博士学位論文

Eco-evolutionary studies on mate choice of the Ryukyu Scops Owls *Otus elegans* on an isolated oceanic island

(隔離海洋島におけるリュウキュウコノハズクの配偶者選択に関わる進化生態学研究)

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Contents

Summary

和文要旨

配偶者選択は特定の形質に関して非ランダムなつがい形成をもたらす行動と定義される。個体の遺伝子や形質は個体の行動を通して集団や環境に影響をもたらし、集団や環境は個体に対する選択圧となる。ゆえに配偶者選択は、その行動のみに着目するのではなく、遺伝子から集団に至る幅広い視点で関連する現象を研究することで、その総合的理解が可能になる。しかし、そのような研究には整った研究基盤と膨大な基礎データが必要なため、これを実践できる野外個体群は多くはない。2002 年より繁殖調査と標識再捕獲調査が続く沖縄県南大東島に生息するリュウキュウコノハズク個体群は、そのような貴重な研究個体群の一つである。私は 2016 年から現在に至るまでのこの個体群の調査を率いてきた。本研究の目的は、本個体群を用いて遺伝子から集団に至る様々なスケールで配偶者選択の進化を理解することである。

はじめに、本種の配偶者選択に関わっていると考えられる形質に関する基礎的記述を行った。17 年間にわたる形態計測値データから本種には、メスがオスよりも大きいという「性的二型の逆転」の程度に年変動があることを明らかにした。「性的二型の逆転」は猛禽類で一般的なものではあるが、その経年的な変化に着目した研究は少ない。巣内雛 99 羽の成長記録からは、それらの形態形質の成長様式を記述した。博物館標本と CT スキャンを用いた頭骨形態の記述からは、南大東島のリュウキュウコノハズクが他の島のリュウキュウコノハズクとは異なる形態的特徴を持つことを示した。南大東島および南西諸島の各島のリュウキュウコノハズクの鳴き声の解析からは、リュウキュウコノハズクの集団には集団内に豊富な声の変異が存在することが明らかになった。

次に、3 種類の配偶者選択行動の記述とその行動に伴う適応度利益の評価を行った。一つ目の配偶者選択行動は体サイズにもとづくものである。2012 年からの調査データから、南大東島のリュウキュウコノハズクは、嘴峰長と翼長に関して同類交配を行っている傾向があることが分かった。この傾向は地理的に近く

にいるものが出会う事で生じたものではなく、積極的にサイズに関して配偶者を選んでいることによるものであることが示唆された。さらに、翼長の小さいオスほど一度の繁殖で生産するリクルートの数が多い傾向があることも示唆された。このことから、メスが体サイズに関してオスを選ぶことには適応度利益があると考えられた。

二つ目の配偶者選択行動は主要組織適合抗原複合体遺伝子（MHC 遺伝子）にもとづくものである。2016 年のつがいの MHC 遺伝子の違いを、ランダム交配のシミュレーションで生成されたつがいの MHC 遺伝子の違いの値と比較した。その結果、実際のつがいの MHC 遺伝子の違いは、シミュレーションで生成したつがいの MHC 遺伝子の違いよりも大きいことが分かった。しかし、2016 年に巣立った同時出生集団の予後を追跡した結果からは、MHC 遺伝子の違いが大きいつがいから生まれた雛が長生きするという傾向は見出されず、MHC 遺伝子に関して配偶者を選ぶことの明確な適応度利益は見出されなかった。

三つ目の配偶者選択行動は近親交配回避である。2016 年のヒナに対して、実際の母親と実際の父親の間の血縁度と、実際の母親と父親以外のオス個体の間の血縁度を比較した。その結果、実際の母親と実際の父親の間の血縁度は低い傾向があることがわかった。

最後に、配偶者選択が集団に与える影響に関連する事象の記述を行った。配偶者を探索する手段でもある個体の分散行動の記述では、出生地からの分散距離は、メスの方がオスよりも大きいこと、繁殖期の中で早い時期に巣立った個体ほど大きいことが分かった。南大東島内での空間的遺伝構造の記述では、オスに関しては有意な空間自己相関構造が検出された一方、メスではそのような有意な空間構造が見出されなかった。すべての個体の行動の帰結の一つである個体群動態の記述からは、個体数、生存率、産仔数、性比、個体群成長率の年変動を明らかにした。2013 年以降の平均個体群成長率は 0.98 と推定され、わずかな個体数の減少傾向が見出された。

本研究で見出された体サイズと遺伝子に関する配偶者選択では、鳴き声や化学物質がそれらの配偶者選びの実際の基準になっている可能性が考えられる。

フクロウは夜行性であり音声コミュニケーションが発達している。多くの動物で声の周波数は体サイズと相関関係がある。さらに、フクロウは鳴き声を学習しないと考えられている。ゆえに、体サイズに関する情報が鳴き声によって正直に伝えられると考えられる。また、視覚に頼ることが難しい状況では、視覚以外の情報伝達手段として匂いが重要である可能性がある。MHC 遺伝子の違いが個体の匂いの違いに対応していることは他の鳥類で示されている。MHC 遺伝子に関する配偶者選択はこうした匂いの情報をもとに実現しているかもしれない。フクロウ類は鳥類の嗅覚の研究対象としては用いられていないため、今後の展開が期待される。

本研究で示唆された体の小さいオスの繁殖成績における有利さは、猛禽類特有の性的二型の逆転を説明する理論の一つである small male hypothesis に沿う結果である。猛禽類のオスは繁殖期に給餌の大半を担うことが多い。体の小ささがもたらす飛翔能力と採餌効率の向上は、オスに対してよりサイズが小さくなるような選択圧として働くと考えられている。一方で本研究でも見出された体サイズの同類交配の生じるメカニズムの一つでは、大きく繁殖能力の優れたメスをめぐるオス同士の争いにおける、大きいオスの有利さを仮定する。これはサイズが小さくなるような選択圧とは逆の選択圧である。今回の研究ではそのような大きいオスの競争上の有利さを支持する結果は得られていない。単にサイズの同類交配だけに着目するのではなく、異なる視点からも対象種の生態的特徴を研究することで、配偶者選択にかかわる選択圧の実態をより詳しく検討することができた。

近親交配回避の傾向は分散距離に性差があることで実現していると考えられる。すなわち、メスがオスよりも遠くに定着することで、近親者の出会いが妨げられていると考えられる。これは従来の研究で広く述べられてきた考え方である。一方で、もし遺伝子にもとづく配偶者選択が声や匂いのような手段で実現しているとすれば、メスが出生地近隣の近親者のオスたちを積極的に回避するという行動をとることで、結果的に分散距離に性差が生じるとも考えられる。それゆえに従来の考え方とは異なり、近親交配回避と分散距離の性差の関係は、互い

が互いの因果となり得るような複雑な関係であると考えられる。

本学位論文にまとめられた一連の研究は、長期研究個体群の確立した研究基盤と、自身で蓄積し、および、過去に蓄積されてきた膨大な基礎データがなければ実現しなかったものである。長期研究個体群のデータは研究者の意思によってありとあらゆる課題解決に用いることができ、進化生態学に関する最先端の重要な研究を多く生み出してきた。特に島の個体群は、明瞭な集団の境界、系としての単純さ、島ごとに異なる環境や地史が、研究を行う上での良い性質となる。南大東島のリュウキュウコノハズク個体群は東アジア地域において、現在も調査が続く貴重な長期研究個体群の一つである。森林の破壊や移入種による捕食被害など個体群に対する人為的影響の多い島ではあるが、これらの困難さは研究者の知恵と工夫次第で克服できるだけでなく、研究の強みとすることもできる。この 5 年間私が引き受けてきた南大東島のリュウキュウコノハズクの長期研究がこの先何十年と継続され、それが日本と世界の進化生態学の発展に貢献し続けることを願ってやまない。

Chapter 1

General introduction

Introduction

Behaviors of individual animals are related to all aspects of biological systems from gene to population and environment (Sutherland 1996; Bowler and Benton 2005). Among the behaviors, choice of mate is of importance because it determines which individuals contribute to the following generations. Mate choice is defined as the behavior which leads to non-random mating with respect to one or more traits (Kokko et al. 2003). Because genotype of offspring depends on that of parents, if the trait under the mate choice has genetic background, such mating bias influence transgenerational inheritance of the alleles behind the traits and the frequencies of them (Servedio and Lande 2006; Kokko et al. 2007).

Individuals often assess potential mates through various traits (Figure 1-1, Andersson and Simmons 2006). Preferences towards individuals with specific coloration, morphological traits and vocal characteristics are well known (Andersson 1994). Assortative mating with respect to body size (Crespi 1989; Jiang et al. 2013; Wang et al. 2019) and age (Jouventin et al. 1999; Ludwig and Becker 2008) are also known from various taxonomic groups. Mate choice based on chemical characteristics is also known (Santos et al. 2016b; Slade et al. 2016). These mate choices sometimes lead to non-random mating with respect to genetic make-up and inbreeding avoidance (Pusey and Wolf 1996; Tregenza and Wedell 2000; Szulkin et al. 2013). If the traits on which these mate choices act are under the genetic control, and if they have genetic variance, mate choice imposes sexual selection on the traits (Kokko et al. 2003). Therefore, mate choice is often invoked when explaining elaborated characteristics which could not be explained by natural selections (Darwin 1874; Andersson 1994; Kokko et al. 2003).

The entity of the selection pressures is the difference in fitness depending on individuals' genetic composition. Some traits convey information of the individual and provide choosers direct material benefits of choosing them as mates. For example, males with specific morphological characteristics such as long tail may be good food providers, and females may be able to benefit from breeding with them (Møller and Jennions 2001). On the other hand, some traits provide choosers indirect genetic benefits from increased fitness in the following generations (Penn and Potts 1999). For example, mating with males with specific genotype for immune gene could produce offspring of high immunocompetence and increase the probability of females' genes to be inherited in the following generations. Such genetic effects have been explained by good gene and genetic compatibility (Puurtinen et al. 2009).

Mate choice also accompanies cost for the choosers (Pomiankowski 1987; Candolin 2003; Lykou and Ntzoufras 2011). For example, mate search behavior can have the risk of predation (Godin and Briggs 1996). Obvious cost of being choosy is time and energy

consumed to choose preferable mate (Pomiankowski 1987). If breeding season is limited in time, too choosy individuals even loses breeding opportunity (Kokko et al. 2003).

Therefore, choosers must conduct their choice based on the trade-off between these benefits and costs (Pomiankowski 1987; Kokko et al. 2003). What makes the matter difficult is that the trade-off relationships vary depending on external factors (Figure 1-1). Abiotic environment such as weather condition can affect energy metabolism and affect the trade-off in relation to body size (Hunt et al. 2005; Wong and Candolin 2005). Large-sized individuals may suffer from harsh weather condition more severely than small-sized individuals, due to their large energy requirement (Blanckenhorn 2000). Biotic environment also matters. For example, spatial distribution of food resources leads heterogeneity in quality of habitat (Hakkarainen et al. 1997). Resultant variation in the quality of territory holders directly translate into the material benefit which they can provide to their mates (e.g. food for offspring, Møller and Jennions 2001).

Furthermore, mate choice is intimately related to population-level processes through eco-evolutionary dynamics (Pelletier et al. 2009): individual's behavior influence population dynamics, and the population dynamics influences the environment, and the population dynamics and the environment influences the selection pressures on individual's behavior (Figure 1-1). For example, dispersal behavior for mate search influence local population characteristics such as density, sex ratio, age structure and kin structure of the place where the individuals settle (Bowler and Benton 2005). For predatory species, changes in their density directly influence local environment by altering population dynamics of prey species and "quality" of territories (Korpimeki and Norrdahl 1989; Korpimaki and Norrdahl 1991). Change in kin structure determines genetic relationships of chooser and their potential mates (Bowler and Benton 2005). Such changes in turns determines cost and benefit of choosing mate there, in other words, affect selection pressure on the choosing behavior. Therefore, for thorough understanding of mate choice, it is necessary to conduct researches from various aspects of hierarchical biological system (gene, trait, individual and population).

I studied a population of the Ryukyu Scops Owls *Otus elgans* on Minami-daito Island from scales of gene to population, aiming to understand their mate choice (Figure1-1). The owls are small sized owls weighing about 85g (Takagi et al. 2007a) ranging from Okinoshima Island, Japan to Babuyan Batanes Islands, Philippine (Severinghaus 2000; Warburton 2009; Ornithological Society of Japan 2012; Takagi et al. 2015). A population on Minami-daito Island is classified as subspecies *O. e. interpositus* (Kuroda 1923). This population has been a target of long-term study since 2002 (Takagi et al. 2007a; Takagi 2020; Sawada et al. 2021a,b). They are monogamous and strictly territorial (Akatani et al. 2011). Pairs rarely divorce and they defend territories for all purpose (food, nest, mating opportunities) around year and in successive years at most cases (Akatani 2011; Akatani et al. 2011; Sawada et al. 2018a). They lay single clutch of one to four eggs from mid-March to mid-May (Akatani 2011; Akatani et al. 2011; Sawada et al. 2021b). Incubation and nestling period last about one-month each (Takagi et al. 2007a; Akatani

et al. 2011). Population size is estimated to be around 200 pairs (Takagi et al. 2007a; Takagi 2020). Minami-daito Island is a small oceanic island of 32km^2 located at 360 km east from Okinawa Island. It is an up-lifted atoll and wind shelter belts planted on the circumference of the island is the main habitat of the owls (Takagi et al. 2007b; Sawada et al. 2018a). Isolation and smallness of the population promote the occurrence of inbreeding (Frankham 1997), and such inbred pairs of the owls have been actually observed (Sawada unpublished data).

These properties of the population on Minami-daito Island provide multiple advantages for studying mate choice from various biological scales. 1) Data accumulation: Various fundamental ecological data obtained through long-term monitoring can be used to test various theories of ecology and evolution. Proportion of marked individuals nearly 90% allows high-resolution individual-based study. 2) Easy data collection: Their small size allows easy handling and measuring. Frequent usage of introduced nest boxes allows to obtain breeding data systematically. Isolation to small island enables to follow individuals circumventing many problems concerning immigration and emigration. Simply structured forest and roads laid entire the island allows easy access to all territories in the island. 3) Life-long monogamy and risk of inbreeding: As is often the case with raptors, their high mate fidelity requires careful mate choice because it heavily influences their lifetime reproductive success. In addition, smallness and isolation of the population increase the risk of inbreeding and probably promote evolution of inbreeding avoidance. 4) Simple ecosystem on small isolated island: Because Minami-datio Island is a small, oceanic, isolated island, its ecosystem comprises of small number of species and environmental factors. This property offers strong advantages for studies of various biological scale since the number of relationships between the components of the system to consider is far smaller than large, continental, open population.

This dissertation documents the studies of the owls I conducted in these five years (Figure1-1). In chapter 2 to 5, I treat topics related to fundamental descriptions of the traits which are representative targets of the owl's mate choice. Chapter 2 describes external morphometrics of *O. e. interpositus* using 17-year measurement dataset. This study focuses on sexual size dimorphism and also offers a methodology for age determination. Chapter 3 describes growth patterns of the traits considered in Chapter 2. Chapter 4 scrutinizes internal skull structures of the owls. This study is motivated from an expectation that the population of *O. e. interpositus* has some characteristics derived from inbreeding in the small isolated island. Chapter 5 describes variation of vocal characteristics of the owls. Because of nocturnality, variation in vocalization is expected to convey information for mate choice. Although I also analyzed genetic variation in my researches, results of the analyses are included later in subsequent Chapter 7 and Chapter 8 to avoid repetition of the contents.

In chapter 6 to 7, I treat topics related to mate choice behaviors of the owls. Chapter 6 focuses on mate choice based on body size and age. Chapter 7 focuses on mate choice based on genes. Several results in relation to benefits of the choice are also included in

these chapters. I do not include mate choice based on vocal characteristics in this dissertation because this is an ongoing project and I do not have enough results yet.

In chapter 8 to 10, I treat topics related to the population consequence of the mate choice behavior. Chapter 8 describes dispersal pattern of the owls within Minami-daito Island. Because dispersal is a part of mate search behavior and a main cause of spatial distribution of individuals within a population, fundamental description of dispersal is necessary to extend our viewpoint on mate choice from individuals to a population. Chapter 9 describes fine-scale spatial genetic structure of the owls on Minami-daito Island, which is a consequence of the dispersal pattern in the Chapter 8. Chapter 10, as the consequences of the all processes treated in the previous chapters, describes population dynamics of the owls using a population dynamics model. This model estimates multiple aspects of demography, such as survival, reproduction, sex ratio and population size.

Combining all results in the previous chapters, Chapter 11 discusses the ecology and evolution of mate choice in *O. e. interpositus*. As a study of mate choice on a bird or on an animal from a total view of various biological scales, significances of the results are discussed from general perspectives.

Figure

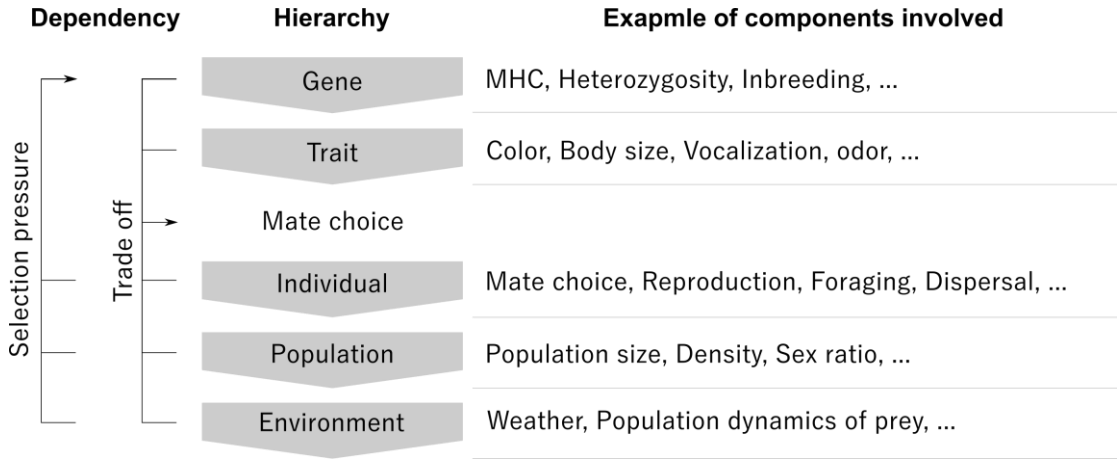


Figure 1-1

Relationships between mate choice and various aspects of hierarchical biological system. Dependency of ecological scales in the hierarchy is shown by arrows. Trade off with respect to mate choice behavior depends on all aspects of the hierarchy. Selection pressures derived from the mate choice exert on genes by individual processes to environmental processes. Examples of components involved in each aspect of the hierarchy are raised in the right half of this diagram.

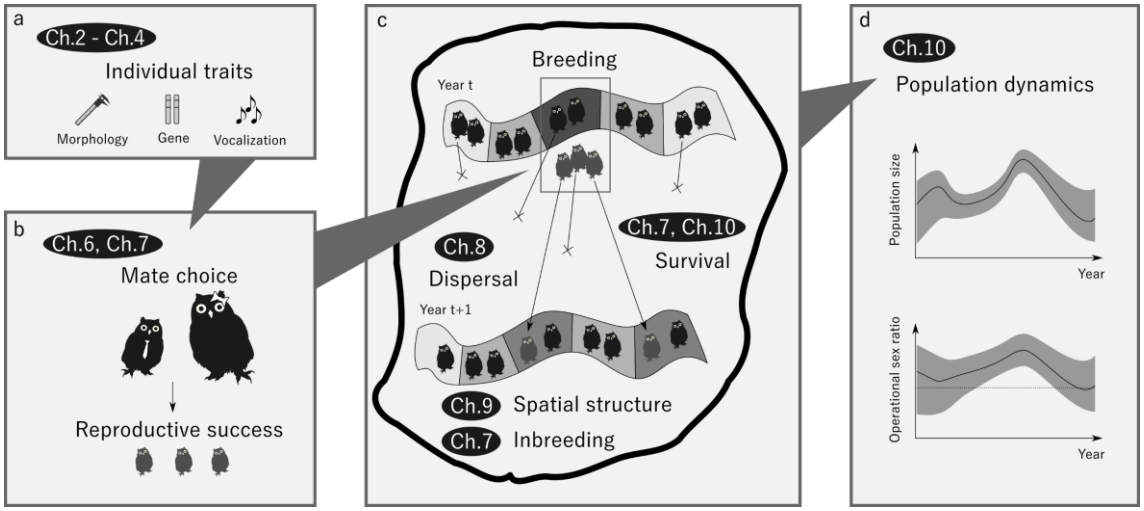


Figure 1-2

Relationships between mate choice and various ecological processes which I focused on in this dissertation. Numbers of chapters corresponding to each process are denoted. Individuals choose mate with respect to traits (a) and produce offspring (b). Each of territories on a wind shelter belt is held by a pair (c). A part of parents and offspring survive to the next year (c) and their dispersal and settlement patterns generate spatial genetic structure (c). Sometimes inbreeding occurs (c). These processes result in population dynamics (d).

Chapter 2

Reversed sexual size dimorphism in the Ryukyu Scops Owl on Minami-daito Island

Abstract
One of the consequences of selections acting on body size is the difference in body size between the sexes or sexual size dimorphism. Although many hypotheses have been proposed for reversed sexual size dimorphism (RSD) in raptors, ornithologists have rarely paid attention to temporal aspects of RSD when testing their hypotheses. Because selection pressures can vary temporally, describing temporal variation in RSD is a first step towards understanding evolutionary mechanism which shape and maintain the dimorphism. Here, I describe RSD in the population of Ryukyu Scops Owls *Otus elegans* on Minami-daito Island using a dataset of the external measurements of 770 individuals obtained during a 17-year long-term population monitoring project. Females were larger than males in body mass, culmen length, bill depth, bill width, tail length and flattened wing length, whereas males were larger than females in tarsus and head lengthes. Among those traits, the degree and direction of RSD of body mass, tarsus length, bill depth and flattened wing length varied across years. There were neither increasing nor decreasing trend in RSD. This is a rare study which addressed temporal variation in RSD in a raptor species.

Introduction

Body size is an important factor in various aspect of ecology and evolutionary biology implying the existence of various selection pressures acting on body size. One consequence of such selection is the difference in body size between the sexes known as sexual size dimorphism (SSD). As Darwin (1874) noted, SSD might be shaped by both natural and sexual selection. For example, natural selection may favour the sexes having different body sizes in relation to sexual difference in diet, and sexual selection may favour males having larger bodies because of mate choice by females (Shine 1989). Furthermore, SSD is known to vary in degree and direction not only among species but also within species (Earhart and Johnson 1970; Shine and Fitzgerald 1995; Reimchen and Nosil 2004; Le Galliard et al. 2006). If such variations in SSD are shaped and maintained by several selection pressures, we may able to infer the underlying selection pressures from long-term changes in body size. Therefore, describing the temporal variation in SSD is a promising way of understanding the evolutionary mechanism of SSD.

In raptorial birds, females are often larger than congeneric males (Krüger 2005). This phenomenon is specifically called reversed sexual size dimorphism (RSD). Detailed

intraspecific studies began to accumulate after 1990s (Hakkarainen and Korpimäki 1991), whereas interspecific comparative analyses in RSD studies began much earlier (Earhart and Johnson 1970; Mueller 1986; Krüger 2005; Pérez-Camacho et al. 2018). However, very few studies have exploited intraspecific temporal variation in body size in the context of RSD (Tornberg et al. 1999; Warkentin et al. 2016). It is somewhat surprising that ornithologists have rarely focused on the temporal aspects of RSD, although major hypotheses for RSD based on foraging behaviour are related to selection pressure, such as food availability, which can vary temporally (reviewed in Mueller 1986).

Ryukyu Scops Owls *Otus elegans* is a well-studied owl in tropical to subtropical area (Severinghaus and Rothery 2001). It occurs from Batan Island and Calayan Island in the Philippine to Okinoshima Island in Japan (Ornithological Society of Japan 2012; Gill and Donsker 2019). Subspecies *O. e. botelensis* on the Lanyu Island has been studied since the 1980s (Severinghaus and Rothery 2001; Severinghaus 2007) and subspecies *O. e. interpositus* on the Miami-daito island has been studied since 2002 (Takagi et al. 2007a; Sawada et al. 2018a). Although SSD in some traits has been reported in the *O. e. botelensis* population (Lee and Severinghaus 2004), it has not yet been reported in detail for other populations of this species including *O. e. interpositus*. The availability of a large data set of morphometric data of *O. e. interpositus* offers a precious opportunity to test whether the degree of RSD varies among years. The aim of this study was first to describe fundamental aspect of RSD in *O. e. interpositus* and then to examine annual variation in RSD.

Material and Methods

Material

Subspecies *O. e. interpositus* is endemic to Minami-daito Island, a small, isolated, oceanic island about 360 km east of Okinawa Island in the north-western Pacific (Ornithological Society of Japan 2012). We have been marking individuals and monitoring the breeding ecology of the population since 2002 (Takagi et al. 2007a; Sawada et al. 2018a; Takagi 2020). There are ca. 200 monogamous pairs on the island (Takagi et al. 2007a; Takagi 2020). Some individuals commence breeding in their first year (Akatani 2011). Females lay one to four eggs from mid-March to mid-May (Takagi et al. 2007a, Sawada & Iwasaki unpublished data), incubation lasts 26 to 30 days and chicks fledge at 28 to 32 days old (Takagi et al. 2007a, Sawada & Iwasaki unpublished data). Males feed their mates and chicks until the chicks are about 10 to 15 days old after which both parents share feeding duties (Akatani 2011, Sawada & Iwasaki unpublished data). Males and females both feed on insects and geckos and there are no apparent differences in the prey they deliver to nestlings (Murakami unpublished data). The diet of nestlings mainly consists of cockroaches, Orthoptera species and gecko species (Takagi and Akatani 2011).

Body size measurement

I used morphometric data from 770 individual owls collected during ongoing long-term population monitoring. Because the focus of the monitoring since 2002 has been for a study of breeding ecology, most measurements have been obtained during the breeding season (March to June, Table 2-1). Body mass was measured using Pesola spring balance or digital weighing scale to the nearest 0.1 g. Tarsus length (from the base to the tip of the tarsometatarsus), culmen length (from the base to the tip of the bill), bill depth (height of the closed bill at the anterior end of nostril vertical to the gape), bill width (width of the bill at the anterior end of nostril), head length (from the back of the skull to the tip of the bill) and tail length (from the root to the tip of the central rectrix) were measured with an electronic digital calliper to the nearest 0.01 mm. Natural wing length (from the bend of the wing to the tip of the longest primary in an un-flattened state) and flattened wing length (from the bend of the wing to the tip of the longest primary in a flattened state) were measured with a stainless steel ruler to the nearest 0.5 mm. Sample sizes differed between the traits since not all traits were measured for all individuals (Table 2-1, 2-2).

Sex determination

Sex was determined by vocal characteristics (Takagi et al. 2007a,b) or by the presence or absence of a brood patch (Takagi 2020). However, I also used a molecular method for those individuals for which sex could not be determined by field observations. DNA samples extracted from blood samples were used for molecular sexing by PCR amplification of the CHD gene (Fridolfsson and Ellegren 1999). The PCR reaction volume was 10 μL, containing 1×Ex Taq Buffer (TaKaRa), 200 μM of each dNTP Mixture (TaKaRa), 0.5 μM of each primer (Applied Biosystems), 0.25 units of Ex Taq (TaKaRa), and about 10 ng of genomic DNA. Reaction condition was 2 min at 94°C followed by 30 cycles of 30 s at annealing temperature (1°C down per cycle from 60°C to 50°C) and 40 s at 72°C, and finally 5 min at 72°C. PCR products were separated by gel electrophoresis and sex was determined by the band patterns.

Age determination

Age class was estimated from plumage characteristics. From the beginning of our long-term monitoring, the research group empirically recognized that, when compared with adults, yearlings have more pointed primaries, softer primary rachides and more worn secondaries. On this basis, we recorded three binary answers for each individual: 1) Primaries pointed or not pointed? 2) Primary rachides soft or not soft 3) Secondaries worn or not worn. If two or more criteria were positive, we judged that individual to be a yearling, conversely if two or more criteria were negative, we judged that individual to be an adult.

To confirm validity of this aging method, aging result of 111 known-aged individuals (41 yearlings and 70 adults) were compared with their actual age. Out of 41 yearlings, 36 (87.8%) were correctly assigned as yearlings, but five (12.2%) were incorrectly considered adult. Out of 70 adults, 68 (97.1%) were correctly assigned as adults but two

(2.9%) were incorrectly considered yearling. Since I could confirm the validity of our ageing method, we used ageing results for unknown-aged individuals in subsequent analyses.

Statistical analysis

(a) Fundamental RSD

I analysed RSD in *O. e. interpositus* by generalized linear mixed models (GLMM) implemented in the *lme4* package (Bates et al. 2015) on R (R Core Team 2019). This approach superior to using the t-test between the two sexes because it can test for sexual difference while controlling for other confounding factors such as annual variation or systematic difference between measurers. Morphometric data were used as the response variable, which follows a normal distribution. Sex and other factors (see below) were used as fixed effects. Since some of the 770 individuals had been measured multiple times over several years, individual ID was included as a random effect. The identity link function was used. Based on the repeated measurement data from certain individuals, the repeatability of measurements across years was calculated from the mixed models, following Nakagawa and Schielzeth (2010).

I analysed each trait separately. Firstly, I compared models with all possible combinations of three explanatory variables: *Year* (categorical variable denoting the year when the measurement was taken), *Measurer* (categorical variable denoting who measured) and *Age* (categorical variable denoting age class as "yearling" or "adult"). By including *Measurer*, systematic bias between researchers was controlled for when the model evaluates sexual difference. Because body mass is known to vary depending on breeding activity (Hirons et al. 1984; Wijnandts 1984), I added a further variable to the preceding three when analysing body mass: *Breeding* (categorical variable denoting the season when the measurement was taken: "breeding (February to July)" or "non-breeding (August to January)"). Model comparison was based on AIC using the dredge function in the *MuMIn* pacakage (Barton 2019). To consider possible annual variation depending on age, for traits which had Age and Year in the final model, interaction between them was included and its significance was tested using the likelihood ratio (LR) test applied on the models before and after inclusion. Then, the final model was chosen as a base model (hereafter, $Model_{base}$) for subsequent analyses.

To test the statistical significance of RSD, the effect of *Sex* (categorical variable denoting sex) was included into the base model (hereafter, $Model_{sex}$) and the statistical significance of the effect was determined by an LR test between $Model_{base}$ and $Model_{sex}$. As *Breeding* was included in the $Model_{base}$ of body mass and the effect of *Sex* was supported for body mass (see result), their interaction was added to the $Model_{sex}$ of body mass (hereafter, $Model_{breed*sex}$). The significance of the interaction effect was determined by LR test between $Model_{sex}$ and $Model_{breed*sex}$. Although the effect was not significant (but marginal, P = 0.09, see results), I used $Model_{breed*sex}$ in the further analysis of RSD of body size. This is because a sex-dependen effect of breeding is common in raptors (i.e.

females gain body mass early in the breeding season, but males have relatively stable body mass, Korpimäki (1990)) and body mass estimates of adults from $Model_{breed*sex}$ were consistent with this pattern.

To describe the average-level of RSD throughout the study period, for all the traits except body mass, I excluded *Year* from $Model_{sex}$ if *Year* was included in $Model_{sex}$, and then the mean values of adult males and females were estimated from the model. From the estimates, three commonly used measures of RSD were calculated for each trait: 1) *Difference* = M_f - M_m, 2) *Dimorphism index* = $100 \times (M_f - M_m) / (0.5 \times (M_f + M_m))$, 3) *Ratio* = M_f / M_m. Here, M_f and M_m are the previously estimated mean size of females and males, respectively. As for body mass, I used $Model_{breed*sex}$ instead of $Model_{sex}$ in the preceding procedures to obtain mean values and the three measures of RSD during the breeding and non-breeding season. All estimates were reported as mean ± SE.

(b) Temporal variation in RSD

For the traits showing statistically significant RSD, except for body mass, I generated $Model_{year*sex}$ (a model which includes the interaction term of *Year* and *Sex* in $Model_{sex}$) to describe annual variation in RSD. The significance of the interaction term was determined by LR test between $Model_{sex}$ and $Model_{year*sex}$. The significance indicates that the degree of RSD differs among years. For traits with significant interactions, the mean values of adults and three measures of RSD (*Difference, Dimorphism index, Ratio*) were calculated for each year. Because each of the three measures showed similar annual variation, for simplicity I have only shown the results of the *Dimorphism index*. Whether there was an increasing or decreasing trend in RSD was determined from the significance of Spearman's rank correlation between year and *Dimorphism index*. As for body mass, I used $Model_{breed*sex}$ and $Model_{breed*sex+year*sex}$ (a model including interaction terms of *Year* and *Sex* in $Model_{breed*sex}$) were used instead of $Model_{sex}$ and $Model_{breed*sex}$ in the procedures above. The mean value of adults, three measures of RSD during the breeding and non-breeding season, and rank correlations, were obtained by the procedures above. To address correlated change in RSD between traits, the *Dimorphism index* of the traits on an annual basis were correlated in a pairwise manner.

(c) Association between RSD and climate

To assess the possible ecological background behind temporal variation in RSD, Spearman's rank correlation between *Dimorphism index* and the following three climate variable were estimated: *Temperature* (average during the previous winter, from November to February), *Precipitation* (average during the previous winter, from November to February) and *Typhoon* (number approaching during the previous year, from June to December). Climate data were based on records from the local Minami-daito metrological office (https://www.data.jma.go.jp/gmd/risk/obsdl/index.php). These variables were chosen based on the expectation that sex or age dependent survival during the previous season might affect the body size distribution on the owls. For body mass,

the association was assessed for RSD during the breeding season only as the sample size during non-breeding season was very small.

Results

RSD in each trait

(a) Body mass

$Model_{base}$ included *Year*, *Measurer*, *Age*, *Breeding* and *Year*Age* (LR test for *Year*Age*, N = 969, $\chi^2_{16} = 31.26$, P = 0.012). There was a significant sexual difference in body mass (Figure 2-1a, LR test between $Model_{base}$ and $Model_{sex}$, N = 969, $\chi^2_1 = 338.65$, P < 0.001). The effect of breeding season did not differ between the sexes (LR test between $Model_{sex}$ and $Model_{sex*breed}$, N = 969, $\chi^2_1 = 2.92$, P = 0.09). Estimates of long-term average for adult males and adult females were 88.43 ± 1.47 g and 92.24 ± 3.42 g in non-breeding season and 85.95 ± 0.44 g and 96.33 ± 0.49 g in breeding season (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were 10.38 g, 11.38 and 1.12 in breeding season and 3.81 g, 4.22 and 1.04 in non-breeding season, respectively. Thus, the body mass of males was smaller than that of females, regardless of the season. Also, males were lighter, and females were heavier in the breeding season than in the non-breeding season. The degree of dimorphism differed between years (Figure 2-2a, LR test between $Model_{breed*sex}$ and $Model_{breed*sex+year*sex}$, N = 969, $\chi^2_{15} = 78.39$, P < 0.001), but there was no apparent trend (increasing or decreasing) in RSD in either the non-breeding season (Spearman's r = -0.24, P = 0.35) or the breeding season (Spearman's r = -0.24, P = 0.35). There were also no significant associations with climate variables (N = 17; Temperature, r = -0.21, P = 0.41; Precipitation, r = 0.01, P = 0.97; Typhoon, r = 0.06, P = 0.82). In the final model, $Model_{breed*sex+year*sex}$, the coefficient of *Age* was -3.47 ± 9.33 and coefficients of *Year*Age* ranged from -1.40 to 5.33 (i.e. yearlings differed from adults by -4.87 to 1.86 g depending on years). Other regression coefficients of the models for body mass can be seen in Table 2-3. Repeatability across years was 0.19 (Figure 2-3).

(b) Tarsus length

$Model_{base}$ included *Year*. There was a significant sexual difference in tarsus length (Figure 2-1b, LR test between $Model_{base}$ and $Model_{sex}$, N = 939, $\chi^2_1 = 20.90$, P < 0.001). The estimate of the long-term average for adult males was 29.59 ± 0.05 mm and for adult females it was 29.59 ± 0.05 mm, respectively (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were -0.20 mm, -0.68 and 0.99, respectively. Thus, males had longer tarsi than females. Although the degree of dimorphism differed between years (Figure 2-2b, LR test between $Model_{sex}$ and $Model_{year*sex}$, N = 939, $\chi^2_{15} = 30.32$, P = 0.011), no trend (increasing or decreasing) in RSD was apparent (Spearman's r = -0.07, P = 0.79). There were also no significant associations with climate variables (N = 17; Temperature, r = -0.03, P = 0.91; Precipitation, r = 0.04, P = 0.87; Typhoon, r = 0.04, P = 0.86). Other regression coefficients of the models for tarsus length can be seen in Table 2-4. Repeatability across years was 0.68 (Figure 2-3).

(c) Culmen length

$Model_{base}$ included *Measurer*. There was a significant sexual difference in culmen length (Figure 2-1c, LR test between $Model_{base}$ and $Model_{sex}$, N = 893, $\chi^2_1 = 15.22$, $P < 0.001$). The estimate of the long-term average for adult males was 20.03 ± 0.03 mm and for adult females it was 20.19 ± 0.04 mm, respectively (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were 0.16 mm, 0.82 and 1.01, respectively. As the main effect of *Year* was not included in the $Model_{base}$, I did not address further the interaction between *Year* and *Sex*. Other regression coefficients of the models for culmen length can be seen in Table 2-5. Repeatability across years was 0.73 (Figure 2-3).

(d) Bill depth

$Model_{base}$ included *Year*, *Measurer*, *Age* and *Year*Age* (LR test for *Year*Age*, N = 969, $\chi^2_{16} = 35.93$, P = 0.003). There was a significant sexual difference in bill depth (Figure 2-1d, LR test between $Model_{base}$ and $Model_{sex}$, N = 913, $\chi^2_1 = 52.50$, $P < 0.001$). The estimates of the long-term average for adult males was 9.55 ± 0.02 mm and for adult females it was 9.78 ± 0.03 mm, respectively (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were 0.23 mm, 2.35 and 1.02, respectively. Thus, males had smaller bill depth than females. Although the degree of dimorphism differed between years (Figure 2-2c, LR test between $Model_{sex}$ and $Model_{year*sex}$, N = 913, $\chi^2_{15} = 28.56$, P = 0.018), no trend (increasing or decreasing) in RSD was apparent (Spearman's r = -0.05, P = 0.84). There were also no significant associations with climate variables (N = 17; Temperature, r = -0.23, P = 0.36; Precipitation, r = 0.08, P = 0.76; Typhoon, r = -0.42, P = 0.09). In the final model, $Model_{year*sex}$, coefficient of *Age* was -0.56 ± 0.03 and coefficients of *Year*Age* ranged from 0.24 to 0.92 (i.e. yearlings were -0.32 to 0.36 mm different from adults depending on years). Other regression coefficients of the models for bill depth can be seen in Table 2-6. Repeatability across years was 0.39 (Figure 2-3).

(e) Bill width

$Model_{base}$ included *Year* and *Measurer*. There was a significant sexual difference in bill width (Figure 2-1e, LR test between $Model_{base}$ and $Model_{sex}$, N = 887, $\chi^2_1 = 19.87$, $P < 0.001$). The estimates of long-term average for adult males was 5.57 ± 0.02 mm and for adult females it was 5.66 ± 0.03 mm (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were 0.10 mm, 1.75 and 1.02, respectively. Thus, males had narrower bills width than females. However, the degree of dimorphism did not differ significantly between years (LR test between $Model_{sex}$ and $Model_{year*sex}$, N = 887, $\chi^2_{13} = 10.87$, P = 0.622). Other regression coefficients of the models for bill width can be seen in Table 2-7. Repeatability across years was 0.13 (Figure 2-3).

(f) Head length

$Model_{base}$ included *Year* and *Measurer*. There was a significant sexual difference in head

length (Figure 2-1f, LR test between $Model_{base}$ and $Model_{sex}$, N = 916, $\chi^2_1 = 5.01$, P = 0.025). The estimate of the long-term average for adult males was 43.01 ± 0.04 mm and for adult females it was 42.91 ± 0.05 mm (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were -0.09 mm, -0.22, 1.00, respectively. Thus, males had longer head length than females. However, the degree of dimorphism did not differ significantly between years (LR test between $Model_{sex}$ and $Model_{year*sex}$, N = 916, χ^2_{15} = 21.50, P = 0.122). Other regression coefficients of the models for head length can be seen in Table 2-8. Repeatability across years was 0.59 (Figure 2-3).

(g) Tail length

$Model_{base}$ included *Year*, *Measurer* and *Age* (LR test for *Year*Age*, N = 776, $\chi^2_{11} = 13.45$, P = 0.265). There was a significant sexual difference in tail length (Figure 2-1g, LR test between $Model_{base}$ and $Model_{sex}$, N = 776, $\chi^2_1 = 35.54$, P < 0.001). The estimate of the long-term average for adult males was 73.22 ± 0.13 mm and for adult females it was 74.30 ± 0.15 mm, respectively (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were 1.08 mm, 1.46 and 1.01, respectively. Thus, males had shorter tails than females. However, the degree of dimorphism did not differ significantly between years (LR test between $Model_{sex}$ and $Model_{year*sex}$, N = 776, $\chi^2_{11} = 9.63$, P = 0.564). In the final model, $Model_{sex}$, coefficient of *Age* was -1.71 ± 0.16 (i.e. yearling averaged 1.71 mm smaller than adults). Other regression coefficients of the models for tail length can be seen in Table 2-9. Repeatability across years was 0.54 (Figure 2-3).

(h) Natural wing length

$Model_{base}$ included *Year*, *Measurer* and *Age* in its base model (LR test for *Year*Age*, N = 923, $\chi^2_{16} = 19.62$, P = 0.238). There was no significant sexual difference in natural wing length (Figure 2-1h, LR test between $Model_{base}$ and $Model_{sex}$, N = 923, $\chi^2_1 = 0.00$, P = 0.982). The estimate of the long-term average for adult males was 155.65 ± 0.19 mm and for adult females it was 155.74 ± 0.23 mm (Table 2-2). Corresponding *Difference*, *Dimorphism index* and *Ratio* were 0.09 mm, 0.06 and 1.00, respectively. As including the main effect of *Sex* was not supported, I did not further address the interaction between *Sex* and *Year*. In the final model, $Model_{base}$, the coefficient of *Age* was -2.25 ± 0.21 (i.e. yearling averaged 2.25 mm smaller than adults). Other regression coefficients of the models for natural wing length can be seen in Table 2-10. Repeatability across years was 0.54 (Figure 2-3).

(i) Flattened wing length

$Model_{base}$ included *Year*, *Measurer* and *Age* in its base model (LR test for *Year*Age*, N = 829, $\chi^2_{10} = 14.34$, P = 0.158). There was a significant sexual difference in flattened wing length (Figure 2-1i, LR test between $Model_{base}$ and $Model_{sex}$, N = 829, $\chi^2_1 = 6.13$, P = 0.012). The estimates of long-term average for adult males was 160.17 ± 0.20 mm and for adult females it was 160.85 ± 0.23 mm (Table 2-2). Corresponding *Difference*,

Dimorphism index and *Ratio* were 0.68 mm, 0.43 and 1.00, respectively. Thus, males had shorter flattened wing length than females. Furthermore, the degree of dimorphism differed between years (Figure 2-2d, LR test between $Model_{sex}$ and $Model_{year*sex}$, N = 829, χ^2_{10} = 18.31, P = 0.0499). However, no trend (increasing or decreasing in RSD was apparent (Spearman's r = -0.55, P = 0.08). There were also no significant associations with climate variables (N = 11; Temperature, r = -0.56, P = 0.07; Precipitation, r = -0.14, P = 0.70; Typhoon, r = -0.07, P = 0.83). In the final model, $Model_{year*sex}$, coefficient of *Age* was -2.16 ± 0.23 (i.e. yearling averaged 2.16 mm shorter than adults). Other regression coefficients of the models for flattened wing length can be seen in Table 2-11. Repeatability across years was 0.65 (Figure 2-3).

Correlation between RSD in multiple traits

To address correlated change in RSD between the traits, pairwise correlations were calculated for the *Dimorphism index* of the traits which had significant annual variation in RSD (body mass, tarsus length, bill depth and flattened wing length). No trait pairs reached significance after Bonferroni adjustment for multiple testing (Table 2-12, Figure 2-4).

Discussion

This is a rare study describing in detail RSD in owls using an exceptionally large sample size. Long-term morphometric data of *O. e. interpositus* revealed statistically significant sexual difference in all traits except natural wing length. Females had larger body mass, culmen length, bill depth, bill width, tail length and flattened wing length, than males. Conversely, males were larger in tarsus and head length than females. Although the degree of RSD was small in all traits except body mass, it fluctuated among years in body mass, tarsus length, bill depth and flattened wing length. The analyses also revealed effects of age class, year, measurer and breeding season on measurement values.

The smaller size of yearlings than adults in some traits has several explanations. First, yearlings are full-grown but are small in some parts especially in plumage traits such as wing length (Mueller and Berger 1967; Bildstein and Hamerstrom 1980). Second, yearlings are not full-grown in some bony traits such as bill depth. Third, only large yearlings survive to become adults (Massemin et al. 2000; Warkentin et al. 2016). Annual variation implies that morphological traits are under selection pressures dependent on the year, such as food availability (Grant and Grant 2002), since possible systematic measurement bias and errors between researchers across years were controlled for by including the effect of measurer in the GLMM analyses.

I found a significant effect of the measurer and a not particularly high repeatability of measurements for all traits. However, our RSD results are not greatly impacted by these factors, firstly because possible systematic differences between measurer were controlled for by including the fixed effect of measurer in the GLMM and secondly

because the effect of large measurement error lowers the power of detection of true associations which could be overcome by large sample size as used here. Hence, my results are conservative. However, I may have missed some associations between traits and some explanatory variables due to measurement error. Changing measurers is unavoidable in a long-term study. It is important to confirm sufficiently the measurement methods between measurers, and it would be good practice to have multiple measurers measure some individuals to estimate and statistically control for inter-measurer differences.

This study revealed a small RSD in the Ryukyu Scops Owls in the Minami-daito Island. From body mass estimates in Table 2-2, the *Dimorphism index* of the cube-root transformation of body mass become 3.71 for this owl. This falls in line with the finding by Earhart and Johnson (1970) that insectivorous owls tend to have a small (2–5) *Dimorphism index* for the trait, compared with large, vertebrate-eating owls with an index reaching 10. Relatively small size, an abundance of insect prey and specialization on prey are suggested to alleviate competition thereby enabling sexual overlap in body size (Earhart and Johnson 1970). Because most compartive studies of RSD in owls have focused on body mass and/or wing length (e.g. Earhart and Johnson 1970; Mueller 1986; Krüger 2005), whether the tendency also applies to the dimorphism of other morphological traits is unknown. For examples, vertebrate-eating Great Horned Owl *Bubo virginianus* (McGillivray 1985) and Barn Owl *Tyto alba* (Pande and Dahanukar 2012) have bill length indices of 5.20 and 5.19 respectively. In contrast, insectivorous Seychelles Scops Owl *Otus insularis* (Currie et al. 2002) and Ryukyu Scops Owls (this study) have bill length indices of 1.00 and 0.82, respectively. These numerical exapmles suggest that the diet-dependence of an owl species's RSD also applies to the dimorphism of traits other than body mass and wing length. Since different selection pressures operate on different body parts, more descriptive studies addressing multiple traits will help to understand evolutionary mechanism of RSD in raptors.

Hereafter I will discuss RSD for each trait. First, body mass showed the most pronounced sexual dimorphism among all the traits. At least a certain part of this size can be explained by seasonal variation in body mass, because measures of dimorphisms were smaller during the non-breeding season than in the breeding season. The small body mass of males during the breeding season could be related to hunting effort during that season and/or adaptive improvement in hunting efficiency resulting from reduced wing loading (Marti 1990). The large body mass of females during the breeding season could result from weight gain early in the breeding season which is a well-known phenomenon in raptors (Korpimäki 1990). However, sample size from the non-breeding season is too small for us to make this interpretation. More measurements from the non-breeding season are necessary to re-evaluate the effect of breeding season on RSD in this species.

The fact that all three bill measurements (culmen length, bill depth and bill width) are larger in females implies that females have a wholly larger bill than males. Such sexual

divergence in trophic apparatus occurs not only under natural selection but also under sexual selection (Shine 1989). If the difference in bill structure is an adaptation to dietary difference between the sexes, then natural selection is responsible. However, if males prefer females with a large bill (i.e. male choice) and/or such females have some reproductive advantage, then sexual selection may also explain the difference in bill structure. Since we have no quantitative data on the prey taken by the adult owls and no data on mate preference based on body size at present, addressing these questions remains as one of the directions of our future work.

In contrast to RSD in other traits, tarsus length and head length followed the ordinary SSD pattern in which males are larger than females. This means that males have longer legs and a larger head (anteroposteriorly) relative to their overall body size than females. Male *O. e. botellensis* also have longer tarsi, although other body parts are larger in females (Lee and Severinghaus 2004). It has been suggested that long tarsi in males may be an adaptation to improve hunting efficiency (Lee and Severinghaus 2004). Although this selection pressure has been considered for adults, election during the growing period may also be responsible for this sexual difference (Badyaev 2002). During sibling competition, smaller nestlings need to reach as close as possible to the feeding parents. This pressure might explain long male tarsi that complement the disadvantage in sibling competition if male nestlings are smaller than female nestlings (Fargallo et al. 2007). To test this hypothesis, we need to know when the sexual difference in tarsus length is established in their ontogeny (Badyaev 2002).

Having a relatively long head might also be associated with function. Male Great Horned Owls *Bubo virginianus* have wider heads than females, a difference that has been explained as a means of enlarging the distance between the ears and thus helping improve the ability to locate prey by sound (McGillivray 1985). It is worth measuring the head width in the Ryukyu Scops Owls in future. Since male Ryukyu Scops Owls contribute considerably to feeding duties during the breeding season, any selection pressure acting on feeding efficiency may act more strongly on males than females. Sexual differences in skull measurements found in this study contradict the previous morphological analysis by Sawada et al. (2018b) who reported an absence of sexual difference in skull size. However, that absence seems likely to have been due to the small sample size.

The short tail length and short flattened wing length of males may have adaptive significance. An approximate measure of wing loading can be obtained by the formula (body mass) / (wing length)^2 (Mueller 1986). Applying this formula to our body size estimates (Table 2-2) yields 0.0033 for males and 0.0037 for females during the breeding season, and 0.0034 for males and 0.0038 for females during the non-breeding season. Estimates are slightly smaller in males than females and male smallness might have adaptive significance facilitating improved flight performance in males despite their short wing length. Such flight performance is probably important for efficient feeding and male-male competition (Andersson and Norberg 1981). The absence of

sexual dimorphism in natural wing length seemed to result from a greater error in measuring the un-flattened wing than the flattened wing.

It should be noted that sample size (700 to nearly 1000) of this study is exceptionally large compared with other studies of raptor RSD. Large sample size enables us to detect even small differences among noise and errors and give small *P*-values. Although *P*-values were very small for most of the traits we measured, absolute sexual differences of estimates were also small (e.g. 0.20 mm for tarsus length and 0.09 mm for head length). Further study is needed to establish whether such small difference have biologically meaningful significance in the context of each trait discussed above. Because the direction of dimorphism in traits other than tarsus length and head length were the same as that of body mass, the sexual difference identified for these traits may be explained simply by allometric change and may not have adaptive significance.

Finally, considering the annual variation in RSD, yearly selection pressures can act differentially on both sexes (Hakkarainen and Korpimäki 1991; Sergio et al. 2007; Pérez-Camacho et al. 2015; Warkentin et al. 2016). This pressure can lead to changes in body size distribution depending on sex, which in turn causes a change in the degree and direction of RSD (Tornberg et al. 1999). Our results, showing that traits intimately relate to feeding behaviour (bill depth and tarsus length) had annually varying RSD, might imply that there are selection pressures associated with diet or hunting efficiency behind their RSD. In addition, neither decreasing nor increasing trends in the degree of RSD were found throughout this 17-year study. This suggests that counter-balancing selection pressures exist (Ydenberg and Forbes 1991; Warkentin et al. 2016). However, there were no significant correlations between RSD in multiple traits. There were also no significant correlations between RSD and climate variables. These results require re-evaluation in the future after more data accumulates during our ongoing long-term study, coupled with the documentation of prey availability and prey taken by adult owls on the island.

Figure

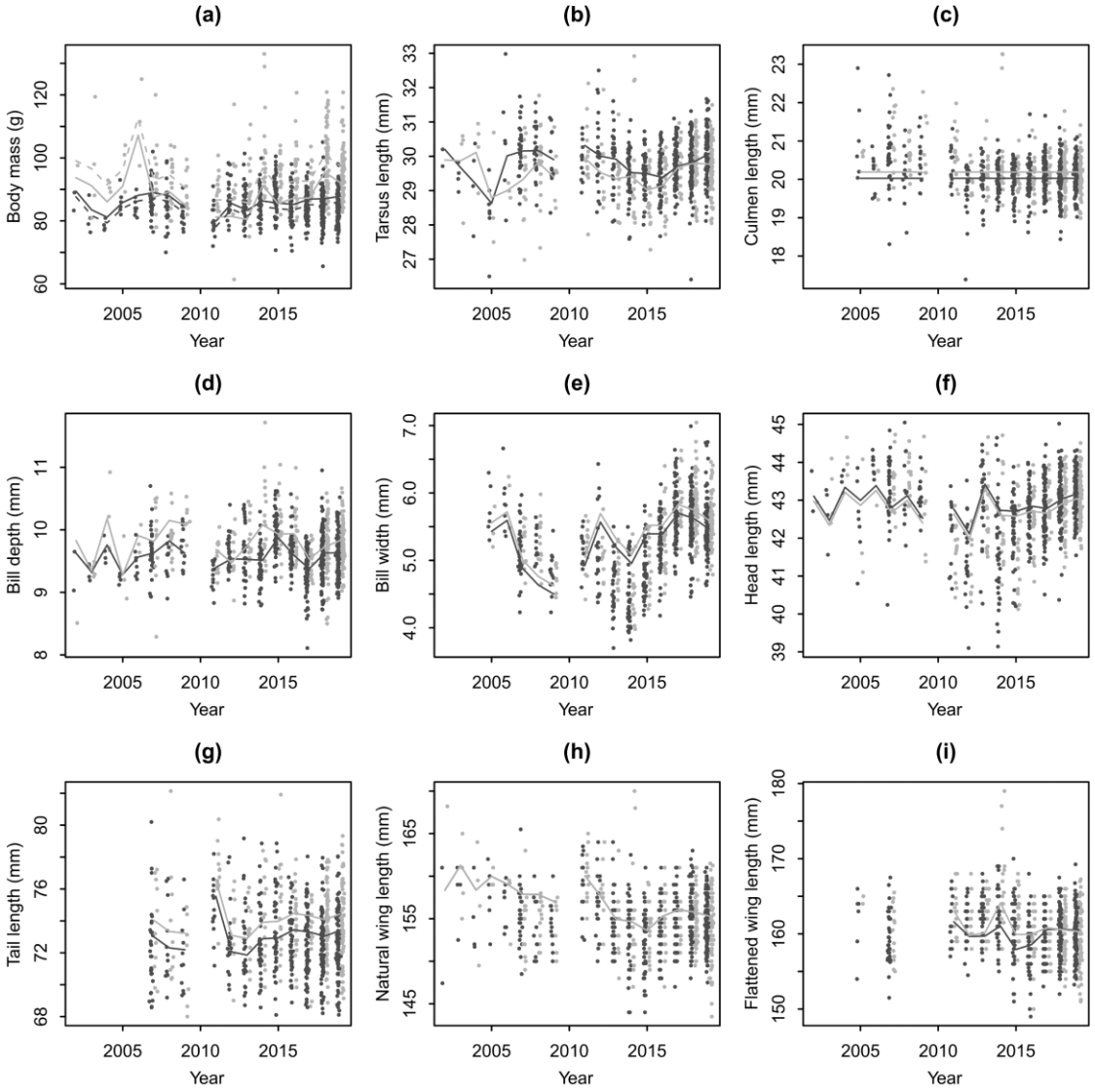


Figure 2-1

Distribution of measurement data (black dots: male, grey dots: female) and estimates of mean of adults (black lines: male, grey lines: female). Only for body mass, estimates in non-breeding season and breeding season are depicted in solid line and dashed line, respectively. (a) body mass, (b) tarsus length, (c) culmen length, (d) bill depth, (e) bill width, (f) head length, (g) tail length, (h) natural wing length, (i) flattened wing length. For the traits which had significant effect of *Sex* but had no significant effect of interaction between *Sex* and *Year* (e, f, g), estimates calculated from $Model_{sex}$ are provided. For the traits which had statistically significant interaction between *Sex* and *Year* (a, b, d, i), estimates calculated from $Model_{year*sex}$ are provided. For the traits which had no significant effect of *Sex* (h), sex-independent estimates calculated from $Model_{base}$ are provided in grey line.

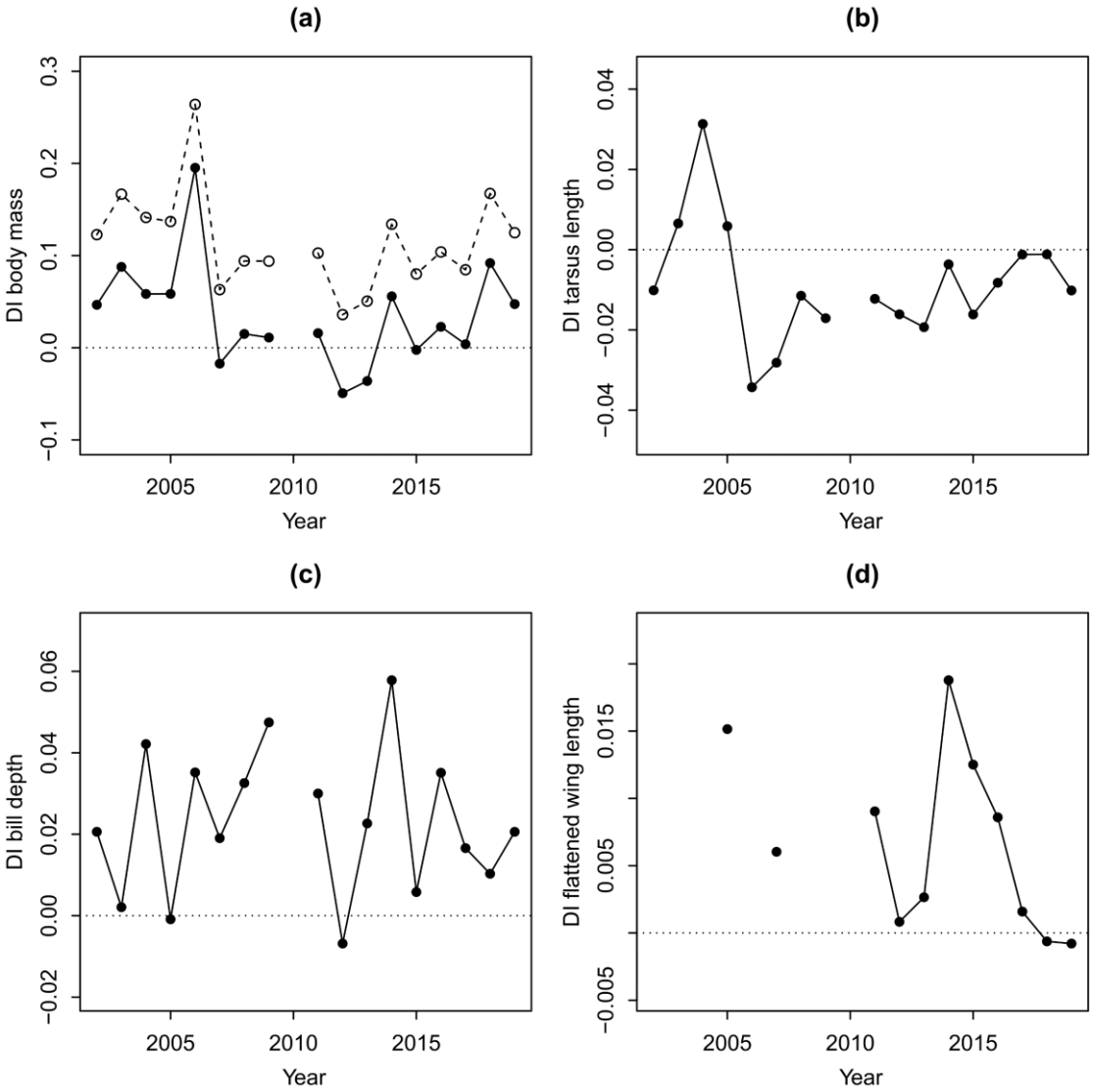


Figure 2-2
Annual variation of *Dimorphism index* of (a) body mass, (b) tarsus length, (c) bill depth and (d) flattened wing length. Only for body mass, estimates in non-breeding season and breeding season are depicted in solid line and dashed line, respectively.

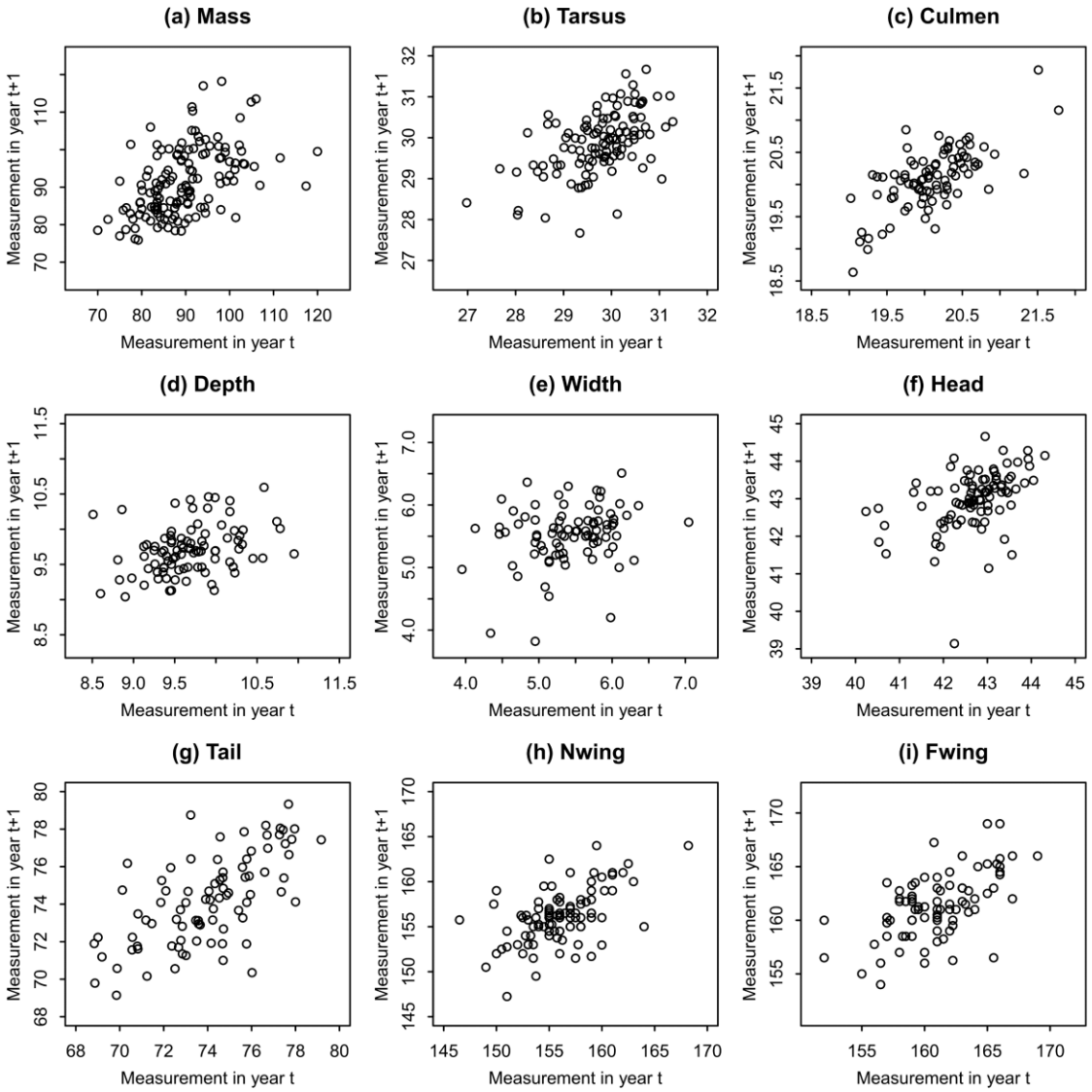


Figure 2-3

Scatter plots of multiple measurement data from same individuals across years. Measurement data are plotted against the previous measurement. Note that some individuals appear as more than one point because they are measured more than two years.

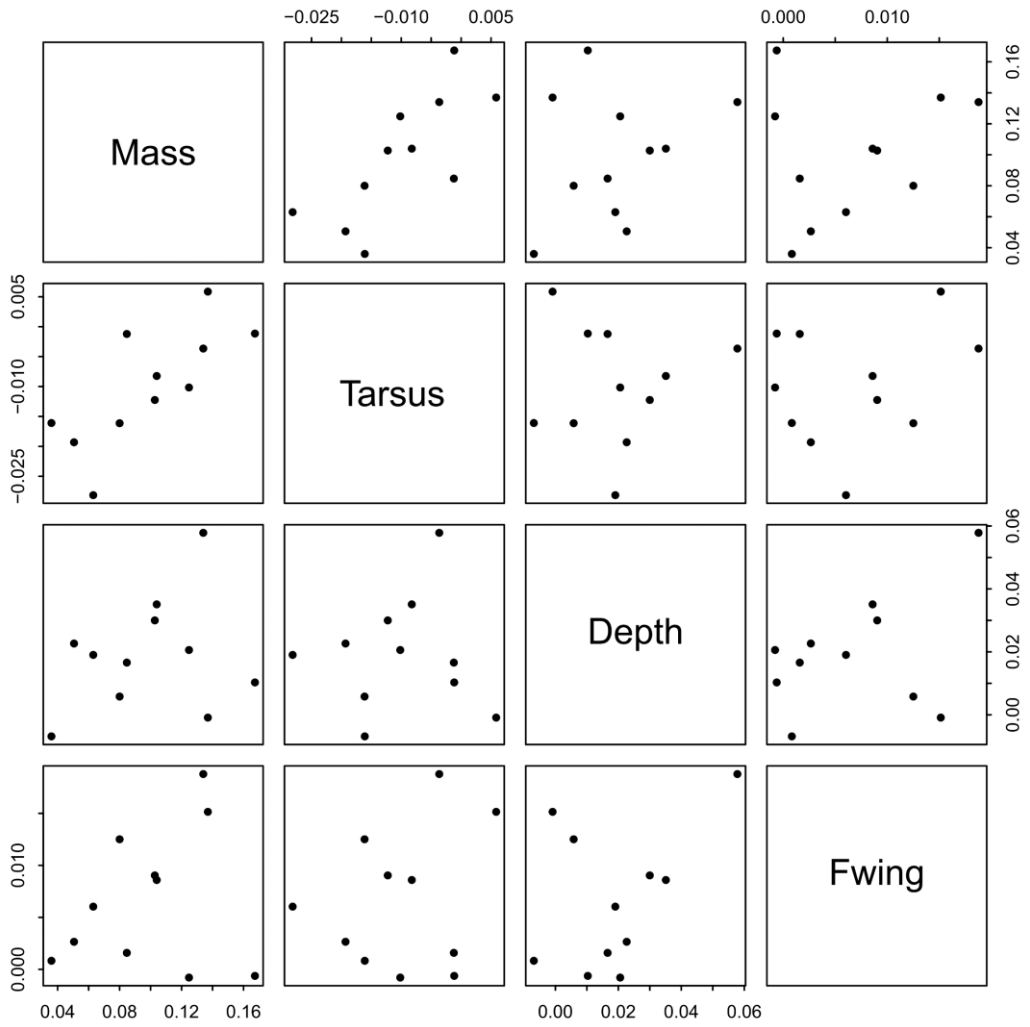


Figure 2-4
Pairwise correlation between RSD in multiple traits. Each point represents a pair of RSD values in a year. Body mass, tarsus length and bill depth had measurements in 2002, …, 2009, 2011, …, 2019. However, flattened wing length had measurements only in 2005, 2007, 2011, …, 2019. Therefore, correlation analyses were based on measurements in 2005, 2007, 2011, …, 2019.

Table

Table 2-1 Sample size per month and per season

	Month												Season		
Trait	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Breed	Non-breed	Total
Body mass	9	18	99	197	325	226	75	16	0	2	1	1	922	47	969
Tarsus length	9	18	96	189	316	219	74	15	0	1	1	1	894	45	939
Culmen length	9	18	94	181	308	197	69	15	0	0	1	1	849	44	893
Bill depth	9	18	94	185	312	205	71	15	0	2	1	1	867	46	913
Bill width	9	18	93	181	304	196	69	15	0	0	1	1	843	44	887
Head length	9	18	95	186	312	207	70	15	0	2	1	1	870	46	916
Tail length	9	15	72	157	274	177	60	9	0	0	1	2	740	36	776
Natural wing length	9	18	97	190	314	205	71	15	0	2	1	1	877	46	923
Flattened wing length	9	18	92	168	286	170	69	15	0	0	1	1	785	44	829

Breed: breeding season (February to July), Non-breed: non-breeding season (August to January)

Table 2-2 Body size estimates of long-term average of adult male and adult female

Trait	N_t	N_m	Ny_m	$Mean_m$	SE_m	$2.5\%_m$	$97.5\%_m$	N_f	Ny_f	$Mean_f$	SE_f	$2.5\%_f$	$97.5\%_f$
Body mass (Breed) (g)	922	606	240	85.93	0.44	85.06	86.79	316	84	96.18	0.49	95.22	97.15
Body mass (Non-breed) (g)	47	36	9	87.25	1.06	85.17	89.33	11	2	97.51	1.13	95.30	99.71
Tarsus length (mm)	939	622	252	29.79	0.04	29.72	29.86	317	85	29.59	0.05	29.49	29.69
Culmen length (mm)	893	592	248	20.03	0.03	19.97	20.09	301	82	20.19	0.04	20.12	20.27
Bill depth (mm)	913	603	251	9.55	0.02	9.50	9.59	310	84	9.78	0.03	9.72	9.83
Bill width (mm)	887	587	247	5.57	0.02	5.52	5.61	300	82	5.66	0.03	5.61	5.72
Head length (mm)	916	606	251	43.01	0.04	42.92	43.09	310	84	42.91	0.05	42.81	43.02
Tail length (mm)	776	512	193	73.22	0.13	72.96	73.49	264	60	74.30	0.15	74.00	74.60
Natural wing length (mm)	923	609	251	155.65	0.19	155.27	156.03	314	85	155.74	0.23	155.30	156.19
Flattened wing length (mm)	829	552	231	160.17	0.20	159.77	160.57	277	73	160.85	0.23	160.39	161.31

N: sample size, Ny: sample size of yearling, Mean: estimate of mean, SE: standard error, 2.5% and 97.5%: lower and upper boundary of 95% confidence interval

Table 2-2 (continued)

Trait	Difference	Dimorphism Index	Ratio
Body mass (Breed) (g)	10.26	11.27	1.12
Body mass (Non-breed) (g)	10.26	11.10	1.12
Tarsus length (mm)	-0.20	-0.68	0.99
Culmen length (mm)	0.16	0.82	1.01
Bill depth (mm)	0.23	2.35	1.02
Bill width (mm)	0.10	1.75	1.02
Head length (mm)	-0.09	-0.22	1.00
Tail length (mm)	1.08	1.46	1.01
Natural wing length (mm)	0.09	0.06	1.00
Flattened wing length (mm)	0.68	0.43	1.00

N: sample size, Ny: sample size of yearling, Mean: estimate of mean, SE: standard error, 2.5% and 97.5%: lower and upper boundary of 95% confidence interval

Table 2-3 Regression coefficients of Model$_{breed*sex+Year*sex}$ for body mass

Variable	Estimate	SE	t
Intercept	98.65	6.79	14.54
Measurer (Iwasaki)	5.07	5.06	1.00
Measurer (Matsuo)	-2.72	1.99	-1.37
Measurer (Nakanishi)	3.10	5.50	0.56
Measurer (Nishi)	2.55	9.84	0.26
Measurer (Sawada)	0.43	5.44	0.08
Measurer (Takagi)	3.31	4.46	0.74
Year (2003)	-2.52	7.77	-0.32
Year (2004)	-7.63	7.63	-1.00
Year (2005)	-2.68	8.69	-0.31
Year (2006)	13.52	7.89	1.71
Year (2007)	-6.24	7.06	-0.88
Year (2008)	-4.41	7.06	-0.62
Year (2009)	-8.58	7.12	-1.21
Year (2011)	-12.48	8.30	-1.50
Year (2012)	-12.28	8.67	-1.42
Year (2013)	-13.27	8.60	-1.54
Year (2014)	-2.42	8.61	-0.28
Year (2015)	-8.23	8.58	-0.96
Year (2016)	-6.47	8.73	-0.74
Year (2017)	-6.44	8.85	-0.73
Year (2018)	1.77	8.74	0.20
Year (2019)	-1.58	8.68	-0.18
Age (Y)	-3.47	9.33	-0.37
Breeding (Non-breeding)	-5.39	3.33	-1.62
Year (2003): Age (Y)	5.33	12.01	0.44
Year (2004): Age (Y)	2.98	10.55	0.28
Year (2005): Age(Y)	3.11	10.84	0.29
Year (2006): Age (Y)	0.95	10.18	0.09
Year (2007): Age(Y)	4.37	9.55	0.46
Year (2008): Age (Y)	2.13	9.64	0.22
Year (2009): Age (Y)	2.46	9.79	0.25

Table 2-3 (continued)

Variable	Estimate	SE	t
Year (2011): Age (Y)	-0.03	10.41	0.00
Year (2012): Age (Y)	0.81	9.97	0.08
Year (2013): Age (Y)	1.55	9.65	0.16
Year (2014): Age (Y)	-1.40	9.49	-0.15
Year (2015): Age (Y)	0.89	9.46	0.09
Year (2016): Age (Y)	4.80	9.44	0.51
Year (2017): Age (Y)	3.03	9.42	0.32
Year (2018): Age (Y)	0.74	9.39	0.08
Year (2019): Age (Y)	-1.13	9.39	-0.12
Sex (M)	-11.45	1.01	-11.39
Sex (M): Breeding (Non-breeding)	7.19	3.66	1.97
Sex (M): Year (2003)	-3.40	5.09	-0.67
Sex (M): Year (2004)	-0.62	4.84	-0.13
Sex (M): Year (2005)	-0.91	4.77	-0.19
Sex (M): Year (2006)	-14.81	4.60	-3.22
Sex (M): Year (2007)	5.78	2.33	2.48
Sex (M): Year (2008)	2.94	2.24	1.31
Sex (M): Year (2009)	3.33	2.92	1.14
Sex (M): Year (2011)	2.99	2.59	1.15
Sex (M): Year (2012)	8.38	2.55	3.28
Sex (M): Year (2013)	7.22	2.07	3.49
Sex (M): Year (2014)	-0.69	2.28	-0.30
Sex (M): Year (2015)	4.46	1.98	2.25
Sex (M): Year (2016)	2.30	1.87	1.23
Sex (M): Year (2017)	3.93	1.97	1.99
Sex (M): Year (2018)	-4.12	1.39	-2.97

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-4 Regression coefficients of Model$_{year*sex}$ for tarsus length

Variable	Estimate	SE	t
Intercept	29.89	0.49	60.75
Sex (M)	0.30	0.10	2.92
Year (2003)	-0.03	0.63	-0.04
Year (2004)	0.22	0.59	0.36
Year (2005)	-1.10	0.67	-1.65
Year (2006)	-0.89	0.67	-1.34
Year (2007)	-0.58	0.53	-1.09
Year (2008)	-0.07	0.52	-0.14
Year (2009)	-0.50	0.57	-0.88
Year (2011)	0.05	0.52	0.10
Year (2012)	-0.37	0.54	-0.68
Year (2013)	-0.55	0.52	-1.05
Year (2014)	-0.48	0.52	-0.91
Year (2015)	-0.87	0.51	-1.69
Year (2016)	-0.75	0.51	-1.48
Year (2017)	-0.21	0.52	-0.41
Year (2018)	-0.09	0.49	-0.19
Year (2019)	-0.12	0.49	-0.25
Sex (M): Year (2003)	-0.50	0.52	-0.96
Sex (M): Year (2004)	-1.23	0.48	-2.55
Sex (M): Year (2005)	-0.47	0.54	-0.88
Sex (M): Year (2006)	0.71	0.52	1.36
Sex (M): Year (2007)	0.53	0.25	2.13
Sex (M): Year (2008)	0.04	0.23	0.18
Sex (M): Year (2009)	0.20	0.36	0.56
Sex (M): Year (2011)	0.06	0.26	0.25
Sex (M): Year (2012)	0.17	0.29	0.61
Sex (M): Year (2013)	0.27	0.24	1.13
Sex (M): Year (2014)	-0.20	0.23	-0.87
Sex (M): Year (2015)	0.17	0.21	0.80
Sex (M): Year (2016)	-0.06	0.19	-0.34
Sex (M): Year (2017)	-0.27	0.20	-1.34
Sex (M): Year (2018)	-0.27	0.13	-2.15

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-5 Regression coefficients of $Model_{base}$ for culmen length

Variable	Estimate	SE	t
Intercept	20.69	0.06	342.72
Measurer (Iwasaki)	-0.65	0.07	-9.47
Measurer (Matsuo)	-0.37	0.12	-3.14
Measurer (Nakanishi)	-0.24	0.19	-1.26
Measurer (Sawada)	-0.60	0.07	-9.23
Measurer (Takagi)	-0.13	0.09	-1.43

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-6 Regression coefficients of Model$_{year*sex}$ for bill depth

Variable	Estimate	SE	t
Intercept	9.85	0.37	26.89
Sex (M)	-0.20	0.05	-3.76
Year (2003)	-0.48	0.42	-1.15
Year (2004)	0.35	0.41	0.84
Year (2005)	-0.55	0.47	-1.17
Year (2006)	0.08	0.43	0.19
Year (2007)	-0.01	0.38	-0.03
Year (2008)	0.32	0.42	0.77
Year (2009)	0.27	0.39	0.67
Year (2011)	-0.14	0.45	-0.32
Year (2012)	-0.36	0.47	-0.75
Year (2013)	-0.08	0.47	-0.18
Year (2014)	0.25	0.47	0.54
Year (2015)	0.10	0.47	0.22
Year (2016)	0.11	0.47	0.23
Year (2017)	-0.29	0.48	-0.61
Year (2018)	-0.10	0.47	-0.21
Year (2019)	0.00	0.47	0.01
Measurer (Iwasaki)	0.11	0.28	0.39
Measurer (Matsuo)	-0.38	0.18	-2.09
Measurer (Nakanishi)	-0.24	0.30	-0.79
Measurer (Nishi)	-1.34	0.50	-2.68
Measurer (Sawada)	-0.02	0.29	-0.08
Measurer (Takagi)	-0.13	0.24	-0.53
Age (Y)	-0.56	0.50	-1.12
Sex (M): Year (2003)	0.18	0.28	0.64
Sex (M): Year (2004)	-0.22	0.26	-0.84
Sex (M): Year (2005)	0.21	0.26	0.80
Sex (M): Year (2006)	-0.14	0.25	-0.56
Sex (M): Year (2007)	0.02	0.13	0.12
Sex (M): Year (2008)	-0.12	0.15	-0.84
Sex (M): Year (2009)	-0.27	0.18	-1.51

Table 2-6 (continued)

Variable	Estimate	SE	t
Sex (M): Year (2011)	-0.09	0.14	-0.61
Sex (M): Year (2012)	0.27	0.15	1.78
Sex (M): Year (2013)	-0.02	0.12	-0.15
Sex (M): Year (2014)	-0.37	0.13	-2.77
Sex (M): Year (2015)	0.14	0.11	1.31
Sex (M): Year (2016)	-0.14	0.10	-1.42
Sex (M): Year (2017)	0.04	0.11	0.41
Sex (M): Year (2018)	0.10	0.07	1.41
Year (2003): Age (Y)	0.44	0.65	0.68
Year (2004): Age (Y)	0.24	0.57	0.43
Year (2005): Age (Y)	0.92	0.58	1.58
Year (2006): Age (Y)	0.26	0.54	0.47
Year (2007): Age (Y)	0.62	0.51	1.22
Year (2008): Age (Y)	0.54	0.52	1.04
Year (2009): Age (Y)	0.78	0.53	1.49
Year (2011): Age (Y)	0.80	0.55	1.46
Year (2012): Age (Y)	0.55	0.53	1.03
Year (2013): Age (Y)	0.64	0.52	1.24
Year (2014): Age (Y)	0.34	0.51	0.66
Year (2015): Age (Y)	0.58	0.51	1.15
Year (2016): Age (Y)	0.62	0.50	1.23
Year (2017): Age (Y)	0.50	0.50	0.99
Year (2018): Age (Y)	0.36	0.50	0.72
Year (2019): Age (Y)	0.45	0.50	0.90

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-7 Regression coefficients of $Model_{sex}$ for bill width

Variable	Estimate	SE	t
Intercept	5.80	0.29	20.36
Sex (M)	-0.13	0.03	-4.44
Year (2006)	0.16	0.29	0.56
Year (2007)	-0.55	0.29	-1.89
Year (2008)	-0.79	0.33	-2.39
Year (2009)	-0.93	0.30	-3.13
Year (2011)	-0.51	0.15	-3.36
Year (2012)	0.14	0.21	0.65
Year (2013)	-0.24	0.20	-1.15
Year (2014)	-0.48	0.19	-2.52
Year (2015)	-0.04	0.20	-0.18
Year (2016)	-0.04	0.21	-0.17
Year (2017)	0.27	0.22	1.20
Year (2018)	0.19	0.22	0.86
Year (2019)	0.03	0.22	0.14
Measurer (Iwasaki)	-0.77	0.32	-2.39
Measurer (Matsuo)	0.40	0.19	2.11
Measurer (Nakanishi)	-1.09	0.35	-3.12
Measurer (Sawada)	-0.25	0.34	-0.73
Measurer (Takagi)	-0.08	0.29	-0.26

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-8 Regression coefficients of $Model_{sex}$ for head length

Variable	Estimate	SE	t
Intercept	43.52	0.49	88.55
Sex (M)	0.13	0.06	2.22
Year (2003)	-0.64	0.51	-1.26
Year (2004)	0.23	0.54	0.43
Year (2005)	-0.11	0.64	-0.17
Year (2006)	0.28	0.54	0.52
Year (2007)	-0.30	0.50	-0.60
Year (2008)	0.01	0.59	0.02
Year (2009)	-0.58	0.52	-1.13
Year (2011)	-0.34	0.68	-0.50
Year (2012)	-0.99	0.74	-1.33
Year (2013)	0.32	0.74	0.43
Year (2014)	-0.37	0.72	-0.52
Year (2015)	-0.40	0.73	-0.54
Year (2016)	-0.26	0.74	-0.36
Year (2017)	-0.32	0.75	-0.43
Year (2018)	-0.06	0.75	-0.08
Year (2019)	0.07	0.75	0.10
Measurer (Iwasaki)	-1.06	0.54	-1.97
Measurer (Matsuo)	-0.20	0.36	-0.56
Measurer (Nakanishi)	-3.19	0.60	-5.29
Measurer (Nishi)	-1.10	0.80	-1.38
Measurer (Sawada)	-0.54	0.57	-0.95
Measurer (Takagi)	-1.32	0.46	-2.89

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-9 Regression coefficients of $Model_{sex}$ for tail length

Variable	Estimate	SE	t
Intercept	73.79	0.35	211.13
Sex (M)	-1.03	0.17	-5.99
Year (2008)	-0.70	1.05	-0.66
Year (2009)	-0.81	0.58	-1.39
Year (2011)	2.53	0.50	5.10
Year (2012)	-0.94	0.94	-1.00
Year (2013)	-1.14	0.90	-1.27
Year (2014)	-0.13	0.79	-0.16
Year (2015)	-0.06	0.89	-0.07
Year (2016)	0.43	0.97	0.45
Year (2017)	0.30	1.03	0.29
Year (2018)	0.04	1.02	0.04
Year (2019)	0.41	1.02	0.40
Measurer (Iwasaki)	1.06	0.79	1.34
Measurer (Matsuo)	0.99	1.10	0.90
Measurer (Nakanishi)	1.38	1.05	1.32
Measurer (Sawada)	0.25	0.96	0.26
Age (Y)	-1.71	0.16	-10.63

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-10 Regression coefficients of $Model_{base}$ for natural wing length

Variable	Estimate	SE	t
Intercept	156.57	2.04	76.63
Year (2003)	2.92	2.14	1.36
Year (2004)	0.01	2.27	0.01
Year (2005)	1.62	2.68	0.60
Year (2006)	0.72	2.23	0.32
Year (2007)	-0.47	2.09	-0.23
Year (2008)	-0.51	2.44	-0.21
Year (2009)	-1.32	2.15	-0.62
Year (2011)	1.71	2.82	0.61
Year (2012)	-0.66	3.07	-0.22
Year (2013)	-3.40	3.05	-1.12
Year (2014)	-3.68	2.99	-1.23
Year (2015)	-4.75	3.04	-1.56
Year (2016)	-3.06	3.08	-0.99
Year (2017)	-2.31	3.12	-0.74
Year (2018)	-2.54	3.11	-0.82
Year (2019)	-3.04	3.12	-0.97
Measurer (Iwasaki)	1.59	2.23	0.71
Measurer (Matsuo)	-0.93	1.49	-0.63
Measurer (Nakanishi)	3.56	2.45	1.45
Measurer (Nishi)	7.65	3.37	2.27
Measurer (Sawada)	1.78	2.35	0.76
Measurer (Takagi)	0.99	1.88	0.53
Age (Y)	-2.25	0.21	-10.62

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-11 Regression coefficients of $Model_{year*sex}$ for flattened wing length

Variable	Estimate	SE	t
Intercept	164.50	2.29	71.94
Sex (M)	-2.47	2.64	-0.94
Year (2007)	-3.39	2.46	-1.38
Year (2011)	-1.43	2.42	-0.59
Year (2012)	-4.71	2.60	-1.82
Year (2013)	-4.37	2.51	-1.74
Year (2014)	-0.39	2.53	-0.16
Year (2015)	-4.58	2.48	-1.84
Year (2016)	-4.55	2.37	-1.92
Year (2017)	-3.68	2.39	-1.54
Year (2018)	-3.96	2.31	-1.71
Year (2019)	-4.19	2.31	-1.81
Measurer (Iwasaki)	2.85	0.73	3.88
Measurer (Nakanishi)	3.03	1.43	2.12
Age (Y)	-2.16	0.23	-9.48
Sex (M): Year (2007)	1.50	2.84	0.53
Sex (M): Year (2011)	1.01	2.86	0.35
Sex (M): Year (2012)	2.34	2.89	0.81
Sex (M): Year (2013)	2.05	2.79	0.73
Sex (M): Year (2014)	-0.58	2.82	-0.21
Sex (M): Year (2015)	0.49	2.75	0.18
Sex (M): Year (2016)	1.10	2.73	0.40
Sex (M): Year (2017)	2.22	2.75	0.81
Sex (M): Year (2018)	2.57	2.68	0.96
Sex (M): Year (2019)	2.60	2.68	0.97

All variables are categorical. Level of the variables are indicated in parentheses.

Table 2-12 Pearson's correlation between yearly dimorphism index of traits

	Body mass	Tarsus length	Bill depth	Flattened wing length
Body mass	-	0.74	0.26	0.23
Tarsus length	0.01	-	0.02	0.23
Bill depth	0.43	0.95	-	0.40
Flattened wing length	0.50	0.49	0.22	-

Upper diagonal: Pearson's correlation coefficient. Lower diagonal: non-adjusted P-value. Critical P-value for significance level of 0.05 after Bonferroni correction is 0.0083.

Chapter 3

Growth curves of Ryukyu Scops Owl nestlings, an owl species with asynchronous hatching and reversed sexual dimorphism

Abstract

The growth pattern of an organism is influenced by multiple factors, such as its own sex, the amount of parental resources invested in it, food abundance, and sibling competition. For species showing sexual size dimorphism, the sex of nest mates is expected to affect the growth of nestlings because sexual size dimorphism contributes to competitive hierarchies through body size differences, although this topic has rarely been investigated. This study describes the growth curve of the Ryukyu Scops Owl *Otus elegans* nestlings based on the analysis of body mass, wing length and tarsus length measurements from 99 individuals. Overall, I detected significant effects of several of the investigated predictor variables, though it is important to note the differences between groups were often small. Males and later hatched chicks had smaller body mass throughout their growth curves. The smaller the brood, the significantly heavier the chicks were on days 0–1 and 30–32, although this relationship reversed on days 8–13. Males and later hatched chicks also had shorter wing lengths. Males had significantly shorter tarsi than females from day 0 to day 4; however, dimorphism in this trait was reversed afterwards. Chicks in a large brood had longer tarsi. Earlier hatched chicks had longer tarsi in the first half of the growth period, but the difference had disappeared by the second half. From day 0 to day 3, individuals with an older brother had longer tarsi than those with an older sister. However, by the middle of the growth period and thereafter, individuals with an older brother had shorter tarsi than those with an older sister. Because males had smaller body mass and shorter wings than females in the middle of the growth period, the results suggest that male nestlings are more competitive than females during this period despite their smallness, for a reason other than body size difference between the sexes.

Introduction

The growth pattern of an organism is an outcome of multiple factors. For example, the organism's own sex (Zárybnická et al. 2015; Loonstra et al. 2018; Nogueira et al. 2019), the amount of parental resources invested (Eising et al. 2001; Hsu et al. 2019), food abundance (Zárybnická et al. 2015) and sibling competition (Nilsson and Svensson 1996; Royle et al. 1999) have all been shown to affect growth. Because body size is a

major determinant of individual fitness (Peters 1983), how it develops and what factors influence it are important questions in evolutionary ecology.

Many bird species grow with nest mates. Therefore, sibling rivalry is an unavoidable aspect when discussing growth patterns in avian species. Hatching order often shapes competitive hierarchies between nestlings (Lack 1947; Mock and Parker 1998), as later-hatched chicks are usually allocated less food, which results in poor growth or death. Furthermore, hormone levels may also alter the hierarchy, as androgens are related to the intensity of nestling behaviours such as begging and aggressiveness (Groothuis and Schwabl 2008).

It is important to note that a relative power balance among siblings is what determines the hierarchy. Whether a nestling can win in such a competition is dependent not only on its own status but also on that of its siblings. However, when analysing the possible outcomes of competition, explanatory variables derived from 'others' are often overlooked in favour of those derived from 'self'. For example, although previous avian studies have documented the effect of sex on nestling growth (Zárybnická et al. 2015; Loonstra et al. 2018; Nogueira et al. 2019), the effects of a sibling's sex have been rarely evaluated (but see Becker and Wink 2003; Scandolara et al. 2014). However, in the contemporary human population, older brothers, compared with older sisters, have been shown to lead to lower birth weights of later-born siblings (Nielsen et al. 2008). Such effects of having an older brother have been documented mainly in humans (Blanchard and Ellis 2001; Christiansen et al. 2004; Nielsen et al. 2008; Rickard 2008). Among avian species exhibiting sexual size dimorphism, the sex of nest mates can matter because of the associated relative difference in body size. An individual with a sibling of the smaller-sex may be more competitive than an individual with a sibling of the larger-sex (Fargallo et al. 2007; Müller et al. 2007). This may translate into different growth patterns dependent on whether the sibling is a sister or a brother.

This study describes the growth pattern of the Ryukyu Scops Owl *Otus elegans*. Females of this owl commence incubation before clutch completion, thus asynchronous hatching is common (Iwasaki unpublished data). Sexual dimorphism in body size among adults of this species has been documented recently (Sawada et al. 2021b). Thus, this owl can serve as a model for investigating the effect of sex of nest mates on growth patterns. In this study I aim to determine the factors affecting the growth pattern of Ryukyu Scops Owls, specifically including not only the effects of factors associated with the individual itself, but also the effects of its nest mates.

Materials and Methods

Material

Ryukyu Scops Owls are distributed on islands ranging from Batan Island and Calayan Island, in the northern part of the Philippines, to Okinoshima Island, off Kyushu, the southern main island of Japan (Ornithological Society of Japan 2012; Takagi et al.

2015; Gill and Donsker 2019). I focused on the Ryukyu Scops Owl (subspecies *O. e. interpositus*) population on Minami-daito Island (25˚50′N, 131˚ 14′E, 30.5 km^2), an oceanic island 360 km east of Okinawa Island. The species exhibits reversed sexual dimorphism (Lee and Severinghaus 2004). Adult females are larger and heavier than males (Akatani 2011; Sawada et al. 2021b). According to Sawada et al. (2021b), average body mass is 85.93 g (N = 606) in males and 96.18 g (N = 316) in females; average tarsus length is 29.79 mm (N = 622) in males and 29.59 mm (N = 317) in females; average wing length is 155.65 (N = 609) in males and 155.74 (N = 314) in females. Although tarsus length is slightly smaller in females than males, females are larger than males as a whole. They lay a single clutch (1–4 eggs) from mid-March to mid-May (Takagi et al. 2007a; Akatani et al. 2011; Sawada and Iwasaki unpublished data). Incubation and the nestling period last about one-month each (Takagi et al. 2007a). Females lay eggs with an interval of one egg per three or four days (Iwasaki unpublished data). They commence incubation before clutch completion (often from when they lay the second egg), thus asynchronous hatching is common (all chicks in a clutch typically hatch within three days in most cases, Iwasaki unpublished data). The breeding behaviour of the Ryukyu Scops Owl on Minami-daito Island has been monitored since 2002 (Takagi et al. 2007a,b; Sawada et al. 2018a; Takagi 2020).

Data collection

Members of the long-term research group monitored the breeding activity of the owls by visiting their nests regularly from late February to late July from 2004 to 2008. From a few days before the estimated hatching date, they checked the nests daily so as to confirm hatching order. Nestlings were captured after sundown (19:00 to 20:30). They measured body mass (by Pesola spring balance to nearest 0.1 g), tarsus length (by electronic digital calliper to nearest 0.01 mm) and wing length (by stainless steel ruler to nearest 0.1 mm) of 99 nestlings (10 in 2004, 17 in 2005, 10 in 2006, 27 in 2007, 35 in 2008) during the 32 days from hatching. Other than the 99 nestlings, four chicks died before measurements and blood samples had been taken (hence we had no data on body size and sex for them); they were also excluded because such chicks seem to follow a fundamentally different growth curve from healthy chicks. I also did not include 15 chicks for which we had measurements but no data on their precise hatching date and/or data from their older siblings. Measurements were taken at least twice during each measuring occasion and their averages were used as data points for our analyses. Blood samples were collected by brachial venepuncture from day 15 to day 27. DNA samples (extracted from the blood samples) were used for molecular sexing by PCR amplification of the CHD gene (Fridolfsson and Ellegren 1999). Procedures for sexing the owls are detailed in Sawada et al. (2021b).

Growth analysis

Step 1) determining the growth model

I used a non-linear mixed effect model and model selection to describe the growth curve of the traits (Sofaer et al. 2013). To determine which types of growth model (Gompertz, Logistic and von Bertalanffy) to use in the subsequent analyses, measurement data for each trait were first fitted to the three growth models without any explanatory variables. The best model for each trait was then chosen for further investigation with explanatory variables. In this step, the three models were parameterised according to model formulas given in Narinç et al. (2017).

$$\text{Gompertz: } f(t|\beta_0, \beta_1, \beta_2) = \beta_0 \exp[-\beta_1 \exp(-\beta_2 t)]$$
$$\text{Logistic: } f(t|\beta_0, \beta_1, \beta_2) = \beta_0 \exp[1-\beta_1 \exp(-\beta_2 t)]^{-1}$$
$$\text{von Bertalanffy: } f(t|\beta_0, \beta_1, \beta_2) = \beta_0 \exp[1+\beta_1 \exp(-\beta_2 t)]^{3}$$

These functions describe body size at time *t*, where *t* denotes days from hatching. β_0 is an asymptotic value, β_1 is a parameter related to the position of the growth curve along the t-axis and β_2 is a parameter related to growth rate (Narinç et al. 2017). The above interpretation follows from the mathematical expression of the models and its derivatives (Table 3-1, Narinç et al. 2017). In other words, the larger β_0 becomes, the larger size the individual reaches; the larger β_1 becomes, the larger the individual becomes at any given time; the larger β_2 becomes, the more rapidly the individual grows. These three parameters collectively shape the growth curves.

I fitted the growth models using Bayesian non-linear regression (Karaman et al. 2014). To account for repeated measurements of the same individuals, I included a random effect of individual ID and nest ID into the asymptotic value β_0, which is denoted as β_{0i}:

$$\beta_{0i} = \exp(ind_i + nest_i)$$
$$ind_i \sim \text{Normal}(0, sigma_{ind})$$
$$nest_i \sim \text{Normal}(0, sigma_{nest})$$

The exponential guarantees that an asymptotic value will become positive. I avoided including random effects in other parameters (β_1 and β_2) following Loonstra et al. (2018). Then I modelled measurement value Y of individual *i* at day *t*, Y_{it}, as a sum of the function of growth model $f(t|\beta_0, \beta_1, \beta_2)$ (this is one of the above defined formulae of Gompertz, Logistic and von Bertalanffy) and normal measurement error e_i as in the following formula:

$$Y_{it} = f(t|\beta_0, \beta_1, \beta_2) + e_i$$
$$e_i \sim \text{Normal}(0, sigma_{error})$$

I used the probabilistic programming language Stan (Carpenter et al. 2017) and R package *rstan* (Stan Development Team 2016) for model fitting. MCMC parameters were set as follows: chains = 4, iter = 25000, warmup = 5000, thin = 5. I used priors of t-distributions for β following prior recommendations in Stan (Gelman 2020). Further statistical details including the priors are given in Appendix. After fitting the three models with Stan, the models were compared based on predictive accuracy using the Watanabe-Akaike Information Criteria (WAIC) implemented in R package *loo* (Vehtari

et al. 2018). Unlike AIC, the widely used information criteria, WAIC can be used for complex hierarchical models as used in this study (Watanabe 2010).

Step 2) including explanatory variables into the growth model

To determine which factors influence the growth pattern, the fixed effects of explanatory variables were included into the three parameters of the previously chosen best model (in step 1). The explanatory variables are as follows: 1) *Intercept*, a constant which takes 1 for all individuals, 2) *Sex*, a two-level categorical variable that indicates the sex of the chick, "female" (reference) or "male", 3) *Year*, a five-level categorical variable indicating the sampling year, "2004" (reference), "2005", "2006", "2007" and "2008", 4) *Brood*, a continuous variable of 0, 1, or 2 depending on whether the individual belongs to a brood of 1, 2, or 3 chicks, respectively, 5) *Order*, a three-level categorical variable indicating hatching order, "a-chick" (reference), "b-chick" and "c-chick", 6) *Older*, a two-level factor variable indicating whether or not the individual has an older male sibling, "no" (reference) and "yes". Expressions of the model are:

$$\beta_{0i} = \exp(\mathbf{x_i}\boldsymbol{\alpha_0} + ind_i + nest_i)$$
$$\beta_{1i} = \exp(\mathbf{x_i}\boldsymbol{\alpha_1})$$
$$\beta_{2i} = \exp(\mathbf{x_i}\boldsymbol{\alpha_2})$$
$$ind_i \sim \text{Normal}(0, sigma_{ind})$$
$$nest_i \sim \text{Normal}(0, sigma_{nest})$$

Here, $\mathbf{x}_i$ is a p dimensional row vector which has the values of p explanatory variables (i.e. *Intercept*, *Sex*, …, *Older*) of individual i. Three parameters, $\boldsymbol{\alpha}_0$, $\boldsymbol{\alpha}_1$ and $\boldsymbol{\alpha}_2$, are p dimensional column vectors whose elements are the regression coefficients of the p explanatory variables. I fitted the model with all possible combinations of the explanatory variables under two conditions: 1) all models must include the *Intercept*, 2) all models that include *Older* must include *Order*. Since only younger siblings experience the effects of having an older brother (those with *Order* = "b-chick" or "c-chick"), the effect can be interpreted as changes in the effects of *Order* depending on the sex of their older sibling. This is the reason why I pose the second condition above. Then, I again implemented the models with Stan and R. MCMC parameters were set as follows: chains = 4, iter = 28000, warmup = 8000, thin = 5. Further statistical details including the priors for regression coefficients are given in Appendix. Models were ranked by WAIC and model averaging was applied based on model weight calculated from the WAIC values (see Appendix). Please note that what I averaged is prediction (i.e. value of Y) (Banner and Higgs 2017).

I focused on explanatory variables which were included in models with delta WAIC (difference from the best model) values smaller than four. Interpretations of the effects of the included explanatory variables were based on the model-averaged prediction of growth curves depending on the effects and 95% credible interval (95% CRI) of their differences. Although my analyses are based on Bayesian statistics and information theoretic approaches, I used the term "significant" for convenience. The "significance"

of the differences between the curves at a given time point (e.g. difference between tarsus length of a-chick in 2004 at day 10 and tarsus length of b-chick in 2004 at day 10) were decided based on whether the 95% CRI of the differences include zero or not. I did not discuss the significance of regression coefficients in each model (i.e. whether 95% CRI of the coefficients include zero or not), because the inclusion of explanatory variables into models was already evaluated through the information theoretic approach.

I obtained some biologically important statistics of the growth curve dependent on the effects of explanatory variables. Specifically, asymptotic size A, day of inflection point IP_{day} and growth rate at the inflection point IP_{rate} were calculated using formulas in Table 3-1 with setting variables to fixed values given in Table 3-2. Growth rates reach their maxima at the inflection point. Because these statistics can be calculated for each model, I took their weighted averages using the WAIC weight (Appendix).

Results

Determining the growth model

The Gompertz model performed best for body mass and tarsus length, however, the Logistic model performed best for wing length (Table 3-3, Figure 3-1). Fitted models were:

$$\text{Body mass: } Y = 89.116\exp[-2.128\exp(-0.148t)]$$

$$\text{Tarsus length: } Y = 30.389\exp[-1.175\exp(-0.139t)]$$

$$\text{Wing length: } Y = 123.968\exp[1-11.996\exp(-0.164t)]^{-1}$$

For each trait the contributions of explanatory variables were evaluated using model averaging based on WAIC (see below).

Body mass

For body mass, *Sex*, *Year*, *Brood* and *Order* were included in the best set of models with delta WAIC < 4 (Table 3-4, regression coefficients were given in Table 3-5). I describe below the results related to these four explanatory variables.

From model averaging, all the explanatory variables had significant effects on growth curves (Figure 3-2, Table 3-6). Females had larger body mass than males and the difference was significant from day 4 to day 16 (Figure 3-2a). Estimated differences between males and females ranged from 0.235 g to 0.307 g during this period (Table 3-7). Asymptotic size was slightly larger in females (89.340 g) than males (89.306 g), indicating a slight sign of reversed sexual size dimorphism (Table 3-6). Body mass also varied on an annual basis (Figure 3-2b).

The smaller the brood size the heavier the chicks were on day 0 and day 1 (Figure 3-2c). However, this relationship reversed from day 8 to day 13 and then reversed again from day 30 to day 32 (Figure 3-2c). Estimated differences on days 0 and 1 and from day 30 to day 32 between one-chick-broods and two-chick broods ranged from 0.514 g to 0.698 g, between two-chick-broods and three-chick broods ranged from 0.471 g to 0.741 g, between three-chick-broods and one-chick broods ranged from -1.439 g to -

0.984 g (Table 3-7). Estimated differences from day 8 to day 13 between one-chick-broods and two-chick broods ranged from -0.435 g to -0.580 g, between two-chick-broods and three-chick broods ranged from -0.506 g to -0.607 g, between three-chick-broods and one-chick broods ranged from 0.941 g to 1.187 g (Table 3-7). Asymptotic size also decreased with increasing brood size by about one gram per chick: 89.340 g (one chick), 88.351 g (two chicks) and 87.385 g (three chicks) (Table 3-6).

Earlier hatched chicks were heavier than later hatched chicks (Figure 3-2d). The difference between the a-chick and the b-chick was significant from day 1 to day 21 and the difference between the b-chick and the c-chick was significant from day 3 to day 32. Last-hatched c-chicks had significantly smaller body mass than first hatched a-chicks throughout their growth period (Figure 3-2d). Estimated differences between a-chicks and b-chicks ranged from 0.164 g to 0.215 g from day 1 to day 21, between b-chicks and c-chicks ranged from 0.191 g to 0.392 g from day 3 to day 32, between c-chicks and a-chicks ranged from -0.573 to -0.225 g from day 0 to day 32 (Table 3-7). Asymptotic size decreased with hatching order: 87.385 g (a-chick), 87.217 g (b-chick), 86.890 g (c-chick) (Table 3-6; Table 3-7 provides more detailed numerical differences between growth curves in Figure 3-2).

Wing length

For wing length, *Sex*, *Year*, *Brood* and *Order* were included in the best set of models with delta WAIC < 4 (Table 3-8, regression coefficients were given in Table 3-9). I describe below the results related to these four explanatory variables.

From model averaging, all explanatory variables except *Brood* had significant effects on the growth curve (Figure 3-3, Table 3-10). Females had larger wing length than males and the difference was significant after day 5 (Figure 3-3a, Table 3-10). Estimated differences between the sexes increased from 0.094 mm to 0.422 mm during this period (Table 3-11). Asymptotic size was slightly larger in females (123.745 mm) than males (123.276 mm), indicating a slight sign of reversed sexual size dimorphism (Table 3-10). Wing length also varied on an annual basis (Figure 3-3b).

Brood size did not significantly affect the growth curve (Figure 3-3c). First-hatched a-chicks had longer wings than later-hatched b-chicks and c-chicks (Figure 3-3d). These differences between a-chicks and others were significant before day 11 and after day 22 (Figure 3-3d). For example, estimated differences during the period between a-chicks and b-chicks were 0.193–0.790 mm, between b-chicks and c-chicks were 0.067–0.570 mm, between c-chicks and a-chicks were -0.259–-1.360 mm (Table 3-11). Asymptotic size decreased with hatching order: 123.938 mm (a-chick), 122.805 mm (b-chick), 122.040 mm (c-chick) (Table 3-10; see also Table 3-11 for more detailed numerical differences between growth curves in Figure 3-3).

Tarsus length

For tarsus length, *Sex*, *Year*, *Brood*, *Order* and *Older* (presence of older male sibling) were included in the best set of models with delta WAIC < 4 (Table 3-12, regression coefficients were given in Table 3-13). I describe below the results related to these five effects.

From model averaging, all the explanatory variables had significant effects on growth curves (Figure 3-4, Table 3-14). Females had larger tarsi than males from day 0 to day 4; however, this relationship reversed from day 11 to day 17 (Figure 3-4a, Table 3-14). Estimated differences between males and females decreased from 0.394 mm to 0.131 mm from day 0 to day 4, and ranged from -0.141 mm to -0.116 mm from day 11 to day 17 (Table 3-15). Asymptotic size was slightly larger in females (30.608 mm) than males (30.530 mm) (Table 3-14). Tarsus length also varied on an annual basis (Figure 3-4b).

The larger the brood size the larger tarsi the chicks had throughout the growth period (Figure 3-4c). Estimated differences during the growth period between one-chick broods and two-chick-broods ranged from -0.074 to -0.052 mm, between two-chick-broods and three-chick-broods ranged from -0.078 to -0.052 mm, and between three-chick broods and one-chick-broods ranged from 0.104 to 0.153 mm (Table 3-15). Asymptotic size also increased with brood size by about 0.07 mm per chick: 30.608 mm (one chick), 30.681 mm (two chicks), 30.755 mm (three chicks) (Table 3-14). Earlier hatched chicks were larger than later hatched chicks until about day 15 (Figure 3-4d). However, only last-hatched c-chicks were smaller than the others after day 21 (Figure 3-4d). Estimated differences before day 15 between a-chicks and b-chicks ranged from 0.144 to 0.446 mm, between b-chicks and c-chicks ranged from 0.123 to 0.570 mm, between c-chicks and a-chicks ranged from -0.952 to -0.293 mm (Table 3-15). Estimated differences after day 21 between a-chicks and b-chicks ranged from -0.218 to -0.214 mm (Table 3-15). Asymptotic size was smallest in c-chicks and largest in b-chicks: 30.755 mm (a-chick), 31.068 mm (b-chick), 30.526 mm (c-chick) (Table 3-14).

Chicks with an older brother had significantly longer tarsi than those without an older brother from day 0 to day 3 (Figure 3-4e). Although, the difference was non-significant from day 4 to day 10, the relationship reversed from day 11 to day 28 (Figure 3-4e). Estimated differences of chicks with an older brother from chicks without an older brother ranged from -0.495 to -0.267 mm from day 0 to day 3, and ranged from 0.242 to 0.336 mm from day 11 to day 28 (Table 3-15). Asymptotic size was smaller in chicks with an older brother (30.794 mm) than those without (30.994 mm) (Table 3-14; and see Table 3-12 for more detailed numerical differences between growth curves in Figure 3-4).

Discussion

In this study I aimed to describe the growth pattern of the Ryukyu Scops Owl *Otus elegans* nestlings. After determining which growth curve fitted each body size measure best, I investigated effects of sex of the nestlings, brood size, hatching order and having an older brother on the growth trajectories. Below I discuss our findings with possible

biological interpretations, though it must be noted that most detected significant differences between the growth curves were small. Therefore, we should be cautious when making conclusions on their biological relevance and further research is needed.

Body mass

Females had larger body mass estimates throughout the growth period and the difference was significant in the middle of the growth curve. Because females are larger than males also in adults, this result indicates that the sexual size dimorphism emerges during the nestling period. Non significance at hatching and fledging seems to be due to small sample sizes at these time points. Annual variation might result from the rearing conditions in the year (Brommer et al. 2003). However, as I have no data on prey availability in the field, I do not discuss annual variation any further here.

Large brood size resulted in small body mass at hatching. This indicates that there is a trade-off between clutch size and the size of hatchlings (Pellerin *et al*. 2016). Analysis of egg volume and content would provide useful data; however, collection of such egg data is difficult for this owl because it can induce nest abandonment (Iwasaki unpublished data). Reversed relationships after hatching may be explained by increased feeding efforts of parents disproportionately to brood size and/or an uneven share of food among nestlings. Low body mass at fledging linked to increased brood size indicates that parental provisioning does not meet the demands of large broods.

It was reasonable that later hatched chicks weighed less than earlier hatched chicks, because later hatched chicks experience competition immediately after their hatching. Conversely, earlier hatched chicks do not have competitors until their siblings hatch. Please note that the independent variable in our growth model was “days from hatching date”, not “days from the hatching date of the first-hatched chick within a brood”. If I draw the growth curves of nestlings in a brood on an x-axis representing “days from hatching date of the first-hatched chick within a brood”, the curves of later hatched chicks slide horizontally and the size difference at a given time becomes greater (Figure 3-5).

Wing length

Females had longer wings than males in the middle of the growth curve. This result indicates the emergence of sexual size dimorphism in adults (Sawada et al. 2021b). There was an effect of year on wing length. This effect too might be explained by rearing conditions of the year (Brommer et al. 2003). In contrast to body mass, wing length did not vary with brood size. Furthermore, although there was a tendency of wing length to decrease with hatching order, it was not as significant as body mass. These results indicate that chicks prioritize wing growth even though they have small body mass (Nilsson and Svensson 1996). This might confer better flying ability on younger siblings within large broods after fledging and enable them to keep up with their older siblings (Nilsson and Svensson 1996).

Tarsus length

At hatching, females had longer tarsi than males. However, this sexual difference reversed in the middle of the growth period, although it disappeared afterwards. Because females weighed more than males at hatching, the longer tarsi of females would be an allometric difference proportional to overall body size. The sexual difference in tarsus length illustrated above is in accordance with sexual size dimorphism in adults (Sawada et al. 2021b). That is, females have slightly shorter tarsi than males (see methods, Sawada et al. 2021b). Tarsus length also varied on an annual basis, which might be one result of yearly differences in rearing conditions (Brommer et al. 2003). Although variation with respect to *Year* was larger than variation with respect to other variables, this does not influence discussion. This is because the focus is not on the difference between chicks sampled across years, but on the size and growth difference of chicks within a brood.

It was surprising that chicks had longer tarsi when they were in a large brood. Considering that chicks in a large brood had low body mass, this result implies that they have disproportionally longer tarsi compared to their body mass. Competition within a brood might prioritise development of legs to facilitate obtaining food from parents (Gil et al. 2008).

Later hatched chicks had shorter tarsi than earlier hatched chicks during the first half of the growth period. This suggests a declining investment into eggs based on the laying order. However, in the remaining period, the difference between a-chicks and c-chicks was not significant, and b-chicks even had longer tarsi than a-chicks. This suggests an adaptive growth pattern of later hatched chicks. As fledglings need to climb from their nest and around their natal tree, later-hatched nestlings should have sufficiently grown legs even though there has been less investment in them (Kristan et al. 1996). In order to fledge successfully, younger siblings may allocate resources to tarsus growth to allow them to acquire sufficiently strong tarsi for climbing (Kristan et al. 1996).

Having an older brother resulted in greater tarsus length at the beginning of the growth curve (days 0–3) but smaller tarsus length in the middle of the curve (days 11–28). The effect at the beginning has two explanations. First, because males are smaller than females at first (at least for tarsus length), brothers would be less competitive than sisters. Therefore, nestlings with an older brother can grow better. Second, if initial body size corresponds to egg content volume, the results suggest that there was greater investment into the eggs laid after the male egg.

In the middle of the growth curve, females were larger than males in both body mass and wing length. Therefore, the effect of having an older brother, which resulted in smallness, is not simply explained by body-size-related competitive ability. Small brothers seem to be less competitive than large sisters, hence, when they have brothers, chicks are expected to have better, rather than worse, growth. Sexual differences in aggression may be an explanation. Androgens are known to increase the aggressiveness

and begging intensity of nestlings (Groothuis and Schwabl 2008). If male owl nestlings have more androgens and stronger aggressive behaviour than females (even though they are smaller than females), then their younger nest mates may suffer from reduced growth.

Although sexual differences in testosterone levels have been investigated in many avian species (Ottinger et al. 2001; Verboven et al. 2003; Goymann et al. 2005; Goodship and Buchanan 2006; Fargallo et al. 2007), there have been few such studies of owl species. It may be adaptive for mothers to increase the baseline levels of testosterone in the smaller sex to better compete with the larger sex (Fargallo et al. 2007). In addition to studying egg volume, I aim to measure the androgen levels of nestling owls in the near future.

Conclusion

Although the detected effects were often small, the effect of sex was consistently in the direction of sexual size dimorphism in adults across the multiple traits. This suggests that dimorphism begins to appear in nestlings. The effects of brood size and hatching order were also small and inconsistent across traits. However, the effect of having an older brother was relatively large. As the effect of having an older brother has been, so far, mostly studied in humans (Blanchard and Ellis 2001; Christiansen et al. 2004; Nielsen et al. 2008; Rickard 2008), we suggest that the effects of having an older brother in other species is worth investigating.

Figure

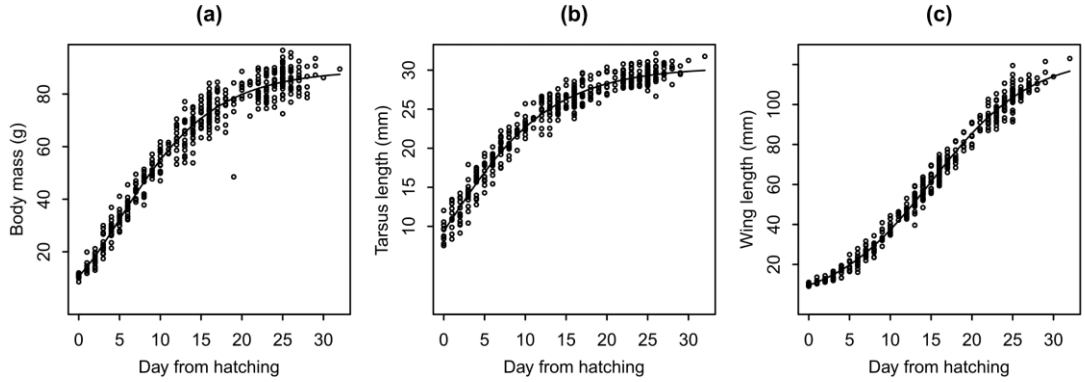


Figure 3-1

Growth curves of (a) body mass, (b) wing length, (c) tarsus length. Points: raw data, lines: estimates calculated from null model chosen by analyses in the step 1 fundamental model selection.

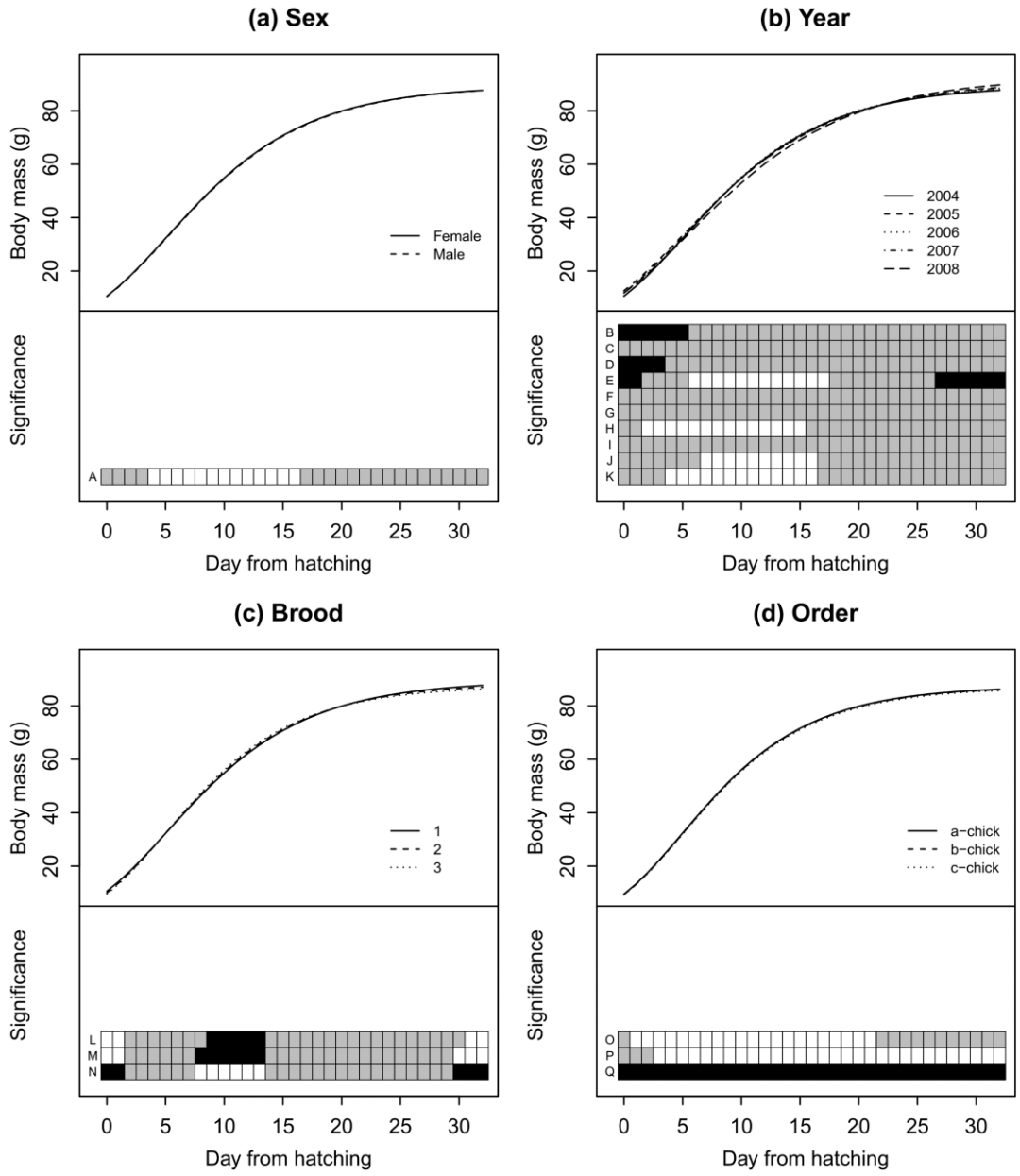


Figure 3-2

Growth curves of body mass depending on (a) sex, (b) year, (c) brood size and (d) hatching order. Variables settings used to obtain these estimates are given in Table 3-2. Heat maps under the graphs show the significance of the difference between curves in pairwise manner at each day. Black: upper boundary of 95% CRI of difference is smaller than zero, grey: 95% CRI of difference include zero, white: lower boundary of 95% CRI of difference is larger than zero. A: female – male, B: 2004 – 2005, C: 2004 – 2006, D: 2004 – 2007, E: 2004 – 2008, F: 2005 – 2006, G: 2005 – 2007, H: 2005 – 2008, I: 2006 – 2007, J: 2006 – 2008, K: 2007 – 2008, L: 1 chick – 2 chicks, M: 2 chicks – 3 chicks, N: 3 chicks – 1 chick, O: a chick – b chick, P: b chick – c chick, Q: c chick – a chick.

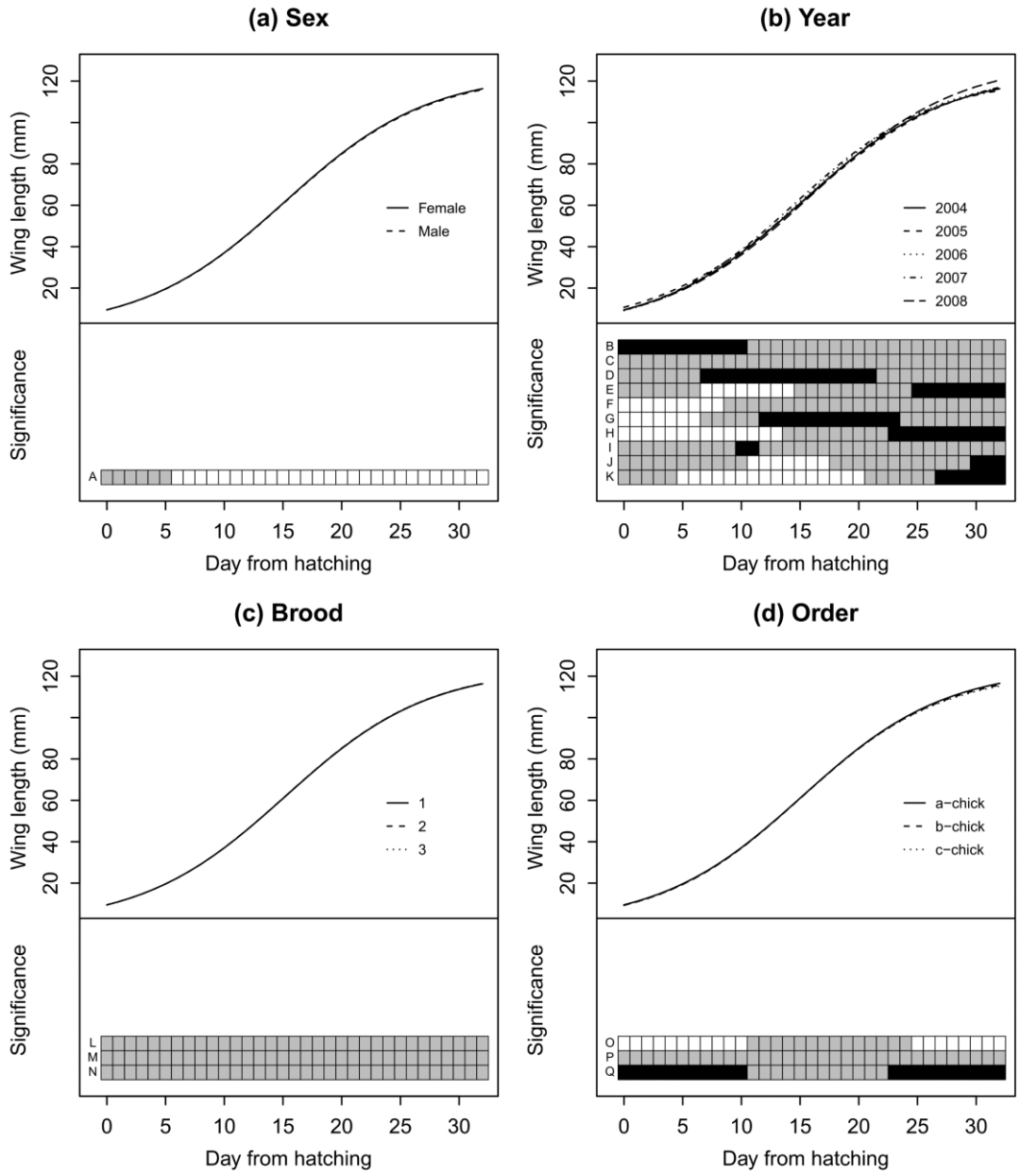


Figure 3-3

Growth curves of wing length depending on (a) sex, (b) year, (c) brood size and (d) hatching order. Variables settings used to obtain these estimates are given in Table 3-2. Heat maps under the graphs show the significance of the difference between curves in pairwise manner at each day. Black: upper boundary of 95% CRI of difference is smaller than zero, grey: 95% CRI of difference include zero, white: lower boundary of 95% CRI of difference is larger than zero. A: female – male, B: 2004 – 2005, C: 2004 – 2006, D: 2004 – 2007, E: 2004 – 2008, F: 2005 – 2006, G: 2005 – 2007, H: 2005 – 2008, I: 2006 – 2007, J: 2006 – 2008, K: 2007 – 2008, L: 1 chick – 2 chicks, M: 2 chicks – 3 chicks, N: 3 chicks – 1 chick, O: a chick – b chick, P: b chick – c chick, Q: c chick – a chick.

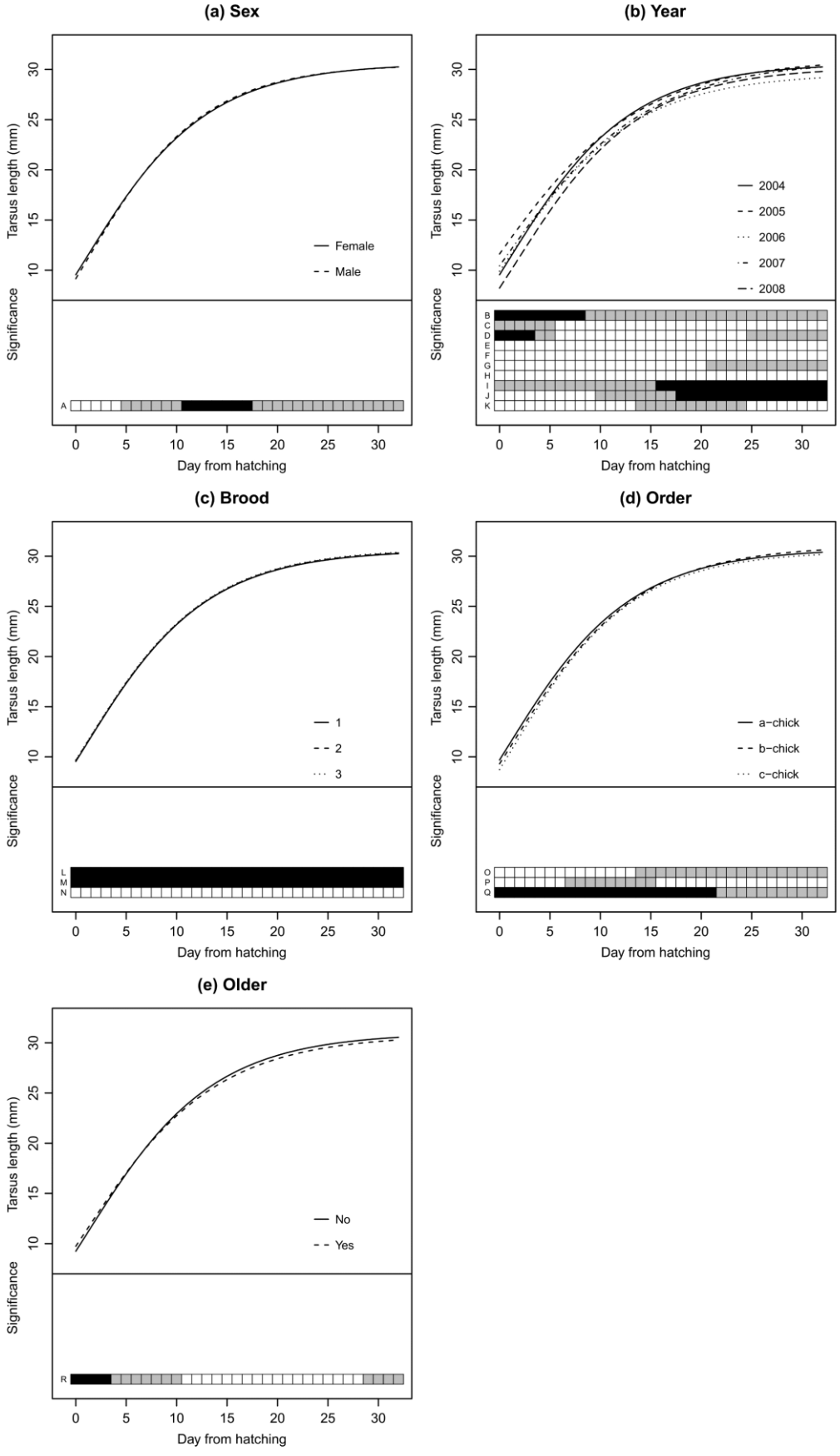

(a) Sex
Tarsus length (mm)
Female
Male
Significance
A
Day from hatching
(b) Year
2004
2005
2006
2007
2008
B
C
D
E
F
G
H
I
J
K
(c) Brood
1
2
3
L
M
N
(d) Order
a−chick
b−chick
c−chick
O
P
Q
(e) Older
No
Yes
R

Figure 3-4

Growth curves of tarsus length depending on (a) sex, (b) year, (c) brood size, (d) hatching order and (e) presence of older male sibling. Variables settings used to obtain these estimates are given in Table 3-2. Heat maps under the graphs show the significance of the difference between curves in pairwise manner at each day. Black: upper boundary of 95% CRI of difference is smaller than zero, grey: 95% CRI of difference include zero, white: lower boundary of 95% CRI of difference is larger than zero. A: female – male, B: 2004 – 2005, C: 2004 – 2006, D: 2004 – 2007, E: 2004 – 2008, F: 2005 – 2006, G: 2005 – 2007, H: 2005 – 2008, I: 2006 – 2007, J: 2006 – 2008, K: 2007 – 2008, L: 1 chick – 2 chicks, M: 2 chicks – 3 chicks, N: 3 chicks – 1 chick, O: a chick – b chick, P: b chick – c chick, Q: c chick – a chick, R: No – Yes.

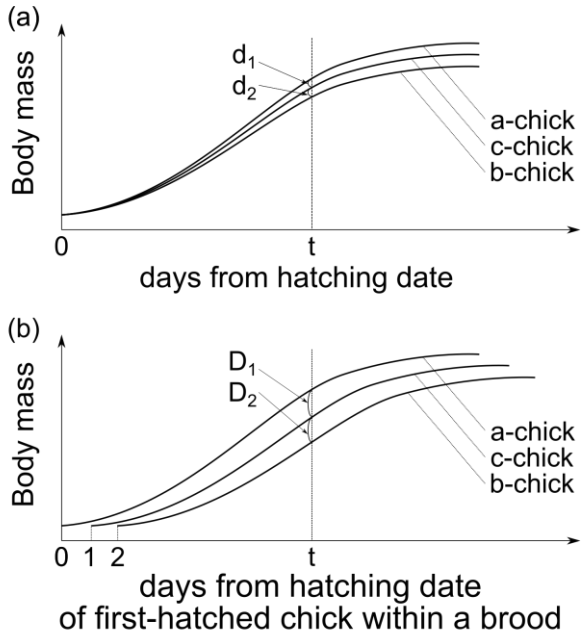


Figure 3-5

Growth curves of the members of a hypothetical three-chick-brood drawn on the x-axis of (a) days from hatching date, and (b) days from the hatching date of the first-hatched chick within the brood. The three chicks are assumed to hatch on consecutive days. To obtain actual size differences in a brood at given time t, we should focus on D_1 and D_2 in (b), not on d_1 and d_2 in (a).

Table

Table 3-1 Model formulation and derived parameters

model	Y_t	Y_0	Y_{max}	IP_{day}	IP_{rate}
Gompertz	$\beta_0 exp[-\beta_1 exp(-\beta_2 t)]$	$\beta_0 exp(-\beta_1)$	β_0	$log(\beta_1)/\beta_2$	$\beta_0\beta_2/e$
Logistic	$\beta_0 exp[1-\beta_1 exp(-\beta_2 t)]^{-1}$	$\beta_0 exp(1-\beta_1)^{-1}$	β_0	$log(\beta_1)/\beta_2$	$\beta_0\beta_2/4$
von Bertalanffy	$\beta_0 exp[1+\beta_1 exp(-\beta_2 t)]^3$	$\beta_0 exp(1+\beta_1)^3$	β_0	$log(3\beta_1)/\beta_2$	$4\beta_0\beta_2/9$

Formulae of Y_t and IP_{day} are the expressions given in Table 1 of Narinç et al. (2017). Y_0 is the value of Y_t at $t = 0$. A follows from taking the limit of Y_t as t approaches infinity. IP_{day} follows from resolve an equation "second derivative of $Y_t = 0$" about t. IP_{rate} follows from taking the derivative coefficient of Y_t at $t = IP_{day}$.

Table 3-2 Variable settings used to obtain prediction value and statistics of growth models in Figure 3-2, 3-3, 3-4 and Table 3-6, 3-9, 3-12

Trait	Effect	Varied	Fixed	Figure	Table
Body mass	Sex	Sex = female, male	Year = 2004, Brood = 0, Order = a-chick	Figure 3-2a	Table 3-6
	Year	Year = 2004, …, 2008	Sex = female, Brood = 0, Order = a-chick	Figure 3-2b	Table 3-6
	Brood	Brood = 0, 1, 2	Sex = female, Year = 2004, Order = a-chick	Figure 3-2c	Table 3-6
	Order	Order = a-chick, b-chick, c-chick	Sex = female, Year = 2004, Brood = 2	Figure 3-2d	Table 3-6
Wing length	Sex	Sex = female, male	Year = 2004, Brood = 0, Order = a-chick	Figure 3-3a	Table 3-9
	Year	Year = 2004, …, 2008	Sex = female, Brood = 0, Order = a-chick	Figure 3-3b	Table 3-9
	Brood	Brood = 0, 1, 2	Sex = female, Year = 2004, Order = a-chick	Figure 3-3c	Table 3-9
	Order	Order = a-chick, b-chick, c-chick	Sex = female, Year = 2004, Brood = 2	Figure 3-3d	Table 3-9
Tarsus length	Sex	Sex = female, male	Year = 2004, Brood = 0, Order = a-chick, Older = no	Figure 3-4a	Table 3-10
	Year	Year = 2004, …, 2008	Sex = female, Brood = 0, Order = a-chick, Older = no	Figure 3-4b	Table 3-10
	Brood	Brood = 0, 1, 2	Sex = female, Year = 2004, Order = a-chick, Older = no	Figure 3-4c	Table 3-10
	Order	Order = a-chick, b-chick, c-chick	Sex = female, Year = 2004, Brood = 2, Older = no	Figure 3-4d	Table 3-10
	Older	Older = no, yes	Sex = female, Year = 2004, Brood = 1, Order = b-chick	Figure 3-4e	Table 3-10

Effect: focused variable, Varied: range of focused variables, Fixed: variable settings used for calculating estimates, Figure number: corresponding figures

Table 3-3 Results of model comparison for each trait

	Model	WAIC	Delta
Mass	Gompertz	2439.44	0.00
	Logistic	2482.99	43.55
	von Bertalanffy	2444.15	4.70
Tarsus	Gompertz	1225.18	0.00
	Logistic	1229.49	4.30
	von Bertalanffy	1242.68	17.49
Wing	Gompertz	2113.04	51.07
	Logistic	2189.48	127.51
	von Bertalanffy	2061.97	0.00

WAIC: Watanabe Akaike information criteria, Delta: difference from the minimum WAIC

Table 3-4 Results of model comparison for body mass

ID	Model	WAIC	Delta	Weight	CumWeight
15	Intercept + Year + Brood	2390.082	0.000	0.353	0.353
3	Intercept + Brood	2391.844	1.762	0.146	0.499
16	Intercept + Sex + Year + Brood	2392.037	1.955	0.133	0.632
19	Intercept + Year + Brood + Order	2393.032	2.951	0.081	0.712
1	Intercept	2393.410	3.328	0.067	0.779
11	Intercept + Year	2394.435	4.354	0.040	0.819
4	Intercept + Sex + Brood	2394.566	4.484	0.037	0.857
21	Intercept + Sex + Year + Brood + Order	2395.363	5.282	0.025	0.882
2	Intercept + Sex	2395.702	5.621	0.021	0.903
7	Intercept + Brood + Order	2396.002	5.921	0.018	0.921
5	Intercept + Order	2396.399	6.318	0.015	0.936
13	Intercept + Sex + Year	2396.627	6.545	0.013	0.950
17	Intercept + Year + Order	2397.202	7.120	0.010	0.960
23	Intercept + Year + Brood + Order + Older	2397.602	7.520	0.008	0.968
9	Intercept + Sex + Brood + Order	2397.811	7.730	0.007	0.975
6	Intercept + Sex + Order	2398.072	7.990	0.006	0.982
18	Intercept + Sex + Year + Order	2398.079	7.997	0.006	0.988
24	Intercept + Sex + Year + Brood + Order + Older	2398.725	8.643	0.005	0.993
12	Intercept + Brood + Order + Older	2400.051	9.969	0.002	0.995
20	Intercept + Year + Order + Older	2401.084	11.002	0.001	0.997
8	Intercept + Order + Older	2401.453	11.372	0.001	0.998
14	Intercept + Sex + Brood + Order + Older	2401.896	11.814	0.001	0.999
22	Intercept + Sex + Year + Order + Older	2402.817	12.735	0.001	0.999
10	Intercept + Sex + Order + Older	2402.957	12.875	0.001	1.000

ID: model ID corresponding to model name in Table 3-5, WAIC: Watanabe Akaike information criteria, Delta: difference from the minimum WAIC, Weight: model weight based on WAIC value, CumWeight: cumulate value of Weight from the best model

Table 3-5 Regression coefficients in the best models for body mass

Model	Variables	α_0	α_1	α_2
Model1	Intercept	4.490 (4.478, 4.502)	0.755 (0.733, 0.777)	-1.909 (-1.936, -1.883)
Model3	Intercept	4.493 (4.478, 4.508)	0.758 (0.728, 0.788)	-1.923 (-1.959, -1.888)
	Brood	-0.006 (-0.019, 0.008)	0.003 (-0.024, 0.030)	0.019 (-0.014, 0.052)
Model15	Intercept	4.492 (4.476, 4.509)	0.759 (0.728, 0.790)	-1.913 (-1.951, -1.874)
	Year (2005)	0.030 (-0.027, 0.088)	-0.104 (-0.218, 0.014)	-0.129 (-0.273, 0.012)
	Year (2006)	0.007 (-0.056, 0.072)	-0.004 (-0.175, 0.185)	-0.006 (-0.220, 0.205)
	Year (2007)	0.023 (-0.024, 0.070)	-0.072 (-0.166, 0.024)	-0.095 (-0.209, 0.018)
	Year (2008)	0.057 (0.010, 0.103)	-0.048 (-0.129, 0.032)	-0.189 (-0.297, -0.081)
	Brood	-0.017 (-0.038, 0.003)	0.037 (-0.007, 0.080)	0.064 (0.012, 0.114)
Model16	Intercept	4.493 (4.476, 4.509)	0.757 (0.726, 0.789)	-1.909 (-1.948, -1.870)
	Sex (male)	-0.003 (-0.035, 0.029)	0.027 (-0.042, 0.096)	-0.006 (-0.094, 0.080)
	Year (2005)	0.034 (-0.023, 0.094)	-0.119 (-0.238, 0.000)	-0.139 (-0.287, 0.004)
	Year (2006)	0.009 (-0.055, 0.076)	-0.018 (-0.188, 0.170)	-0.010 (-0.225, 0.198)
	Year (2007)	0.022 (-0.026, 0.071)	-0.080 (-0.176, 0.021)	-0.090 (-0.209, 0.029)
	Year (2008)	0.058 (0.011, 0.108)	-0.059 (-0.144, 0.026)	-0.191 (-0.307, -0.077)
	Brood	-0.017 (-0.038, 0.003)	0.034 (-0.010, 0.078)	0.062 (0.009, 0.113)
Model19	Intercept	4.492 (4.475, 4.509)	0.759 (0.728, 0.789)	-1.913 (-1.951, -1.874)
	Year (2005)	0.033 (-0.025, 0.092)	-0.116 (-0.232, 0.003)	-0.143 (-0.291, 0.001)
	Year (2006)	0.005 (-0.056, 0.071)	0.003 (-0.169, 0.191)	0.001 (-0.213, 0.205)
	Year (2007)	0.024 (-0.023, 0.073)	-0.072 (-0.166, 0.023)	-0.097 (-0.209, 0.015)
	Year (2008)	0.056 (0.010, 0.105)	-0.050 (-0.134, 0.033)	-0.195 (-0.308, -0.081)
	Brood	-0.013 (-0.035, 0.010)	0.026 (-0.024, 0.075)	0.068 (0.008, 0.126)
	Order (b-chick)	-0.010 (-0.044, 0.024)	0.036 (-0.041, 0.115)	0.009 (-0.087, 0.105)
	Order (c-chick)	-0.024 (-0.069, 0.021)	0.037 (-0.063, 0.139)	-0.029 (-0.157, 0.099)

Model: model name corresponding to model ID in Table 3-4

Table 3-6 Statistics of growth curve of body mass depending on the effects of explanatory variables

Variables	Y_0	Y_{10}	Y_{20}	Y_{30}	A	IP_{rate}	IP_{day}
Sex (female)	10.588 (10.289, 10.896)	54.910 (54.196, 55.630)	79.938 (79.298, 80.583)	87.097 (86.505, 87.700)	89.340 (88.740, 89.959)	5.128 (5.019, 5.240)	5.128 (5.019, 5.240)
Sex (male)	10.464 (10.092, 10.849)	54.606 (53.865, 55.356)	79.759 (79.086, 80.438)	87.010 (86.342, 87.673)	89.306 (88.585, 90.038)	5.183 (5.067, 5.303)	5.183 (5.067, 5.303)
Year (2004)	10.588 (10.289, 10.896)	54.910 (54.196, 55.630)	79.938 (79.298, 80.583)	87.097 (86.505, 87.700)	89.340 (88.740, 89.959)	5.128 (5.019, 5.240)	5.128 (5.019, 5.240)
Year (2005)	12.594 (11.342, 13.923)	54.732 (53.699, 55.773)	79.840 (78.579, 81.143)	88.028 (86.430, 89.650)	91.168 (89.162, 93.290)	5.039 (4.827, 5.248)	5.039 (4.827, 5.248)
Year (2006)	10.746 (9.076, 12.495)	55.221 (53.830, 56.659)	80.163 (78.763, 81.611)	87.340 (85.597, 89.116)	89.681 (87.523, 92.054)	5.102 (4.837, 5.372)	5.102 (4.837, 5.372)
Year (2007)	11.856 (10.892, 12.907)	54.729 (53.707, 55.794)	79.891 (78.707, 81.090)	87.766 (86.379, 89.145)	90.589 (88.909, 92.269)	5.090 (4.900, 5.281)	5.090 (4.900, 5.281)
Year (2008)	11.801 (10.983, 12.668)	52.978 (52.061, 53.916)	79.483 (78.524, 80.470)	88.840 (87.643, 90.072)	92.790 (91.153, 94.538)	5.569 (5.348, 5.804)	5.569 (5.348, 5.804)
Brood (0)	10.588 (10.289, 10.896)	54.910 (54.196, 55.630)	79.938 (79.298, 80.583)	87.097 (86.505, 87.700)	89.340 (88.740, 89.959)	5.128 (5.019, 5.240)	5.128 (5.019, 5.240)
Brood (1)	10.023 (9.582, 10.478)	55.471 (54.818, 56.121)	79.960 (79.271, 80.638)	86.475 (85.725, 87.228)	88.351 (87.528, 89.174)	5.043 (4.948, 5.136)	5.043 (4.948, 5.136)
Brood (2)	9.506 (8.771, 10.277)	56.077 (55.186, 56.993)	79.897 (78.836, 80.964)	85.799 (84.538, 87.074)	87.385 (85.994, 88.795)	4.954 (4.826, 5.081)	4.954 (4.826, 5.081)
Order (a-chick)	9.506 (8.771, 10.277)	56.077 (55.186, 56.993)	79.897 (78.836, 80.964)	85.799 (84.538, 87.074)	87.385 (85.994, 88.795)	4.954 (4.826, 5.081)	4.954 (4.826, 5.081)
Order (b-chick)	9.363 (8.635, 10.130)	55.883 (54.993, 56.796)	79.733 (78.660, 80.803)	85.634 (84.364, 86.916)	87.217 (85.817, 88.635)	4.983 (4.855, 5.111)	4.983 (4.855, 5.111)
Order (c-chick)	9.280 (8.550, 10.052)	55.507 (54.607, 56.421)	79.361 (78.295, 80.422)	85.292 (84.011, 86.576)	86.890 (85.475, 88.307)	5.011 (4.882, 5.141)	5.011 (4.882, 5.141)

Y_0, Y_{10}, Y_{20}, Y_{30}: body mass (g) at day 0, 10, 20, 30, A: asymptotic size, IP_{rate}: growth rate at inflection point (g/day), IP_{day}: the day of inflection point. Parenthesis indicates 95% credible interval. See Table 3-2 for variables settings used to calculate these statistics

Table 3-7 Numerical differences of growth curves of body mass in Figure 3-2

Figure legend	Contrast	Y_0	Y_1	Y_2	Y_3	Y_4	Y_5
A	female - male	0.124 (-0.116, 0.349)	0.159 (-0.083, 0.390)	0.194 (-0.043, 0.419)	0.225 (-0.003, 0.441)	0.252 (0.041, 0.455)	0.274 (0.075, 0.467)
B	2004 - 2005	-2.006 (-3.342, -0.753)	-1.974 (-3.296, -0.713)	-1.848 (-3.114, -0.620)	-1.644 (-2.841, -0.478)	-1.385 (-2.494, -0.298)	-1.094 (-2.127, -0.079)
C	2004 - 2006	-0.159 (-1.923, 1.511)	-0.162 (-1.928, 1.572)	-0.174 (-1.883, 1.517)	-0.194 (-1.799, 1.389)	-0.219 (-1.683, 1.243)	-0.246 (-1.599, 1.095)
D	2004 - 2007	-1.268 (-2.320, -0.288)	-1.248 (-2.296, -0.250)	-1.163 (-2.186, -0.190)	-1.026 (-2.016, -0.085)	-0.851 (-1.793, 0.052)	-0.656 (-1.562, 0.219)
E	2004 - 2008	-1.213 (-2.095, -0.366)	-0.987 (-1.881, -0.116)	-0.667 (-1.557, 0.209)	-0.282 (-1.158, 0.585)	0.137 (-0.732, 0.994)	0.559 (-0.305, 1.409)
F	2005 - 2006	1.847 (-0.128, 3.772)	1.812 (-0.147, 3.753)	1.674 (-0.203, 3.547)	1.450 (-0.289, 3.191)	1.166 (-0.424, 2.752)	0.848 (-0.601, 2.299)
G	2005 - 2007	0.738 (-0.469, 1.957)	0.726 (-0.476, 1.929)	0.685 (-0.479, 1.837)	0.618 (-0.473, 1.691)	0.534 (-0.474, 1.532)	0.438 (-0.500, 1.364)
H	2005 - 2008	0.793 (-0.417, 2.057)	0.987 (-0.224, 2.236)	1.181 (0.007, 2.385)	1.362 (0.252, 2.490)	1.522 (0.478, 2.574)	1.652 (0.666, 2.642)
I	2006 - 2007	-1.110 (-2.824, 0.664)	-1.086 (-2.845, 0.678)	-0.989 (-2.702, 0.702)	-0.832 (-2.427, 0.749)	-0.632 (-2.082, 0.826)	-0.410 (-1.772, 0.949)
J	2006 - 2008	-1.055 (-2.743, 0.734)	-0.825 (-2.560, 0.959)	-0.493 (-2.192, 1.222)	-0.088 (-1.696, 1.512)	0.356 (-1.114, 1.819)	0.804 (-0.552, 2.154)
K	2007 - 2008	0.055 (-0.850, 0.982)	0.261 (-0.651, 1.196)	0.496 (-0.399, 1.417)	0.744 (-0.127, 1.637)	0.989 (0.143, 1.856)	1.214 (0.377, 2.061)
L	1 chick - 2 chicks	0.564 (0.156, 0.966)	0.514 (0.090, 0.933)	0.415 (-0.006, 0.835)	0.280 (-0.129, 0.691)	0.124 (-0.270, 0.521)	-0.038 (-0.430, 0.354)
M	2 chicks - 3 chicks	0.518 (0.144, 0.859)	0.471 (0.077, 0.839)	0.369 (-0.026, 0.745)	0.226 (-0.155, 0.598)	0.060 (-0.313, 0.426)	-0.111 (-0.492, 0.268)
N	3 chicks - 1 chick	-1.082 (-1.826, -0.298)	-0.984 (-1.771, -0.166)	-0.784 (-1.584, 0.031)	-0.506 (-1.287, 0.283)	-0.184 (-0.945, 0.582)	0.148 (-0.616, 0.919)
O	a chick - b chick	0.142 (-0.008, 0.294)	0.168 (0.011, 0.325)	0.188 (0.033, 0.343)	0.203 (0.054, 0.350)	0.212 (0.072, 0.349)	0.215 (0.080, 0.350)
P	b chick - c chick	0.083 (-0.108, 0.275)	0.116 (-0.083, 0.315)	0.153 (-0.042, 0.347)	0.191 (0.008, 0.376)	0.230 (0.056, 0.401)	0.265 (0.096, 0.433)
Q	c chick - a chick	-0.225 (-0.424, -0.029)	-0.284 (-0.488, -0.081)	-0.341 (-0.541, -0.142)	-0.394 (-0.583, -0.206)	-0.441 (-0.618, -0.264)	-0.481 (-0.651, -0.308)

Table 3-7 (continued)

Figure legend	Contrast	Y_6	Y_7	Y_8	Y_9	Y_{10}	Y_{11}
A	female - male	0.291 (0.097, 0.482)	0.301 (0.105, 0.498)	0.307 (0.102, 0.511)	0.307 (0.092, 0.521)	0.304 (0.079, 0.525)	0.297 (0.066, 0.524)
B	2004 - 2005	-0.793 (-1.777, 0.170)	-0.503 (-1.473, 0.439)	-0.238 (-1.210, 0.709)	-0.009 (-1.020, 0.970)	0.177 (-0.871, 1.194)	0.320 (-0.777, 1.384)
C	2004 - 2006	-0.270 (-1.543, 0.992)	-0.289 (-1.579, 0.973)	-0.303 (-1.636, 1.008)	-0.310 (-1.729, 1.062)	-0.311 (-1.824, 1.142)	-0.307 (-1.883, 1.196)
D	2004 - 2007	-0.454 (-1.343, 0.415)	-0.262 (-1.158, 0.607)	-0.087 (-1.006, 0.818)	0.062 (-0.895, 1.013)	0.181 (-0.815, 1.174)	0.269 (-0.764, 1.302)
E	2004 - 2008	0.954 (0.077, 1.817)	1.301 (0.409, 2.181)	1.585 (0.671, 2.483)	1.796 (0.847, 2.723)	1.931 (0.955, 2.884)	1.993 (0.994, 2.954)
F	2005 - 2006	0.523 (-0.844, 1.901)	0.213 (-1.138, 1.575)	-0.065 (-1.473, 1.328)	-0.301 (-1.785, 1.147)	-0.488 (-2.046, 1.026)	-0.627 (-2.261, 0.950)
G	2005 - 2007	0.339 (-0.558, 1.230)	0.241 (-0.651, 1.119)	0.151 (-0.764, 1.049)	0.071 (-0.883, 1.013)	0.003 (-0.992, 0.986)	-0.051 (-1.090, 0.983)
H	2005 - 2008	1.747 (0.790, 2.704)	1.804 (0.851, 2.747)	1.823 (0.862, 2.781)	1.805 (0.811, 2.790)	1.754 (0.726, 2.772)	1.673 (0.611, 2.726)
I	2006 - 2007	-0.185 (-1.485, 1.117)	0.028 (-1.273, 1.353)	0.216 (-1.140, 1.616)	0.372 (-1.058, 1.855)	0.492 (-1.002, 2.051)	0.576 (-0.967, 2.190)
J	2006 - 2008	1.224 (-0.087, 2.534)	1.591 (0.286, 2.906)	1.888 (0.526, 3.255)	2.106 (0.702, 3.563)	2.242 (0.773, 3.783)	2.300 (0.788, 3.896)
K	2007 - 2008	1.408 (0.559, 2.273)	1.563 (0.681, 2.462)	1.672 (0.753, 2.610)	1.734 (0.778, 2.703)	1.751 (0.751, 2.752)	1.724 (0.694, 2.753)
L	1 chick - 2 chicks	-0.191 (-0.594, 0.203)	-0.326 (-0.749, 0.089)	-0.435 (-0.880, 0.008)	-0.513 (-0.987, -0.039)	-0.561 (-1.057, -0.067)	-0.580 (-1.093, -0.065)
M	2 chicks - 3 chicks	-0.269 (-0.673, 0.127)	-0.403 (-0.838, 0.023)	-0.506 (-0.971, -0.045)	-0.573 (-1.070, -0.083)	-0.606 (-1.122, -0.097)	-0.607 (-1.140, -0.085)
N	3 chicks - 1 chick	0.461 (-0.327, 1.267)	0.730 (-0.109, 1.580)	0.941 (0.038, 1.849)	1.087 (0.124, 2.052)	1.167 (0.162, 2.175)	1.187 (0.151, 2.233)
O	a chick - b chick	0.215 (0.078, 0.351)	0.211 (0.069, 0.352)	0.206 (0.059, 0.353)	0.200 (0.049, 0.352)	0.194 (0.039, 0.349)	0.188 (0.034, 0.343)
P	b chick - c chick	0.297 (0.124, 0.468)	0.325 (0.144, 0.503)	0.347 (0.155, 0.536)	0.364 (0.165, 0.563)	0.376 (0.174, 0.580)	0.385 (0.181, 0.589)
Q	c chick - a chick	-0.512 (-0.685, -0.339)	-0.536 (-0.716, -0.356)	-0.553 (-0.744, -0.363)	-0.564 (-0.763, -0.367)	-0.570 (-0.774, -0.368)	-0.573 (-0.778, -0.368)

Table 3-7 (continued)

Figure legend	Contrast	Y_{12}	Y_{13}	Y_{14}	Y_{15}	Y_{16}	Y_{17}
A	female - male	0.288 (0.054, 0.519)	0.276 (0.040, 0.511)	0.263 (0.028, 0.494)	0.250 (0.016, 0.480)	0.235 (0.005, 0.464)	0.221 (-0.010, 0.448)
B	2004 - 2005	0.418 (-0.710, 1.521)	0.474 (-0.691, 1.618)	0.493 (-0.705, 1.663)	0.480 (-0.744, 1.671)	0.439 (-0.806, 1.647)	0.376 (-0.889, 1.604)
C	2004 - 2006	-0.299 (-1.910, 1.240)	-0.289 (-1.914, 1.269)	-0.278 (-1.879, 1.287)	-0.266 (-1.842, 1.293)	-0.255 (-1.801, 1.286)	-0.245 (-1.771, 1.270)
D	2004 - 2007	0.326 (-0.747, 1.390)	0.355 (-0.748, 1.452)	0.359 (-0.766, 1.471)	0.341 (-0.807, 1.470)	0.305 (-0.861, 1.447)	0.255 (-0.922, 1.403)
E	2004 - 2008	1.986 (0.970, 2.965)	1.917 (0.898, 2.912)	1.797 (0.776, 2.797)	1.632 (0.615, 2.634)	1.434 (0.420, 2.425)	1.210 (0.203, 2.199)
F	2005 - 2006	-0.717 (-2.398, 0.908)	-0.763 (-2.467, 0.884)	-0.771 (-2.483, 0.882)	-0.746 (-2.452, 0.899)	-0.694 (-2.371, 0.939)	-0.621 (-2.289, 1.005)
G	2005 - 2007	-0.092 (-1.164, 0.989)	-0.119 (-1.225, 0.996)	-0.134 (-1.263, 0.999)	-0.139 (-1.289, 1.018)	-0.134 (-1.308, 1.043)	-0.122 (-1.316, 1.070)
H	2005 - 2008	1.568 (0.479, 2.652)	1.443 (0.326, 2.551)	1.303 (0.165, 2.426)	1.152 (0.004, 2.284)	0.995 (-0.161, 2.135)	0.833 (-0.322, 1.980)
I	2006 - 2007	0.626 (-0.962, 2.276)	0.645 (-0.977, 2.316)	0.637 (-0.992, 2.294)	0.607 (-1.008, 2.240)	0.560 (-1.037, 2.166)	0.499 (-1.072, 2.067)
J	2006 - 2008	2.285 (0.728, 3.897)	2.207 (0.637, 3.832)	2.074 (0.522, 3.681)	1.898 (0.361, 3.469)	1.689 (0.173, 3.230)	1.454 (-0.039, 2.970)
K	2007 - 2008	1.660 (0.610, 2.702)	1.562 (0.490, 2.606)	1.437 (0.369, 2.494)	1.291 (0.217, 2.353)	1.129 (0.062, 2.188)	0.955 (-0.102, 2.010)
L	1 chick - 2 chicks	-0.572 (-1.103, -0.048)	-0.542 (-1.081, -0.006)	-0.494 (-1.037, 0.045)	-0.431 (-0.975, 0.104)	-0.357 (-0.900, 0.180)	-0.277 (-0.818, 0.262)
M	2 chicks - 3 chicks	-0.581 (-1.124, -0.051)	-0.532 (-1.074, -0.003)	-0.466 (-1.007, 0.060)	-0.387 (-0.927, 0.135)	-0.301 (-0.834, 0.221)	-0.210 (-0.744, 0.315)
N	3 chicks - 1 chick	1.153 (0.098, 2.227)	1.074 (0.006, 2.154)	0.959 (-0.104, 2.041)	0.818 (-0.238, 1.901)	0.658 (-0.397, 1.735)	0.487 (-0.576, 1.554)
O	a chick - b chick	0.183 (0.031, 0.336)	0.178 (0.030, 0.329)	0.175 (0.029, 0.322)	0.172 (0.029, 0.316)	0.169 (0.027, 0.311)	0.167 (0.024, 0.308)
P	b chick - c chick	0.390 (0.188, 0.592)	0.392 (0.193, 0.589)	0.392 (0.197, 0.585)	0.391 (0.199, 0.579)	0.388 (0.199, 0.575)	0.384 (0.197, 0.572)
Q	c chick - a chick	-0.573 (-0.777, -0.370)	-0.570 (-0.771, -0.371)	-0.567 (-0.762, -0.372)	-0.562 (-0.753, -0.372)	-0.557 (-0.744, -0.370)	-0.552 (-0.738, -0.364)

Table 3-7 (continued)

Figure legend	Contrast	Y_{18}	Y_{19}	Y_{20}	Y_{21}	Y_{22}	Y_{23}
A	female - male	0.207 (-0.025, 0.433)	0.193 (-0.041, 0.422)	0.180 (-0.058, 0.412)	0.167 (-0.077, 0.405)	0.155 (-0.096, 0.401)	0.144 (-0.116, 0.400)
B	2004 - 2005	0.296 (-0.983, 1.545)	0.202 (-1.101, 1.465)	0.099 (-1.227, 1.384)	-0.010 (-1.372, 1.300)	-0.122 (-1.514, 1.209)	-0.234 (-1.660, 1.129)
C	2004 - 2006	-0.236 (-1.740, 1.250)	-0.229 (-1.718, 1.231)	-0.224 (-1.700, 1.224)	-0.221 (-1.701, 1.237)	-0.219 (-1.725, 1.245)	-0.219 (-1.743, 1.272)
D	2004 - 2007	0.193 (-0.989, 1.348)	0.123 (-1.069, 1.292)	0.048 (-1.149, 1.239)	-0.031 (-1.244, 1.170)	-0.110 (-1.338, 1.106)	-0.190 (-1.432, 1.040)
E	2004 - 2008	0.968 (-0.040, 1.949)	0.714 (-0.294, 1.693)	0.456 (-0.561, 1.442)	0.197 (-0.829, 1.191)	-0.059 (-1.094, 0.942)	-0.308 (-1.355, 0.710)
F	2005 - 2006	-0.532 (-2.186, 1.095)	-0.431 (-2.077, 1.186)	-0.323 (-1.980, 1.302)	-0.211 (-1.882, 1.430)	-0.097 (-1.793, 1.564)	0.016 (-1.716, 1.715)
G	2005 - 2007	-0.103 (-1.312, 1.110)	-0.079 (-1.308, 1.150)	-0.051 (-1.308, 1.199)	-0.021 (-1.292, 1.258)	0.011 (-1.285, 1.315)	0.044 (-1.285, 1.378)
H	2005 - 2008	0.672 (-0.489, 1.828)	0.512 (-0.656, 1.676)	0.357 (-0.823, 1.546)	0.207 (-0.992, 1.425)	0.063 (-1.170, 1.314)	-0.074 (-1.339, 1.209)
I	2006 - 2007	0.429 (-1.106, 1.981)	0.352 (-1.161, 1.892)	0.272 (-1.239, 1.815)	0.190 (-1.328, 1.742)	0.109 (-1.428, 1.677)	0.029 (-1.523, 1.616)
J	2006 - 2008	1.204 (-0.259, 2.690)	0.944 (-0.509, 2.416)	0.680 (-0.759, 2.152)	0.417 (-1.025, 1.890)	0.160 (-1.309, 1.640)	-0.090 (-1.579, 1.426)
K	2007 - 2008	0.775 (-0.275, 1.827)	0.591 (-0.460, 1.648)	0.408 (-0.659, 1.472)	0.227 (-0.846, 1.303)	0.051 (-1.043, 1.147)	-0.118 (-1.230, 1.003)
L	1 chick - 2 chicks	-0.193 (-0.732, 0.348)	-0.107 (-0.649, 0.437)	-0.022 (-0.571, 0.527)	0.062 (-0.487, 0.615)	0.142 (-0.417, 0.700)	0.218 (-0.348, 0.783)
M	2 chicks - 3 chicks	-0.118 (-0.654, 0.410)	-0.026 (-0.568, 0.508)	0.063 (-0.484, 0.602)	0.148 (-0.410, 0.692)	0.228 (-0.338, 0.786)	0.303 (-0.274, 0.868)
N	3 chicks - 1 chick	0.311 (-0.759, 1.383)	0.133 (-0.942, 1.215)	-0.041 (-1.130, 1.050)	-0.209 (-1.304, 0.897)	-0.370 (-1.478, 0.753)	-0.521 (-1.654, 0.621)
O	a chick - b chick	0.166 (0.019, 0.309)	0.165 (0.016, 0.313)	0.164 (0.010, 0.318)	0.164 (0.003, 0.326)	0.164 (-0.005, 0.334)	0.164 (-0.015, 0.342)
P	b chick - c chick	0.381 (0.190, 0.571)	0.376 (0.181, 0.572)	0.372 (0.169, 0.574)	0.368 (0.156, 0.580)	0.364 (0.142, 0.585)	0.360 (0.128, 0.592)
Q	c chick - a chick	-0.546 (-0.737, -0.357)	-0.541 (-0.737, -0.348)	-0.537 (-0.738, -0.336)	-0.532 (-0.741, -0.324)	-0.528 (-0.748, -0.311)	-0.524 (-0.755, -0.297)

Table 3-7 (continued)

Figure legend	Contrast	Y_{24}	Y_{25}	Y_{26}	Y_{27}	Y_{28}	Y_{29}
A	female - male	0.134 (-0.135, 0.399)	0.124 (-0.153, 0.400)	0.116 (-0.172, 0.401)	0.108 (-0.190, 0.402)	0.100 (-0.205, 0.404)	0.093 (-0.220, 0.406)
B	2004 - 2005	-0.346 (-1.800, 1.049)	-0.455 (-1.935, 0.972)	-0.560 (-2.077, 0.907)	-0.660 (-2.214, 0.842)	-0.756 (-2.345, 0.781)	-0.846 (-2.466, 0.723)
C	2004 - 2006	-0.220 (-1.768, 1.291)	-0.222 (-1.818, 1.332)	-0.225 (-1.867, 1.376)	-0.229 (-1.915, 1.414)	-0.233 (-1.959, 1.455)	-0.238 (-2.009, 1.486)
D	2004 - 2007	-0.268 (-1.528, 0.989)	-0.344 (-1.622, 0.934)	-0.416 (-1.718, 0.882)	-0.485 (-1.807, 0.838)	-0.551 (-1.896, 0.788)	-0.612 (-1.987, 0.752)
E	2004 - 2008	-0.549 (-1.618, 0.487)	-0.779 (-1.879, 0.295)	-0.997 (-2.126, 0.102)	-1.203 (-2.359, -0.067)	-1.396 (-2.583, -0.220)	-1.576 (-2.795, -0.361)
F	2005 - 2006	0.126 (-1.632, 1.871)	0.233 (-1.563, 2.007)	0.335 (-1.501, 2.163)	0.432 (-1.443, 2.308)	0.523 (-1.405, 2.443)	0.608 (-1.386, 2.585)
G	2005 - 2007	0.078 (-1.284, 1.440)	0.111 (-1.285, 1.508)	0.143 (-1.282, 1.571)	0.175 (-1.275, 1.641)	0.205 (-1.278, 1.704)	0.234 (-1.285, 1.773)
H	2005 - 2008	-0.203 (-1.501, 1.112)	-0.324 (-1.664, 1.033)	-0.437 (-1.823, 0.966)	-0.542 (-1.970, 0.902)	-0.640 (-2.116, 0.851)	-0.730 (-2.248, 0.801)
I	2006 - 2007	-0.048 (-1.632, 1.566)	-0.122 (-1.749, 1.536)	-0.191 (-1.857, 1.518)	-0.257 (-1.966, 1.489)	-0.318 (-2.061, 1.470)	-0.374 (-2.161, 1.461)
J	2006 - 2008	-0.329 (-1.861, 1.205)	-0.557 (-2.128, 1.017)	-0.772 (-2.389, 0.845)	-0.974 (-2.637, 0.693)	-1.163 (-2.877, 0.559)	-1.338 (-3.103, 0.437)
K	2007 - 2008	-0.281 (-1.422, 0.869)	-0.435 (-1.607, 0.743)	-0.581 (-1.786, 0.628)	-0.717 (-1.958, 0.529)	-0.845 (-2.124, 0.441)	-0.964 (-2.278, 0.353)
L	1 chick - 2 chicks	0.290 (-0.287, 0.865)	0.358 (-0.227, 0.944)	0.420 (-0.176, 1.011)	0.478 (-0.131, 1.073)	0.530 (-0.087, 1.136)	0.578 (-0.048, 1.197)
M	2 chicks - 3 chicks	0.372 (-0.216, 0.945)	0.436 (-0.164, 1.019)	0.494 (-0.116, 1.089)	0.547 (-0.072, 1.152)	0.594 (-0.034, 1.206)	0.637 (-0.002, 1.259)
N	3 chicks - 1 chick	-0.662 (-1.815, 0.500)	-0.793 (-1.952, 0.391)	-0.914 (-2.090, 0.293)	-1.024 (-2.225, 0.202)	-1.125 (-2.348, 0.119)	-1.216 (-2.452, 0.049)
O	a chick - b chick	0.164 (-0.021, 0.350)	0.164 (-0.028, 0.358)	0.164 (-0.036, 0.365)	0.164 (-0.043, 0.372)	0.165 (-0.050, 0.380)	0.165 (-0.056, 0.386)
P	b chick - c chick	0.357 (0.114, 0.600)	0.354 (0.101, 0.606)	0.351 (0.086, 0.612)	0.348 (0.073, 0.620)	0.346 (0.062, 0.627)	0.343 (0.052, 0.631)
Q	c chick - a chick	-0.521 (-0.762, -0.284)	-0.518 (-0.770, -0.270)	-0.515 (-0.775, -0.258)	-0.513 (-0.780, -0.248)	-0.510 (-0.786, -0.238)	-0.508 (-0.791, -0.229)

Table 3-7 (continued)

Figure legend	Contrast	Y_{30}	Y_{31}	Y_{32}
A	female - male	0.087 (-0.234, 0.409)	0.082 (-0.248, 0.410)	0.077 (-0.261, 0.413)
B	2004 - 2005	-0.931 (-2.577, 0.674)	-1.010 (-2.690, 0.626)	-1.083 (-2.791, 0.584)
C	2004 - 2006	-0.243 (-2.057, 1.530)	-0.248 (-2.100, 1.554)	-0.254 (-2.143, 1.582)
D	2004 - 2007	-0.669 (-2.072, 0.720)	-0.722 (-2.146, 0.691)	-0.771 (-2.213, 0.659)
E	2004 - 2008	-1.743 (-2.992, -0.492)	-1.898 (-3.173, -0.614)	-2.041 (-3.346, -0.729)
F	2005 - 2006	0.688 (-1.367, 2.717)	0.761 (-1.350, 2.843)	0.829 (-1.337, 2.952)
G	2005 - 2007	0.262 (-1.289, 1.837)	0.287 (-1.301, 1.904)	0.312 (-1.305, 1.953)
H	2005 - 2008	-0.812 (-2.379, 0.762)	-0.888 (-2.495, 0.723)	-0.958 (-2.599, 0.693)
I	2006 - 2007	-0.426 (-2.257, 1.455)	-0.474 (-2.347, 1.447)	-0.518 (-2.429, 1.441)
J	2006 - 2008	-1.500 (-3.321, 0.325)	-1.650 (-3.523, 0.229)	-1.787 (-3.706, 0.146)
K	2007 - 2008	-1.074 (-2.420, 0.277)	-1.176 (-2.551, 0.201)	-1.270 (-2.672, 0.128)
L	1 chick - 2 chicks	0.622 (-0.013, 1.252)	0.662 (0.016, 1.297)	0.698 (0.042, 1.343)
M	2 chicks - 3 chicks	0.676 (0.026, 1.306)	0.710 (0.054, 1.348)	0.741 (0.077, 1.384)
N	3 chicks - 1 chick	-1.298 (-2.551, -0.014)	-1.372 (-2.645, -0.066)	-1.439 (-2.726, -0.119)
O	a chick - b chick	0.165 (-0.061, 0.391)	0.165 (-0.065, 0.395)	0.166 (-0.069, 0.399)
P	b chick - c chick	0.342 (0.043, 0.636)	0.340 (0.034, 0.641)	0.338 (0.026, 0.646)
Q	c chick - a chick	-0.507 (-0.795, -0.221)	-0.505 (-0.800, -0.213)	-0.504 (-0.805, -0.206)

Table 3-8 Results of model comparison for wing length

ID	Model	WAIC	Delta	Weight	CumWeight
11	Intercept + Year	1982.197	0.000	0.504	0.504
17	Intercept + Year + Order	1983.806	1.609	0.225	0.729
13	Intercept + Sex + Year	1985.128	2.931	0.116	0.845
15	Intercept + Year + brood	1986.062	3.865	0.073	0.918
18	Intercept + Sex + Year + Order	1988.096	5.900	0.026	0.945
19	Intercept + Year + brood + Order	1988.400	6.203	0.023	0.967
20	Intercept + Year + Order + Older	1989.472	7.275	0.013	0.981
16	Intercept + Sex + Year + brood	1989.841	7.644	0.011	0.992
21	Intercept + Sex + Year + brood + Order	1992.281	10.084	0.003	0.995
22	Intercept + Sex + Year + Order + Older	1992.823	10.626	0.002	0.997
23	Intercept + Year + brood + Order + Older	1992.854	10.657	0.002	1.000
24	Intercept + Sex + Year + brood + Order + Older	1997.585	15.388	0.000	1.000
1	Intercept	2026.281	44.085	0.000	1.000
3	Intercept + brood	2026.935	44.739	0.000	1.000
5	Intercept + Order	2029.704	47.508	0.000	1.000
7	Intercept + brood + Order	2029.738	47.541	0.000	1.000
2	Intercept + Sex	2029.954	47.758	0.000	1.000
4	Intercept + Sex + brood	2031.163	48.966	0.000	1.000
8	Intercept + Order + Older	2032.525	50.328	0.000	1.000
12	Intercept + brood + Order + Older	2032.714	50.517	0.000	1.000
6	Intercept + Sex + Order	2033.220	51.024	0.000	1.000
9	Intercept + Sex + brood + Order	2033.691	51.494	0.000	1.000
10	Intercept + Sex + Order + Older	2036.504	54.308	0.000	1.000
14	Intercept + Sex + brood + Order + Older	2037.251	55.054	0.000	1.000

ID: model ID corresponding to model name in Table 3-9, WAIC: Watanabe Akaike information criteria, Delta: difference from the minimum WAIC, Weight: model weight based on WAIC value, CumWeight: cumulate value of Weight from the best model

Table 3-9 Regression coefficients in the best models for wing length

Model	Variables	α_0	α_1	α_2
Model11	Intercept	4.818 (4.801, 4.834)	2.489 (2.464, 2.514)	-1.808 (-1.825, -1.791)
	Year (2005)	0.016 (-0.033, 0.067)	-0.097 (-0.158, -0.032)	-0.058 (-0.114, -0.003)
	Year (2006)	-0.007 (-0.061, 0.050)	0.050 (-0.076, 0.189)	0.035 (-0.047, 0.116)
	Year (2007)	-0.025 (-0.058, 0.008)	-0.006 (-0.061, 0.050)	0.046 (0.008, 0.084)
	Year (2008)	0.043 (0.004, 0.083)	0.076 (0.003, 0.151)	-0.018 (-0.069, 0.033)
Model13	Intercept	4.819 (4.803, 4.835)	2.488 (2.463, 2.514)	-1.806 (-1.823, -1.789)
	Sex (male)	-0.024 (-0.055, 0.009)	0.014 (-0.042, 0.072)	0.007 (-0.035, 0.048)
	Year (2005)	0.023 (-0.026, 0.074)	-0.103 (-0.172, -0.033)	-0.061 (-0.120, -0.003)
	Year (2006)	0.003 (-0.053, 0.061)	0.045 (-0.085, 0.187)	0.030 (-0.056, 0.115)
	Year (2007)	-0.017 (-0.053, 0.019)	-0.013 (-0.075, 0.051)	0.041 (-0.003, 0.085)
	Year (2008)	0.054 (0.013, 0.097)	0.070 (-0.007, 0.149)	-0.023 (-0.079, 0.031)
Model15	Intercept	4.816 (4.800, 4.833)	2.489 (2.462, 2.516)	-1.811 (-1.830, -1.793)
	Year (2005)	0.013 (-0.044, 0.071)	-0.114 (-0.194, -0.033)	-0.069 (-0.133, -0.004)
	Year (2006)	-0.009 (-0.067, 0.052)	0.040 (-0.092, 0.181)	0.030 (-0.055, 0.112)
	Year (2007)	-0.028 (-0.073, 0.017)	-0.026 (-0.106, 0.052)	0.032 (-0.020, 0.085)
	Year (2008)	0.041 (-0.004, 0.087)	0.063 (-0.017, 0.147)	-0.026 (-0.081, 0.030)
	Brood	0.003 (-0.016, 0.023)	0.011 (-0.023, 0.046)	0.009 (-0.014, 0.032)
Model17	Intercept	4.819 (4.803, 4.835)	2.488 (2.463, 2.514)	-1.810 (-1.828, -1.793)
	Year (2005)	0.032 (-0.020, 0.086)	-0.124 (-0.193, -0.052)	-0.077 (-0.136, -0.018)
	Year (2006)	0.001 (-0.055, 0.060)	0.042 (-0.090, 0.181)	0.030 (-0.055, 0.111)
	Year (2007)	-0.007 (-0.042, 0.029)	-0.030 (-0.092, 0.033)	0.027 (-0.015, 0.068)
	Year (2008)	0.054 (0.014, 0.096)	0.055 (-0.021, 0.134)	-0.031 (-0.085, 0.022)
	Order (b-chick)	-0.031 (-0.063, 0.001)	0.043 (-0.020, 0.106)	0.035 (-0.008, 0.079)
	Order (c-chick)	-0.053 (-0.093, -0.012)	0.053 (-0.022, 0.132)	0.054 (0.001, 0.107)

Model: model name corresponding to model ID in Table 3-8

Table 3-10 Statistics of growth curve of wing length depending on the effects of explanatory variables

Variables	Y_0	Y_{10}	Y_{20}	Y_{30}	A	IP_{rate}	IP_{day}
Sex (female)	9.484 (9.337, 9.638)	37.054 (36.529, 37.591)	85.081 (84.057, 86.114)	113.705 (112.647, 114.769)	123.745 (122.620, 124.874)	0.494 (0.484, 0.504)	15.187 (15.041, 15.334)
Sex (male)	9.431 (9.266, 9.600)	36.904 (36.374, 37.445)	84.791 (83.754, 85.829)	113.297 (112.196, 114.402)	123.276 (122.072, 124.486)	0.495 (0.484, 0.507)	15.185 (15.030, 15.340)
Year (2004)	9.484 (9.337, 9.638)	37.054 (36.529, 37.591)	85.081 (84.057, 86.114)	113.705 (112.647, 114.769)	123.745 (122.620, 124.874)	0.494 (0.484, 0.504)	15.187 (15.041, 15.334)
Year (2005)	10.696 (10.210, 11.201)	37.980 (37.275, 38.685)	84.183 (82.787, 85.585)	114.032 (111.797, 116.278)	126.389 (123.004, 130.003)	0.417 (0.392, 0.442)	15.503 (15.146, 15.882)
Year (2006)	9.078 (8.329, 9.861)	37.170 (36.079, 38.258)	86.415 (84.603, 88.269)	114.268 (111.713, 116.867)	123.328 (119.682, 127.209)	0.537 (0.479, 0.604)	14.971 (14.576, 15.408)
Year (2007)	9.442 (9.101, 9.789)	38.420 (37.801, 39.031)	87.120 (85.922, 88.297)	113.272 (111.639, 114.920)	121.415 (119.328, 123.567)	0.506 (0.483, 0.531)	14.524 (14.327, 14.727)
Year (2008)	9.348 (8.895, 9.814)	36.064 (35.463, 36.668)	85.138 (84.154, 86.118)	117.322 (115.764, 118.936)	129.764 (127.146, 132.567)	0.517 (0.485, 0.552)	15.965 (15.682, 16.273)
Brood (0)	9.484 (9.337, 9.638)	37.054 (36.529, 37.591)	85.081 (84.057, 86.114)	113.705 (112.647, 114.769)	123.745 (122.620, 124.874)	0.494 (0.484, 0.504)	15.187 (15.041, 15.334)
Brood (1)	9.485 (9.334, 9.637)	37.088 (36.567, 37.622)	85.179 (84.159, 86.209)	113.812 (112.748, 114.886)	123.840 (122.708, 124.982)	0.494 (0.485, 0.504)	15.183 (15.037, 15.329)
Brood (2)	9.486 (9.326, 9.646)	37.124 (36.594, 37.660)	85.279 (84.242, 86.321)	113.920 (112.830, 115.012)	123.938 (122.757, 125.118)	0.495 (0.485, 0.506)	15.178 (15.030, 15.327)
Order (a-chick)	9.486 (9.326, 9.646)	37.124 (36.594, 37.660)	85.279 (84.242, 86.321)	113.920 (112.830, 115.012)	123.938 (122.757, 125.118)	0.495 (0.485, 0.506)	15.178 (15.030, 15.327)
Order (b-chick)	9.293 (9.080, 9.511)	36.909 (36.355, 37.473)	85.074 (84.000, 86.150)	113.217 (112.023, 114.429)	122.805 (121.383, 124.262)	0.507 (0.492, 0.523)	15.096 (14.922, 15.269)
Order (c-chick)	9.212 (8.982, 9.449)	36.842 (36.271, 37.417)	84.930 (83.821, 86.043)	112.702 (111.420, 114.015)	122.040 (120.514, 123.641)	0.512 (0.495, 0.531)	15.030 (14.850, 15.219)

Y_0, Y_{10}, Y_{20}, Y_{30}: body mass (g) at day 0, 10, 20, 30, A: asymptotic size, IP_{rate}: growth rate at inflection point (g/day), IP_{day}: the day of inflection point. Parenthesis indicates 95% credible interval. See Table 3-2 for variables settings used to calculate these statistics

Table 3-11 Numerical differences of growth curves of wing length in Figure 3-2

Figure legend	Contrast	Y_0	Y_1	Y_2	Y_3	Y_4	Y_5
A	female - male	0.053 (-0.024, 0.129)	0.060 (-0.022, 0.140)	0.068 (-0.018, 0.152)	0.076 (-0.014, 0.165)	0.085 (-0.008, 0.177)	0.094 (-0.001, 0.188)
B	2004 - 2005	-1.212 (-1.739, -0.703)	-1.276 (-1.828, -0.735)	-1.330 (-1.905, -0.759)	-1.368 (-1.966, -0.774)	-1.389 (-2.010, -0.770)	-1.387 (-2.029, -0.742)
C	2004 - 2006	0.406 (-0.391, 1.178)	0.417 (-0.433, 1.244)	0.420 (-0.482, 1.304)	0.412 (-0.538, 1.351)	0.391 (-0.601, 1.384)	0.355 (-0.677, 1.390)
D	2004 - 2007	0.042 (-0.333, 0.410)	-0.013 (-0.417, 0.385)	-0.083 (-0.517, 0.344)	-0.173 (-0.636, 0.286)	-0.283 (-0.776, 0.208)	-0.415 (-0.942, 0.112)
E	2004 - 2008	0.136 (-0.351, 0.609)	0.188 (-0.332, 0.691)	0.249 (-0.301, 0.784)	0.321 (-0.259, 0.887)	0.402 (-0.204, 1.000)	0.492 (-0.143, 1.114)
F	2005 - 2006	1.618 (0.709, 2.521)	1.693 (0.727, 2.649)	1.749 (0.737, 2.760)	1.780 (0.719, 2.843)	1.780 (0.677, 2.890)	1.741 (0.601, 2.885)
G	2005 - 2007	1.254 (0.672, 1.845)	1.264 (0.648, 1.887)	1.246 (0.601, 1.902)	1.195 (0.523, 1.877)	1.106 (0.406, 1.812)	0.971 (0.253, 1.698)
H	2005 - 2008	1.349 (0.696, 2.011)	1.464 (0.777, 2.161)	1.579 (0.862, 2.306)	1.689 (0.946, 2.446)	1.791 (1.020, 2.572)	1.879 (1.081, 2.678)
I	2006 - 2007	-0.364 (-1.184, 0.477)	-0.429 (-1.307, 0.466)	-0.503 (-1.432, 0.445)	-0.585 (-1.567, 0.413)	-0.674 (-1.701, 0.368)	-0.770 (-1.837, 0.312)
J	2006 - 2008	-0.270 (-1.145, 0.626)	-0.229 (-1.169, 0.722)	-0.170 (-1.165, 0.833)	-0.091 (-1.142, 0.965)	0.011 (-1.087, 1.107)	0.137 (-0.987, 1.264)
K	2007 - 2008	0.094 (-0.466, 0.643)	0.201 (-0.399, 0.785)	0.333 (-0.299, 0.955)	0.494 (-0.170, 1.148)	0.685 (-0.011, 1.366)	0.907 (0.185, 1.612)
L	1 chick - 2 chicks	0.000 (-0.032, 0.030)	-0.002 (-0.035, 0.031)	-0.003 (-0.039, 0.032)	-0.005 (-0.043, 0.032)	-0.007 (-0.047, 0.032)	-0.010 (-0.052, 0.031)
M	2 chicks - 3 chicks	-0.001 (-0.033, 0.029)	-0.002 (-0.036, 0.030)	-0.004 (-0.040, 0.030)	-0.006 (-0.044, 0.030)	-0.008 (-0.049, 0.030)	-0.011 (-0.054, 0.029)
N	3 chicks - 1 chick	0.002 (-0.059, 0.064)	0.004 (-0.061, 0.071)	0.007 (-0.062, 0.079)	0.011 (-0.062, 0.087)	0.016 (-0.061, 0.096)	0.022 (-0.059, 0.106)
O	a chick - b chick	0.193 (0.037, 0.341)	0.206 (0.040, 0.363)	0.218 (0.044, 0.384)	0.229 (0.047, 0.401)	0.237 (0.047, 0.415)	0.242 (0.049, 0.424)
P	b chick - c chick	0.081 (-0.122, 0.284)	0.085 (-0.130, 0.301)	0.089 (-0.137, 0.315)	0.091 (-0.143, 0.328)	0.092 (-0.148, 0.336)	0.092 (-0.154, 0.340)
Q	c chick - a chick	-0.274 (-0.451, -0.088)	-0.291 (-0.481, -0.095)	-0.307 (-0.507, -0.100)	-0.320 (-0.529, -0.105)	-0.329 (-0.548, -0.107)	-0.334 (-0.560, -0.106)

Table 3-11 (continued)

Figure legend	Contrast	Y_6	Y_7	Y_8	Y_9	Y_{10}	Y_{11}
A	female - male	0.104 (0.007, 0.201)	0.115 (0.017, 0.214)	0.126 (0.026, 0.227)	0.138 (0.036, 0.241)	0.150 (0.045, 0.257)	0.163 (0.052, 0.275)
B	2004 - 2005	-1.358 (-2.030, -0.681)	-1.299 (-2.002, -0.590)	-1.208 (-1.951, -0.450)	-1.083 (-1.875, -0.268)	-0.926 (-1.785, -0.043)	-0.740 (-1.683, 0.229)
C	2004 - 2006	0.301 (-0.767, 1.372)	0.227 (-0.873, 1.332)	0.133 (-1.002, 1.276)	0.018 (-1.152, 1.199)	-0.116 (-1.343, 1.110)	-0.266 (-1.551, 1.018)
D	2004 - 2007	-0.570 (-1.136, 0.002)	-0.745 (-1.356, -0.127)	-0.940 (-1.603, -0.269)	-1.149 (-1.875, -0.416)	-1.366 (-2.159, -0.562)	-1.583 (-2.456, -0.691)
E	2004 - 2008	0.590 (-0.072, 1.238)	0.693 (0.007, 1.368)	0.798 (0.085, 1.505)	0.899 (0.147, 1.645)	0.990 (0.197, 1.785)	1.064 (0.213, 1.910)
F	2005 - 2006	1.659 (0.496, 2.826)	1.526 (0.337, 2.723)	1.341 (0.126, 2.564)	1.101 (-0.147, 2.353)	0.810 (-0.482, 2.112)	0.474 (-0.893, 1.823)
G	2005 - 2007	0.788 (0.046, 1.536)	0.554 (-0.217, 1.332)	0.268 (-0.539, 1.075)	-0.066 (-0.916, 0.783)	-0.440 (-1.356, 0.468)	-0.843 (-1.827, 0.130)
H	2005 - 2008	1.948 (1.133, 2.764)	1.992 (1.160, 2.821)	2.006 (1.157, 2.843)	1.982 (1.105, 2.852)	1.916 (1.006, 2.819)	1.804 (0.845, 2.761)
I	2006 - 2007	-0.870 (-1.977, 0.243)	-0.972 (-2.110, 0.161)	-1.073 (-2.241, 0.090)	-1.167 (-2.368, 0.015)	-1.250 (-2.505, -0.013)	-1.318 (-2.623, -0.015)
J	2006 - 2008	0.289 (-0.862, 1.440)	0.466 (-0.702, 1.630)	0.665 (-0.521, 1.862)	0.881 (-0.312, 2.086)	1.106 (-0.115, 2.337)	1.330 (0.068, 2.626)
K	2007 - 2008	1.160 (0.414, 1.893)	1.439 (0.666, 2.189)	1.738 (0.942, 2.518)	2.048 (1.225, 2.854)	2.356 (1.506, 3.203)	2.647 (1.749, 3.537)
L	1 chick - 2 chicks	-0.014 (-0.057, 0.029)	-0.018 (-0.063, 0.027)	-0.023 (-0.070, 0.024)	-0.028 (-0.078, 0.022)	-0.034 (-0.088, 0.020)	-0.041 (-0.099, 0.017)
M	2 chicks - 3 chicks	-0.015 (-0.059, 0.027)	-0.019 (-0.065, 0.025)	-0.024 (-0.073, 0.023)	-0.030 (-0.081, 0.020)	-0.036 (-0.091, 0.018)	-0.042 (-0.102, 0.015)
N	3 chicks - 1 chick	0.029 (-0.056, 0.117)	0.037 (-0.051, 0.129)	0.047 (-0.047, 0.143)	0.058 (-0.042, 0.159)	0.070 (-0.037, 0.178)	0.083 (-0.033, 0.201)
O	a chick - b chick	0.244 (0.049, 0.429)	0.242 (0.046, 0.430)	0.237 (0.037, 0.427)	0.227 (0.025, 0.423)	0.215 (0.006, 0.417)	0.199 (-0.018, 0.414)
P	b chick - c chick	0.090 (-0.160, 0.343)	0.087 (-0.167, 0.343)	0.081 (-0.176, 0.343)	0.074 (-0.189, 0.341)	0.067 (-0.206, 0.343)	0.059 (-0.231, 0.351)
Q	c chick - a chick	-0.334 (-0.565, -0.100)	-0.329 (-0.562, -0.093)	-0.318 (-0.558, -0.076)	-0.302 (-0.550, -0.054)	-0.281 (-0.540, -0.024)	-0.259 (-0.531, 0.019)

Table 3-11 (continued)

Figure legend	Contrast	Y_{12}	Y_{13}	Y_{14}	Y_{15}	Y_{16}	Y_{17}
A	female - male	0.176 (0.057, 0.295)	0.189 (0.060, 0.317)	0.203 (0.064, 0.341)	0.217 (0.067, 0.366)	0.232 (0.071, 0.390)	0.246 (0.078, 0.412)
B	2004 - 2005	-0.530 (-1.565, 0.529)	-0.303 (-1.440, 0.845)	-0.070 (-1.314, 1.184)	0.159 (-1.189, 1.510)	0.374 (-1.063, 1.819)	0.563 (-0.961, 2.097)
C	2004 - 2006	-0.427 (-1.799, 0.943)	-0.593 (-2.078, 0.864)	-0.758 (-2.358, 0.811)	-0.912 (-2.625, 0.770)	-1.050 (-2.877, 0.727)	-1.165 (-3.092, 0.714)
D	2004 - 2007	-1.791 (-2.754, -0.813)	-1.977 (-3.032, -0.909)	-2.132 (-3.275, -0.968)	-2.247 (-3.478, -1.001)	-2.312 (-3.622, -0.980)	-2.325 (-3.703, -0.919)
E	2004 - 2008	1.113 (0.200, 2.037)	1.129 (0.153, 2.128)	1.105 (0.055, 2.179)	1.036 (-0.093, 2.190)	0.915 (-0.292, 2.139)	0.744 (-0.528, 2.036)
F	2005 - 2006	0.103 (-1.348, 1.525)	-0.290 (-1.852, 1.239)	-0.687 (-2.375, 0.952)	-1.072 (-2.893, 0.694)	-1.424 (-3.390, 0.485)	-1.728 (-3.788, 0.300)
G	2005 - 2007	-1.261 (-2.326, -0.203)	-1.674 (-2.834, -0.521)	-2.062 (-3.322, -0.804)	-2.406 (-3.772, -1.043)	-2.686 (-4.156, -1.232)	-2.887 (-4.457, -1.340)
H	2005 - 2008	1.643 (0.612, 2.670)	1.433 (0.329, 2.544)	1.176 (-0.016, 2.385)	0.876 (-0.417, 2.182)	0.542 (-0.843, 1.940)	0.181 (-1.291, 1.656)
I	2006 - 2007	-1.364 (-2.749, 0.015)	-1.384 (-2.876, 0.095)	-1.375 (-2.973, 0.214)	-1.334 (-3.056, 0.372)	-1.262 (-3.092, 0.566)	-1.160 (-3.086, 0.775)
J	2006 - 2008	1.540 (0.213, 2.890)	1.723 (0.313, 3.155)	1.863 (0.363, 3.402)	1.948 (0.336, 3.589)	1.966 (0.239, 3.717)	1.909 (0.080, 3.753)
K	2007 - 2008	2.904 (1.951, 3.848)	3.106 (2.085, 4.115)	3.238 (2.131, 4.327)	3.282 (2.087, 4.458)	3.228 (1.962, 4.474)	3.068 (1.721, 4.388)
L	1 chick - 2 chicks	-0.048 (-0.111, 0.015)	-0.055 (-0.123, 0.013)	-0.062 (-0.136, 0.012)	-0.069 (-0.150, 0.010)	-0.076 (-0.163, 0.009)	-0.083 (-0.174, 0.009)
M	2 chicks - 3 chicks	-0.050 (-0.114, 0.014)	-0.057 (-0.127, 0.012)	-0.064 (-0.141, 0.010)	-0.071 (-0.155, 0.009)	-0.078 (-0.168, 0.009)	-0.085 (-0.179, 0.008)
N	3 chicks - 1 chick	0.097 (-0.028, 0.225)	0.112 (-0.026, 0.251)	0.126 (-0.022, 0.277)	0.141 (-0.019, 0.304)	0.154 (-0.018, 0.331)	0.167 (-0.016, 0.354)
O	a chick - b chick	0.183 (-0.046, 0.411)	0.167 (-0.078, 0.412)	0.154 (-0.110, 0.419)	0.144 (-0.136, 0.429)	0.140 (-0.158, 0.443)	0.144 (-0.169, 0.459)
P	b chick - c chick	0.053 (-0.260, 0.363)	0.048 (-0.292, 0.384)	0.046 (-0.322, 0.412)	0.049 (-0.347, 0.440)	0.057 (-0.363, 0.472)	0.070 (-0.370, 0.503)
Q	c chick - a chick	-0.236 (-0.527, 0.065)	-0.215 (-0.528, 0.111)	-0.200 (-0.537, 0.151)	-0.193 (-0.556, 0.183)	-0.197 (-0.581, 0.202)	-0.214 (-0.618, 0.206)

Table 3-11 (continued)

Figure legend	Contrast	Y_{18}	Y_{19}	Y_{20}	Y_{21}	Y_{22}	Y_{23}
A	female - male	0.261 (0.086, 0.435)	0.276 (0.095, 0.455)	0.291 (0.105, 0.474)	0.305 (0.112, 0.494)	0.319 (0.119, 0.515)	0.333 (0.124, 0.535)
B	2004 - 2005	0.717 (-0.884, 2.329)	0.830 (-0.833, 2.509)	0.898 (-0.819, 2.646)	0.919 (-0.845, 2.706)	0.894 (-0.925, 2.749)	0.827 (-1.047, 2.736)
C	2004 - 2006	-1.252 (-3.272, 0.706)	-1.309 (-3.398, 0.718)	-1.334 (-3.483, 0.750)	-1.329 (-3.522, 0.807)	-1.297 (-3.533, 0.890)	-1.242 (-3.516, 0.978)
D	2004 - 2007	-2.281 (-3.721, -0.821)	-2.185 (-3.681, -0.672)	-2.038 (-3.581, -0.469)	-1.849 (-3.428, -0.248)	-1.626 (-3.238, 0.021)	-1.378 (-3.027, 0.308)
E	2004 - 2008	0.522 (-0.809, 1.870)	0.253 (-1.132, 1.646)	-0.057 (-1.483, 1.381)	-0.399 (-1.864, 1.064)	-0.766 (-2.266, 0.721)	-1.147 (-2.665, 0.360)
F	2005 - 2006	-1.969 (-4.120, 0.152)	-2.139 (-4.367, 0.066)	-2.232 (-4.554, 0.045)	-2.248 (-4.646, 0.112)	-2.192 (-4.665, 0.213)	-2.069 (-4.600, 0.408)
G	2005 - 2007	-2.999 (-4.641, -1.363)	-3.015 (-4.729, -1.291)	-2.936 (-4.715, -1.143)	-2.769 (-4.618, -0.907)	-2.521 (-4.433, -0.610)	-2.205 (-4.187, -0.214)
H	2005 - 2008	-0.195 (-1.750, 1.351)	-0.577 (-2.204, 1.038)	-0.955 (-2.646, 0.725)	-1.318 (-3.078, 0.418)	-1.660 (-3.492, 0.141)	-1.975 (-3.886, -0.096)
I	2006 - 2007	-1.029 (-3.028, 0.997)	-0.876 (-2.954, 1.233)	-0.704 (-2.846, 1.481)	-0.520 (-2.721, 1.729)	-0.329 (-2.573, 1.983)	-0.136 (-2.451, 2.246)
J	2006 - 2008	1.774 (-0.129, 3.701)	1.561 (-0.422, 3.562)	1.277 (-0.760, 3.329)	0.930 (-1.155, 3.047)	0.532 (-1.591, 2.719)	0.095 (-2.067, 2.324)
K	2007 - 2008	2.803 (1.394, 4.184)	2.437 (0.979, 3.867)	1.982 (0.465, 3.468)	1.450 (-0.122, 2.985)	0.861 (-0.756, 2.444)	0.231 (-1.450, 1.859)
L	1 chick - 2 chicks	-0.088 (-0.185, 0.008)	-0.094 (-0.195, 0.007)	-0.098 (-0.203, 0.006)	-0.101 (-0.211, 0.005)	-0.104 (-0.217, 0.007)	-0.106 (-0.222, 0.008)
M	2 chicks - 3 chicks	-0.090 (-0.190, 0.007)	-0.095 (-0.199, 0.006)	-0.099 (-0.208, 0.005)	-0.103 (-0.215, 0.005)	-0.105 (-0.220, 0.007)	-0.107 (-0.226, 0.009)
N	3 chicks - 1 chick	0.179 (-0.015, 0.375)	0.189 (-0.013, 0.394)	0.197 (-0.011, 0.411)	0.204 (-0.011, 0.425)	0.209 (-0.014, 0.437)	0.213 (-0.016, 0.449)
O	a chick - b chick	0.156 (-0.171, 0.481)	0.176 (-0.162, 0.510)	0.205 (-0.143, 0.547)	0.242 (-0.119, 0.593)	0.285 (-0.086, 0.646)	0.333 (-0.052, 0.707)
P	b chick - c chick	0.089 (-0.367, 0.539)	0.114 (-0.356, 0.576)	0.144 (-0.337, 0.616)	0.178 (-0.316, 0.663)	0.215 (-0.295, 0.716)	0.255 (-0.287, 0.775)
Q	c chick - a chick	-0.245 (-0.666, 0.194)	-0.290 (-0.725, 0.166)	-0.349 (-0.795, 0.124)	-0.420 (-0.878, 0.067)	-0.500 (-0.970, 0.004)	-0.588 (-1.080, -0.059)

Table 3-11 (continued)

Figure legend	Contrast	Y_{24}	Y_{25}	Y_{26}	Y_{27}	Y_{28}	Y_{29}
A	female - male	0.346 (0.127, 0.557)	0.359 (0.129, 0.582)	0.370 (0.127, 0.608)	0.381 (0.123, 0.633)	0.391 (0.117, 0.657)	0.400 (0.110, 0.681)
B	2004 - 2005	0.723 (-1.204, 2.689)	0.588 (-1.420, 2.626)	0.429 (-1.677, 2.548)	0.252 (-1.945, 2.447)	0.063 (-2.227, 2.355)	-0.131 (-2.520, 2.252)
C	2004 - 2006	-1.168 (-3.484, 1.104)	-1.079 (-3.439, 1.251)	-0.981 (-3.428, 1.425)	-0.877 (-3.402, 1.630)	-0.771 (-3.399, 1.845)	-0.666 (-3.402, 2.037)
D	2004 - 2007	-1.113 (-2.793, 0.608)	-0.840 (-2.543, 0.913)	-0.567 (-2.305, 1.216)	-0.298 (-2.066, 1.526)	-0.040 (-1.851, 1.827)	0.204 (-1.656, 2.115)
E	2004 - 2008	-1.534 (-3.086, 0.014)	-1.920 (-3.513, -0.329)	-2.296 (-3.931, -0.659)	-2.657 (-4.352, -0.965)	-3.000 (-4.770, -1.256)	-3.321 (-5.165, -1.511)
F	2005 - 2006	-1.891 (-4.500, 0.652)	-1.668 (-4.345, 0.984)	-1.410 (-4.189, 1.363)	-1.129 (-4.025, 1.776)	-0.835 (-3.864, 2.209)	-0.535 (-3.720, 2.659)
G	2005 - 2007	-1.836 (-3.900, 0.243)	-1.429 (-3.609, 0.761)	-0.996 (-3.249, 1.270)	-0.550 (-2.907, 1.826)	-0.104 (-2.556, 2.395)	0.336 (-2.233, 2.951)
H	2005 - 2008	-2.258 (-4.249, -0.307)	-2.508 (-4.600, -0.443)	-2.725 (-4.914, -0.540)	-2.909 (-5.228, -0.595)	-3.063 (-5.499, -0.622)	-3.189 (-5.742, -0.609)
I	2006 - 2007	0.055 (-2.332, 2.494)	0.239 (-2.234, 2.768)	0.414 (-2.133, 3.029)	0.579 (-2.085, 3.321)	0.731 (-2.032, 3.590)	0.870 (-2.006, 3.849)
J	2006 - 2008	-0.367 (-2.617, 1.945)	-0.840 (-3.179, 1.541)	-1.315 (-3.766, 1.163)	-1.780 (-4.337, 0.823)	-2.229 (-4.926, 0.517)	-2.654 (-5.487, 0.228)
K	2007 - 2008	-0.421 (-2.159, 1.265)	-1.080 (-2.891, 0.683)	-1.729 (-3.613, 0.122)	-2.359 (-4.346, -0.418)	-2.960 (-5.034, -0.931)	-3.525 (-5.703, -1.405)
L	1 chick - 2 chicks	-0.108 (-0.227, 0.010)	-0.109 (-0.231, 0.014)	-0.109 (-0.235, 0.016)	-0.109 (-0.239, 0.020)	-0.109 (-0.244, 0.025)	-0.108 (-0.248, 0.030)
M	2 chicks - 3 chicks	-0.108 (-0.230, 0.011)	-0.109 (-0.235, 0.014)	-0.109 (-0.239, 0.017)	-0.109 (-0.243, 0.022)	-0.109 (-0.247, 0.027)	-0.108 (-0.251, 0.032)
N	3 chicks - 1 chick	0.216 (-0.022, 0.457)	0.217 (-0.027, 0.466)	0.218 (-0.034, 0.474)	0.218 (-0.042, 0.482)	0.217 (-0.051, 0.491)	0.216 (-0.061, 0.498)
O	a chick - b chick	0.385 (-0.016, 0.779)	0.439 (0.023, 0.857)	0.495 (0.051, 0.938)	0.549 (0.075, 1.023)	0.603 (0.099, 1.112)	0.654 (0.123, 1.196)
P	b chick - c chick	0.295 (-0.278, 0.843)	0.335 (-0.275, 0.916)	0.375 (-0.271, 0.998)	0.413 (-0.272, 1.074)	0.450 (-0.280, 1.152)	0.484 (-0.287, 1.229)
Q	c chick - a chick	-0.680 (-1.199, -0.132)	-0.775 (-1.323, -0.203)	-0.870 (-1.452, -0.269)	-0.963 (-1.582, -0.329)	-1.053 (-1.711, -0.382)	-1.138 (-1.830, -0.428)

Table 3-11 (continued)

Figure legend	Contrast	Y_{30}	Y_{31}	Y_{32}
A	female - male	0.408 (0.102, 0.705)	0.415 (0.093, 0.728)	0.422 (0.084, 0.750)
B	2004 - 2005	-0.327 (-2.810, 2.143)	-0.520 (-3.120, 2.052)	-0.707 (-3.399, 1.955)
C	2004 - 2006	-0.564 (-3.395, 2.236)	-0.466 (-3.392, 2.436)	-0.374 (-3.382, 2.624)
D	2004 - 2007	0.433 (-1.470, 2.392)	0.644 (-1.295, 2.641)	0.838 (-1.139, 2.870)
E	2004 - 2008	-3.617 (-5.535, -1.728)	-3.890 (-5.920, -1.931)	-4.138 (-6.251, -2.089)
F	2005 - 2006	-0.237 (-3.594, 3.126)	0.054 (-3.461, 3.564)	0.333 (-3.336, 3.995)
G	2005 - 2007	0.760 (-1.914, 3.493)	1.164 (-1.620, 4.013)	1.545 (-1.334, 4.501)
H	2005 - 2008	-3.291 (-5.971, -0.563)	-3.370 (-6.186, -0.492)	-3.431 (-6.378, -0.432)
I	2006 - 2007	0.997 (-1.983, 4.084)	1.110 (-1.973, 4.310)	1.212 (-1.983, 4.517)
J	2006 - 2008	-3.054 (-6.034, -0.026)	-3.424 (-6.532, -0.254)	-3.764 (-7.010, -0.452)
K	2007 - 2008	-4.050 (-6.330, -1.833)	-4.534 (-6.902, -2.214)	-4.976 (-7.426, -2.564)
L	1 chick - 2 chicks	-0.108 (-0.251, 0.035)	-0.107 (-0.254, 0.040)	-0.106 (-0.258, 0.044)
M	2 chicks - 3 chicks	-0.107 (-0.254, 0.037)	-0.107 (-0.258, 0.041)	-0.106 (-0.261, 0.046)
N	3 chicks - 1 chick	0.215 (-0.071, 0.505)	0.213 (-0.081, 0.512)	0.212 (-0.090, 0.518)
O	a chick - b chick	0.702 (0.140, 1.279)	0.748 (0.155, 1.352)	0.790 (0.164, 1.426)
P	b chick - c chick	0.515 (-0.298, 1.303)	0.544 (-0.311, 1.370)	0.570 (-0.324, 1.435)
Q	c chick - a chick	-1.218 (-1.948, -0.469)	-1.292 (-2.055, -0.510)	-1.360 (-2.154, -0.548)

Table 3-12 Results of model comparison for tarsus length

ID	Model	WAIC	Delta	Weight	CumWeight
22	Intercept + Sex + Year + Order + Older	1143.132	0.000	0.311	0.311
20	Intercept + Year + Order + Older	1144.339	1.208	0.170	0.481
17	Intercept + Year + Order	1144.655	1.523	0.145	0.627
18	Intercept + Sex + Year + Order	1145.036	1.904	0.120	0.747
24	Intercept + Sex + Year + brood + Order + Older	1145.317	2.185	0.104	0.851
21	Intercept + Sex + Year + brood + Order	1147.197	4.065	0.041	0.892
11	Intercept + Year	1147.397	4.265	0.037	0.929
23	Intercept + Year + brood + Order + Older	1148.144	5.013	0.025	0.954
19	Intercept + Year + brood + Order	1148.349	5.217	0.023	0.977
13	Intercept + Sex + Year	1148.987	5.855	0.017	0.994
15	Intercept + Year + brood	1151.678	8.546	0.004	0.998
16	Intercept + Sex + Year + brood	1153.500	10.369	0.002	1.000
5	Intercept + Order	1205.899	62.767	0.000	1.000
9	Intercept + Sex + brood + Order	1207.261	64.130	0.000	1.000
1	Intercept	1207.949	64.817	0.000	1.000
6	Intercept + Sex + Order	1208.062	64.930	0.000	1.000
4	Intercept + Sex + brood	1208.325	65.194	0.000	1.000
7	Intercept + brood + Order	1208.572	65.440	0.000	1.000
3	Intercept + brood	1208.866	65.734	0.000	1.000
8	Intercept + Order + Older	1209.234	66.102	0.000	1.000
14	Intercept + Sex + brood + Order + Older	1209.891	66.759	0.000	1.000
2	Intercept + Sex	1210.926	67.794	0.000	1.000
12	Intercept + brood + Order + Older	1211.484	68.352	0.000	1.000
10	Intercept + Sex + Order + Older	1211.541	68.409	0.000	1.000

ID: model ID corresponding to model name in Table 3-13, WAIC: Watanabe Akaike information criteria, Delta: difference from the minimum WAIC, Weight: model weight based on WAIC value, CumWeight: cumulate value of Weight from the best model

Table 3-13 Regression coefficients in the best models for tarsus length

Model	Variables	α_0	α_1	α_2
Model17	Intercept	3.422 (3.411, 3.433)	0.153 (0.131, 0.174)	-1.938 (-1.975, -1.902)
	Year (2005)	0.012 (-0.023, 0.049)	-0.126 (-0.202, -0.048)	-0.106 (-0.248, 0.032)
	Year (2006)	-0.029 (-0.072, 0.019)	-0.061 (-0.175, 0.059)	-0.063 (-0.285, 0.142)
	Year (2007)	0.009 (-0.018, 0.036)	-0.066 (-0.115, -0.016)	-0.135 (-0.234, -0.039)
	Year (2008)	-0.012 (-0.037, 0.014)	0.126 (0.077, 0.177)	0.001 (-0.096, 0.099)
	Order (b-chick)	0.007 (-0.014, 0.030)	0.008 (-0.041, 0.056)	-0.057 (-0.150, 0.034)
	Order (c-chick)	-0.009 (-0.036, 0.019)	0.036 (-0.021, 0.093)	-0.018 (-0.129, 0.087)
Model18	Intercept	3.422 (3.410, 3.432)	0.152 (0.130, 0.174)	-1.939 (-1.977, -1.902)
	Sex (male)	-0.001 (-0.021, 0.020)	0.050 (0.004, 0.095)	0.057 (-0.028, 0.140)
	Year (2005)	0.016 (-0.020, 0.056)	-0.163 (-0.244, -0.077)	-0.153 (-0.309, -0.006)
	Year (2006)	-0.029 (-0.073, 0.020)	-0.088 (-0.204, 0.036)	-0.089 (-0.316, 0.122)
	Year (2007)	0.010 (-0.019, 0.040)	-0.094 (-0.150, -0.037)	-0.167 (-0.278, -0.057)
	Year (2008)	-0.011 (-0.038, 0.018)	0.097 (0.041, 0.154)	-0.030 (-0.136, 0.074)
	Order (b-chick)	0.009 (-0.013, 0.032)	0.010 (-0.039, 0.058)	-0.060 (-0.154, 0.033)
	Order (c-chick)	-0.010 (-0.037, 0.017)	0.044 (-0.014, 0.102)	-0.009 (-0.119, 0.098)
Model20	Intercept	3.422 (3.411, 3.433)	0.152 (0.131, 0.174)	-1.939 (-1.976, -1.903)
	Year (2005)	0.014 (-0.023, 0.055)	-0.160 (-0.243, -0.073)	-0.146 (-0.308, 0.002)
	Year (2006)	-0.033 (-0.074, 0.014)	-0.043 (-0.161, 0.085)	-0.030 (-0.250, 0.174)
	Year (2007)	0.011 (-0.017, 0.039)	-0.054 (-0.106, -0.003)	-0.126 (-0.226, -0.027)
	Year (2008)	-0.013 (-0.038, 0.013)	0.126 (0.077, 0.176)	0.007 (-0.089, 0.101)
	Order (b-chick)	0.014 (-0.013, 0.043)	0.055 (-0.013, 0.122)	-0.023 (-0.142, 0.094)
	Order (c-chick)	-0.002 (-0.036, 0.034)	0.090 (0.010, 0.169)	0.026 (-0.122, 0.171)
	Older (yes)	-0.015 (-0.048, 0.019)	-0.073 (-0.146, -0.002)	-0.050 (-0.187, 0.085)
Model22	Intercept	3.422 (3.410, 3.433)	0.151 (0.129, 0.173)	-1.941 (-1.978, -1.904)
	Sex (male)	-0.006 (-0.027, 0.015)	0.057 (0.011, 0.103)	0.073 (-0.011, 0.157)
	Year (2005)	0.023 (-0.016, 0.066)	-0.209 (-0.300, -0.115)	-0.216 (-0.393, -0.052)
	Year (2006)	-0.032 (-0.074, 0.015)	-0.069 (-0.189, 0.059)	-0.055 (-0.275, 0.150)
	Year (2007)	0.014 (-0.016, 0.044)	-0.085 (-0.141, -0.028)	-0.165 (-0.274, -0.058)
	Year (2008)	-0.009 (-0.037, 0.019)	0.094 (0.037, 0.150)	-0.031 (-0.134, 0.072)
	Order (b-chick)	0.012 (-0.015, 0.041)	0.064 (-0.003, 0.133)	-0.011 (-0.132, 0.106)
	Order (c-chick)	-0.008 (-0.043, 0.029)	0.109 (0.028, 0.189)	0.059 (-0.092, 0.206)
	Older (yes)	-0.009 (-0.044, 0.026)	-0.086 (-0.160, -0.013)	-0.078 (-0.216, 0.063)

Table 3-13 (continued)

Model	Variables	α_0	α_1	α_2
Model24	Intercept	3.420 (3.408, 3.431)	0.156 (0.133, 0.178)	-1.948 (-1.987, -1.908)
	Sex (male)	-0.007 (-0.028, 0.015)	0.064 (0.018, 0.111)	0.081 (-0.004, 0.165)
	Year (2005)	0.008 (-0.035, 0.053)	-0.185 (-0.280, -0.088)	-0.187 (-0.374, -0.014)
	Year (2006)	-0.044 (-0.086, 0.004)	-0.044 (-0.171, 0.089)	-0.014 (-0.239, 0.193)
	Year (2007)	-0.001 (-0.035, 0.032)	-0.061 (-0.127, 0.004)	-0.139 (-0.262, -0.017)
	Year (2008)	-0.021 (-0.051, 0.009)	0.110 (0.050, 0.171)	-0.009 (-0.122, 0.102)
	Brood	0.013 (-0.002, 0.028)	-0.026 (-0.061, 0.008)	-0.022 (-0.084, 0.039)
	Order (b-chick)	0.010 (-0.019, 0.039)	0.078 (0.008, 0.148)	0.003 (-0.124, 0.128)
	Order (c-chick)	-0.013 (-0.051, 0.026)	0.132 (0.047, 0.217)	0.085 (-0.082, 0.247)
	Older (yes)	-0.008 (-0.043, 0.027)	-0.084 (-0.157, -0.013)	-0.082 (-0.221, 0.057)

Model: model name corresponding to model ID in Table 3-12

Table 3-14 Statistics of growth curve of tarsus length depending on the effects of explanatory variables

Variables	Y_0	Y_{10}	Y_{20}	Y_{30}	A	IP_{rate}	IP_{day}
Sex (female)	9.546 (9.436, 9.657)	23.190 (23.018, 23.359)	28.648 (28.498, 28.797)	30.128 (29.987, 30.269)	30.608 (30.464, 30.752)	0.062 (0.060, 0.063)	1.065 (1.001, 1.128)
Sex (male)	9.152 (8.930, 9.377)	23.308 (23.106, 23.508)	28.730 (28.540, 28.919)	30.113 (29.884, 30.342)	30.530 (30.272, 30.795)	0.067 (0.064, 0.070)	1.240 (1.137, 1.340)
Year (2004)	9.546 (9.436, 9.657)	23.190 (23.018, 23.359)	28.648 (28.498, 28.797)	30.128 (29.987, 30.269)	30.608 (30.464, 30.752)	0.062 (0.060, 0.063)	1.065 (1.001, 1.128)
Year (2005)	11.619 (11.090, 12.153)	23.245 (23.017, 23.475)	28.498 (28.240, 28.766)	30.275 (29.920, 30.637)	31.079 (30.585, 31.599)	0.045 (0.040, 0.049)	-0.163 (-0.516, 0.153)
Year (2006)	9.893 (9.242, 10.537)	22.385 (22.033, 22.745)	27.527 (27.215, 27.843)	29.037 (28.635, 29.446)	29.607 (29.085, 30.168)	0.056 (0.049, 0.064)	0.645 (0.283, 0.970)
Year (2007)	10.435 (10.132, 10.730)	22.547 (22.329, 22.767)	28.175 (27.959, 28.395)	30.059 (29.791, 30.327)	30.875 (30.524, 31.231)	0.050 (0.047, 0.053)	0.651 (0.480, 0.818)
Year (2008)	8.224 (7.965, 8.488)	22.028 (21.800, 22.254)	27.973 (27.789, 28.161)	29.652 (29.408, 29.904)	30.221 (29.909, 30.548)	0.068 (0.064, 0.072)	1.860 (1.725, 1.997)
Brood (0)	9.546 (9.436, 9.657)	23.190 (23.018, 23.359)	28.648 (28.498, 28.797)	30.128 (29.987, 30.269)	30.608 (30.464, 30.752)	0.062 (0.060, 0.063)	1.065 (1.001, 1.128)
Brood (1)	9.622 (9.502, 9.742)	23.242 (23.069, 23.413)	28.705 (28.552, 28.854)	30.194 (30.048, 30.340)	30.681 (30.529, 30.832)	0.061 (0.060, 0.062)	1.035 (0.967, 1.102)
Brood (2)	9.699 (9.550, 9.850)	23.297 (23.116, 23.476)	28.762 (28.598, 28.922)	30.260 (30.094, 30.425)	30.755 (30.578, 30.933)	0.061 (0.059, 0.062)	1.003 (0.922, 1.082)
Order (a-chick)	9.699 (9.550, 9.850)	23.297 (23.116, 23.476)	28.762 (28.598, 28.922)	30.260 (30.094, 30.425)	30.755 (30.578, 30.933)	0.061 (0.059, 0.062)	1.003 (0.922, 1.082)
Order (b-chick)	9.317 (8.960, 9.672)	23.002 (22.758, 23.240)	28.808 (28.578, 29.036)	30.479 (30.182, 30.788)	31.068 (30.695, 31.459)	0.062 (0.058, 0.066)	1.332 (1.162, 1.498)
Order (c-chick)	8.747 (8.348, 9.152)	22.876 (22.593, 23.160)	28.538 (28.270, 28.800)	30.044 (29.673, 30.413)	30.526 (30.077, 30.985)	0.068 (0.062, 0.074)	1.511 (1.330, 1.686)
Older (no)	9.241 (8.892, 9.588)	22.948 (22.708, 23.184)	28.751 (28.525, 28.972)	30.413 (30.120, 30.713)	30.994 (30.628, 31.380)	0.062 (0.058, 0.067)	1.363 (1.196, 1.524)
Older (yes)	9.736 (9.432, 10.038)	22.742 (22.500, 22.982)	28.419 (28.196, 28.637)	30.142 (29.854, 30.428)	30.794 (30.423, 31.172)	0.057 (0.053, 0.060)	1.052 (0.892, 1.209)

Y_0, Y_{10}, Y_{20}, Y_{30}: body mass (g) at day 0, 10, 20, 30, A: asymptotic size, IP_{rate}: growth rate at inflection point (g/day), IP_{day}: the day of inflection point. Parenthesis indicates 95% credible interval. See Table 3-2 for variables settings used to calculate these statistics

Table 3-15 Numerical differences of growth curves of tarsus length in Figure 3-4

Figure legend	Contrast	Y_0	Y_1	Y_2	Y_3	Y_4	Y_5
A	female - male	0.394 (0.194, 0.592)	0.335 (0.161, 0.506)	0.268 (0.121, 0.413)	0.198 (0.074, 0.325)	0.131 (0.016, 0.246)	0.069 (-0.045, 0.183)
B	2004 - 2005	-2.073 (-2.612, -1.540)	-1.856 (-2.325, -1.389)	-1.615 (-2.026, -1.211)	-1.365 (-1.724, -1.019)	-1.118 (-1.431, -0.814)	-0.884 (-1.167, -0.608)
C	2004 - 2006	-0.347 (-1.000, 0.300)	-0.227 (-0.794, 0.335)	-0.097 (-0.584, 0.378)	0.037 (-0.382, 0.442)	0.170 (-0.198, 0.526)	0.299 (-0.047, 0.632)
D	2004 - 2007	-0.889 (-1.198, -0.574)	-0.686 (-0.964, -0.405)	-0.475 (-0.727, -0.218)	-0.265 (-0.502, -0.027)	-0.068 (-0.295, 0.160)	0.111 (-0.116, 0.338)
E	2004 - 2008	1.322 (1.043, 1.597)	1.389 (1.135, 1.638)	1.430 (1.197, 1.660)	1.446 (1.225, 1.664)	1.441 (1.219, 1.659)	1.418 (1.189, 1.641)
F	2005 - 2006	1.727 (0.930, 2.550)	1.629 (0.939, 2.332)	1.518 (0.930, 2.112)	1.402 (0.901, 1.904)	1.288 (0.853, 1.717)	1.183 (0.789, 1.571)
G	2005 - 2007	1.184 (0.673, 1.709)	1.169 (0.722, 1.629)	1.140 (0.751, 1.540)	1.099 (0.761, 1.448)	1.050 (0.752, 1.358)	0.995 (0.717, 1.278)
H	2005 - 2008	3.395 (2.900, 3.900)	3.245 (2.811, 3.691)	3.045 (2.667, 3.432)	2.811 (2.482, 3.149)	2.559 (2.264, 2.866)	2.302 (2.020, 2.592)
I	2006 - 2007	-0.542 (-1.195, 0.094)	-0.460 (-1.023, 0.093)	-0.378 (-0.853, 0.097)	-0.302 (-0.708, 0.104)	-0.238 (-0.599, 0.125)	-0.188 (-0.527, 0.158)
J	2006 - 2008	1.668 (1.011, 2.314)	1.616 (1.043, 2.180)	1.527 (1.040, 2.008)	1.410 (0.995, 1.824)	1.271 (0.902, 1.642)	1.119 (0.770, 1.470)
K	2007 - 2008	2.211 (1.911, 2.510)	2.076 (1.803, 2.344)	1.905 (1.658, 2.149)	1.712 (1.479, 1.942)	1.509 (1.278, 1.737)	1.307 (1.072, 1.539)
L	1 chick - 2 chicks	-0.076 (-0.129, -0.024)	-0.074 (-0.121, -0.029)	-0.072 (-0.112, -0.032)	-0.069 (-0.105, -0.033)	-0.066 (-0.099, -0.033)	-0.063 (-0.096, -0.030)
M	2 chicks - 3 chicks	-0.078 (-0.134, -0.024)	-0.076 (-0.125, -0.029)	-0.074 (-0.117, -0.033)	-0.071 (-0.109, -0.034)	-0.068 (-0.103, -0.034)	-0.065 (-0.099, -0.032)
N	3 chicks - 1 chick	0.153 (0.048, 0.263)	0.151 (0.058, 0.247)	0.146 (0.064, 0.229)	0.140 (0.068, 0.214)	0.134 (0.067, 0.202)	0.128 (0.062, 0.194)
O	a chick - b chick	0.382 (0.042, 0.724)	0.414 (0.117, 0.713)	0.436 (0.182, 0.690)	0.446 (0.229, 0.660)	0.445 (0.254, 0.633)	0.436 (0.259, 0.611)
P	b chick - c chick	0.570 (0.261, 0.874)	0.518 (0.253, 0.782)	0.457 (0.228, 0.683)	0.392 (0.191, 0.592)	0.330 (0.139, 0.523)	0.273 (0.078, 0.468)
Q	c chick - a chick	-0.952 (-1.340, -0.554)	-0.932 (-1.271, -0.584)	-0.892 (-1.181, -0.595)	-0.838 (-1.086, -0.586)	-0.775 (-0.997, -0.550)	-0.709 (-0.923, -0.492)
R	sister - brother	-0.495 (-0.840, -0.151)	-0.428 (-0.730, -0.127)	-0.350 (-0.610, -0.092)	-0.267 (-0.492, -0.043)	-0.182 (-0.385, 0.018)	-0.101 (-0.293, 0.092)

Table 3-15 (continued)

Figure legend	Contrast	Y_6	Y_7	Y_8	Y_9	Y_{10}	Y_{11}
A	female - male	0.014 (-0.104, 0.132)	-0.032 (-0.155, 0.089)	-0.070 (-0.197, 0.056)	-0.098 (-0.226, 0.029)	-0.118 (-0.247, 0.007)	-0.132 (-0.258, -0.009)
B	2004 - 2005	-0.668 (-0.935, -0.407)	-0.476 (-0.741, -0.216)	-0.310 (-0.578, -0.050)	-0.170 (-0.442, 0.093)	-0.056 (-0.331, 0.214)	0.035 (-0.245, 0.310)
C	2004 - 2006	0.421 (0.072, 0.756)	0.533 (0.179, 0.878)	0.635 (0.269, 0.996)	0.726 (0.345, 1.101)	0.805 (0.419, 1.189)	0.873 (0.484, 1.260)
D	2004 - 2007	0.268 (0.036, 0.499)	0.399 (0.156, 0.638)	0.505 (0.250, 0.749)	0.585 (0.323, 0.837)	0.643 (0.375, 0.900)	0.679 (0.407, 0.938)
E	2004 - 2008	1.382 (1.142, 1.619)	1.335 (1.083, 1.584)	1.281 (1.020, 1.538)	1.222 (0.956, 1.485)	1.162 (0.894, 1.426)	1.102 (0.833, 1.366)
F	2005 - 2006	1.089 (0.710, 1.458)	1.010 (0.628, 1.380)	0.945 (0.557, 1.327)	0.896 (0.496, 1.290)	0.860 (0.449, 1.267)	0.838 (0.422, 1.249)
G	2005 - 2007	0.936 (0.667, 1.208)	0.876 (0.604, 1.147)	0.815 (0.539, 1.091)	0.756 (0.474, 1.035)	0.698 (0.410, 0.985)	0.644 (0.351, 0.937)
H	2005 - 2008	2.050 (1.774, 2.333)	1.811 (1.532, 2.095)	1.591 (1.304, 1.879)	1.393 (1.101, 1.688)	1.218 (0.923, 1.516)	1.066 (0.771, 1.367)
I	2006 - 2007	-0.153 (-0.493, 0.192)	-0.134 (-0.484, 0.224)	-0.130 (-0.498, 0.244)	-0.140 (-0.522, 0.248)	-0.162 (-0.551, 0.235)	-0.193 (-0.587, 0.208)
J	2006 - 2008	0.961 (0.609, 1.315)	0.801 (0.435, 1.168)	0.646 (0.261, 1.028)	0.497 (0.104, 0.890)	0.357 (-0.040, 0.756)	0.229 (-0.169, 0.629)
K	2007 - 2008	1.114 (0.869, 1.357)	0.936 (0.679, 1.189)	0.776 (0.511, 1.038)	0.637 (0.363, 0.906)	0.519 (0.241, 0.791)	0.422 (0.145, 0.695)
L	1 chick - 2 chicks	-0.060 (-0.093, -0.027)	-0.057 (-0.092, -0.022)	-0.055 (-0.092, -0.019)	-0.054 (-0.091, -0.016)	-0.053 (-0.091, -0.014)	-0.052 (-0.090, -0.013)
M	2 chicks - 3 chicks	-0.062 (-0.096, -0.029)	-0.060 (-0.095, -0.025)	-0.057 (-0.093, -0.022)	-0.056 (-0.093, -0.019)	-0.054 (-0.092, -0.016)	-0.053 (-0.091, -0.015)
N	3 chicks - 1 chick	0.122 (0.056, 0.189)	0.117 (0.048, 0.187)	0.113 (0.040, 0.185)	0.109 (0.034, 0.184)	0.107 (0.031, 0.183)	0.105 (0.028, 0.181)
O	a chick - b chick	0.418 (0.244, 0.591)	0.394 (0.216, 0.571)	0.364 (0.182, 0.547)	0.331 (0.146, 0.516)	0.295 (0.110, 0.482)	0.258 (0.075, 0.443)
P	b chick - c chick	0.225 (0.022, 0.427)	0.185 (-0.023, 0.396)	0.156 (-0.059, 0.373)	0.137 (-0.080, 0.356)	0.126 (-0.086, 0.342)	0.123 (-0.082, 0.333)
Q	sister - brother	-0.643 (-0.862, -0.418)	-0.579 (-0.810, -0.345)	-0.520 (-0.758, -0.277)	-0.467 (-0.709, -0.221)	-0.421 (-0.663, -0.177)	-0.380 (-0.619, -0.144)

Table 3-15 (continued)

Figure legend	Contrast	Y_{12}	Y_{13}	Y_{14}	Y_{15}	Y_{16}	Y_{17}
A	female - male	-0.139 (-0.261, -0.020)	-0.141 (-0.258, -0.027)	-0.139 (-0.253, -0.028)	-0.133 (-0.243, -0.024)	-0.126 (-0.235, -0.018)	-0.116 (-0.226, -0.006)
B	2004 - 2005	0.104 (-0.181, 0.383)	0.153 (-0.133, 0.433)	0.185 (-0.101, 0.467)	0.203 (-0.085, 0.485)	0.208 (-0.081, 0.491)	0.204 (-0.086, 0.488)
C	2004 - 2006	0.930 (0.544, 1.316)	0.978 (0.595, 1.361)	1.017 (0.640, 1.393)	1.049 (0.678, 1.417)	1.073 (0.709, 1.433)	1.092 (0.734, 1.445)
D	2004 - 2007	0.697 (0.425, 0.956)	0.700 (0.426, 0.958)	0.689 (0.416, 0.945)	0.668 (0.397, 0.924)	0.638 (0.369, 0.893)	0.602 (0.335, 0.855)
E	2004 - 2008	1.042 (0.776, 1.303)	0.985 (0.724, 1.241)	0.930 (0.675, 1.180)	0.879 (0.629, 1.122)	0.831 (0.585, 1.068)	0.786 (0.544, 1.020)
F	2005 - 2006	0.826 (0.410, 1.239)	0.825 (0.412, 1.238)	0.832 (0.423, 1.242)	0.846 (0.442, 1.248)	0.865 (0.466, 1.261)	0.888 (0.494, 1.279)
G	2005 - 2007	0.594 (0.295, 0.890)	0.547 (0.248, 0.847)	0.504 (0.202, 0.807)	0.465 (0.162, 0.770)	0.430 (0.124, 0.737)	0.398 (0.089, 0.708)
H	2005 - 2008	0.938 (0.643, 1.241)	0.832 (0.537, 1.134)	0.745 (0.454, 1.042)	0.676 (0.389, 0.971)	0.622 (0.337, 0.915)	0.582 (0.296, 0.874)
I	2006 - 2007	-0.233 (-0.627, 0.165)	-0.278 (-0.671, 0.117)	-0.328 (-0.716, 0.061)	-0.381 (-0.764, 0.003)	-0.435 (-0.814, -0.057)	-0.490 (-0.861, -0.118)
J	2006 - 2008	0.112 (-0.287, 0.507)	0.006 (-0.387, 0.395)	-0.087 (-0.473, 0.291)	-0.170 (-0.545, 0.199)	-0.243 (-0.611, 0.119)	-0.306 (-0.666, 0.051)
K	2007 - 2008	0.345 (0.067, 0.617)	0.285 (0.012, 0.555)	0.241 (-0.027, 0.507)	0.211 (-0.052, 0.474)	0.192 (-0.067, 0.452)	0.184 (-0.073, 0.440)
L	1 chick - 2 chicks	-0.052 (-0.090, -0.013)	-0.052 (-0.089, -0.013)	-0.052 (-0.089, -0.014)	-0.052 (-0.089, -0.015)	-0.053 (-0.090, -0.016)	-0.054 (-0.090, -0.018)
M	2 chicks - 3 chicks	-0.053 (-0.091, -0.014)	-0.052 (-0.090, -0.014)	-0.052 (-0.090, -0.015)	-0.053 (-0.090, -0.015)	-0.053 (-0.091, -0.016)	-0.054 (-0.091, -0.017)
N	3 chicks - 1 chick	0.104 (0.027, 0.180)	0.104 (0.027, 0.180)	0.104 (0.029, 0.179)	0.105 (0.030, 0.179)	0.106 (0.033, 0.180)	0.108 (0.035, 0.182)
O	a chick - b chick	0.220 (0.042, 0.402)	0.182 (0.007, 0.356)	0.144 (-0.023, 0.313)	0.108 (-0.051, 0.270)	0.074 (-0.083, 0.230)	0.041 (-0.114, 0.192)
P	b chick - c chick	0.126 (-0.069, 0.326)	0.136 (-0.048, 0.323)	0.149 (-0.026, 0.326)	0.166 (-0.002, 0.333)	0.185 (0.023, 0.347)	0.205 (0.045, 0.366)
Q	sister - brother	-0.346 (-0.577, -0.120)	-0.317 (-0.538, -0.101)	-0.293 (-0.501, -0.086)	-0.274 (-0.472, -0.075)	-0.258 (-0.451, -0.064)	-0.246 (-0.437, -0.054)

Table 3-15 (continued)

Figure legend	Contrast	Y_{18}	Y_{19}	Y_{20}	Y_{21}	Y_{22}	Y_{23}
A	female - male	-0.105 (-0.219, 0.008)	-0.094 (-0.212, 0.024)	-0.082 (-0.205, 0.042)	-0.070 (-0.200, 0.060)	-0.058 (-0.194, 0.078)	-0.047 (-0.190, 0.096)
B	2004 - 2005	0.192 (-0.100, 0.476)	0.173 (-0.122, 0.459)	0.150 (-0.149, 0.442)	0.123 (-0.182, 0.421)	0.094 (-0.218, 0.400)	0.063 (-0.258, 0.378)
C	2004 - 2006	1.106 (0.751, 1.450)	1.115 (0.763, 1.458)	1.121 (0.770, 1.465)	1.124 (0.771, 1.470)	1.125 (0.767, 1.475)	1.124 (0.758, 1.482)
D	2004 - 2007	0.562 (0.295, 0.813)	0.518 (0.254, 0.769)	0.473 (0.209, 0.725)	0.427 (0.160, 0.681)	0.381 (0.112, 0.638)	0.336 (0.064, 0.598)
E	2004 - 2008	0.746 (0.507, 0.976)	0.708 (0.472, 0.937)	0.675 (0.437, 0.906)	0.644 (0.405, 0.878)	0.616 (0.374, 0.854)	0.591 (0.343, 0.833)
F	2005 - 2006	0.914 (0.522, 1.304)	0.942 (0.550, 1.333)	0.972 (0.575, 1.365)	1.002 (0.598, 1.401)	1.031 (0.618, 1.442)	1.061 (0.634, 1.483)
G	2005 - 2007	0.370 (0.058, 0.681)	0.345 (0.028, 0.662)	0.324 (0.002, 0.646)	0.304 (-0.027, 0.634)	0.288 (-0.051, 0.629)	0.273 (-0.075, 0.625)
H	2005 - 2008	0.554 (0.267, 0.848)	0.535 (0.243, 0.834)	0.525 (0.224, 0.830)	0.521 (0.212, 0.833)	0.523 (0.204, 0.845)	0.528 (0.201, 0.860)
I	2006 - 2007	-0.544 (-0.917, -0.180)	-0.597 (-0.966, -0.233)	-0.648 (-1.018, -0.286)	-0.697 (-1.069, -0.329)	-0.744 (-1.120, -0.372)	-0.788 (-1.170, -0.408)
J	2006 - 2008	-0.360 (-0.714, -0.008)	-0.407 (-0.756, -0.058)	-0.447 (-0.794, -0.097)	-0.480 (-0.829, -0.129)	-0.509 (-0.862, -0.150)	-0.533 (-0.894, -0.164)
K	2007 - 2008	0.184 (-0.073, 0.437)	0.190 (-0.064, 0.442)	0.201 (-0.056, 0.456)	0.217 (-0.046, 0.477)	0.235 (-0.034, 0.502)	0.255 (-0.019, 0.529)
L	1 chick - 2 chicks	-0.055 (-0.091, -0.019)	-0.056 (-0.093, -0.020)	-0.057 (-0.094, -0.021)	-0.058 (-0.096, -0.021)	-0.059 (-0.097, -0.022)	-0.060 (-0.099, -0.022)
M	2 chicks - 3 chicks	-0.055 (-0.092, -0.018)	-0.056 (-0.093, -0.019)	-0.057 (-0.095, -0.020)	-0.058 (-0.096, -0.020)	-0.059 (-0.098, -0.020)	-0.060 (-0.099, -0.021)
N	3 chicks - 1 chick	0.110 (0.037, 0.184)	0.112 (0.038, 0.186)	0.114 (0.040, 0.189)	0.116 (0.042, 0.192)	0.118 (0.042, 0.195)	0.120 (0.042, 0.199)
O	a chick - b chick	0.010 (-0.145, 0.161)	-0.019 (-0.177, 0.136)	-0.046 (-0.209, 0.115)	-0.071 (-0.242, 0.098)	-0.094 (-0.273, 0.085)	-0.115 (-0.305, 0.074)
P	b chick - c chick	0.227 (0.063, 0.392)	0.248 (0.076, 0.421)	0.270 (0.088, 0.451)	0.291 (0.097, 0.484)	0.311 (0.105, 0.517)	0.331 (0.110, 0.550)
Q	sister - brother	-0.237 (-0.431, -0.042)	-0.229 (-0.429, -0.030)	-0.224 (-0.435, -0.015)	-0.220 (-0.444, -0.001)	-0.217 (-0.454, 0.015)	-0.215 (-0.466, 0.031)

Table 3-15 (continued)

Figure legend	Contrast	Y_{24}	Y_{25}	Y_{26}	Y_{27}	Y_{28}	Y_{29}
A	female - male	-0.036 (-0.185, 0.114)	-0.026 (-0.181, 0.130)	-0.016 (-0.178, 0.146)	-0.008 (-0.176, 0.161)	0.001 (-0.173, 0.175)	0.008 (-0.171, 0.188)
B	2004 - 2005	0.031 (-0.297, 0.355)	0.000 (-0.336, 0.333)	-0.031 (-0.376, 0.312)	-0.062 (-0.415, 0.291)	-0.091 (-0.454, 0.272)	-0.120 (-0.491, 0.252)
C	2004 - 2006	1.121 (0.748, 1.487)	1.118 (0.736, 1.493)	1.113 (0.724, 1.499)	1.108 (0.708, 1.503)	1.102 (0.691, 1.507)	1.097 (0.673, 1.511)
D	2004 - 2007	0.292 (0.017, 0.558)	0.250 (-0.030, 0.519)	0.209 (-0.075, 0.484)	0.171 (-0.118, 0.452)	0.135 (-0.158, 0.422)	0.101 (-0.197, 0.394)
E	2004 - 2008	0.569 (0.316, 0.817)	0.549 (0.289, 0.802)	0.531 (0.266, 0.790)	0.515 (0.244, 0.780)	0.500 (0.222, 0.769)	0.487 (0.204, 0.762)
F	2005 - 2006	1.090 (0.651, 1.519)	1.118 (0.666, 1.559)	1.144 (0.679, 1.603)	1.170 (0.689, 1.644)	1.194 (0.696, 1.681)	1.216 (0.703, 1.722)
G	2005 - 2007	0.261 (-0.099, 0.621)	0.250 (-0.122, 0.620)	0.241 (-0.143, 0.622)	0.233 (-0.163, 0.624)	0.226 (-0.180, 0.626)	0.220 (-0.196, 0.631)
H	2005 - 2008	0.537 (0.198, 0.881)	0.549 (0.198, 0.904)	0.562 (0.200, 0.931)	0.576 (0.203, 0.956)	0.592 (0.207, 0.983)	0.607 (0.211, 1.010)
I	2006 - 2007	-0.829 (-1.220, -0.441)	-0.868 (-1.270, -0.471)	-0.904 (-1.319, -0.494)	-0.937 (-1.365, -0.513)	-0.968 (-1.406, -0.534)	-0.996 (-1.445, -0.547)
J	2006 - 2008	-0.552 (-0.924, -0.175)	-0.569 (-0.954, -0.179)	-0.582 (-0.978, -0.179)	-0.593 (-1.002, -0.175)	-0.602 (-1.023, -0.172)	-0.609 (-1.043, -0.165)
K	2007 - 2008	0.277 (-0.004, 0.558)	0.299 (0.010, 0.586)	0.321 (0.025, 0.615)	0.344 (0.039, 0.647)	0.365 (0.054, 0.678)	0.387 (0.067, 0.707)
L	1 chick - 2 chicks	-0.061 (-0.101, -0.022)	-0.062 (-0.103, -0.022)	-0.063 (-0.105, -0.022)	-0.064 (-0.107, -0.021)	-0.065 (-0.108, -0.021)	-0.065 (-0.110, -0.021)
M	2 chicks - 3 chicks	-0.061 (-0.101, -0.021)	-0.062 (-0.103, -0.021)	-0.063 (-0.105, -0.021)	-0.063 (-0.107, -0.020)	-0.064 (-0.108, -0.020)	-0.065 (-0.110, -0.020)
N	3 chicks - 1 chick	0.122 (0.043, 0.202)	0.124 (0.043, 0.206)	0.126 (0.043, 0.209)	0.127 (0.042, 0.213)	0.129 (0.042, 0.217)	0.131 (0.041, 0.220)
O	a chick - b chick	-0.134 (-0.335, 0.064)	-0.152 (-0.364, 0.057)	-0.168 (-0.391, 0.052)	-0.183 (-0.418, 0.048)	-0.196 (-0.442, 0.044)	-0.208 (-0.464, 0.042)
P	b chick - c chick	0.349 (0.115, 0.582)	0.366 (0.120, 0.614)	0.382 (0.124, 0.644)	0.397 (0.127, 0.673)	0.411 (0.128, 0.697)	0.424 (0.130, 0.719)
Q	sister - brother	-0.214 (-0.478, 0.046)	-0.214 (-0.491, 0.060)	-0.214 (-0.507, 0.074)	-0.214 (-0.521, 0.087)	-0.215 (-0.533, 0.098)	-0.216 (-0.543, 0.109)

Table 3-15 Numerical differences of growth curves of tarsus length in Figure 3-4

Figure legend	Contrast	Y_{30}	Y_{31}	Y_{32}
A	female - male	0.015 (-0.168, 0.200)	0.022 (-0.166, 0.210)	0.028 (-0.165, 0.219)
B	2004 - 2005	-0.147 (-0.527, 0.234)	-0.172 (-0.563, 0.219)	-0.196 (-0.597, 0.204)
C	2004 - 2006	1.091 (0.658, 1.517)	1.085 (0.641, 1.521)	1.079 (0.627, 1.524)
D	2004 - 2007	0.069 (-0.234, 0.368)	0.040 (-0.268, 0.343)	0.012 (-0.301, 0.322)
E	2004 - 2008	0.476 (0.188, 0.756)	0.466 (0.172, 0.751)	0.457 (0.157, 0.748)
F	2005 - 2006	1.238 (0.710, 1.758)	1.257 (0.714, 1.794)	1.276 (0.718, 1.826)
G	2005 - 2007	0.216 (-0.210, 0.637)	0.212 (-0.223, 0.643)	0.208 (-0.234, 0.650)
H	2005 - 2008	0.623 (0.218, 1.036)	0.638 (0.223, 1.061)	0.653 (0.229, 1.086)
I	2006 - 2007	-1.022 (-1.481, -0.562)	-1.046 (-1.514, -0.575)	-1.067 (-1.546, -0.588)
J	2006 - 2008	-0.615 (-1.059, -0.160)	-0.619 (-1.077, -0.155)	-0.623 (-1.093, -0.148)
K	2007 - 2008	0.407 (0.080, 0.735)	0.426 (0.091, 0.760)	0.445 (0.101, 0.785)
L	1 chick - 2 chicks	-0.066 (-0.111, -0.021)	-0.067 (-0.113, -0.021)	-0.067 (-0.114, -0.021)
M	2 chicks - 3 chicks	-0.066 (-0.112, -0.020)	-0.067 (-0.113, -0.020)	-0.067 (-0.115, -0.020)
N	3 chicks - 1 chick	0.132 (0.041, 0.223)	0.133 (0.040, 0.226)	0.135 (0.040, 0.229)
O	a chick - b chick	-0.219 (-0.483, 0.040)	-0.229 (-0.501, 0.038)	-0.238 (-0.519, 0.036)
P	b chick - c chick	0.436 (0.132, 0.740)	0.446 (0.133, 0.758)	0.456 (0.132, 0.775)
Q	sister - brother	-0.216 (-0.553, 0.119)	-0.217 (-0.563, 0.129)	-0.218 (-0.572, 0.138)

Appendix

Priors for models in step 1

I used a t distribution as priors for parameters (β_1, β_2, $sigma_{ind}$, $sigma_{nest}$) in the model described in the step1 (Gelman 2020). Specifically, coefficients β_1 and β_2 were assumed to follow a t distribution with degree of freedom nu = 5, mean = 0, and scale sigma = 3 (Stan Development Team 2018). The standard deviation $sigma_{ind}$, $sigma_{nest}$ and $sigma_{error}$ of the normal distributions were also assumed to follow a t distribution with degree of freedom nu = 5, mean = 0, and scale sigma = 3.

Priors for models in step 2

I used a t-distribution and a normal distribution as priors for regression coefficients (elements of α_0, α_1, α_2) in the model described in the step 2. To explain this precisely, I wrote down linear predictor $x_i\alpha_j$ (j = 0, 1, 2) in the models:

$\log(\beta_0) = x_i\alpha_0 + ind_i + nest_i = \alpha_{00} + \alpha_{01}Sex + \alpha_{02}Year2005 + \alpha_{03}Year2006 + \alpha_{04}Year2007 + \alpha_{05}Year2008 + \alpha_{06}Brood + \alpha_{07}OrderB + \alpha_{08}OrderC + \alpha_{09}Older$

$\log(\beta_j) = x_i\alpha_j = \alpha_{j0} + \alpha_{j1}Sex + \alpha_{j2}Year2005 + \alpha_{j3}Year2006 + \alpha_{j4}Year2007 + \alpha_{j5}Year2008 + \alpha_{j6}Brood + \alpha_{j7}OrderB + \alpha_{j8}OrderC + \alpha_{j9}Older$ (j = 1, 2)

Note that α_{j0} is an intercept and therefore $\exp(\alpha_{j0})$ determines the base-line value of β_j without any fixed effects and random effects. Because values of β_j without any effects are already estimated from the models in the step 1, I used information of the posterior distribution of β_j estimated in the step 1 for priors of the models in the step 2. That is, I assumed α_{j0} to follow a normal distribution with a mean = "mean of posterior distribution of $\log(\beta_j)$ in the step 1 model" and standard deviation = "standard deviation of posterior distribution of $\log(\beta_j)$ in the step 1 model". On the other hand, regression coefficients α_{ji} (i = 1, …, 9) were assumed to a follow t distribution with degree of freedom nu = 5, mean = 0, and scale sigma = 3.

I also used information of posterior distribution of $sigma_{ind}$, $sigma_{nest}$ and $sigma_{error}$ estimated in the step1 for priors of the models in the step 2. That is, I assumed standard deviation $sigma_{ind}$, $sigma_{nest}$ and $sigma_{error}$ to follow a normal distribution with mean = "mean of posterior distribution of focal sigma in the step 1 model" and standard deviation = "standard deviation of posterior distribution of focal sigma in the step 1 model". From my preliminary analyses, fitting speed improved by using these informative priors, but results were essentially unchanged compared to when I used uninformative priors.

WAIC and weight

From the model fitting results, I calculated WAIC and model weight which were used for model averaging. The definition of WAIC depends on the values of log likelihood of each data point (Vehtari et al. 2017). As Stan record the values, I can immediately obtain WAIC value through simple codes. After obtaining single WAIC value for each model, the weight of the model i was calculated following formula (11) in Dormann et al. (2018).

$$weight\ of\ model_i = w_i = \frac{e^{-0.5(WAICi - WAICmin)}}{\sum_{k=1}^{m} e^{-0.5(WAICk - WAICmin)}}$$

Using this model weight, model averaged value of statistics $\bar{T}$ was obtained by following formula:

$$\bar{T} = \sum_{k}^{m} w_k T_k$$

Here, T represents body size Y, asymptotic size A, day of inflection point IP_{day} and growth rate at the inflection point IP_{rate}.

Chapter 4

Distinctive features of the skull of the Ryukyu Scops Owl from Minami-daito Island, revealed by computed tomography scanning

Abstract
Morphological differentiation of island-dwelling organisms provides model systems for studying evolution. Computed tomography (CT) scanning is an entirely non-destructive technique that provides detailed three-dimensional (3D) images of physical structures. Geometric morphometrics has been increasingly used in avian morphology studies by analyzing 3D data obtained from CT scans. I used geometric morphometrics to evaluate the morphological details of the skulls of three, genetically distinct, island populations of the Ryukyu Scops Owl *Otus elegans*: *O. e. elegans* from the northern part of the Ryukyu Archipelago, *O. e. elegans* from the southern part of the Ryukyu Archipelago, and *O. e. interpositus* from Minami-daito Island. Skulls were scanned using an X-ray CT system and the digitized 3D coordinates of 16 landmarks for each skull were analyzed in order to describe geometric morphometric features. *O. e. interpositus* was found to have a significantly smaller skull than either population of *O. e. elegans*. From principal component analysis of shape variation, I also found that the skull shape of *O. e. interpositus* differed significantly from both the northern and southern groups of *O. e. elegans*. This difference was in terms of PC1, which mainly represented relative anteroposterior length, and angle of the orbit. I inferred that the small skull of *O. e. interpositus* is partly a consequence of the particular founders of the population, or evolutionary selection that has taken place on Minami-daito Island and that the distinctive shape of the skull of *O. e. interpositus* is partly a consequence of adaptations for foraging efficiency, or of morphological integration.

Introduction

Morphological features of organisms can reflect their evolutionary histories. In addition, population differentiation between islands can provide model systems for studying evolution (Santos et al. 2016a). Classic studies of evolutionary biology have focused on the morphology of island birds, such as Darwin's Finches (Geospizinae) (Grant and Grant 2008) and the Hawaiian Honeycreepers (Drepanididae) (Pratt 2005). Herrel et al. (2007) suggested that the internal cranial skeleton has crucial importance in both ecological and behavioral contexts. Therefore, I considered that evaluating the differentiation of skulls between populations of island birds has the potential for providing insights into the ways in which ecological and behavioral factors affect evolution.

The Ryukyu Scops Owl *Otus elegans* is an island species with a very restricted range of no more than 1,000 km from north to south. It is mainly distributed throughout the Ryukyu Archipelago of Japan, a small island off southeast Taiwan, and south to small islands north of Luzon, Philippines (Ornithological Society of Japan 2012; Takagi et al. 2015; Gill & Donsker 2017). Four subspecies are currently recognised: *O. e. elegans, O. e. interpositus, O. e. botelensis*, and *O. e. calayensis* (Gill and Donsker 2017). Two subspecies occur in Japan: nominate *O. e. elegans*, which occurs widely on the continental islands of the Ryukyu Archipelago, and the isolated *O. e. interpositus*, which is endemic to oceanic Minami-daito Island (Figure 4-1)

The current subspecific classification is mainly based on plumage characteristics (Kuroda 1923), but more recently, (Takagi 2011) revealed that the three populations, those on island groups north and south of the Kerama Gap, and those on Minami-daito Island (Figure 4-1) differed in their vocalisations. Features of their morphology seem to be largely attributable to their geohistorical isolation. A recent mitochondrial cytochrome c oxidase subunit I (COI) analysis has supported the subdivision of *O. e. elegans* into northern and southern populations (Saitoh et al. 2015). The genetic independence of the Minami-daito Island *O. e. interpositus* population has also been revealed by a STRUCTURE analysis (Pritchard et al. 2000) of microsatellite regions (Takagi & Saitoh unpublished data). Although their plumage, acoustic, and genetic characteristics have been described in the previous studies mentioned above, their internal morphology has never been described.

I used landmark-based geometric morphometrics to evaluate morphological variation in Computed tomography (CT) scanned skulls of the Ryukyu Scops Owl. CT scanning has become increasingly popular among natural science disciplines as it is entirely non-destructive and provides detailed three-dimensional (3D) images of structures (Matthews and Plessis 2016). The CT images allow us to manipulate, section, dissect and measure internal morphology as well as external morphology (Abel et al. 2012). This characteristic of CT scanning is a necessary property for obtaining internal morphological data of objects that must not be damaged or destroyed, such as precious museum specimens.

Landmark-based geometric morphometrics has been increasingly applied in a range of ornithological studies, such as those on the relationships between ecology and morphology (Kulemeyer et al. 2009; Bright et al. 2016; Matsui et al. 2016) and avian evolution (Bhullar et al. 2012, 2015). As traditional morphometrics is based on multivariate analysis of focused variables, such as linear measurements, ratios, angles, areas, and volumes, the results are restricted to those relevant to these *a priori* selected variables and their combinations (Mitteroecker and Gunz 2009). However, as landmark-based geometric morphometrics analyze Cartesian landmark coordinates (Mitteroecker and Gunz 2009), results can be drawn from any possible relative positioning of the landmarks. Therefore, landmark-based geometric morphometrics is superior to traditional morphometrics, in terms of finding unexpected morphological differences.

In this study, I explored the skull morphology of three different populations of the Ryukyu Scops Owl in order to establish whether any characteristics differ among them, and sought explanations for the differences I found.

Materials and Method

A total of 28 specimens were derived as follows: six (two males, one female, three of unknown sex) from the Ryukyu Archipelago north of the Kerama Gap; seven (two males, five of unknown sex) from the Ryukyu Archipelago south of the Kerama Gap; and 15 (seven males, four females, four of unknown sex) from Minami-daito Island. Twenty of the specimens were dry museum skins and eight were frozen bodies; 20 were adult, one was a yearling, and seven were of unknown age. All of the specimens of unknown age were sufficiently ossified to allow CT imaging: they were considered to be either yearlings or adults, not juveniles (see Table 4-1).

All 28 skulls were scanned using an X-ray CT system (La Theta LTC-100, Hitachi Aloka Medical, Tokyo, Japan) with slice thickness set to 0.2 mm. Superficial models of the skulls were reconstructed from their CT-data. The digitized 3D-coordinates of the 16 landmarks on the surfaces of model skulls were acquired by means of ImageJ 1.49 (Schneider et al. 2012) (Figure 4-2, Table 4-2). As avian adult neurocranium bones are fused (Zusi 1993), it proved difficult to place landmarks on skulls. Furthermore, some specimens had been damaged around the *foramen magnum* by taxidermists removing brain tissue from the cranium, making it difficult for us to put landmarks on the skull images. Accordingly, I chose 16 landmarks as a compromise between maximizing the number of landmarks and avoiding missing data, which emerged in the data of damaged specimens when I put landmarks around the *foramen magnum*. The geometric features of the skulls were summarized into landmark configurations.

In order to describe the geometric morphometric features of the skulls, first I captured size and shape variation from landmark configurations. Second, I compared skull size and shape between the three groups. Finally, I examined whether the differences found were explained by allometry or not.

Size and shape information were extracted from the original landmark dataset using Generalized Procrustes Analysis (GPA). GPA is based on a least-square approach that minimizes the distance between homologous landmarks by translating, scaling, and rotating the original landmark configurations (Slice 2007). The scaling factor extracted through GPA is called “centroid size”. The coordinates of the resulting centered, scaled, and rotated landmark configurations are called “Procrustes shape coordinates”. Size was represented in centroid size and shape by Procrustes shape coordinates. GPA was conducted using the *ProcGPA* function, implemented in R version 3.1.3 (R Core Team 2015) with the package *Morpho* (Schlager 2015).

To evaluate the significance of differences in skull centroid size, I used the Kruskal-Wallis test and the pairwise Wilcoxon rank sum test. Principal component analysis (PCA) summarized variation in Procrustes shape coordinates. First, major principal

components (PC), which explained more than 80% of total variance, were compared by MANOVA to compare PC scores among three groups. Subsequently, the significance of the difference in each PC score was assessed by ANOVA and pairwise t test if MANOVA indicated significance. Holm's correction for *P*-value adjustment (Holm 1979) was used for all ANOVAs and pairwise comparisons. Before all intergroup comparisons were made, I assessed sexual dimorphism using specimens from Minami-daito Island, as there were multiple samples of both sexes. As no sexual dimorphism either in centroid size or first major PCs of Procrustes shape coordinates was detected (see results), I conducted all analyses on pooled data without separating for sex. I also conducted all analyses without separating for age because all samples including unknown age were deemed to be yearling or adult. Sufficient ossification of yearlings, combined with knowing that the owls first commence breeding when yearlings, support the fact that yearlings have a full-grown skeleton and do not differ from adults. I excluded samples of juveniles because they may have different skull structure (Hogg 1980). Visualization of the deformation of skulls along PC axes was obtained from thin plate spline interpolation (Mitteroecker and Gunz 2009). All statistical analyses were conducted with R version 3.1.3. Calculation of thin plate spline interpolation was done using the *tps3d* function implemented in the R package *Morpho*. Deformed skulls were visualized and captured using MeshLab version 1.3.3 (Cignoni et al. 2008).

Explaining shape variation between the three groups by allometry requires one regression line that relates shape to size for the merged group. For the purpose of drawing this regression line, I adopted a procedure consisting of two steps. The first step involved fitting a regression line for each of the three groups. Depending on the results of the first step, I followed one of the following three sub-procedures in the second step: a) If no significant regression line was detected in any of the three groups, or detected for only one group, I conducted a regression analysis using merged data; b) If significant regression lines were obtained for at least two of the groups and these lines did not differ statistically from each other, I also conducted merged data analysis; c) If regression lines for at least two of the groups proved to be significantly different, pooled analysis was not justifiable, and not conducted.

I conducted Procrustes ANOVA (Goodall 1991) using the *procD.lm* function of R package *geomorph* (Adams and Otárola-Castillo 2013) in order to test the significance of regressions with a permutation test in the first step. In cases when significant regression lines were detected (i.e., cases (b) or (c) above), I aimed to test the homogeneity of slopes and intercepts using the *advanced.procD.lm* function of R package *geomorph*. To summarize variation in the Procrustes shape coordinates, which was not explained by the size factor, I performed PCA on the residual of the regression analysis of merged data. I used the same statistical procedures for analysing residual Procrustes shape coordinates as described above.

Results

Size difference

Centroid size did not differ significantly between males and females (Wilcoxon rank sum test, $n_1 = 7$, $n_2 = 4$, $W = 19$, $P > 0.05$), but differed significantly between the three population groups (Kruskal-Wallis test, $\chi^2_2 = 10.58$, $P < 0.01$). Pairwise Wilcoxon rank sum tests revealed that the centroid size of *O. e. interpositus* was significantly smaller than that of the northern ($n_1 = 15$, $n_2 = 6$, $W = 83$, adjusted $P < 0.05$, Figure 4-3) and that of the southern ($n_1 = 15$, $n_2 = 7$, $W = 85$, adjusted $P < 0.05$, Figure 4-3) groups of *O. e. elegans*. However, differences between the two groups of *O. e. elegans* ($n_1 = 6$, $n_2 = 7$, $W = 29$, $P > 0.05$, Figure 4-3) were not significant.

Shape difference

The first eight PCs in the original Procrustes shape coordinates explained 81.3% of the total shape variation (see Table 4-3 for detailed data). These PC scores did not differ significantly between males and females (MANOVA, $F_{8, 2} = 2.85$, Pillai Trace = 0.92, $P > 0.05$), but did differ significantly between the three regional groups (MANOVA, $F_{16, 38} = 2.96$, Pillai Trace = 1.11, $P < 0.01$). PC1, which explained 22.9% of total shape variation, showed a significant difference among the three groups (ANOVA, $F_{2, 25} = 39.32$, $P < 0.01$, Table 4-3, Figure 4-4). With the exception of PC1, none of the other major PCs differed significantly between the three groups (see Table 4-3 for detailed results of ANOVA). Further analysis was conducted only for PC1. The PC1 score of *O. e. interpositus* was significantly smaller than those of the northern (t-test, $t_{8.36} = 6.51$, $P < 0.001$) and the southern groups (t-test, $t_{10.37} = 7.28$, $P < 0.001$). The northern and southern groups of *O. e. elegans* did not differ from each other (t-test, $t_{10.79} = 0.43$, $P > 0.05$). Deformation of the average-shaped skull along the PC1 axis showed that PC1 mainly represented relative anteroposterior length and the angle of the orbit (Figure 4-4). In other words, birds belonging to *O. e. interpositus* have relatively short skulls with orbits positioned further forward than in other populations.

Allometry

I did not detect any significant regression lines for the three groups by multivariate regression analysis of Procrustes shape coordinates on log centroid size (permutation test; 10,000 permutations, $P > 0.05$ for all groups). I obtained a significant regression line when analyzing the merged data (permutation test; 10,000 permutations, $P < 0.001$). The first eight PCs from the PCA based on residual Procrustes shape coordinates explained 80.5% of the total shape variation (see Table 4-4 for detailed data). As none of these PC scores differed significantly between the three groups (MANOVA, $F_{16, 38} = 1.80$, Pillai Trace = 0.86, $P > 0.05$), I did not perform any subsequent ANOVAs for each PC.

Discussion

The objective of this research was to study, detect and evaluate any differences between

the skulls of three geographically separated populations of the Ryukyu Scops Owl, to infer causal factors for any differences, and to propose explanations for how differences might have evolved. Analyses revealed differences both in size and shape between *O. e. interpositus* and *O. e. elegans*. Multivariate regression of Procrustes shape coordinates on the logarithm of centroid size for each group did not indicate significant allometric relationships. However, regression analysis of a merged group provided significance. Analyses based on residual Procrustes shape coordinates did not indicate subspecific shape differences.

Pairwise comparisons revealed that centroid size differed between *O. e. interpositus* and *O. e. elegans*. I inferred that small skull size on the small (ca. 30 km^2), isolated, oceanic Minami-daito Island might be partly attributable to founder effects. A STRUCTURE analysis of microsatellite regions (Takagi & Saitoh unpublished data) suggests that the population on Minami-daito Island was founded by individuals from the population on Okinawa Island, which is included within the northern group of *O. e. elegans*. Our results showed that some individual *O. e. elegans* had skulls as small as those of *O. e. interpositus* (Figure 4-3), and I propose that founders reaching Minami-daito Island may have had such characteristics. Conversely, however, other evolutionary selection processes may have favored small skull size on Minami-daito Island after initial arrival. Clegg and Owens (2002) discussed how the effects of changes in feeding ecology, intraspecific competition, energetic constraints and physiological optimization in birds on small islets seem to have an important role in size evolution. However, as yet I do not have data supporting or confirming either perspective.

Principal component analysis revealed that cranial shape also differed substantially between *O. e. interpositus* and *O. e. elegans*, for which there seem to be three possible explanations. The first possibility is allometry, one of the factors causing morphological variation among organisms that differ in body size (Mitteroecker et al. 2013). The results of the PCA of residual Procrustes shape coordinates suggest the possibility that variation between subspecies can be simply explained as an allometric effect of skull size. The disappearance of significance of PC1, after controlling for size, suggest that the PC1 of original Procrustes shape coordinates mainly represents allometric variation in the data. Actually, allometry is the most dominant factor of shape and form variation (Mitteroecker et al. 2013). However, explanation by allometry requires careful interpretation of results, because multivariate regressions in each group did not indicate significant allometric relationships. If each group actually has a different regression line, then multivariate regression analysis for merged data is not justified and I need a different explanation, such as that offered below.

The second possibility is that adaptation to foraging behaviour using binocular vision has occurred. Orientation of the orbits may be related to variation in the visual field (Heesy 2004; Fernández-Juricic et al. 2008), which may reveal a trade-off relationship between foraging and predator detection (Martin 2014). Hunting owls swing their feet up into the area of binocular vision just prior to prey capture (Martin 2007). Although

forward positioned eyes increase accuracy during this prey capturing behavior, such positioning decreases lateral vision rendering the hunting owl more susceptible to predators attacking from the side. Potential nocturnal predators, such as *Protobothrops* snakes, do not occur on oceanic Minami-daito Island, whereas they do occur on almost all of the other continental islands in the Ryukyu Archipelago. Adaptations among the owls on Minami-daito Island might have led to them having eyes positioned further forward thus increasing their hunting accuracy. To verify this trade-off relationship, future studies should include analysis of morphometric data in relation to the presence or absence of predators on each island. Quantitative evaluation of visual fields is also desirable (i.e., Fernández-Juricic et al. 2008; Martin and Piersma 2009).

The third explanation for the difference in skull shape is morphological integration. Each part of the skull is integrated with other parts because they develop, function, and evolve together (Klingenberg 2013). The observed shape difference may result from such covariation of skull parts. In other words, part of the observed variation may be caused by variation in other parts, i.e. variation that is explained by other factors such as adaptation. In this study, I was compelled to adopt a small number of landmarks due to the limitation of the material properties of the specimens (as described above). To accurately evaluate shape covariation among parts, many more landmarks including semi-landmarks are needed (Kulemeyer et al. 2009; Mitteroecker et al. 2013).

This study has shown that two subspecies of Ryukyu Scops Owl exhibit substantially different skull size and shape. Such differences may be explained by allometry, adaptation, or morphological integration. However, the variation detected should be interpreted carefully. The results are based on a relatively small sample size including individuals of unknown sex. A larger sample with sexed specimens would help to improve our understanding of their morphological evolution.

Figure

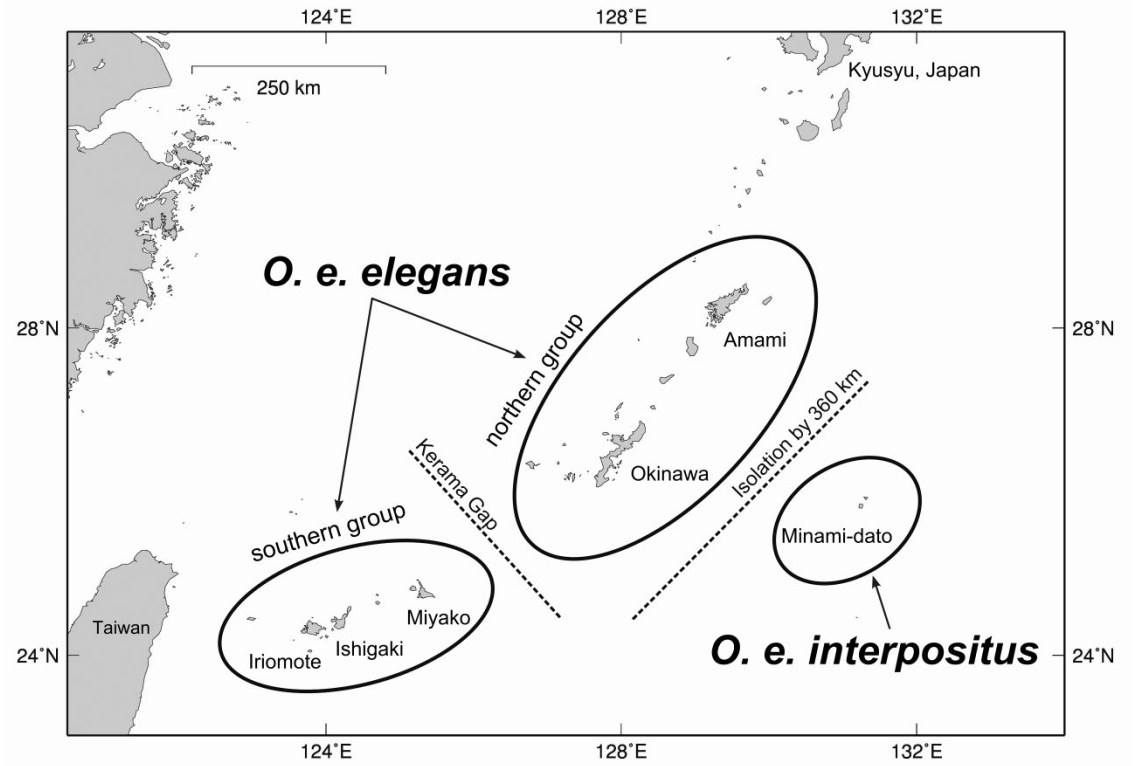


Figure 4-1

Three groups of the Ryukyu Scops Owl, the northern and southern groups, and Minami-daito Island, based on genetic analyses (Saitoh et al. 2015; Takagi & Saitoh in preparation). Ovals show the three groups; the dotted line indicates the Kerama Gap. The Kerama Gap geographically divides subspecies *O. e. elegans* into northern and southern groups. *O. e. interpositus*, isolated on Minami-daito Island, is separated by 360 km from Okinawa, the nearest island.

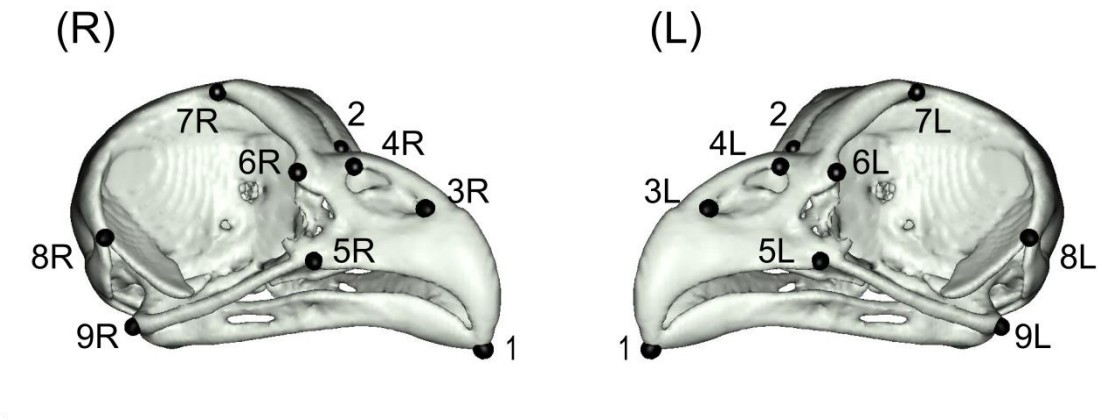


Figure 4-2
Landmarks (black dots) on right (R) and left (L) hemispheres of a Ryukyu Scops Owl skull.

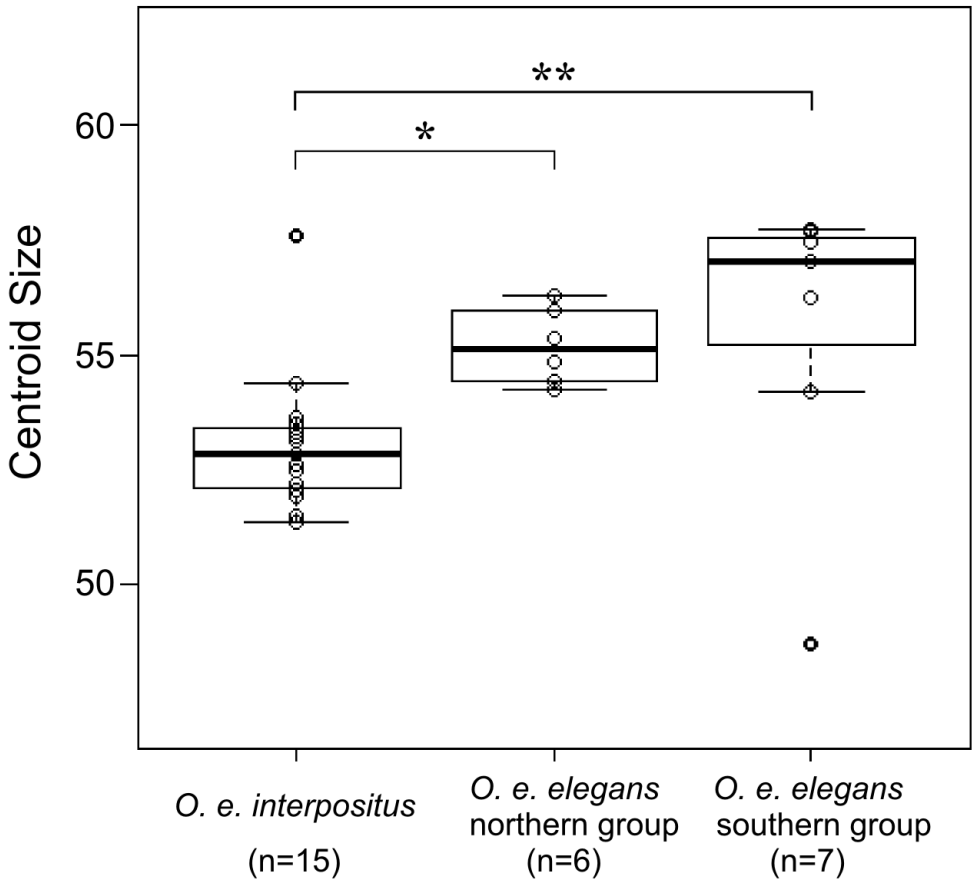


Figure 4-3
Comparison of centroid size between three groups of Ryukyu Scops Owls. *P < 0.05, **P < 0.01

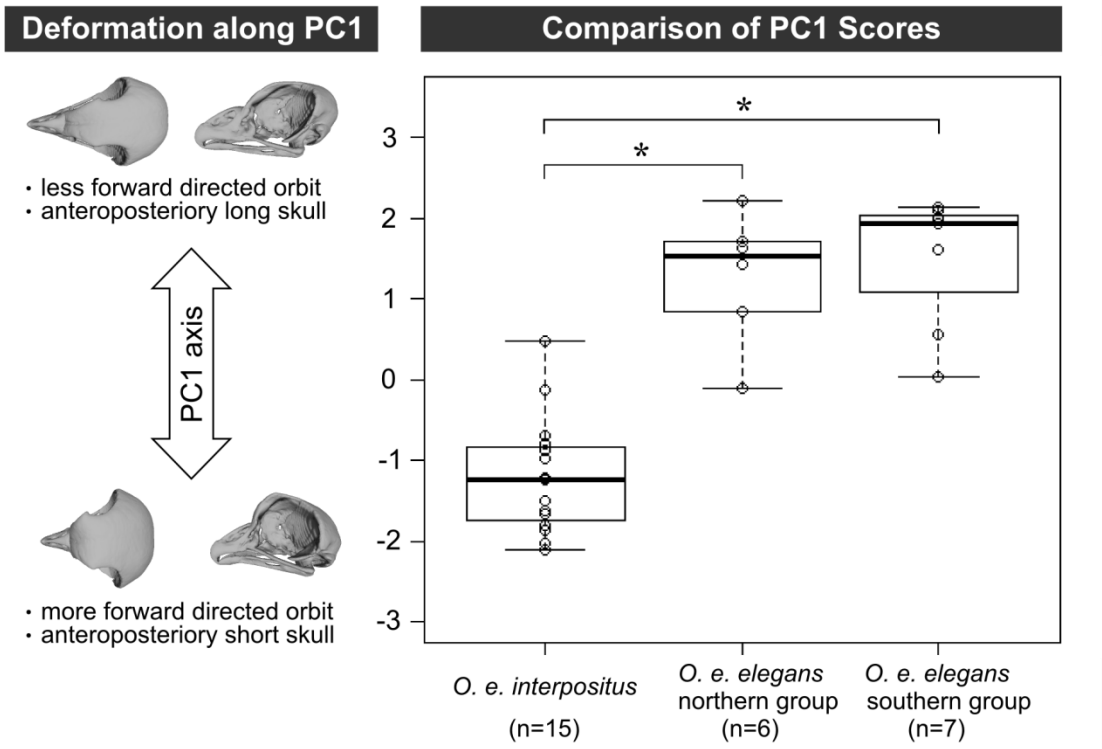


Figure 4-4

Comparison of PC1 score of original Procrustes shape coordinates and deformation of the skull along the PC1 axis in the Ryukyu Scops Owl. *P < 0.001. Landmarks on average shaped skulls were moved along the PC1 axis so that the resultant landmark configuration has a mean + 4SD PC1 score (upper row) or mean -4SD PC1 score (lower row). Each skull is expressed as a vector whose components are coordinates of landmarks on the skull. PC score consists of a linear combination of coordinates of landmarks. Therefore, moving landmarks on a skull, i.e. adding a vector to the vector of coordinates of landmarks, causes changes in PC scores of the skull. Actually, adding a scaled eigenvector of PCA can increase or decrease the corresponding PC score. Extent of the change depends on the scaling factor (see Appendix of Mitteroecker et al. 2013). The remaining surface of an average shaped skull was deformed by thin plate spline interpolation in accordance with the changes in the landmark positions. Deformed skulls are shown from lateral (right) and dorsal views (left).

Table

Table 4-1 Ryukyu Scops Owl specimens examined in this study

Specimen No.	Owner	Island	Subspecies	Group	Sex	Stage	State
YIO-19205	YIO	Minami-daito	*interpositus*		Female	Unknown	Museum skin
YIO-19207	YIO	Minami-daito	*interpositus*		Male	Unknown	Museum skin
YIO-19208	YIO	Minami-daito	*interpositus*		Female	Unknown	Museum skin
YIO-19210	YIO	Minami-daito	*interpositus*		Male	Unknown	Museum skin
YIO-19216	YIO	Okinawa	*elegans*	northern	Male	Adult	Museum skin
YIO-19229	YIO	Iriomote	*elegans*	southern	Unknown	Adult	Museum skin
YIO-62371	YIO	Ishigaki	*elegans*	southern	Unknown	Unknown	Museum skin
YIO-64984	YIO	Iriomote	*elegans*	southern	Unknown	Adult	Museum skin
2004-0129	YIO	Iriomote	*elegans*	southern	Unknown	Unknown	Frozen body
2015-1084	YIO	Minami-daito	*interpositus*		Female	Adult	Museum skin
2015-1086	YIO	Minami-daito	*interpositus*		Male	Adult	Museum skin
2015-1087	YIO	Minami-daito	*interpositus*		Unknown	Adult	Frozen body
2015-1089	YIO	Minami-daito	*interpositus*		Unknown	Adult	Frozen body
2015-1092	YIO	Minami-daito	*interpositus*		Unknown	Adult	Frozen body
2015-1093	YIO	Minami-daito	*interpositus*		Female	Yearling	Museum skin
2015-1094	YIO	Minami-daito	*interpositus*		Male	Adult	Frozen body
2015-1104	YIO	Minami-daito	*interpositus*		Unknown	Adult	Frozen body
2015-1105	YIO	Minami-daito	*interpositus*		Male	Adult	Museum skin

Table 4-1 (continued)

Specimen No.	Owner	Island	Subspecies	Group	Sex	Stage	State
2015-1106	YIO	Minami-daito	interpositus		Male	Adult	Frozen body
2015-1110	YIO	Minami-daito	interpositus		Male	Adult	Frozen body
NSMTA-13193	NMNS	Iriomote	*elegans*	southern	Unknown	Unknown	Museum skin
NSMTA-17395	NMNS	Okinawa	*elegans*	northern	Male	Adult	Museum skin
NSMTA-17402	NMNS	Okinawa	*elegans*	northern	Female	Adult	Museum skin
NSMTA-17501	NMNS	Amami	*elegans*	northern	Unknown	Adult	Museum skin
NSMTA-17504	NMNS	Amami	*elegans*	northern	Unknown	Adult	Museum skin
NSMTA-17511	NMNS	Amami	*elegans*	northern	Unknown	Adult	Museum skin
NSMTA-17615	NMNS	Iriomote	*elegans*	southern	Male	Adult	Museum skin
NSMTA-17616	NMNS	Iriomote	*elegans*	southern	Male	Adult	Museum skin

Abbreviations: YIO, Yamashina Institute for Ornithology; NMNS, National Museum of Nature and Science.

Table 4-2 Landmarks on the skull of the Ryukyu Scops Owl

Landmark No.	description
1	tip of premaxillary
2	midpoint of craniofacial hinge
3L/3R	maximum curvature point of anterior end of left/right nares
4L/4R	maximum curvature point of posterior end of left/right nares
5L/5R	left/right attachment point of jugal and maxillary
6L/6R	outermost point of left/right lacrimal
7L/7R	tip of left/right dorsal process on orbit
8L/8R	diverging point of left/right postorbital process and tympanic wing
9L/9R	outermost point of left/right quadrate

Description follows nomenclature used in Zusi (1993).
Landmark No. corresponds to Figure 4-2.

Table 4-3 Results of the principal component analysis (PCA) on original Procrustes shape coordinates and the analysis of variance (ANOVA)

Principal component	Explained variance (%)	Cumulative explained variance (%)	ANOVA		
			$F_{2, 25}$	P	Significance
PC1	22.9	22.9	39.32	0.000	*
PC2	16.6	39.5	0.01	0.995	
PC3	13.8	53.3	0.46	0.637	
PC4	8.0	61.3	3.31	0.053	
PC5	7.0	68.3	0.51	0.608	
PC6	5.4	73.7	0.06	0.947	
PC7	4.3	78.1	0.18	0.838	
PC8	3.2	81.3	0.64	0.536	

Significance: * $P < 0.01$ after Holm's P-value correction

Table 4-4 Results of the principal component analysis (PCA) on residual Procrustes shape coordinates and the analysis of variance (ANOVA)

Principal component	Explained variance (%)	Cumulative explained variance (%)	ANOVA		
			$F_{2, 25}$	P	Significance
PC1	19.8	19.8	2.98	0.069	
PC2	15.8	35.6	2.43	0.108	
PC3	14.1	49.7	2.53	0.100	
PC4	8.9	58.6	3.44	0.048	
PC5	7.9	66.5	0.51	0.606	
PC6	5.6	72.1	0.22	0.807	
PC7	4.8	76.9	0.23	0.797	
PC8	3.6	80.5	0.68	0.519	

Significance: * $P < 0.05$ after Holm's P-value correction

Chapter 5

Decomposing vocal variation of the Ryukyu Scops Owl

Abstract
Relative importance of the factors contributing the vocal variation in owls are not known, despite plentiful studies on their vocalization. I decomposed variation in vocal characteristics of the Ryukyu Scops Owls using a data set of 205 individuals from 16 island populations. A quarter of the total variation was attributed to between-island and three quarters were to within-island. Effects of environment, geographic isolation, neutral genetic variation and body size account for the 69%, 75%, 44% and 54% of the between-island variation, respectively, with considerable overlaps of the effects.

Introduction

Existence of variation within a population is an important assumption in evolution, because selections works by fitness variation between individuals depending on their genotypes (Endler 1986; Lynch and Walsh. 1998). On the other hand, existence of variation between populations is an indicative of neutral process or selection pressures contributing the differentiation (Walsh and Lynch 2018). Therefore, recognizing the variation is one of the most fundamental but important task for evolutionary biology.

Which traits became under the selection pressures depend on ecological background of the organisms (Endler 1992). Owls would be the one of the most studied animals whose characteristics suggest strong selection pressures or adaptation to become nocturnal aerial predators. Large front-facing eyes, asymmetrical ear openings and fluffy feathers are suggesting their adaptation to hunting in the night (König and Weick 2008). Apart from these structural characteristics, their diverse vocalization is also suggested as an outcome of adaptation to nocturnality (König and Weick 2008). Previous studies on vocalization of owls have documented geographic variation (Galeotti et al. 1996; Takagi 2011; Odom and Mennill 2012), individuality (reviewed in Terry et al. 2005) and functionality (Appleby and Redpath 1997; Galeotti 1998; Penteriani 2002; Hardouin et al. 2009). Although these studies collectively and convincingly suggest their vocalization is under the control of selection pressures, relative importance of the factors generating their vocal variation is rarely focused on.

This study focuses on the Ryukyu Scops Owl *Otus elegans*, an owl species whose vocalization is well-documented. The owls occur through the islands from the Okinoshima Island in Japan to the Batanes and Babuyan Islands in the northern Philippines (Warburton 2009; Ornithological Society of Japan 2012; Takagi et al. 2015; Gill and Donsker 2019). Takagi (2011) previously found significant vocal differences among the island populations and suggested the contribution of neutral processes

(vicariance and dispersal) to the differentiations. On the other hand, the owls intensively use vocal contest when they claim their territories (Severinghaus 2000; Takagi 2020) and males and females shows duet calls even in non-breeding seasons at least in the population of the Minami-daito Island (Sawada unpublished data), suggesting the functional processes are also involved in their vocal variation. The aim of this study is two-folded: 1) Decomposing the vocal variation into between-island variation and within-island variation. 2) Further decomposing the two variations by possible origins of the variations, such as environment, geography, genetic differentiation and body size.

Material and Methods

Material

The Ryukyu Scops Owl is a small owl weighing about 90 g (Akatani et al. 2011). They are territorial and monogamous with pair bond lasting multiple years (Hsu et al. 2006a; Akatani et al. 2011; Bai and Severinghaus 2012). Four subspecies are known: nominate *elegance* on the Okinoshima Island and the Ryukyu Archipelago (Ornithological Society of Japan 2012; Takagi et al. 2015; Inoue et al. 2019), *interpositus* on the Minami-daito Island (Takagi et al. 2007a), *botelensis* on the Layu Island (Severinghaus and Rothery 2001), *calayensis* on some islands of the northern Philippines (Warburton 2009).

Vocalization

Vocalization data used in this study was based on vocal records collected by Masaoki Takagi. The data consists of hoot recordings of 205 male Ryukyu Scops Owls, from 16 islands across the Ryukyu archipelago (Figure 5-1): Okinoshima, Nakanoshima, Amami-Oshima, Tokunoshima, Okinawa, Minami-daito, Iheya, Izena, Kume, Zamami, Miyako, Irabu, Ishigaki, Hateruma, Iriomote, Yonaguni. The recordings were done from 2011 to 2016 by Marantz PMD 660 or 670 solid-state recorders (D&M Holdings Inc., Tokyo, Japan) and Audio-Technica AT4073A directional microphones (Audio-Technica Corporation, Tokyo, Japan). A hoot of the owl consists of two syllables (Takagi 2011). By spectrographic analysis, he extracted five variables from single hoot: Int (interval between two syllables), Freq1 (maximum frequency in the first syllable), Freq2 (maximum frequency in the second syllable), Du1 (duration of the first syllable), Du2 (duration of the second syllable) (Takagi 2011). Mean values of these variables across 10 successive hoots were used. Geographic locations of recording site in Universal Transversal Mercator (UTM) coordinate system were obtained for each individual. For further information on field procedures to the vocal data collection, see (Takagi 2011, 2013).

Body size measurement

Morphometric data of the 205 individuals used in this study was also collected by Masaoki Takagi. These data were obtained when he captured owls immediately after the vocal recordings. Eight variables were recorded: tarsus length, culmen length, bill depth,

bill width, head length, wing length, tail length, body mass (Table 5-1). Mean values of two measurements were used. For further information on the field procedures of the morphometric data collection, see Sawada et al. (2021b).

Microsatellite

Eleven microsatellite loci were genotyped for the 205 individuals. The loci typed are Oe085, Oe022, Oe081, Oe129, Oe171, Oe084, Oe3-7, Oe045, Oe029, Oe149, Oe128 (Hsu et al. 2003, 2006b). I followed the genotyping procedures described in Sawada et al. (2018a). I did not perform any test of linkage disequilibrium or Hardy Weinberg equilibrium here, because analyses in below does not need assumptions about them.

Statistical analysis

To decompose and explain variations in the vocal characteristics, this study analyzed the vocal data with the multiple explanatory variables by redundancy analysis (RDA). RDA is a multivariate analysis which combines multiple regression and principal component analysis (PCA) (Legendre and Legendre 1988). Response variable matrix Y is firstly regressed on Explanatory variable matrix X, and matrix of fitted value Y_{hat} (= Xβ) and residual value Y_{res} (= Y - Y_{hat}) is obtained. Secondly, PCA is applied to Y_{hat}, and summarizes variation in Y which is explained by X. Resultant extracted axes are referred to RDA1, RDA2, and so on. Thirdly, PCA is applied to Y_{res}, and summarizes variation in Y which is not explained by X. Resultant extracted axes are referred to PC1, PC2, and so on. Based on the decomposition of Y = Y_{hat} + Y_{res}, and independence between Y_{hat} and Y_{res}, total variation of the RDAs (often called as constrained variance) and total variation of the PCs (often called as unconstrained variance) sum up to total variation of Y. Below, I describe data matrixes Y and X which were used in this study.

(a) Response variables Y

Response variable matrix Y was a matrix which included data on five vocal characteristics: Int, Freq1, Freq2, Du1, Du2 (Figure 2 of Takagi 2011).

(b) Explanatory variables X

For the purpose of subsequent analysis, I prepared five matrixes X_{isl}, X_{env}, X_{body}, X_{geo} and X_{genet} as explanatory variable matrixes. X_{isl} is a 1-column matrix which contains island names of sampling location. X_{env} is a six-column matrix which contains Elevation, Slope, Annual precipitation, Annual average temperature, Annual total day length, Annual average total solar radiation of sampling location. These data were extracted from GIS data available at a website of Ministry of Land, Infrastructure, Transport and Tourism, Japan (Table 5-2). X_{body} is an eight-column matrix of which columns are all principal components of a PCA applied to a matrix containing body size measurement data. X_{genet} is a 48-column matrix of which columns are the first 50 principal components of a PCA applied to a matrix containing microsatellite genotypes. In the original matrix containing

microsatellite genotypes, rows represent individuals and columns represent alleles. If an individual has an allele, corresponding element of the matrix is 1 and otherwise 0. I used the first 48 PCs as these accounted for more than 90% of the variance in the genotype data. X_{geo} is a five-column matrix of which columns are the first five Moran's eigen vector map (MEM) of a matrix containing sampling locations. By using MEMs, instead of original geographic coordinates, as explanatory variables, regression models become able to grasp complex spatial pattern (Dray et al. 2006). For examples, linear regression on latitude and longitude implicitly assume linear spatial pattern along latitude and longitude. However, as MEMs takes more various value on the network of sampling locations, regression on MEMs can deal with non-linear spatial pattern among sampling locations. I used the first five MEMs because these had significant spatial autocorrelation, which was confirmed by *moran.randtest* in *adespatial* (Dray et al. 2019).

(c) Redundancy analysis

I took three steps to analyse vocal variation. First, I conducted an RDA with response variable Y and explanatory variable X_{isl}. By doing this, between-island variation in the Y was obtained as Y_{hat}, and residual within island variation was obtained as Y_{res}. Significance of regression model was confirmed by *anova.cca* function. Proportion of variance in Y accounted for by X_{isl} was determined by adjusted R^2 statistic.

Second, I conducted an RDA with response variable Y_{hat} and explanatory variable X_{env}, X_{geo}, X_{genet} and X_{body}. By doing this, between-island components extracted as Y_{hat} was further decomposed into the combination of effects of environment (X_{env}), geographic isolation (X_{geo}), neutral genetic variation (X_{genet}), and body size (X_{body}). Significance of regression model was confirmed by *anova.cca* function. Proportion of variance in Y_{hat} accounted for by X_{env}, X_{geo}, X_{genet} and X_{body} was determined by variance partitioning implemented in *varpart* function.

Third, I conducted an RDA with response variable Y_{res} and explanatory variable X_{env}, X_{geo}, X_{genet} and X_{body}. By doing this, within-island components extracted as Y_{res} was further decomposed into the combination of effects of environment, geographic isolation, neutral genetic variation, and body size. Significance of regression model was confirmed by *anova.cca* function. Since the test did not confirm significant model fitting, variance partitioning was not conduced for Y_{res}.

Results

RDA with response variable Y and explanatory variable X_{isl} revealed significant between island difference in vocal characteristics (ANOVA, $F_{15, 189} = 5.61$, $P = 0.001$). Proportion of constrained and unconstrained variance were 0.31 and 0.69, respectively. Adjusted R^2 was 0.25. Thus, 25% of the total variation in vocal characteristics was attributed to between island differences and remaining 75 % was to within island differences.

RDA with response variable Y_{hat} and explanatory variable X_{env}, X_{geo}, X_{genet} and X_{body} revealed significant effect of these variables on between island difference in vocal

characteristics (ANOVA, $F_{65, 137} = 30.794$, $P = 0.001$). Proportion of constrained and unconstrained variance were 0.94 and 0.06, respectively. Adjusted R^2 was 0.91. Thus, 91% of between island variation in vocal characteristics was attributed to the effect of X_{env}, X_{geo}, X_{genet} and X_{body}. Results of variance partitioning shows relative contribution of these variables and their combinations (Figure 5-2). For examples, effects of the variables were: 69% for environment (X_{env}), 75% for geographic isolation (X_{geo}), 44% neutral genetic variation (X_{genet}), and 54% for body size (X_{body}). However, unique effects of the variables were: 5% for environment (X_{env}), 5% for geographic isolation (X_{geo}), 1% neutral genetic variation (X_{genet}), and 1% for body size (X_{body}), indicating considerable overlap of these effect.

RDA with response variable Y_{res} and explanatory variable X_{env}, X_{geo}, X_{genet} and X_{body} did not detect significant effect of these variables on within island difference in vocal characteristics (ANOVA, $F_{67, 137} = 0.846$, $P = 0.778$). Therefore, I did not further interpret contributions of the explanatory variables.

Discussion

This study confirmed previous results by Takagi (2011) that there are between island variations in vocalization of the Ryukyu Scops Owls. One of the progresses from the previous study is that I was able to estimate proportion of variance attributable to between-island and within-island: only 25% of the vocal variation was attributable to the between-island differences.

Among the between-island variation, 75% was accounted for by geographic location of islands. Because MEMs, which were used to describe spatial location, take spatially autocorrelated values on the networks of sampling locations (Dray et al. 2006), correlation between vocal characteristics and MEMs indicates that the between-island vocal variation corresponds to the geographic isolation between islands (i.e. isolation by distance). This is in accord with clinal pattern in the variation of vocal characteristic found by Takagi (2011). Among the between-island variation, 54 % were accounted for by body size. This indicates that body size difference between islands is contributing to the between-island difference in vocal characteristics.

Among the between-island variation, 69% was accounted for by environment. Although this result apparently indicates local adaptation of vocalization to environments (Podos and Warren 2007), some cautions are needed before reaching this conclusion. Firstly, 32% (overlap of Environment and Gene in Figure 5-2) out of the 69% were also accounted for by neutral genetic variation. That is, nearly half of the effect is attributable to neutral population genetic processes such as dispersal, bottleneck and genetic drift coincided with environment. Secondly, 55% (overlap of Environment and Geography in Figure 5-2) out of the 69% are also accounted for by geographic locations. This large amount of overlap would be due to confounding of difference in environment and geographic isolations. Excluding such overlapped part of variance, the proportion of the variance which is uniquely accounted for by environment was 5%. Therefore, the amount

of variance which could be attributed to local adaptation to the environment seems to be limited.

Finally, I discuss significance of the within-island variation. This study revealed the amount of the within-island variation to be 75% of the total variation. This indicates that large amount (nearly three quarters) of variation in vocal characteristic is due to the variation between individuals within a population, because variation within individual has been shown to be small by previous study (Takagi 2020). Although recording error also contribute to the 75%, its contribution would be also small because I used mean value of 10 successive hoots as data to minimize the errors. Such plentiful between-individual within-population variation provide a basis on which selection pressures can act. For example, vocal characteristics of the Common Scops Owls *Otus scops* contain cue of reproductive success and can become target of sexual selection (Hardouin et al. 2009). Long-term monitoring of the Ryukyu Scops Owls revealed their genetically based mate choice (Sawada et al. 2020). Vocal characteristic might be the traits which convey the information of genetic make-up of individuals to realize the mate choice.

Figure

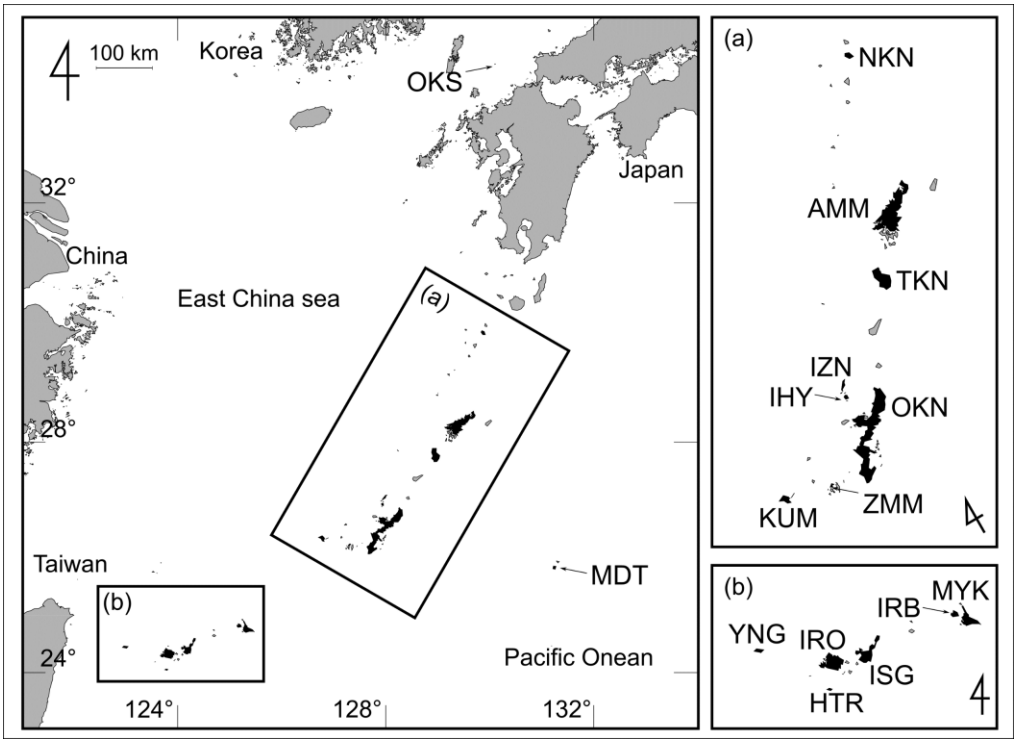


Figure 5-1

Map of the islands around the Ryukyu Archipelago. The islands involved in this study are coloured by black: Okinoshima (OKS), Nakanoshima (NKN), Amami-Oshima (AMM), Tokunoshima (TKN), Okinawa (OKN), Minami-daito (MDT), Iheya (IHY), Izena (IZN), Kume (KUM), Zamami (ZMM), Miyako (MYK), Irabu (IRB), Ishigaki (ISG), Hateruma (HTR), Iriomote (IRO), Yonaguni (YNG).

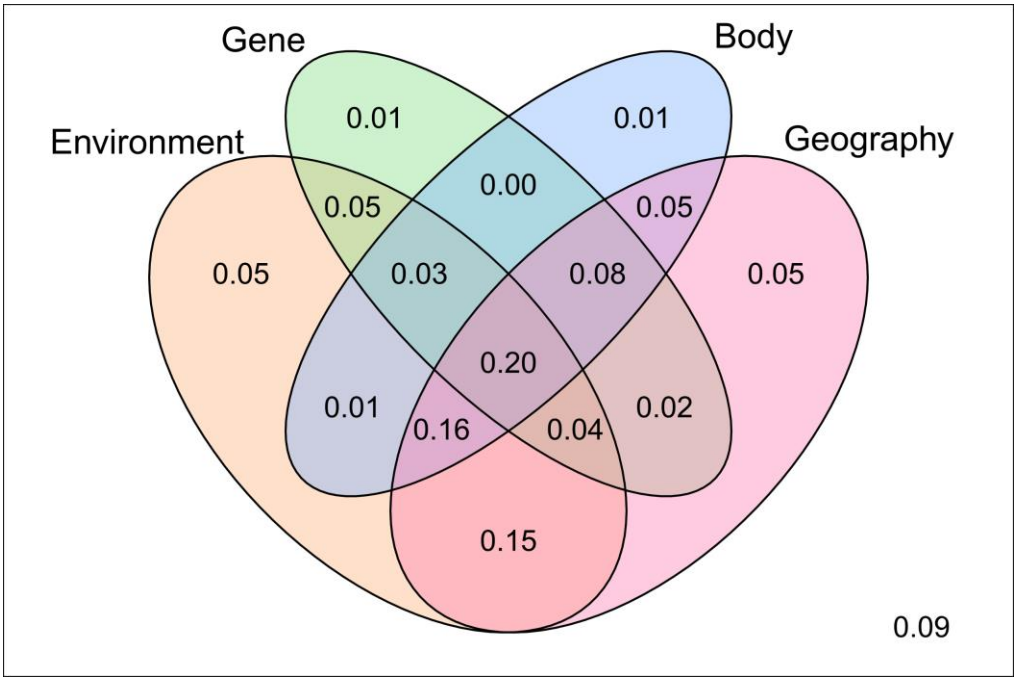


Figure 5-2
Venn's diagram showing the result of variance partitioning. Values are the proportions of variance (total = 1.00) which are accounted for by the factors contributing to each part.

Table

Table 5-1 Definition of the morphometric traits measured in this study

Trait	Definition
Body mass	body mass in mg
Tarsus length	from the base to the tip of the tarsometatarsus
Culmen length	from the base to the tip of the bill
Bill depth	height of the closed bill at the anterior end of nostril vertical to the gape
Bill width	width of the bill at the anterior end of nostril
Head length	from the back of the skull to the tip of the bill
Tail length	from the root to the tip of the central rectrix
Wing length	from the bend of the wing to the tip of the longest primary at an unflattened state

Table 5-2 Data source of explanatory variables for environment

Explanatory variables	Attribute code in source shape file
Elevation[*1]	G04d_002
Slope[*1]	G04d_010
Annual precipitation[*2]	G02_014
Annual average temperature[*2]	G02_053
Annual total day length[*2]	G02_071
Annual average total solar radiation[*2]	G02_084

*1: https://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G04-d.html (accessed on March 29, 2020). *2: https://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html (accessed on March 29, 2020)

Chapter 6

Size assortative mating in the Ryukyu Scops Owl on Minami-daito Island

Abstract
Accurate understanding of evolutionary phenomena involving size assortative mating needs elucidating generating mechanisms on which the assortment occurs. Although some mechanisms have been suggested, relative importance of them may be different across taxonomic groups. For example, male's preference for large fecund females and dominance of large males in the competition for females is suggested as a major mechanism for arthropods. However, raptors do not seem to conform to this theory, mainly because selection for smallness in males (assumed in theory of their reversed sexual size dimorphism) is opposite direction from the selection for largeness in males (assumed in theory of size assortative mating). I studied the generating mechanism of assortative mating in a long-term monitoring population of the Ryukyu Scops Owls *Otus elegans interpositus*. Significant assortative mating was found for culmen length and wing length. Statistical control of spatial and temporal accessibility of potential mates did not cancel the assortment. Furthermore, individuals with small wing length slightly increased fitness components. However, change in territory holders did not accompany body size differences between present and previous holders, suggesting non-significant contribution of body size on competitiveness. I propose active mate choice for small individuals is a likely explanation for the assortative mating in the owl population.

Introduction

There are often correlations in phenotypes between members of mated pairs, that is, assortative mating (Jiang et al. 2013). These correlations are derived from non-random mating with respect to the traits, due to various mechanisms (Crespi 1989). The traits ranged from external morphology or behaviours such as coloration, body size and aggressiveness to internal characteristics such as genotypes, metabolic state and intelligence (reviewed in Jiang et al. 2013; Luo 2017; Wang et al. 2019). Because the assortative mating could be perceived as an incipient process of speciation or assumed as a prerequisite of speciation models (Coyne and Orr. 2004; Bolnick and Fitzpatrick 2007; Elmer et al. 2009), and because it could be an outcome of sexual selection (Crespi 1989; Wang et al. 2019), consequences of assortative mating have significance for evolutionary biology.

To accurately understand evolutionary phenomena involving assortative mating, generating mechanisms on which the assortment (i.e. correlation) occur are also of

importance (Galipaud et al. 2013). Focusing on size assortative mating of avian species, Wang et al. (2019) classified the mechanisms into three categories: 1) mate choice, 2) like meets like, and 3) become alike.

Mechanism 1: ”like meets like” explains the correlation between paired individuals by resemblance between individuals and their potential mates (Wang et al. 2019). This resemblance occurs both spatially and temporally. For example, because individuals in the vicinity can have similar genotypes even within a population, phenotypes of potential mates tend to be similar to own phenotypes (Erlandsson and Rolán-Alvarez 1998; Indykiewicz et al. 2017). Such assortment also arises from temporal separation of individuals (Hendry and Day 2005). For the species of lifelong monogamy, potential mates for the young recruits are often also young recruits, and young recruits often breed later than adults (Warkentin et al. 1992). This leads to assortment for age. If body size differs between the ages, size assortative mating can occur for the reason of the age-related temporal assortment (Wagner 1999)

Mechanism 2: ”become alike” explains the correlation between paired individuals by sharing same environmental effect between mates (Wang et al. 2019). For the species which share resources (e.g. territory and food) among individuals of pairs, mated individuals can resemble each other because they feed similar food, use similar environment and be affected by the similar environmental effects (Class and Brommer 2018).

Mechanism 3: “mate choice” explains the correlation between paired individuals by choice (or preference) of a part or both of the individuals of pairs which leads to similarity for the traits between them (Wang et al. 2019). If the choice exerts on the similarity, correlation between the mates is easy to understand. However, without such a preference for similarity, phenotypic correlation between mates can arise. For example, if the males prefer large females for the reason of their fecundity and large males have advantage in the competition for large females, such competition result in pair of large (competitive) males and large (fecund) females, and pairs of small (uncompetitive) males and small (infecund) females (Crespi 1989). I hereafter call this mechanism competition-based mechanism.

Although such the three mechanisms have been suggested irrespective of taxonomic groups, relative importance of them may different across the groups. As already mentioned, competition-based mechanism assumes male’s preference for large fecund females. In a review for mechanism of size assortative mating, Crespi (1989) suggested that "male choice of large females combined with male-male competition, and increased availability of large females combined with male-male competition" is dominant mechanism for arthropods. However, compared to arthropods, this mechanism may not have much importance for taxonomic groups with small inter-individual variation in fecundity, or groups with little correlation between female body size and fecundity (Pincheira-Donoso and Hunt 2017). Enough variation under the target of choice is needed for the choice to work (Lehmann et al. 2007). In addition, the competition-based

mechanism may also be less important in the species whose female choice for males override the outcome of male-male competition for females. Considering these, if there were size assortative mating in an avian species, what mechanisms would contribute to their assortative mating? Birds lay much smaller number of eggs than arthropods, hence, small interindividual variation in fecundity, and they are traditional study material for sexual selection by female choice. Assortative mating in bird may arise due to the different mechanisms from other taxonomic groups (Wang et al. 2019).

Amongst bird, raptors offer interesting opportunity for investigating the cause of size assortative mating. Firstly, they are long-lived and often show life-long monogamy (McDonald et al. 2005; König and Weick 2008). Such characteristics call for careful mate choice because the choice can heavily influence their life-time reproductive success (Wojczulanis-Jakubas et al. 2018). Secondly, they occur around the world and have large range of body size (Schoenjahn et al. 2020). This enables comparative analysis which seeks for relationships between size assortative mating and various factors. Thirdly, their females are often larger than males: reversed sexual size dimorphism (Mueller 1986; Owens and Hartley 1998; Krüger 2005). One of the major hypotheses for the evolution of the dimorphism is small-male hypothesis, that is, males are selected to be small to improve agility, manoeuvrability, and thus foraging efficiency (Hakkarainen et al. 1996; Krüger 2005). Intriguingly, this selection for smallness is opposite direction from the selection for largeness which is assumed in competition-based mechanism for size assortative mating. Furthermore, one of the other hypotheses suggests size difference between the sexes has been selected due to the reduction of intersexual competition (Krüger 2005; Pande and Dahanukar 2012). If this is the case, size dissimilarity between mates (disassortative mating) rather than size similarity between mates (assortative mating) seems to be preferred. From these consideration, occurrence of size assortative mating per.se. can be questioned for raptors. Even if it exists, underlying mechanism of the assortment is unclear.

Here, I addressed the generating mechanism of assortative mating in a long-term monitoring population of the Ryukyu Scops Owls *Otus elegans interpositus*. Males of the owls are slightly smaller than females (Sawada et al. 2021b). Data of reproductive success, territories, age of breeding pairs have been accumulated since 2002. The aims of this study are 1) describing size assortative mating in the owls, 2) investigating the possible mechanisms contributing to the detected assortative mating patterns.

Material and Methods

Material

O. e. interpositus is endemic to a small, isolated, oceanic island, the Minami-daito Island, Japan (Ornithological Society of Japan 2012). Ongoing long-term study of the owls has recorded their breeding activity and survival history since 2002 (Takagi et al. 2007a; Sawada et al. 2018a; Takagi 2020). They are monogamous and pair-bond, at most case, lasts until a part of the pair dies (Akatani 2011). Extra-pair fertilization is not common

(Sawada et al. 2020). Pairs maintain the same territories around a year and tend to use same nest successive years (Akatani et al. 2011). Females lay a clutch of one to four eggs from mid-March to mid-May (Takagi et al. 2007; Akatani et al. 2011; Sawada and Iwasaki unpublished data). Incubation period and nestling period last about one month each (Takagi et al. 2007; Akatani et al. 2011; Sawada and Iwasaki unpublished data). Males feed females until middle of the nestling period, and parents share feeding duties afterward (Takagi and Akatani 2011). There are about 200 to 300 pairs on the island (Takagi et al. 2007; Takagi 2020; Sawada et al. 2021a).

Breeding monitoring

The reproductive success data since 2002 were obtained from natural cavities or nest boxes by visiting the nests regularly. Analysis of reproduction data in this study used 285 breeding attempts, which were not predated or abandoned and for which I have complete data on social parents' identity, egg laying data and number of fledglings (Table 6-1). All chicks were ringed, measured and collected their blood. Detailed field procedures are described elsewhere (Takagi et al. 2007a; Akatani et al. 2011; Sawada et al. 2020).

Territory identification

I and Tetsuya Iwasaki (a member of the long-term study group) have recorded all territorial owls in the island as a part of mark-recapture (mark-resight) surveys since 2012 (Table 6-1). From late February to late July, I (2016-2019) and Iwasaki (2012-2015) walked around the entire island using playback almost every night (from sundown to about midnight), except when it rained (see Sawada et al. 2020; Takagi 2020). All territorial owls encountered were recorded their sex, ring ID, and Universal Transverse Mercator (UTM) coordinates of the points where we encountered owls. Ring ID was identified by unique combination of coloured reflective tapes wrapped on the metal rings (Takagi 2020).

Body size measurement

Almost all breeding individuals identified by breeding monitoring (from 2002) and no-marked individuals which I and Iwasaki encountered during territory identification survey (from 2012) were captured by mist-net, ringed and measured. Number of individuals whose measurement are used in this study is 778 in total. Body mass (nearest 0.1 g) was measured using Pesola spring balance or digital weighing scale. Tarsus length, culmen length, bill depth, bill width, head length and tail length (nearest 0.01 mm) were measured with an electronic digital calliper. Wing length (nearest 0.5 mm) was measured with a stainless-steel ruler. Measurements were made basically two times or more at each capturing occasion and mean values across them were used. See Table 6-2 for the definitions of these traits. More information on the measurement is available at Sawada et al. (2021b). Analysis of size assortative mating used measurement data of individuals which were confirmed their presence equal or after 2012 because randomization tests (see

below) needs detailed territory data which is only available since 2012. However, analysis of reproductive success used measurement data of individuals equal or after 2007.

Sex and age determination

Sex was determined by vocal characteristics, by the presence of a brood patch, or by PCR amplification of the Chromo Helicase DNA-binding gene (Fridolfsson and Ellegren 1999; Sawada et al. 2021b; Takagi 2020). Age class (yearling or adult) was estimated from plumage characteristics accordingly to Sawada et al. (2021b). Age used in the analyses in below means this dichotomous classification and not exact age in years. Detailed procedures of the sexing and aging are described in Sawada et al. (2021b).

Statistical analysis

(a) Data standardization before analysis

Before analysis, measurement data were statistically controlled for difference between measurers and years (Grant and Grant 2008; Green 2019), using the results of generalized linear mixed models fitted to the dataset collected during the same period in Sawada et al. (2021b). See Appendix and Table 6-3, 6-4 for the detailed standardization procedures. This data standardization and all analysis in below were conducted on R (R Core Team 2019).

(b) Fundamental analysis of assortative mating

To describe size assortative mating, I calculated Pearson's correlation between measurements in males and females of mated pairs. By using the measurement data which is collected for the first-time for the individuals (some individuals were measured in multiple years), effects of "become alike" were excluded as much as possible. Significance test of the correlation was based on two methods: *cor.test* function in R (hereafter, "parametric test") and randomization test (Erlandsson and Rolán-Alvarez 1998). Parametric test was conducted because it is the commonest method to document assortative mating. Randomization test was conducted because assumptions of parametric test can be violated in the data of assortative mating (i.e. non-normality and/or non-independence of samples).

Procedures of the randomization test were similar to the ones described in Sawada et al. (2020): 1) Using data matrix which contains data for all territories of all years, males are randomly assigned to females within each year. Here, I randomly choose the same number of females as the actual pair data. 2) Calculate Pearson's correlation coefficient based on these simulated pairs. 3) Repeat 1) and 2) 1,000 times. 4) Generate a distribution of correlation coefficient from these simulated values. This is the null distribution of correlation coefficient expected under random mating in this owl population. 5) Obtain two tailed *P*-value as twice the proportion of simulated values which are more extreme than the actual value. For the traits for which I found significant assortative mating by both of the parametric and randomization test (culmen length and wing length, see

Results), I further investigated their generating mechanisms by the analyses detailed in the following sections.

(c) Mechanism 1: Like meets like

I took two approaches to test whether the mechanism 1 contribute to the assortment. The first is statistical control of spatial and temporal accessibility in the randomization test. The second is testing whether the spatially accessible individuals are similar-sized or not.

Basic idea of the first approach is that non-significance after controlling for mechanisms 2 is an indicative of contribution of mechanism 2 to the significance detected above (Erlandsson and Rolán-Alvarez 1998). I modified step1 of above-mentioned randomization test to consider the spatial or temporal accessibility to potential mates.

To control for spatial accessibility, I randomly assigned a male within 1145m around the focal female to the female. This distance is median dispersal distance of females (Sawada et al. 2018; Matsuo unpublished data). Then, null distribution and *P*-value were calculated as the same way. If the distribution moves to the direction of actual value of correlation coefficient and *P*-value increases, mating with spatially more accessible mates would explain the size assortment. Because males often settle earlier than females and females often show roaming dispersal patterns which suggest female's mate searching during dispersal (Sawada and Takagi unpublished data), I consider that assignment of females to males is reasonably mimicking their pair formation processes.

To control for temporal accessibility of potential mates, I randomly assigned males while considering the age of females and males. There are three reasons to this treatment: 1) There was a tendency of age assortative mating (see Appendix, Table 6-5). 2) Yearlings tend to breed late probably due to their late pair formation (see Appendix, Table 6-6, 6-7). 3) Yearlings and adults have slight size difference (Sawada et al. 2021b). Let P_{YY}, P_{YA}, P_{AY} and P_{AA} be observed frequency of pairs (first and second subscript denote the age of male and female, respectively). To mimic the pair formation based on age, for yearling females, yearling males were assigned with the probability P_{YY} and adult males were assigned with P_{AY}. For adult females, yearling males were assigned with the probability P_{YA} and adult males were assigned with P_{AA}. Then, null distribution and *P*-value were calculated as the same way. If the distribution moves to the direction of actual value of correlation coefficient and P-value increases, mating with temporally more accessible, similar-aged mates would explain the size assortative mating. I used means of the observed frequencies from 2012 to 2019 as the values of P_{YY}, P_{YA}, P_{AY} and P_{AA} (Table 6-5).

To assess similarity among spatially accessible individuals, I described and tested spatial autocorrelation in body size by Mantel test. I focused on geographic distance and size difference from females to males because our interest is whether spatially accessible males for females are similar to the females. This test was applied to all years (2012 to 2019) separately for each of culmen length and wing length. Holm's correction of P-value was applied to each trait.

I further investigated heritability of culmen length and wing length. This was motivated from: 1) a previous result that there is spatial autocorrelation in genetic structure (Sawada et al. 2018a), and 2) heritable components in body size variation, if exists, can translate into the spatial heterogeneity in morphological variation. To estimate heritability, I applied parent-offspring regression to father-mother-offspring triads identified during breeding monitoring and territory mapping surveys (63 triads for culmen length and 61 triads for wing length). Regression coefficients in the regressions of offspring value over mid-parent value were used as the estimate of heritability (Lynch and Walsh. 1998).

(d) Mechanism 2: Become alike

I took two approaches to test whether the mechanism 2 contribute to the assortment. The first is the comparison of body size difference of paired individuals at first-time measurement to the difference at last-time measurement. Body size at last-time measurement is expected to reflect body size change accumulated after pair formation. If mechanism 2 works, difference at last-time measurement is expected to be smaller than the one at first-time measurement. Furthermore, such change might be more pronounced in labile trait (wing length) than the less variable bony trait (culmen length). I tested these expectations by paired t-test.

The second is comparison between correlation coefficients calculated from first-time measurement and those from last-time measurement. Statistical significance of the two correlation coefficients was determined based on a test using Fisher's Z transformation of correlation coefficients (see Appendix, Zou 2007). Strong positive correlation in the latter suggest contribution of mechanism 2 to assortative mating in the owls.

(e) Mechanism 3: Mate choice

I took three approaches to test whether the mechanism 3 contribute to the assortment. The first is statistical control of other mechanisms in the fundamental correlational analysis described above. Basic idea is that persistent significant correlation after controlling for other mechanisms is an indicative of contribution of mechanism 3 (Erlandsson and Rolán-Alvarez 1998). Because correlation analysis using first-time measurement data already minimizes the effect of mechanism 2 (become alike), I considered to controlling for mechanisms 1 (like-meets-like). Detailed procedures are already described in the above paragraphs for testing mechanisms 1 (like-meets-like)

The second approach is analysis of fitness components. Basic idea behind this is that if there are active mate choice with respect to body size, choosers are likely to benefit from this behaviour (Andersson and Simmons 2006). To test this, I evaluated the effects of body size on number of fledglings and number of recruits at single breeding attempt, and survival rate. Because the owls breed with the same mate for successive years, small increment of reproductive success at single breeding attempt can enlarged when focusing on lifetime reproductive success. Because longevity positively correlates with lifetime reproductive success in this owl population (Sawada et al. 2020), increased survival rate

indicates increased fitness. Generalized linear model (GLM) and GLMM with log-link and Poisson distribution by *glm* and *glmer* function in *lme4* package (Bates et al. 2015) were used for the analysis of fledglings and recruits. Cormack-Jolly-Seber model (CJS model, Stan Development Team 2018) was used for the analysis of survival rate. Here, I describe the essence of the analysis. See Appendix, Table 6-9 and 6-10 for detailed descriptions.

For the number of fledglings and recruits, I constructed models with all possible combinations of fixed effects (Year, Egg laying date, Father age, Mother age, Father culmen length, Father wing length, Mother culmen length, Mother wing length, Difference in culmen length between parents, Difference in wing length between parents), and all possible combinations of random effects (Mother ID, Father ID). Then, I searched for the best combination of them in terms of AIC by *dredge* function in *MuMIn* package (Barton 2019). Top-ranked models with $\Delta AIC < 2$ (difference from minimum AIC smaller than 2) were model-averaged by *model.avg* to obtain model-averaged regression coefficients and corresponding P-values. Results were interpreted from the top mole and the averaged model.

For the survival rate, I constructed a CJS model with survival rate which is modelled by five fixed effects (Year, Sex, Age, Culmen length, Wing length) and detection probability which is modelled by two fixed effects (Sex, Researcher). To consider sex-dependency of the effect of body size, regression coefficients for body size (Culmen length, Wing length) were modelled to be sex-dependent. These effects were introduced by GLM with logit link and Bernoulli distribution. Model implementation was done using Stan (Carpenter et al. 2017) and *rstan* (Stan Development Team 2019). Fitting parameters were as follows: warmup = 15,000; iter = 5,000; thin = 4. Convergence was confirmed based on Rhat diagnostic statistics and the output of *check_hmc_diagnostics* function in the *rstan* package. Significance of the fixed effects were judged based on whether 95% credible interval (95% CRI) include zero or not.

The third approach is a comparison of body size between previous territory holders and present territory holders. Although the owls basically hold the same territory, some individuals moved to another place, which implies competition for territories or mates (Akatani et al. 2011, Sawada and Iwasaki unpublished data). If there are consistent body size differences between previous territory holders and present territory holders, contribution of body size on competitiveness and contribution of body size-based competition to the assortative mating are expected. From the data of territory identification, I obtained 53 cases of such changes for males and 22 cases for females (see Appendix). I compared culmen length and wing length (the traits for which I found significant assortment), between previous and present territory holders by paired t-test.

Results

Fundamental analysis of assortative mating

Parametric test of correlation of body size measurements revealed significant assortative

mating in culmen length, bill depth, bill width, head length and wing length (Figure 6-1, Table 6-11). The significant assortments in the all traits remained after P-value corrections (Table 6-11). Randomization test revealed significant assortative mating in culmen length and wing length (Figure 6-2, Table 6-11). The assortment in culmen length even remained after P-value corrections (Table 6-11). Because null distributions generated by randomization of all traits, except culmen length and tail length, did not have its mean near zero (Figure 6-2, Table 6-11), significance by parametric test seemed to be overestimated. Subsequent analyses for generating mechanisms of assortment focused on culmen length and wing length for which both tests identified significant assortment.

Test of mechanism 1: Like meets like

Statistical control of spatial accessibility of potential mates hardly moved the null distribution towards actual values (Figure 6-3). P-values were almost unchanged (Table 6-12, from P = 0.000 to 0.002 in culmen length, from P = 0.026 to 0.034 in wing length). Heritability were significant for culmen length (Figure 6-4, h^2 ±SE = 0.303 ±0.119, t_{61} = 2.552, P = 0.013) and for wing length (Figure 6-4, h^2 ±SE = 0.245 ±0.109, t_{59} = 2.252, P = 0.028). However, no significant morphological similarity between females and their spatially accessible potential mates were found (Mantel test, all P > 0.05, Table 6-13).

Statistical control of age of potential mates hardly moved the null distribution towards actual values (Figure 6-3). P-values were almost unchanged (Table 6-12, from P = 0.000 to 0.000 in culmen length, from P = 0.026 to 0.050 in wing length).

Test of mechanism 2: Become alike

Difference in last-time measurements were not significantly different from first-time measurements in culmen length (Figure 6-5a, paired t-test, t_{235} = 0.354, P = 0.724). However, last-time measurements were significantly smaller than first-time measurements in wing length (Figure 6-5b, paired t-test, t_{229} = -3.192, P = 0.002).

Correlation coefficients calculated from last-time measurements (Figure 6-6) was not significantly different from ones calculated from first-time measurements (Table 6-11, all P > 0.05). However, correlation coefficients of bill depth had marginally weakened from 0.169 to -0.006 (Table 6-11, Z = 1.906, P = 0.057).

Test of mechanism 3: Mate choice

Statistical control of spatial and temporal accessibility of potential mates did not completely cancel the significance in the correlation coefficients for culmen length and wing length, as described above (Figure 6-3, Table 6-12, further described in the results for mechanism 2).

Best model for number of fledglings was a model including year, male age and male wing length (Table 6-14). From this model, number of fledglings in a pair with yearling males decreased by 0.74 times, compared to a pair with adult males (Figure 6-7a, Table

6-15, coefficient ±SE = -0.30 ±0.13, Z = -2.24, P = 0.03), and 10 mm decrease in male wing length increased number of fledglings by 1.20 times (Figure 6-7a, Table 6-15, coefficient ±SE = -0.02 ±0.01, Z = -1.56, P = 0.12) although it is not significant. Applying model averaging to the best set of models, effect size and significance of male age and male wing length were almost unchanged (Table 6-16).

Best model for number of recruits was a model including year, egg laying date, male age and male wing length (Table 6-17). From this model, number of recruits in a pair with yearling males decreased by 0.62 times, compared to a pair with adult males (Figure 6-7b, Table 6-18, coefficient ±SE = -0.47 ±0.28, Z = -1.67, P = 0.10), 10 days late egg laying decreased number of recruits by 0.85 times (Table 6-18, coefficient ±SE =-0.02 ±0.01, Z =-1.63, P = 0.10), and 10mm decrease in male wing length increased number of recruits by 1.44 times (Figure 6-7b, Table 6-18, coefficient ±SE =-0.04 ±0.02, Z =-1.68, P = 0.09), although the effects were marginal. Applying model averaging to the best set of models, effect size and significance of male age and male wing length were almost unchanged (Table 6-19).

Survival rate was not significantly affected by culmen length in both sexes (Figure 6-7c, Table 6-20, coefficient for male = 0.03, 95%CRI = [-0.14, 0.20]; coefficient for female = -0.16, 95%CRI = [-0.39, 0.07]). However, it was significantly affected by wing length in females and not in males (Figure 6-7c, Table 6-20, coefficient for male = -0.10, 95%CRI = [-0.28, 0.09]; coefficient for female = -0.32, 95%CRI = [-0.62, -0.03]). Sex did not affect survival rate significantly (Table 6-20, mean = -0.24, 95%CRI = [-0.59, 0.10]). Age had significant effect (Table 6-20, mean =4.79, 95%CRI = [2.35, 9.54]).

Comparison of body size between previous male territory holders and present male territory holders did not find significant difference in culmen length (paired t-test, t_{52} = -0.282, P = 0.779) and wing length (paired t-test, t_{52} = 0.384, P = 0.702). Females also did not have significant difference in culmen length (paired t-test, t_{21} = 1.320, P = 0.201) and wing length (paired t-test, t_{21} = 0.421, P = 0.678).

Discussion

This study described size assortative mating of the Ryukyu Scops Owls in the Minami-daito Island. Significant assortative mating was found for culmen length and wing length by two statistical tests (parametric test and randomization test). Statistical control of spatial and temporal accessibility in the test did not cancel the assortment. Furthermore, wing length was suggested to have some contribution for fitness components. However, change in territory holders did not accompany body size differences between present and previous holders. On the other hand, there were smaller differences in wing length of paired individuals later in their paired period compared to early in their paired period. I discuss possible generating mechanism of assortative mating in the owl from these results. Then, I discuss its relevance comparing other taxonomic groups.

Possible mechanism of assortative mating

For both of the culmen length and wing length, active mate choice (mechanism 1) would be a likely explanation for the assortative mating in the owl population. There are three reasons. First, statistical control of spatial accessibility did not cancel the assortment. Second, Mantel test did not find significant similarity between females and potential mates. These two results indicate little contribution of spatial covariation of body size (i.e. mechanism 2: like meets like) to the assortment. Third, our results already minimized the effect of mechanism 3 "become alike" by using first-time measurement data.

For the assortment with respect to culmen length, there were no further support to this interpretation because any fitness components did not correlate with the trait. However, for the assortment with respect to wing length, mate choice is further supported by correlation between wing length and fitness components. Because males with smaller wing length produced slightly more fledglings and recruits, females would benefit from choosing small males. Because the owls breed with the same mate for successive years, Although the effect of wing length on the reproductive success is marginal, such the small increments of reproductive success at single reproductive occasion seems to be enlarged and reach significance at lifetime reproductive success.

Then, which of the preference for similar-sized individual or the competition for large-sized (or small-sized) individuals would be the underlying process of active mate choice? Assortative mating can occur not only when individuals prefer similar-sized individuals but also when individuals of specific size have competitive advantage in acquisition of mates of the same specific size (for example, circumstance in which large-sized males compete for the large female and remaining small individuals mate each other, Crespi 1989; Taborsky et al. 2009). However, there were no significant size differences in previous and present territory holders, indicating little contribution of body size on competition. Therefore, preference for similar-sized individuals, rather than size dependent competitive advantage in acquiring mate with specific size, might be the process of mate choice in this owl.

Nevertheless, contribution of mechanism 3 "become alike" cannot completely be ruled out for assortment by wing length because of small size difference in late after pair formation. I used the measurement at first-time capture to grasp correlations which were similar to the correlation at the pair formation as much as possible. However, this method has a limitation because we cannot obtain measurement at exact timing of pair formation. Therefore, if wing length of mated individuals become alike continuously after pair formation, our measurement at first-time capture have already some similarity due to the mechanism "become alike", which generate positive correlation between males and females. However, because mantel test for spatial autocorrelation structure did not detect similarity in wing length between nearby individuals (Sawada unpublished data), sharing similar environment does not seem to yield similarity between individuals for this population and suggest less contribution of "become alike".

Furthermore, physical constraint (Crespi 1989), a mechanism which I did not addressed in this study, also may not be ruled out. For some species of arthropod with long copulation time and or specific behaviour at copulation, inefficiency in copulation between pairs with large size difference is suggested as a cause of size assortment (Han et al. 2010). However, the duration of copulation is much shorter in birds (within several tens of seconds at long case, Birkhead et al. 1987) than such some species of arthropods which remain to be contacted for more than several hours (Crespi 1989). Therefore, I think the contribution of this mechanism in most of birds are limited because their copulation takes little times to the body size difference considerably matter the success of copulation.

Reason for large females to mate with large males

Given the weak negative correlation of male wing length and number of recruits, why large females mate with large males, not with small males? I propose two explanations here. First, males with small wing length may entail unknown cost for females that I did not find. Because my analysis of breeding data is based on individuals that lay at least one egg, we are ignorant of individuals that failed to reach egg-laying. Such breeding failure may be worth studying as a future direction to illuminate unknown cost in relation to body size difference.

Second, large females may have some disadvantage in acquiring small males. This is a simple corollary for raptors derived from competition-based hypothesis that large males have advantage in acquiring large females. Since I already discussed unlikeliness of contribution of body size on competitiveness, such disadvantage of large females may be derived from aspects other than competition. Females with large wing length actually had worse survival rate than those with small wing length. If adaptive females with small wing length have some advantage in accessing males with small wings, there may not be small males to be chosen by large females. Although not significant, females which settled in their first year tend to have smaller wing length than those settled in their second year or later (Sawada unpublished data), indicating existence of such advantage of females with small wing.

Mechanisms to assess body size

A problem I did not addressed in this study is how the owls know body size of other individuals. I propose that they use vocal characteristic to infer the body size of others. Because of nocturnality, owls heavily rely on vocal communication (König and Weick 2008). Body size measurement correlates with frequency of their hoot in this owl (Takagi unpublished data). Recording of behavioural responses to the hoot of various frequency would be a promising way to answer this problem in the future research (Podos 2010).

Implication for taxonomic variation in generating mechanism of assortative mating

Relative contribution of previously proposed mechanisms for assortative mating may

differ depending on taxonomic group. In a hypothesis for reversed sexual dimorphism in raptors, small males are assumed to have agility, manoeuvrability and thus have good performance in foraging (Mueller 1986; Krüger 2005). Some field studies have actually identified the small male advantage (Hakkarainen and Korpimäki 1991; Hakkarainen et al. 1996), and this study also supported it. However, such selection for smallness in males assumed in the literature of sexual size dimorphism, opposes the selection for largeness in males assumed in the literature of assortative mating. Therefore, contribution of large-male advantage in the competition for large female are questioned for raptor's size assortative mating. On the other hand, intrasexual competition is important for assortative mating at least in arthropod (Crespi 1989) and probably in fish (Taborsky et al. 2009; de Almeida Borghezan et al. 2019). Small clutch size and substantial parental care of offspring in birds compared to them suggests the existence of taxonomic difference in relative importance of generating mechanism of assortative mating.

Because the consequence of assortative mating depends on the mechanism on which the assortment occurs, elucidating taxonomic variation in relative importance of the mechanism is important issue for our understanding of ecology and evolution of assortative mating. One of the largest motivations to document assortative mating would be its importance as an incipient process or as a necessary assumption for sympatric speciation (Bolnick and Fitzpatrick 2007). Although size assortative mating is often only described its presence or absence, fruitful avenues for future studies would be concealed in investigating how the mating bias generated.

Figure

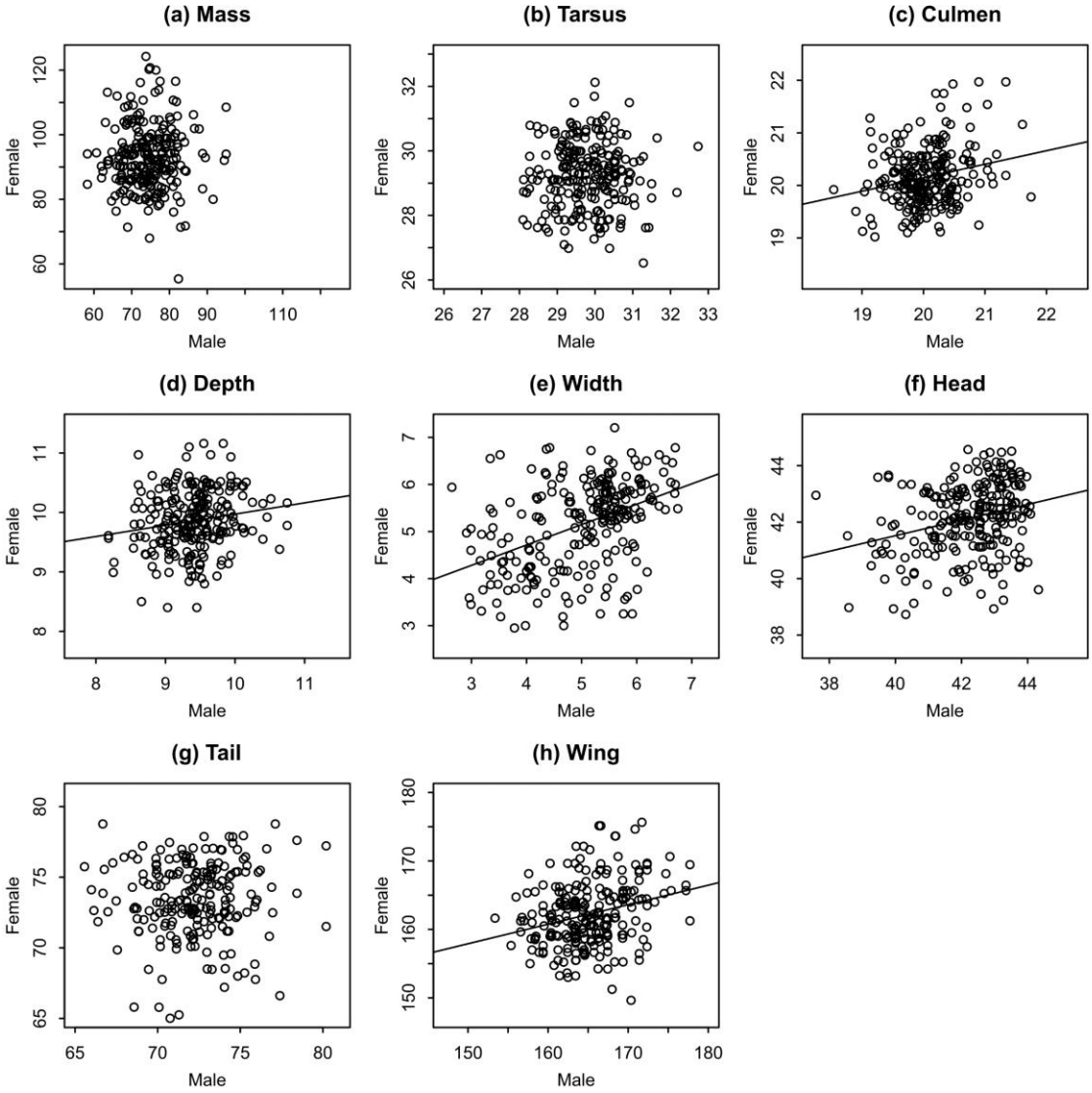


Figure 6-1

Scatter plot of body size measurements of males and females in mated pairs based on first-time measurement data. For the traits which have P-values lower than 0.05 in parametric test for Pearson's correlation, estimated regression lines are depicted.

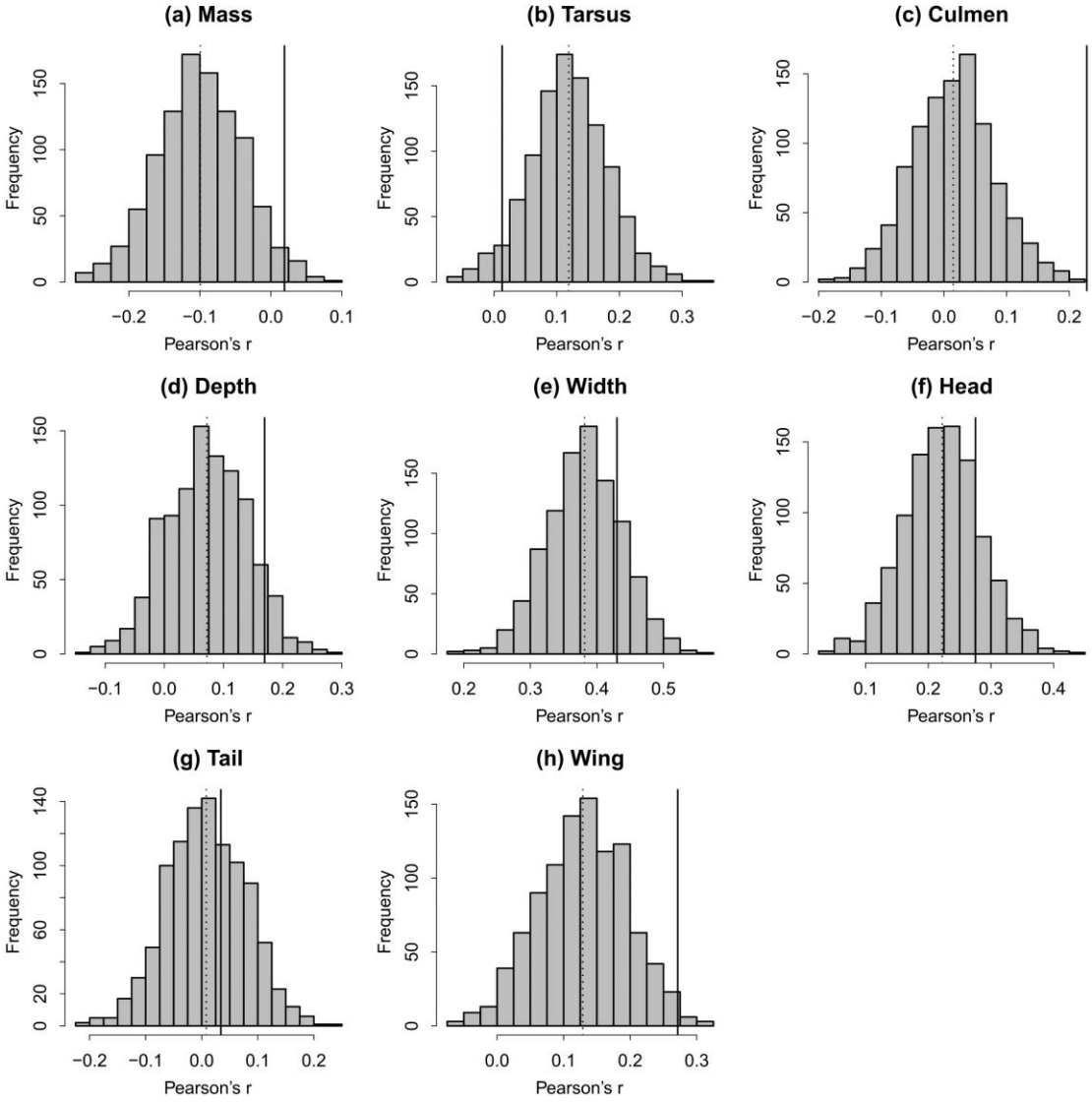


Figure 6-2

Results of randomization tests without any statistical controls. Histograms: distribution of simulated correlation coefficients. Solid line: observed value. Dotted line: mean of the distribution of simulated correlation coefficients.

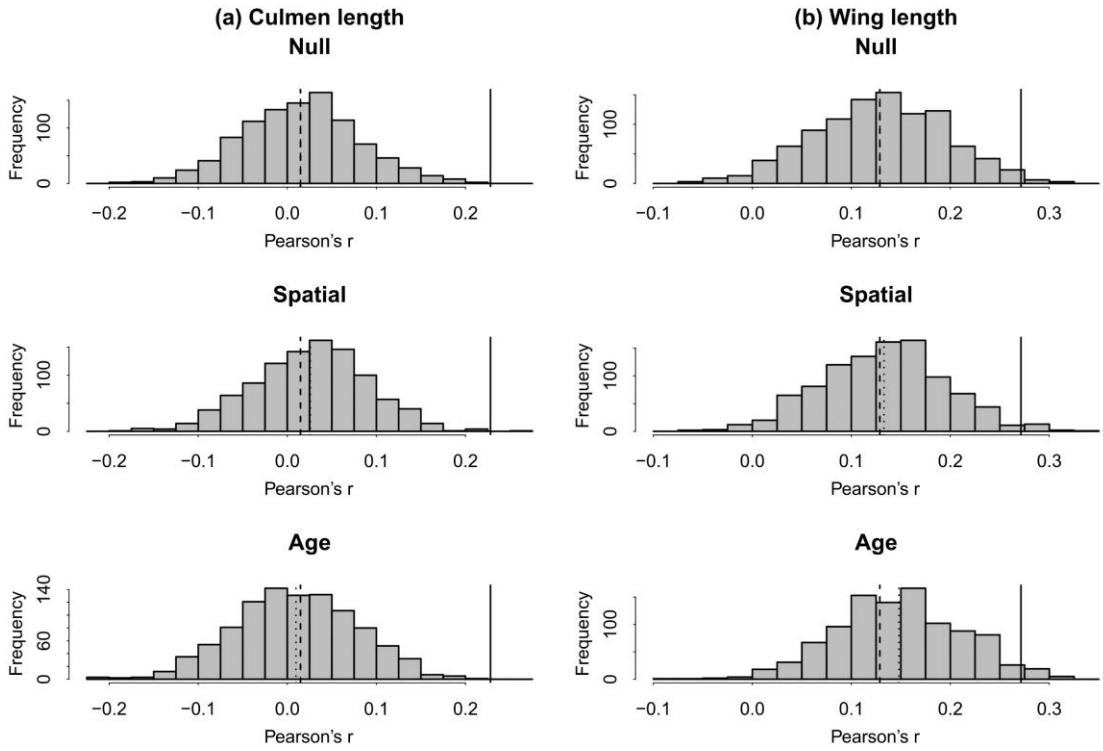


Figure 6-3

Results of statistical control of like-meets-like mechanisms in randomization tests for (a) culmen length and (b) wing length. Histograms: distribution of simulated correlation coefficients. First row: simulation without any controls, second row: simulation with control for spatial accessibility, third row: simulation with control for age-assortment. Solid line: observed value, dotted line: mean of each histogram, dashed line: mean of histogram of simulation without any controls in the first raw.

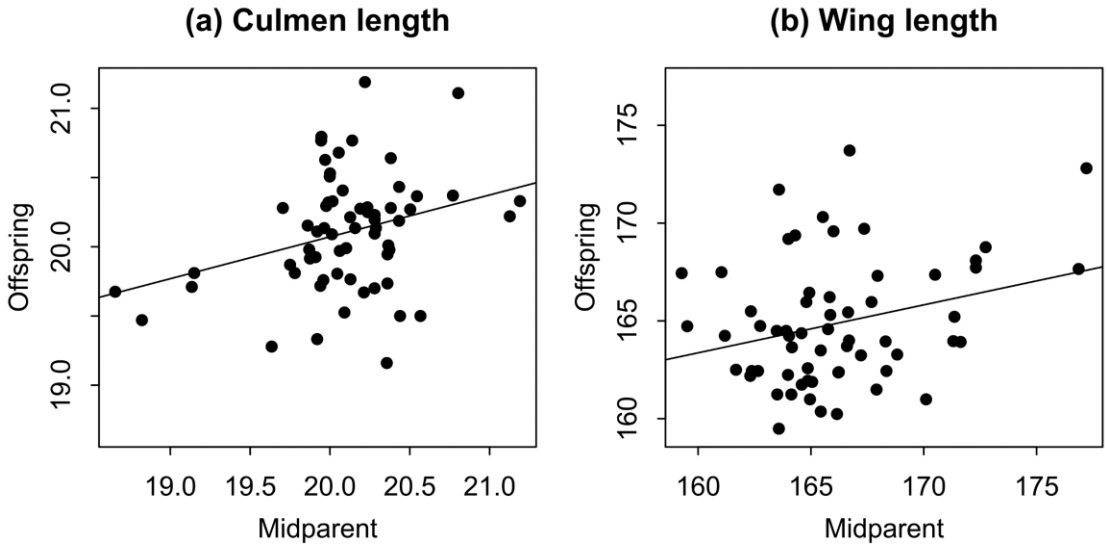


Figure 6-4
Parent offspring regressions of (a) culmen length and (b) wing length.

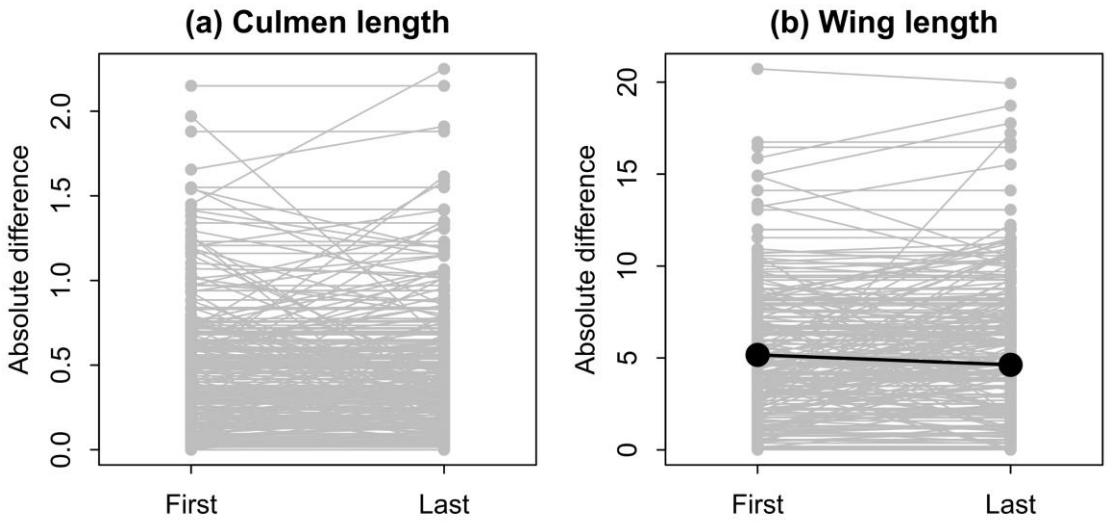


Figure 6-5
Comparison of body size difference of paired individuals at first-time measurement to the difference at last-time measurement. (a): culmen length, (b): wing length. Grey dot and grey line: each pair. Black dot and black line: mean estimate (shown when paired t-test detect significant difference)

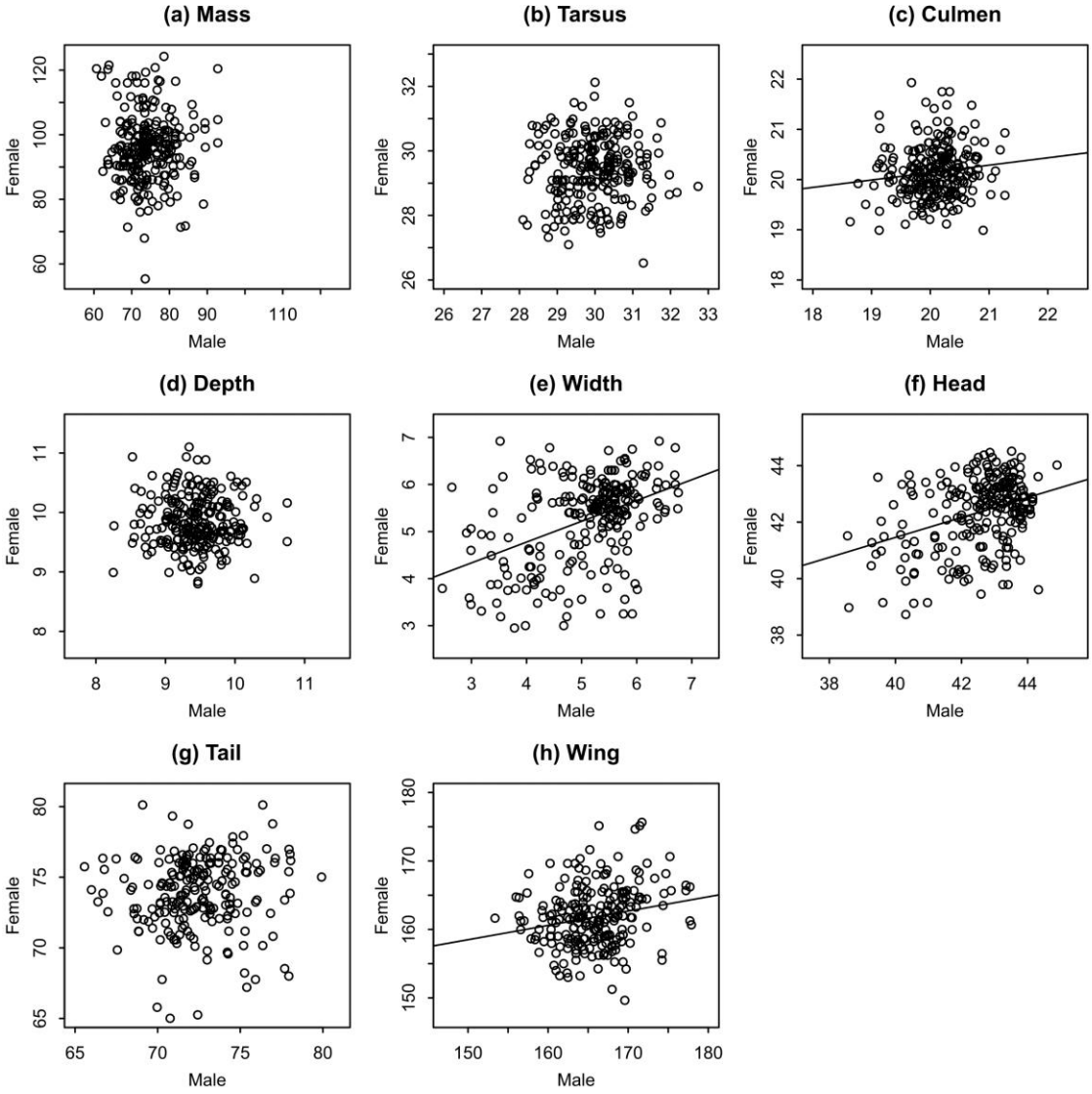


Figure 6-6

Scatter plot of body size measurements of males and females in mated pairs based on last-time measurement data. For the traits which have P-values lower than 0.05 in parametric test for Pearson's correlation, estimated regression lines are depicted.

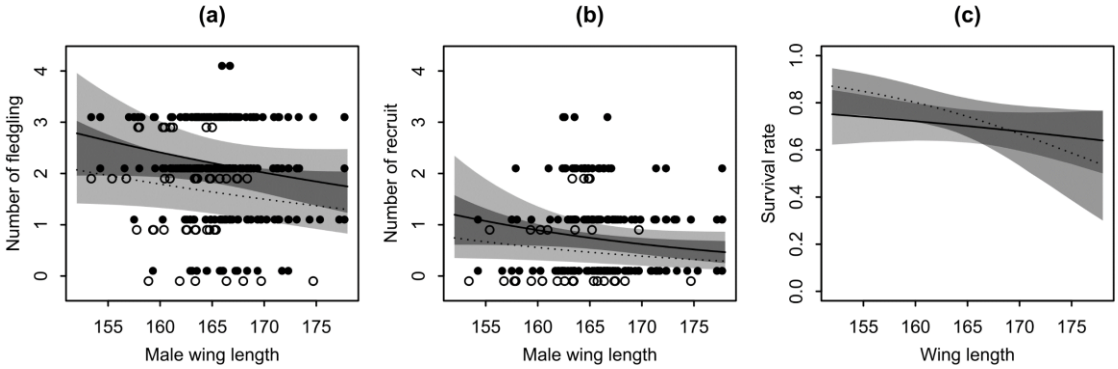


Figure 6-7

Relationships between wing length and fitness components. (a) Wing length of males and number of fledglings they produced at one breeding attempt. (b) Wing length of males and number of recruits they produced at one breeding attempt. Black dot and solid line: data point and mean estimate of adult males, white dot and dotted line: data point and mean estimate of yearling males. (c) Wing length and survival rate. Solid line: male, dotted line: female. Pale grey area: 95% CRI of mean estimates, dark grey area: overlap of the 95% CRI.

Table

Table 6-1 Number of territories and breeding attempts analyzed in this study

Year	$N_{territory}$	N_{fledge}	$N_{recruit}$
2002		0	0
2003		0	0
2004		0	0
2005		0	0
2006		0	0
2007		8	8
2008		6	6
2009		5	5
2010		0	0
2011		13	0
2012	190	4	4
2013	261	25	24
2014	240	25	24
2015	257	24	22
2016	289	38	36
2017	269	36	28
2018	252	51	50
2019	290	50	0
Total	2048	285	207

$N_{territory}$: number of territories (count data of territory are only available after 2011), N_{fledge}: number of breeding attempts which used in the analyses of number of fledglings, $N_{recruit}$: number of breeding attempts which used in the analyses of number of recruits

Table 6-2 Definition of the morphometric traits measured in this study

Trait	Definition
Body mass	body mass in mg
Tarsus length	from the base to the tip of the tarsometatarsus
Culmen length	from the base to the tip of the bill
Bill depth	height of the closed bill at the anterior end of nostril vertical to the gape
Bill width	width of the bill at the anterior end of nostril
Head length	from the back of the skull to the tip of the bill
Tail length	from the root to the tip of the central rectrix
Wing length	from the bend of the wing to the tip of the longest primary at a flattened state

Table 6-3 Values used for controlling for variation between measurers

Measurer	Mass	Tarsus	Culmen	Depth	Width	Head	Tail	Wing
Iwasaki	4.64	0.00	-0.04	0.13	-0.52	-0.53	0.81	2.85
Matsuo	-3.14	0.00	0.21	-0.36	0.65	0.34	0.75	0.00
Nakanishi	2.67	0.00	0.40	-0.22	-0.84	-2.65	1.13	3.03
Nishi	2.13	0.00	0.00	-1.32	0.00	-0.56	0.00	0.00
Sawada	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Takagi	2.88	0.00	0.46	-0.11	0.17	-0.78	-0.25	0.00

These values are from in supplementary tables in Sawada et al. (2021b).

Table 6-4 Values used for controlling for variation between years

Year	Sex	Mass	Tarsus	Culmen	Depth	Width	Head	Tail	Wing
2012	F	-10.69	-0.25	0.00	-0.36	0.10	-1.06	-1.35	-0.52
2013	F	-11.69	-0.43	0.00	-0.09	-0.27	0.24	-1.55	-0.18
2014	F	-0.83	-0.36	0.00	0.25	-0.51	-0.45	-0.54	3.79
2015	F	-6.65	-0.75	0.00	0.10	-0.07	-0.47	-0.47	-0.39
2016	F	-4.88	-0.63	0.00	0.11	-0.07	-0.34	0.02	-0.36
2017	F	-4.86	-0.09	0.00	-0.30	0.24	-0.40	-0.11	0.51
2018	F	3.36	0.03	0.00	-0.10	0.16	-0.13	-0.37	0.22
2019	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2012	M	-13.76	0.23	0.00	-0.29	0.10	-1.06	-1.35	4.46
2013	M	-15.92	0.14	0.00	-0.30	-0.27	0.24	-1.55	4.51
2014	M	-12.98	-0.25	0.00	-0.32	-0.51	-0.45	-0.54	5.86
2015	M	-13.64	-0.28	0.00	0.04	-0.07	-0.47	-0.47	2.73
2016	M	-14.03	-0.39	0.00	-0.24	-0.07	-0.34	0.02	3.38
2017	M	-12.38	-0.06	0.00	-0.45	0.24	-0.40	-0.11	5.37
2018	M	-12.22	0.06	0.00	-0.20	0.16	-0.13	-0.37	5.44
2019	M	-11.45	0.30	0.00	-0.20	0.00	0.00	0.00	5.24

These values are from in supplementary tables in Sawada et al. (2021b).

Table 6-5 Result of Fisher's exact test for age assortative mating

Year	M_YF_Y*	M_YF_A*	M_AF_Y*	M_AF_A*	N	P	$P_{correct}$
2012	0	1	0	21	22	1.000	1.000
2013	1	2	1	16	20	0.284	1.000
2014	2	6	0	11	19	0.164	0.982
2015	1	1	2	11	15	0.371	1.000
2016	7	10	5	12	34	0.721	1.000
2017	4	11	4	10	29	1.000	1.000
2018	7	8	5	27	47	0.034	0.239
2019	13	9	5	27	54	0.001	0.010
Total	35	48	22	135	240	0.000	0.000
Frequency	0.146	0.200	0.092	0.563	1.000		

*: subscript means age of pair of male (M) and female (F). $P_{ccorect}$: P-values adjusted by Holm’s method

Table 6-6 Selection of random effect structure in GLMM for egg laying date

Model	AIC
FatherID + MotherID	1967.705
FatherID	1970.254
MotherID	1967.123
No random effect	2007.349

Table 6-7 Selection of fixed effect structure in GLMM for egg laying date

Model	AIC	Delta
MaleAge + FemaleAge	1967.123	0.000
FemaleAge	1972.605	5.482
MaleAge	1977.458	10.335
No random effect	1991.522	24.399

Table 6-8 Regression coefficients of the top model for egg laying date

Variable	Estimate	SE	df	t	P
Intercept	-1.58	0.64	137.99	-2.45	0.02
MaleAge (Y)	2.97	1.31	257.24	2.27	0.02
FemaleAge (Y)	4.79	1.53	274.23	3.13	0.00

Table 6-9 Selection of random effect structure in GLMM for number of fledglings

Model	AIC
FatherID + MotherID	865.8191
FatherID	863.8191
MotherID	863.8191
No random effect	861.8191

Table 6-10 Selection of random effect structure in GLMM for number of recruits

Model	AIC
FatherID + MotherID	465.4258
FatherID	463.4258
MotherID	463.4258
No random effect	461.4258

Table 6-11 Results of fundamental correlation analyses

Trait	N	r	P_{param}	P_{param}^{*}	P_{rand}	P_{rand}^{*}	r_{last}	P_{param_last}	$P_{param\_last}^{*}$	Z	P_{diff}
Body mass	240	0.019	0.768	1.000	0.056	0.336	0.004	0.954	1.000	0.168	0.867
Tarsus length	237	0.013	0.844	1.000	0.116	0.580	0.034	0.607	1.000	-0.225	0.822
Culmen length	236	0.228	**0.000**	**0.002**	**0.000**	**0.000**	0.131	**0.044**	0.222	1.083	0.279
Bill depth	236	0.169	**0.009**	**0.037**	0.148	0.592	-0.006	0.931	1.000	1.906	0.057
Bill width	236	0.430	**0.000**	**0.000**	0.370	1.000	0.430	**0.000**	0.000	0.006	0.995
Head length	236	0.275	**0.000**	**0.000**	0.366	1.000	0.365	**0.000**	0.000	-1.076	0.282
Tail length	213	0.034	0.620	1.000	0.702	1.000	0.067	0.330	1.000	-0.338	0.736
Wing length	230	0.271	**0.000**	**0.000**	**0.026**	0.182	0.208	**0.001**	0.009	0.712	0.477

r: correlation coefficient calculated from first-time measurements, r_{last}: correlation coefficient calculated from first-time measurements, P_{param}: P-value of parametric test on first-time measurements, P_{rand}: P-value of randomization test on first-time measurements, P_{param_last}: P-value of parametric test on last-time measurements, *: Values after control of multiple testing by Holm's correction, Z: test statistic of difference between r and r_{last}, P_{diff}: P-value corresponding to Z.

Table 6-12 Change in P-value and mean of null distribution by controlling for mechanism 2 in randomization test

Trait	P_{null}	$P_{spatial}$	P_{age}	M_{null}	$M_{spatial}$	M_{age}	r
Culmen length	0.000	0.002	0.000	0.015	0.026	0.010	0.228
Wing length	0.026	0.034	0.050	0.129	0.133	0.148	0.271

P: P-value of randomization test, M: mean of simulated correlation coefficients, r: observed value of correlation coefficient. Subscript “null” denote no statistical control with respect to potential mate, “spatial” denote control of spatial accessibility to potential mate, and “age” denote statistical control of age of potential mate.

Table 6-13 Results of Mantel tests

Year	P_{culmen}	P_{wing}
2012	0.612	0.094
2013	0.418	0.358
2014	0.426	0.104
2015	0.734	0.444
2016	0.932	0.340
2017	0.908	0.908
2018	0.936	0.970
2019	0.578	0.500

P_{culmen}: results of analyses for culmen length, P_{wing}: results of analyses for wing length

Table 6-14 Selection of fixed effect structure in GLMM for number of fledglings

Model	AIC	Delta
Year + MaleAge + MaleWing	851.974	0.000
Year + MaleAge + MaleWing + FemaleWing	852.411	0.437
Year + MaleAge	852.421	0.447
Year + MaleAge + DifferenceWing	852.425	0.451
Year + MaleAge + FemaleAge + MaleWing	852.639	0.665
Year + MaleAge + MaleWing + DifferenceCulmen	852.771	0.797
Year + MaleAge + FemaleAge	853.019	1.045
Year + FemaleAge	853.157	1.183
Year + MaleAge + MaleWing + DifferenceWing	853.299	1.325
Year + LayDate + MaleAge + MaleWing	853.317	1.343
Year + MaleAge + MaleWing + FemaleWing + DifferenceCulmen	853.365	1.391
Year + MaleAge + FemaleAge + MaleWing + DifferenceCulmen	853.382	1.408
Year + MaleAge + FemaleAge + MaleWing + FemaleWing	853.533	1.559
Year + MaleAge + DifferenceCulmen + DifferenceWing	853.607	1.634
Year + MaleAge + FemaleAge + DifferenceWing	853.674	1.700
Year + FemaleAge + MaleWing	853.680	1.706
Year + MaleAge + DifferenceCulmen	853.686	1.712
Year + MaleAge + MaleCulmen + MaleWing	853.753	1.779
Year + LayDate + MaleAge	853.766	1.792
Year + MaleAge + MaleWing + FemaleCulmen	853.768	1.795
Year + MaleAge + FemaleWing	853.811	1.837
Year + LayDate + MaleAge + DifferenceWing	853.989	2.016
Year + FemaleAge + DifferenceWing	854.027	2.053
Year + LayDate + MaleAge + MaleWing + FemaleWing	854.055	2.081
Year + LayDate + MaleAge + MaleWing + DifferenceCulmen	854.060	2.086
Year + MaleAge + MaleWing + FemaleCulmen + FemaleWing	854.121	2.147
Year + MaleAge + MaleWing + DifferenceCulmen + DifferenceWing	854.158	2.184
Year + MaleAge + FemaleCulmen + DifferenceWing	854.195	2.221
Year + MaleAge + FemaleCulmen	854.217	2.243
Year + MaleAge + FemaleAge + DifferenceCulmen	854.218	2.244

Only the top 30 models are shown.

Table 6-15 Regression coefficients of the top model for number of fledglings

Variable	Estimate	SE	Z	P
Intercept	3.75	1.84	2.04	0.04
MaleAge (Y)	-0.30	0.13	-2.24	0.03
MaleWing	-0.02	0.01	-1.56	0.12
Year (2008)	-0.01	0.36	-0.02	0.98
Year (2009)	0.22	0.36	0.61	0.54
Year (2011)	0.08	0.30	0.28	0.78
Year (2012)	0.23	0.42	0.55	0.58
Year (2013)	-0.06	0.30	-0.20	0.84
Year (2014)	-0.84	0.33	-2.52	0.01
Year (2015)	-0.16	0.30	-0.55	0.58
Year (2016)	-0.15	0.28	-0.53	0.60
Year (2017)	-0.18	0.28	-0.67	0.50
Year (2018)	0.10	0.27	0.39	0.70
Year (2019)	0.00	0.27	0.01	0.99

Table 6-16 Model-averaged regression coefficients of models for number of fledglings

Variable	Estimate	SE	Adjusted SE	Z	P
Intercept	2.34	2.22	2.23	1.05	0.29
MaleAge (Y)	-0.26	0.14	0.14	1.91	0.06
MaleWing	-0.02	0.01	0.01	1.55	0.12
Year (2008)	-0.04	0.36	0.36	0.12	0.91
Year (2009)	0.18	0.36	0.36	0.49	0.63
Year (2011)	0.02	0.31	0.31	0.08	0.94
Year (2012)	0.13	0.42	0.43	0.30	0.76
Year (2013)	-0.15	0.30	0.31	0.51	0.61
Year (2014)	-0.94	0.34	0.34	2.76	0.01
Year (2015)	-0.26	0.31	0.31	0.86	0.39
Year (2016)	-0.22	0.28	0.28	0.80	0.43
Year (2017)	-0.26	0.28	0.28	0.92	0.36
Year (2018)	0.04	0.27	0.27	0.13	0.89
Year (2019)	-0.07	0.27	0.27	0.26	0.80
FemaleWing	0.01	0.01	0.01	1.09	0.28
DifferenceWing	-0.02	0.01	0.01	1.18	0.24
FemaleAge (Y)	-0.20	0.17	0.17	1.20	0.23
DifferenceCulmen	-0.10	0.10	0.10	0.99	0.32
LayDate	0.00	0.01	0.01	0.81	0.42
MaleCulmen	-0.04	0.10	0.10	0.47	0.64
FemaleCulmen	-0.03	0.07	0.07	0.45	0.65

Table 6-17 Selection of fixed effect structure in GLMM for number of recruits

Model	AIC	Delta
Year + LayDate + MaleAge + MaleWing	453.019	0.000
Year + MaleAge + MaleWing	453.624	0.605
Year + LayDate + MaleAge + DifferenceWing	453.647	0.628
Year + MaleAge + DifferenceWing	453.689	0.670
Year + LayDate + MaleAge + FemaleWing + DifferenceWing	453.753	0.734
Year + LayDate + DifferenceWing	453.852	0.833
Year + LayDate + MaleAge	453.921	0.902
Year + LayDate	453.964	0.945
Year + LayDate + MaleWing	454.109	1.090
Year + MaleAge	454.341	1.322
Year + LayDate + MaleAge + MaleWing + DifferenceWing	454.375	1.356
Year + MaleAge + FemaleWing + DifferenceWing	454.379	1.360
Year + LayDate + FemaleWing + DifferenceWing	454.405	1.386
Year + LayDate + MaleAge + MaleWing + FemaleCulmen	454.475	1.456
Year + LayDate + MaleAge + MaleWing + DifferenceCulmen	454.560	1.541
Year + MaleAge + MaleWing + DifferenceWing	454.679	1.660
Year + DifferenceWing	454.751	1.732
Year + LayDate + FemaleCulmen	454.799	1.780
Year + LayDate + FemaleCulmen + DifferenceWing	454.807	1.788
Year + LayDate + MaleAge + MaleWing + FemaleWing	454.827	1.808
Year + LayDate + MaleAge + FemaleCulmen + DifferenceWing	454.925	1.906
Year + LayDate + MaleAge + FemaleAge + MaleWing	454.999	1.980
Year + LayDate + MaleAge + MaleCulmen + MaleWing	455.014	1.995
Year + MaleAge + FemaleCulmen + DifferenceWing	455.020	2.001
Year + LayDate + MaleAge + FemaleWing	455.024	2.005
Year + LayDate + MaleAge + FemaleCulmen	455.088	2.069
Year + MaleAge + MaleWing + FemaleCulmen	455.121	2.102
Year + LayDate + MaleWing + FemaleCulmen	455.151	2.132
Year + LayDate + MaleAge + MaleWing + FemaleCulmen + DifferenceCulmen	455.178	2.159
Year + LayDate + MaleAge + FemaleCulmen + FemaleWing + DifferenceWing	455.198	2.179

Table 6-18 Regression coefficients of the top model for number of recruits

Variable	Estimate	SE	Z	P
Intercept	4.86	3.48	1.40	0.16
LayDate	-0.02	0.01	-1.63	0.10
MaleAge (Y)	-0.47	0.28	-1.67	0.10
MaleWing	-0.04	0.02	-1.68	0.09
Year (2008)	-0.79	1.16	-0.68	0.50
Year (2009)	1.19	0.71	1.68	0.09
Year (2012)	1.62	0.78	2.06	0.04
Year (2013)	1.25	0.65	1.92	0.05
Year (2014)	0.39	0.69	0.57	0.57
Year (2015)	1.05	0.65	1.61	0.11
Year (2016)	0.80	0.63	1.28	0.20
Year (2017)	0.91	0.63	1.44	0.15
Year (2018)	0.85	0.62	1.37	0.17

Table 6-19 Model-averaged regression coefficients of models for number of recruits

Variable	Estimate	SE	Adjusted SE	Z	P
Intercept	1.80	4.38	4.40	0.41	0.68
LayDate	-0.02	0.01	0.01	1.65	0.10
MaleAge (Y)	-0.46	0.29	0.29	1.59	0.11
MaleWing	-0.03	0.02	0.02	1.47	0.14
Year (2008)	-0.81	1.16	1.17	0.69	0.49
Year (2009)	1.15	0.71	0.72	1.61	0.11
Year (2012)	1.45	0.78	0.78	1.85	0.06
Year (2013)	1.08	0.65	0.66	1.64	0.10
Year (2014)	0.25	0.69	0.69	0.36	0.72
Year (2015)	0.90	0.66	0.66	1.35	0.18
Year (2016)	0.67	0.63	0.64	1.05	0.29
Year (2017)	0.79	0.63	0.64	1.24	0.21
Year (2018)	0.73	0.62	0.63	1.16	0.25
DifferenceWing	-0.04	0.03	0.03	1.40	0.16
FemaleWing	-0.03	0.03	0.03	1.03	0.30
FemaleCulmen	0.13	0.14	0.14	0.91	0.36
DifferenceCulmen	-0.13	0.19	0.20	0.67	0.51
FemaleAge (Y)	-0.05	0.35	0.35	0.14	0.89
MaleCulmen	-0.01	0.18	0.18	0.07	0.95

Table 6-20 Regression coefficients of explanatory variables for survival rates and detection probability

Model	Variables	Mean	SE	2.5%	97.5%
Survival rate	Year (2012)	2.11	0.00	1.30	3.13
	Year (2013)	1.43	0.00	0.90	2.01
	Year (2014)	1.66	0.00	1.13	2.25
	Year (2015)	1.74	0.00	1.22	2.33
	Year (2016)	0.76	0.00	0.38	1.17
	Year (2017)	1.12	0.00	0.70	1.56
	Year (2018)	1.23	0.00	0.76	1.75
	Sex (Male)	-0.24	0.00	-0.59	0.10
	Age (Juvenile)	4.79	0.02	2.35	9.54
	FemaleCulmen	-0.16	0.00	-0.39	0.07
	MaleCulmen	0.03	0.00	-0.14	0.20
	FemaleWinge	-0.32	0.00	-0.62	-0.03
	MaleWing	-0.10	0.00	-0.28	0.09
Detection probability	Researcher (Iwasaki)	1.02	0.00	0.64	1.42
	Researcher (Sawada)	0.86	0.00	0.55	1.19
	Sex (Male)	0.89	0.00	0.48	1.29

Survival rate was modeled with linear combination of year specific intercept, sex (male of female), age (juvenile or adult), culmen length and wing length. Regression coefficients of culmen length and wing length were separately estimated for each sex. Detection probability was modeled with linear combination of researcher specific intercept and sex. Mean and SE: posterior mean and standard error of the mean. 2.5% and 97.5%: percentile of posterior distribution

Appendix

Standardization procedures

Before analysis, all body size measurement data were statistically controlled for difference between measurers and years to avoid false positive correlation when pooled heterogeneous measurement data. Using Sawada et al.'s (2021b) estimates of the effect of measurers and years, all measurements were standardized to the measurement in 2019 by AS. For examples, as culmen length measurements by TI and AS was estimated to be -0.04 and 0.21 mm larger than by KA, 0.21 - (-0.21) = 0.25 mm was added to measurements by TI so that the value to take the same mean as the measurements by AS. Effect of year was adjusted in the same manner. Values used to this adjustment are given in Table 6-3 and 6-4 of this study or supplementary tables in Sawada et al. (2021b).

Data matrix

Combining the measurement data and data from breeding monitoring, territory mapping, and sex and age determination, six data frames (A-F) were generated on R so that the subsequent analyses can immediately use the data (Figure A6-1).

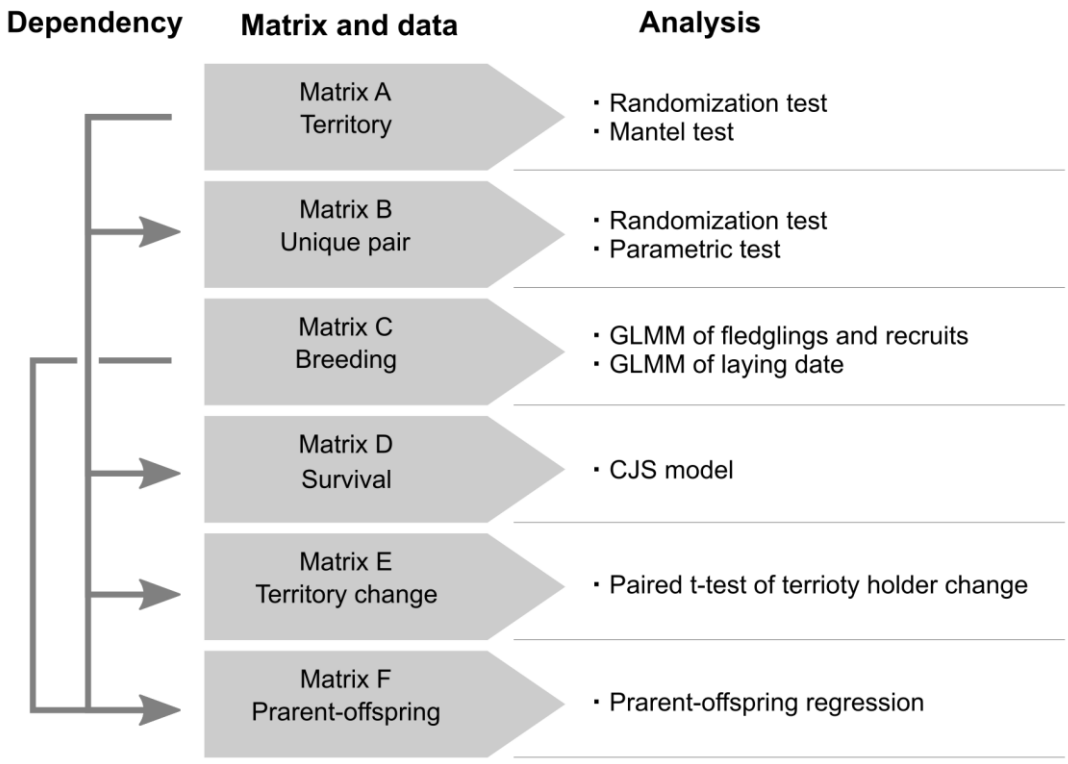


Figure A6-1 Data matrix and on which analyses based

Data matrix A is the one which contains the data for all territories of all years. Each row corresponds to a territory in a year. It contains UTM coordinates, identity of the territory holder male, identity of the territory holder female, age of the territory holders,

and body size measurements of the territory holders in the year. Because not all individuals were measured in the all years when they were present, mean of measurements were used as surrogate measurements in such data-lacking year. This data was used for correlation analysis by randomization test, analysis of similarity of body size between females and their potential mates, and used for generating data matrix B, D, E and F.

Data matrix B is a matrix derived from A. Matrix B contains rows of matrix A which are corresponding to the territories where male and female territory holders are ringed. Duplicated pairs in matrix A are also omitted in matrix B, except the year when they are identified as pair at first. Each row contained UTM coordinates, identity of the territory holder male, identity of the territory holder female, age of the territory holders, first-time measurement data and last-time measurement data for corresponding individuals if they were measured across multiple years. This data was used for correlation analysis by parametric test, correlation analysis by randomization test, analyses for mechanism 3.

Data matrix C is the one which contains the data for all breeding attempts. Each row corresponds to a breeding attempt. It contained, egg laying date, identity of father, identity of mother, age of the parents, and body size measurements of them. Unlike data matrix A, mean across years were used as measurement data in this matrix, because this matrix was used for analysis of relationships between reproductive success and attributes of parents. This data was used for analyses for number of fledglings, number of recruits and egg laying date, and used for generating data matrix F.

Data matrix D is the one which contains survival history. Number of rows equals to the number of individuals which we marked or recaptured (resighted) from 2012 to 2019. Number of columns equals to the number of years in which we marked or recaptured (resighted) the individuals, i.e. 8 (= 2019 – 2012 +1). Each row corresponds to an individual. If individual was captured or recaptured (resighted) in year 2011 + j, (i, j) element of the matrix = 1, otherwise 0. This matrix was generated based on matrix A. This data was used for survival analyses by Cormack-Jolly-Seber model.

Data matrix E is the one which contains attributes of previous and present territory holder. Each row corresponds to a territory change event and contained body size measurement data of the territory holders. This data was used for analyses for body size of previous and present territory holder.

Data matrix F is the one which contains the measurement data for father-mother-offspring triads. As this data was used for parent offspring regression, and therefore there should be one measurement value for an individual, mean values across years were used for measurement data in the matrix. This data was used for analyses parent offspring regression.

Controlling for temporal accessibility

To control for temporal accessibility of potential mates in randomization tests, I randomly assigned males while considering the age of females and males. There are three reasons

to this treatment: 1) There was a tendency of age assortative mating (see below). 2) Yearlings tend to breed late probably due to their late pair formation (see below). 3) Yearlings and adults have slight size difference (Sawada et al. 2021b).

To show the age assortative mating, I applied Fisher's exact test on a cross table which contains frequencies of pairs of 1) yearling male and yearling female, 2) yearling male and adult female, 3) adult male and yearling female, and 4) adult male and adult female. The test is conducted for yearly data and for pooled data.

There were significant age-assortative mattings in some years (Table 6-5, Fisher's exact test, 2018, P = 0.034; 2019, P = 0.001) and throughout the study period (Table 6-5, Fisher's exact test, P = 0.000).

To show the late breeding of yearlings, using data matrix C, I evaluated the effects of age on egg laying date. We constructed Normal GLMM models with all fixed effects (Year, Father age, Mother age), and all possible combinations of random effects (Mother ID, Father ID). Each egg laying date was standardised by subtracting mean egg laying date of the year in which the data was collected.

I included these random effects because our data contained multiple data from the same parents. Varying the combination of random effects, a model with Mother ID gave the smallest AIC value (Table 6-6). Therefore, I used GLMM models with Mother ID in the subsequent analyses.

Then, I searched for best combination of fixed effects in terms of AIC by dredge function in *MuMIn* package. Because the best model gave the AIC value which is much smaller than the second model (ΔAIC = 6.17, Table 6-7), I interpreted the result without doing model averaging.

The best model for egg laying date included significant effect of male age and female age (Table 6-7). From this model, egg laying date in a pair with yearling males had 2.97 days later compared to a pair with adult males (Table 6-8, coefficient ±SE =2.97 ±1.31, $t_{257.24}$ =2.27, P = 0.02) and egg laying date in a pair with yearling females had 4.79 days later compared to a pair with adult females (Table 6-8, coefficient ±SE =4.79 ±1.53, $t_{274.23}$ =3.13, P = 0.00).

Mantel test

To assess similarity among spatially accessible individuals, I described and tested spatial autocorrelation in body size by Mantel test. I focused on geographic distance and size difference from females to males because our interest is whether spatially accessible males for females are similar to the females. Therefore, input matrixes were non-square $n_f \times n_m$ matrix X and Y, where n_f and n_m are the number of female and male, respectively. Elements of the matrixes x_{ij} and y_{ij} are the distance and absolute size difference between the corresponding female and male. Note that this is not a common setting for Mantel test because the test is often applied to square matrix to ask, for example, whether males are similar to spatially neighbouring "males". I followed original description of the test (Mantel 1967) to apply the test to non-square matrixes. Test statistic M was defined as

$\sum\sum x_{ij}y_{ij}$ (summation is taken over all i and j). Null distribution of M and corresponding P-value was obtained by permutation test. This test was applied to all years (2012 to 2019) separately for each of culmen length and wing length.

Number of fledglings

Using data matrix C, I evaluated the effects of body size on number of fledglings. I constructed Poisson GLMM models with all fixed effects (Year, Egg laying date, Father age, Mother age, Father culmen length, Father wing length, Mother culmen length, Mother wing length, Difference in culmen length between parents, Difference in wing length between parents), and all possible combinations of random effects (Mother ID, Father ID). Egg laying date is standardised by subtracting mean egg laying date of the year.

I included these random effects because our data contained multiple data from the same parents. However, variance estimates in relation to the random effects were zero and, the model without the random effect gave smaller AIC value than the model with the random effect (Table 6-5). Therefore, I dropped the random effects from subsequent analyses, i.e. I used GLM instead of GLMM.

Then, I searched for best combination of fixed effects in terms of AIC by *dredge* function in *MuMIn* package. Top-ranked models with ΔAIC < 2 (difference from minimum AIC smaller than 2) were model averaged by *model.avg* to obtain model averaged regression coefficients and corresponding P-values. Specifically, "subset" coefficients in the output of *model.avg* were used for interpretation.

Number of recruits

Using data matrix C, I evaluated the effects of body size on number of recruits. I constructed Poisson GLMM models with all fixed effects (Year, Egg laying date, Father age, Mother age, Father culmen length, Father wing length, Mother culmen length, Mother wing length, Difference in culmen length between parents, Difference in wing length between parents), and all possible combinations of random effects (Mother ID, Father ID). Egg laying date is standardised by subtracting mean egg laying date of the year.

I included these random effects because our data contained multiple data from the same parents. However, variance estimates in relation to the random effects were zero and, the model without the random effect gave smaller AIC value than the model with the random effect (Table 6-6). Therefore, I dropped the random effects from subsequent analyses, i.e. used GLM instead of GLMM.

Then, I searched for best combination of fixed effects in terms of AIC by *dredge* function in *MuMIn* package. Top-ranked models with ΔAIC < 2 (difference from minimum AIC smaller than 2) were model averaged by *model.avg* to obtain model averaged regression coefficients and corresponding P-values. Specifically, "subset" coefficients in the output of *model.avg* were used for interpretation.

Definition of territory change

To evaluate body size dependency of competitiveness, I compared body size between previous territory holders and present territory holders. Because the boundaries of territories were not necessarily obvious, I used following procedures to judge the holder of territory i in year t+1 is different form the holder of territory i in year t:

1) Let (x_{it}, y_{it}) be the coordinate of the capture location (or location of nest if available) of the territory holder of territory i in year t.
2) Define (x_{it}, y_{it}) as the coordinate of the territory i in year t.
3) Obtain distance from (x_{it}, y_{it}) to all coordinate of the territories in year t+1.
4) Let j is the number of the territory which give the smallest distance to (x_{it}, y_{it}) among all territories in year t+1.
5) If the distance is smaller than 4*129m, I considered the territory i in year t and the territory j in year t+1 as identical. That is, I considered the two territories identical if two hypothetical circular territory have non-zero overlap (Figure A6-2).
6) Change of territory holders are judged based on if the holder of territory i in year t is the same as the holder of territory j in year t+1 or not.

After I identified all cases which meet these conditions, I excluded all the cases in which the presence of previous territory holder were not confirmed in the years after the territory changes, because such case can occur simply because death of previous territory holders.

Note that 129 m is the radius of a circle of average-size territory for this owl. Multiplying by 4 was done to consider a situation where coordinate of territory i in year t and coordinate of territory j in year t+1 are exactly on opposite side of least-overlapped territories.

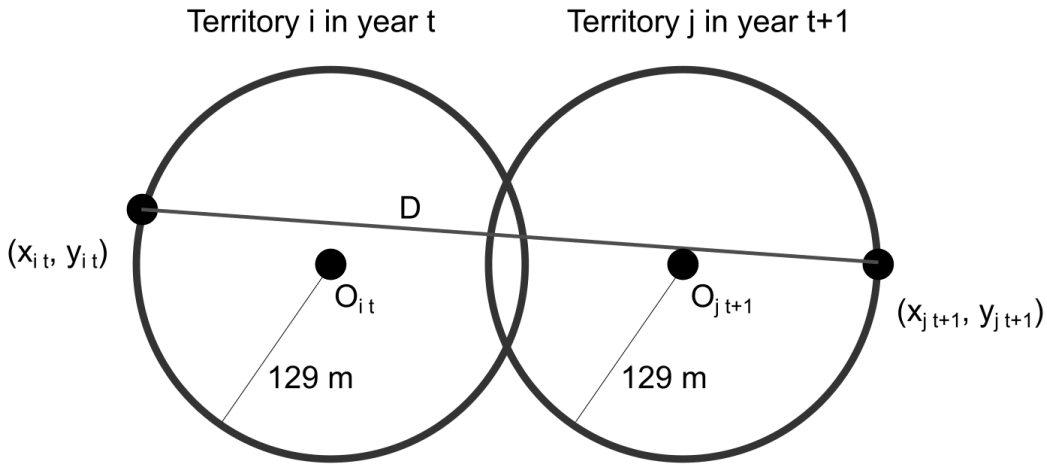


Figure A6-2 Graphical representation of Step 5) in the procedures

O is the centre of territory. If two individuals are captured at just the opposite side of their non-overlapping territories, distance between the individuals should be more than

4*129 m.

Test of difference between two correlation coefficients

I compared correlation coefficients at first-time measurement and those at last-time measurement. Statistical significance was based on Z test using Fisher's Z transformation of correlation coefficients.

Let z_{before} and z_{after} be Fisher's Z transformation of correlation coefficients which are calculated from the first-time measurement and the last-time measurement, respectively. Test statistic Z and P-value were calculated by following formula:

$$Z = \frac{z_{\text{after}} - z_{\text{before}}}{\sqrt{\frac{1}{n_{\text{after}} - 3} + \frac{1}{n_{\text{before}} - 3}}} = \frac{z_{\text{after}} - z_{\text{before}}}{\sqrt{\frac{2}{n - 3}}} \sim Normal(0,1)$$

Here, n_{after} and n_{before} are the sample size. In this study they are identical.

Chapter 7

Evaluating the existence and benefit of major histocompatibility complex-based mate choice in an isolated owl population

Abstract
How mate preferences evolve in the first place has been a major conundrum for sexual selection. Some hypotheses explaining this assume fitness benefit derived from subsequent generations. Major Histocompatibility Complex (MHC)-based mate choice is a representative example of the mate choice that is associated with such trans-generational mechanisms. To provide evidences for fitness benefit of MHC-based mate choice, previous studies assessed the association between own MHC genotype and own fitness components. However, the association between MHC-based mate choice in the parental generation and fitness components in the resultant offspring generation has only rarely been measured in wild populations. Focusing on the isolated population of the monogamous Ryukyu Scops Owl (*Otus elegans interpositus*) on Minami-daito Island, Japan, I found evidence of MHC-based mate choice. However, I found no evidence of MHC-based mate choice increasing own reproductive success or offspring survival. This is a rare case study that directly examines the existence of the trans-generational indirect benefit of MHC-based mate choice for genetic compatibility from trans-generational data in a wild bird population. By investigating the fitness benefits of mate choice, this study serves to facilitate our understanding of the evolution of MHC-based mate choice.

Introduction

The evolution of mate choice or mate preference presents a major conundrum for sexual selection (Kirkpatrick and Ryan 1991; Andersson 1994; Kokko et al. 2003). Mate choice is the tendency for non-random mating with respect to one or more varying traits (Kokko et al. 2003). If such a tendency of mate choice exists, then the evolution of traits is easy to understand. However, how such preferences evolve in the first place is not obvious (Jones and Ratterman 2009). Furthermore, if some traits are preferred, then genetic variance under the traits may be eroded and selection pressures may not act anymore (lek paradox, Miller and Moore 2007). Therefore, a full understanding of sexual selection needs to elucidate how and to what extent preferences provide fitness benefits to choosers and how genetic variation is maintained.

Since the era of Darwin, evolutionary biologists have accumulated many case studies of sexual selection across animal taxa. Morphological traits (e.g. body size and colouration) and behavioural traits (e.g. courtship displays) have often been shown to

become the targets of mate choice. Andersson and Simmons (2006) suggested five mechanisms explaining how mate choice may evolve with respect to such traits. 1) direct phenotypic effects, 2) sensory bias, 3) Fisherian sexy sons, 4) indicator mechanisms, 5) genetic compatibility mechanisms. The latter three are genetically based mechanisms and they accompany problem of lek paradox. Because mechanisms 4) and 5) assume fitness benefit derived from subsequent generations (Møller and Jennions 2001), testing them has proven especially difficult in field studies where trans-generation data is hard to collect.

Major Histocompatibility Complex (MHC)-based mate choice is a representative example of the mate choice that is associated with the previously mentioned genetically based mechanisms (Tregenza and Wedell 2000; Milinski 2006; Eizaguirre et al. 2009). MHC is a gene complex of the vertebrate immune system and a key molecular underpinning for mate choice in vertebrates (Kamiya et al. 2014). Non-random mating with respect to MHC has been studied across vertebrate taxa (Bernatchez and Landry 2003; Ziegler et al. 2005; Milinski 2006; Yamazaki and Beauchamp 2007). Based on the association between MHC property and body odour, olfactory cues have been proposed as the actual target of MHC-based mate choice (Yamazaki et al. 1979; Olsson et al. 2003; Leclaire et al. 2017). Although dependence on smell varies across vertebrates, there is little evidence of phylogenetic variation in the use of MHC in mate choice (Kamiya et al. 2014).

Based on MHC's high-level polymorphism and its relevance to the immune system, we recognize two benefits in MHC-based mate choice: from genetic compatibility and from good genes (Puurtinen et al. 2009). For example, if diverse MHC alleles widen the range of resistible pathogens, choosing a mate with a different set of alleles from one's own would indirectly benefit the chooser because the offspring from such a pair would be expected to have diverse MHC alleles and thus high immunocompetence (Penn and Potts 1999; Milinski 2006). Furthermore, if a specific MHC allele confers resistance to specific parasites, choosing a mate with that allele is indirectly beneficial to the chooser because offspring from such pairs are expected to have the advantageous allele and become adaptive, provided this allele is not present in the chooser individual and/or it is inherited by offspring.

Although the two examples mentioned above focus on the genetic benefit obtained from offspring generation, MHC-based mate choice may also provide direct benefit for the present generation, as the genetic background behind parasite mediated sexual selection (Hamilton and Zuk 1982). Because MHC is an immunologically functional gene complex, the chooser sex might increase its reproductive success when mating with a healthy individual with specific MHC alleles (Hamilton and Zuk 1982; Milinski 2006). Hence, relating mate choice to reproductive success and fitness components of offspring while considering MHC of parents will help to elucidate direct and indirect benefits of the choice. However, previous studies that have sought the fitness benefits of MHC-based mate choice have typically related the subject's MHC genotype to its own

fitness component, not to its offspring's fitness components (Paterson et al. 1998; Banks et al. 2010; Garroway et al. 2013; Bateson et al. 2016). The association between parental MHC genotypes and their offspring's fitness components has been largely overlooked in wild populations (but see, Consuegra and Garcia De Leaniz 2008; Brouwer et al. 2010). From a general perspective, it is necessary to test such associations in order to argue for the adaptive significance of MHC-based mate choice. An interesting aspect of the benefit of MHC-based mate choice is its link to inbreeding avoidance (Zelano and Edwards 2002). Since MHC exhibits great diversity, differences between individuals in their MHC genotypes has the potential to reflect relatedness between them (Potts and Wakeland 1990). If this is the case, MHC-based mate choice might not only be a mate choice in relation to immunocompetence but also a means of inbreeding avoidance (Potts et al. 1994). Because inbreeding avoidance increases the heterozygosity of offspring at a genome-wide level, the benefit of MHC-based mate choice might be enhanced and/or confounded by the effects of being heterozygous at loci other than MHC (Potts et al. 1994; Thoß et al. 2011). Teasing apart these effects is important, firstly because correlation between MHC property and genome-wide relatedness is a fundamental assumption of MHC's role as a cue for kin-recognition, and secondly because beneficial effects of MHC-base mate choice could be overestimated if the choice relieves inbreeding depressions. Therefore, analysis of MHC-based mate choice is better interpreted by coupling the analysis with inbreeding avoidance (Sepil et al. 2015).

In this study, I began by assessing whether MHC-based mate choice occurs in an avian population. Then, as I detected significant MHC-based mate choice (see Results), I assessed whether the mate choice provides both direct and indirect benefits. Specifically, I focused on the isolated population of the monogamous Ryukyu Scops Owl (*Otus elegans interpositus*), which is confined to Minami-daito Island, Japan (Ornithological Society of Japan 2012). This owl population provides an ideal opportunity to study MHC-based mate choice because ongoing long-term monitoring allows us to access individual-level life history data (Takagi et al. 2007a; Akatani et al. 2011; Takagi and Akatani 2011; Sawada et al. 2018a), and because it fulfils certain conditions where MHC-based mate choice might occur (see Methods). Firstly, long-lived monogamous species, such as raptors and owls, might rely on a genetically based mate choice system because the genetic benefits of such a choice are crucial when choosing a single, lifelong mate (Zelano and Edwards 2002). Secondly, species in which there is little or no social context for kin recognition, but in which there is a high probability of inbreeding in isolated habitat, may have a greater requirement for a genetically based kin recognition system, such as MHC-based mate choice, in order to avoid inbreeding (Jordan and Bruford 1998).

The aims of this study were: 1) to establish whether or not MHC-based mate choice and inbreeding avoidance occurs in the Ryukyu Scops Owl, 2) to measure the direct benefit of the choice obtained during one generation, and 3) to measure the indirect

benefit of the choice obtained through subsequent offspring generations. Using two types of analyses, I show signs of MHC-based mate choice and inbreeding avoidance in the Ryukyu Scops Owl. I then tested whether or not such a choice could increase individual reproductive success (direct benefit) and offspring survival (indirect benefit).

Material and Methods

Material

I studied MHC-based mate choice in the Ryukyu Scops Owl population, which is endemic to Minami-daito Island (Ornithological Society of Japan 2012). This small, isolated, oceanic island with an area of about 32 km^2 lies about 360 km east of Okinawa Island in the north-western Pacific. Monogamous scops owl pairs maintain year-round territories in the wind-shelter belt forests on the island (Takagi et al. 2007a,b). Most individuals disappear from their territories after three to five years (indicative of mortality), but some owls have lived for more than 12 years (Sawada unpublished data). Divorce has rarely been observed (Iwasaki unpublished data). Nesting takes place mainly in natural cavities in Fan Palms (*Livistona chinensis*), Australian Pine (*Casuarina* spp.), or in nest boxes (Takagi et al. 2007a,b). The scops owls are strictly nocturnal, and have a population estimated to be 210 pairs (Takagi et al. 2007a). Because of its small size, the population includes closely related individuals (Sawada et al. 2018a). For example, in 2016, there were 60 parent-offspring pairs, 15 full-sibling pairs and six half-sibling pairs among 227 adults (Sawada et al. 2018a). Structure analysis (Pritchard et al. 2000) has shown that the population on Minami-daito differs from those on other islands of the Ryukyu archipelago in regard to microsatellite allele frequency, indicating a low probability of immigration into the population and a high probability of inbreeding (Saito and Takagi unpublished data).

Samples

Sample consisted of 322 individuals (in 2016). This included 50 confirmed families (97 parents and their 95 offspring but note that for three of the 50 families I missed maternal samples) and 16 confirmed pairs (males and females which frequently gave duet calls) (Takagi et al. 2007a). Blood samples of the 322 individuals were collected by brachial venepuncture during a long-term study begun in 2002. Specifically, 157 samples were collected during 2005 to 2015, and 165 were collected during February to July 2016. The samples were preserved in 99.5% ethanol at 4°C until DNA extraction using a DNeasy Blood & Tissue Kit (Qiagen, QIAGEN, Valencia, CA). The locations of all individuals were recorded.

Genotyping

(a) (a) Microsatellite

All 322 individuals were genotyped at 12 microsatellite loci, using markers Oe022, Oe085, Oe3-7, Oe084, Oe171, Oe128, Oe029, Oe53, Oe129, Oe081, Oe045, and Oe149

(Hsu et al. 2006b; Hogan et al. 2007). I followed the same genotyping procedures described in (Sawada et al. 2018a).

(b) (b) MHC

Ninety-three individuals (a subset of parents in total N) were genotyped also at MHC class II genes. To prepare the amplicon library for next generation sequencing using an Ion Personal Genome Machine (Thermo Fisher Scientific, Waltham, MA), I amplified exon 2 of MHC class II using a fusion primer pair. Each of the fusion primer pairs consists of three components in the following manner: adaptor sequence (A in forward, trP1 in reverse) in 5' end, 13-bp of multiplex identifier (MID, Table 7-1), locus specific primer (Os2F in forward, Os2R in reverse) in 3' end. Their sequences are as follows (each component is in brackets):

forward 5'-[CCATCTCATCCCTGCGTGTCTCCGACTCAG][MID][CACACACAGGGGTTTTCC]-3';

reverse 5'-[CCTCTCTATGGGCAGTCGGTGAT][MID][AACGCGTGGCCACGCGCTCA]-3' (See Table 7-1). Os2F and Os2R were newly designed based on part of the sequence for the Eurasian Scops Owl's (*O. scops)* MHC class IIB allele (Accession: EF370937), to which previously designed universal primers for owls bind (Stri2F and Stri2R, Alcaide et al. 2007). The PCR reaction volume was 10 µl containing 1X PrimeSTAR GXL Buffer (Mg2+ plus), 2.0 mM each dNTP Mixture, 0.2 µM each primer, 0.25 units of PrimeSTAR GXL DNA Polymerase (TaKaRa, Japan), and about 10 ng of genomic DNA. Reaction conditions were 1 min at 98°C followed by 35 cycles of 10 s at 98°C, 15 s at 59°C and 30 s at 68°C, and finally 7 min at 68°C. Equal volumes of PCR products were pooled as an amplicon library. The amplicon library was sequenced on Ion PGM with a Hi-Q Sequencing kit (Thermo Fisher Scientific, Waltham, MA) following the manufacturer's instructions, at the National Institute for Environmental Studies (Ibaraki, Japan). Conspecific samples (338) for other projects were run at the same time.

Genotyping of MHC was performed in line with the following procedures: Claident (Tanabe and Toju 2013) was used to filter out short sequences below 200 bp and sequences that did not contain MID sequences from the original FASTQ files. Filtered files were then introduced to AmpliSAT (Sebastian et al. 2016) as input files. AmpliSAT is a set of online tools that provides a series of analyses of amplicon sequencing experiments. Following the pipeline manual, I used three functions included in AmpliSAT, namely AmpliCLEAN, AmpliCHECK, and AmpliSAS. I started analysis with AmpliCLEAN to remove sequences with average Phred quality scores of lower than 20. Subsequently, the output of AmpliCLEAN was used as the input for AmpliCHECK. I chose the "Technology" option as "454/IonTorrent". Then, AmpliSAS genotyped individuals using the "Technology" option as "454/IonTorrent". I set parameters as follows: Maximum number of alleles per amplicon = 20, Minimum amplicon depth =

100, Minimum amplicon frequency for filtering parameters = 4.0%. Parameters not mentioned were set as default values because they were automatically optimized for the selected sequencing technology ("454/IonTorrent"). See Appendix for parameter setting. Although our multilocus amplification does not allow us to assign each sequence to a specific locus, I hereafter refer to the resultant sequences detected in the genotyping procedure as "alleles" and presence or absence of the alleles in individuals as their "genotype".

To validate the allele calling, I directly Sanger-sequenced the MHC locus of 16 individuals out of the 93-typed individuals. The composition of the PCR reaction solution and the condition of the PCR reaction were the same as those used in library preparation, with the exception of using primer OS2F and OS2R instead of the fusion primers. Sequencing reactions were performed using the Big Dye Terminator Cycle Sequencing kit v3.1 (Applied Biosystems, Foster City, CA), and the products were sequenced on an ABI PRISM 3730 Genetic Analyser. I checked whether their chromatograms had duplicate peaks at heterozygous sites, which are to be expected from genotypes determined by Ion PGM and AmpliSAT.

The output of Ion PGM, after quality filtering by Claident and AmpliCLEAN, included 568,607 reads, of which 93,406 were derived from 93 individuals' sequences used in the current study. AmpliSAS genotyped the 93 individuals with a mean reading depth per individual of 957.882 reads (SD = 610.250, range = 179-3345). There were 11 alleles within the 93 individuals, which I named Otel-DAB*01, …, Otel-DAB*10, and Otel-DAB*12 (Table 7-2, DDBJ Accession: LC340383-LC340392 and LC340394). No significant correlation between reading depth and number of alleles was detected for the 93 individuals (Pearson product moment correlation: $r = 0.163$, $N = 93$, $t_{91} = 1.580$, $P = 0.118$). Chromatograms of Sanger-sequencing of 16 individuals had duplicate peaks at heterozygous sites, which were expected from genotypes determined by Ion PGM.

Standard population genetic analysis

For each microsatellite locus, sample size, number of alleles, observed heterozygosity, and expected heterozygosity were calculated using Cervus (Kalinowski et al. 2007). F_{IS} (Weir and Cockerham 1984) and P-values for deviation from the Hardy-Weinberg equilibrium (HWE) were obtained using Genepop (Raymond and Rousset 1995). Analysis parameters were: Dememorization number = 10,000, Number of batches = 10,000, Number of iterations per batch = 10,000. Holm correction was applied to the HWE test (Holm 1979). Results of these analyses are summarized in Table 7-2. No significant deviation from HWE was found (Table 7-3).

I calculated the number of alleles per individual at the MHC locus. I aligned and checked the sequences to characterize sequence length, indels, substitutions, and nonsense mutations. Reading frame and peptide binding region (PBR) were inferred from alignment with human leukocyte antigen class II allele DRB1*0101 (Accession: S40615, Brown et al. 1993). The number of amino-acid substitutions between alleles and the

occurrence of nonsense mutations were checked from translated amino acid sequences with reading frame inferred above. All MHC alleles had lengths of 262-bp and had neither indels nor nonsense mutations. The numbers of nucleotide and amino-acid substitutions between alleles were 1-48 bp and 1-25 aa, respectively. The number of alleles per individual ranged from one to five (mean +SD = 3.237 +0.813), indicating that there are at least three MHC class II loci in the Ryukyu Scops Owl.

Parentage analysis

Cervus was used to detect pairs in which extra-pair fertilization (EPF) might have occurred. I excluded the three offspring for which I had no maternal samples, thus conducted paternity analysis of 92 offspring. Breeding females were considered as mothers and all males were assigned as potential fathers. As a preliminary analysis of population size indicated that there were about 300 males (Sawada unpublished data), the parameter setting used in the simulation step was: Offspring = 10,000, Candidate fathers = 300, Prop. sampled = 0.50, Prop. loci typed = 0.99, Prop. loci mistyped = 0.0216, Minimum typed loci = 11, Calculate confidence using = "LOD". See Figure 7-1 for data utilization and Appendix for parameter settings.

When there were multiple mismatches between a mother and all of her offspring, those individuals were excluded on the assumption that the mother had been misidentified. When there were multiple mismatches between a mother and some of her offspring, those offspring were suspected to be the result of egg dumping. When the father assigned with a confidence level of 80% was the same as that observed in the field, he was considered to be the genetic father. Otherwise, such offspring were suspected to be the result of EPF.

These analyses showed that one female was likely misidentified as a mother (Figure 7-1). Therefore, I excluded her, her mate and two offspring from all subsequent analyses. I detected four offspring suspected of being the results of EPF and one of egg dumping (Figure 7-1). I did not exclude their apparent parents from the mate choice test (see below) because I focused on the choice of social mates. However, I excluded them from the survival analysis (see below) because their survival should be interpreted through the MHC genotype of their genetic parents to consider the genetic benefits of mate choice. Because EPF was suspected in so few cases (four among 92 individuals, see results and Figure 7-1), I did not test for an association between MHC and EPF.

Genetic index to mate choice

In order to test for female MHC-based mate choice, I measured 11 genetic criteria on which females might rely: Relatedness, MHCshare, $AAdist_{nonPBR}$, $AAdist_{PBR}$, MHCdiversity, and MHCallele1, …, MHCallele6. Relatedness was estimated from multilocus microsatellite genotypes using Queller and Goodnight's method (Queller and Goodnight 1989). MHCshare was calculated as the proportion of shared MHC alleles to all of their alleles: $2N_{AB}/ (N_A + N_B)$ where N_A and N_B are the number of alleles in individuals A and B, and N_{AB} is the number of alleles shared by both (Wetton et al. 1987).

$AAdist_{nonPBR}$ was calculated as the mean of the summation of the number of amino acid substitutions within the nonPBR region among possible pairwise combinations of their alleles (Landry et al. 2001; Juola and Dearborn 2012). $AAdist_{PBR}$ was the same as $AAdist_{nonPBR}$ except that it was based on the PBR region. Because functional difference between alleles depends on amino-acid sequences, $AAdist_{nonPBR}$ and $AAdist_{PBR}$ are expected to capture many more functional differences than MHCshare. MHCdiversity was defined as the number of MHC alleles carried by a male (Richardson et al. 2005). Because I found 11 MHC alleles in total (see Results), the previous four indices (MHCshare, $AAdist_{nonPBR}$, $AAdist_{PBR}$ and MHCdiversity) were calculated from the genotypes based on the 11 alleles. Then, MHCallele1, …, MHCallele6 were defined as binary variables (either "1" or "0") depending on whether or not the individual had MHC allele Otel-DAB*01, …, Otel-DAB*06 (see genotyping result in Results). The remaining five MHC alleles were not used because their low frequency became a problem when their presence or absence was used as a binary variable in statistical analyses (see Appendix).

As I found non-random mating in terms of Relatedness and $AAdist_{PBR}$ (see Results), it is possible that the MHC-based mate choice was a means of inbreeding avoidance (Sepil et al. 2015). Therefore, I used Sepil et al.'s (2015) method to control for possible effects of Relatedness on $AAdist_{PBR}$. Firstly, each of Relatedness and $AAdist_{PBR}$ were standardized by z-transformation and then the Relatedness-derived z-value was subtracted from the $AAdist_{PBR}$-derived z-value. I defined this difference as $zzAAdist_{PBR}$. Then I conducted the same mate choice tests on $zzAAdist_{PBR}$ to see if the signs of MHC-based mate choice remained after controlling for the effect of relatedness. I also tested for correlation between Relatedness and $AAdist_{PBR}$ using the Mantel test.

Relatedness was estimated using SPAGeDi 1.5 (Hardy and Vekemans 2002). MHC amino acid substitutions were counted using MEGA7 (Kumar et al. 2016). All genetic indices of MHC were calculated using R 3.1.3 (R Core Team 2017).

Mate choice test

I used two methods to test deviation from random mating. Firstly, I used a randomization test (used in many MHC studies) consisting of the following steps: 1) Randomly assign a male to each female to simulate random mating; 2) Average genetic index of the simulated pairs; 3) Repeat step 1) and step 2) 1,000 times; 4) Generate distribution of mean genetic index; 5) Compare observed value of mean genetic index to the distribution and obtain P-values. In step 1), males within 1,145 m were randomly assigned to females, considering the female's spatial accessibility to males (Sepil et al. 2015). Note that 1,145 m is the median natal dispersal distance of female Ryukyu Scops Owls (Matsuo et al. unpublished data, Sawada et al. 2018a). In step 5), two-tailed P-values for deviations from random mating were calculated as twice the proportion of the simulated means, which have more extreme values than observed means (Sardell et al. 2014). See Figure 7-2 for schematic diagrams of this procedure and Figure 7-3 for data used in this test.

Secondly, I used a recently developed GLMM approach (Santos et al. 2016b, 2017). In this analysis, females are assumed to have opportunities to choose males who will become the fathers of their offspring. Each offspring is considered to be the result of a female's mate choice. Analysis involved the following steps: 1) List candidate fathers of offspring; 2) Define binary response variable CHOICE ("1" if the candidate is the actual father, or "0" if he is not); 3) Model the probability that the male will be selected as the actual father (i.e. probability that CHOICE becomes "1" using GLMM with binomial error and logit link). In step 1), candidates were defined as males within 1,145 m. In step 3), the identity of males and females (random effect) and genetic index (fixed effect) were included. Fitting was done using the *glmer* function of the *lme4* package (Bates et al. 2015). Significance was based on the Wald test on the effect of genetic index. See Figure 7-4 for schematic diagrams of this procedure and Figure 7-5 for data used in this test.

For each randomization test and for the GLMM approach, I used false discovery rate (FDR) correction (Benjamini and Hochberg 1995) with a cut-off q-value = 0.05 (Bateson et al. 2016) to consider multiple testing on 11 genetic indices defined above. However, I did not make such a correction for tests of $zzAAdist_{PBR}$ because the test is an additional independent test after receiving the results of the multiple tests on the 11 genetic indices.

Error rate and power of mate choice test

I estimated the type I error and power of the mate choice tests to better interpret the results. First, I generated "random mating pairs" for Relatedness, $AAdist_{nonPBR}$ and $zzAAdist_{nonPBR}$ by the same procedure described in the randomization test. These indices are the ones giving significance in the mate choice test (see Results). Then, I tested mate choice on this random-mating-pairs data using the randomization test and GLMM approach. After repeating this test 1,000 times (i.e. obtaining 1,000 P-values), the proportion of P-values below 0.05 was calculated as an estimate of type I error. I subsequently generated "non-random mating pairs" by modifying the above procedure. For each female, the most genetically dissimilar male, among spatially accessible males, was assigned. Note that dissimilar means a small value for Relatedness and a large value for $AAdist_{PBR}$ and $zzAAdist_{PBR}$. Then, mate choice was tested on these non-random-mating-pairs data. After repeating this test 1,000 times, the proportion of tests proving significance at an alpha level of 0.05 was calculated as an estimate of power. Confidence intervals of error and power were estimated by means of 1,000 bootstraps of simulated P-values using the *simpleboot* package (Peng 2008).

In summary, randomization tests yielded well controlled type I errors of around 5% and low power ranging from 6% to 13% (Table 7-4). The GLMM approach had an inflated type I error ranging from 10% to 26% and high power ranging from 16% to 29% (Table 7-4). This inflated type I error in the GLMM approach suggests that the mating bias I detected by means of the method may have been a false positive result. As a further check, I estimated the type I error of the GLMM approach with a significance level of 0.004 (this is the actual P-value of the GLMM approach for Relatedness and $AAdist_{PBR}$,

see Results and Table 7-6). This gave a type I error estimate of 0.069 (95% CI = 0.054-0.084) for Relatedness, 0.013 (95% CI = 0.006-0.020) for $AAdist_{PBR}$. Therefore, I considered that the possibility of the result being a false positive was small.

Direct benefit: analysis of own reproductive success

To test the possible direct benefit of mate choice, I estimated the effect of each pair's genetic indices (Relatedness, $AAdist_{nonPBR}$ and $zzAAdist_{nonPBR}$: indices for which I detected signals of mate choice) on own reproductive performance in 2016 (clutch size, hatching failure, number of fledglings). Data from 37 pairs (a subset of the pairs used in the mate choice tests where neither EPF nor egg dumping were suspected) were used when analysing the effect of Relatedness. Reduced data from 34 pairs were used for $AAdist_{nonPBR}$ and $zzAAdist_{nonPBR}$ because three out of the 37 pairs lacked MHC genotype data. See Figure 7-6 for details of data utilization. Separate analyses were done for Relatedness, $AAdist_{nonPBR}$ and $zzAAdist_{nonPBR}$ because subsequent model selection was based on the same dataset.

The three reproductive parameters were modelled separately by GLM (Poisson for clutch size and number of fledglings, binomial for presence or absence of hatching failure) with possible combinations of genetic index, square of genetic index and egg-laying date as explanatory variables. Because clutch size and fledging number take small, non-zero, discrete values (from 0 to 4) in this owl, I used Poisson distribution to model those data. The square of genetic index was introduced to consider the hypothesis that intermediate, rather than extreme, genetic dissimilarity is better (Wegner et al. 2003). Model comparisons, based on AICc, were conducted using the *dredge* function in the *MuMIn* package (Barton 2019). I considered models with AICc – minAICc < 2 as the best set of models. For reasons of parsimony, I considered that the inclusion of the null model in the best set provided no positive support for including the effects.

Indirect benefit: analysis of offspring survival

To test for the possible indirect benefit of mate choice, I estimated the effect of parental genetic indices (Relatedness, $AAdist_{nonPBR}$ and $zzAAdist_{nonPBR}$: indices whose significance was detected in the mate choice test) on offspring survival rate from mark recapture data. Daily monitoring allowed us to check the pre-fledging survival of hatchlings in 2016. After fledging, their survival during 2017 and 2018 was checked by means of whole island censuses. From March to July, I walked around the entire island using playback almost every night, except when it was raining. All owls encountered were identified and recorded. I applied the Bayesian implementation of the Cormack-Jolly-Seber model (Stan Development Team 2018) to the records. Before analysis, all chicks suspected of having misidentified mothers, or being the result of egg dumping or EPF, were excluded. This resulted in survival data of 85 individuals (Figure 7-1). I analysed the effect of Relatedness on survival rate for these 85 individuals. Six individuals were further excluded from this when analysing the effect of $AAdist_{PBR}$ and $zzAAdist_{PBR}$

(reducing the total to 79 individuals), because parents of the six lacked MHC genotype data. See Figure 7-6 for details of data utilization.

As a base model, I included age-dependent intercept and nest identity as random effects for survival rate. Age was defined as a three-level categorical variable: "chick" denotes individuals between hatching and fledging, "juvenile" denotes those between fledging and first spring, and "adult" denotes those after first spring. Estimating survival rate in such a categorical manner assumes that the annual survival rate of adults is constant over their lifetime (Kery and Schaub 2011). Under this assumption, I can obtain the probability of living up to a given year by multiplying the survival rate of chicks, juveniles, and the appropriate number for the annual survival rate of adults. Therefore, increases or decreases in survival rate estimates in our analyses indicate increases or decreases in longevity.

Then, I added all possible combinations of five variables (sex, hatching order within clutch, laying date of the first egg within clutch, genetic index and square of genetic index) to the survival rate. To improve model fitting efficiency, genetic indices (Relatedness, $AAdist_{PBR}$ and $zzAAdist_{PBR}$) were standardized before analysis. Survival rate was modelled as an inverse logit of a linear combination of these variables. Because the sample size of analyses for Relatedness, $AAdist_{PBR}$ and $zzAAdist_{PBR}$ were different, the effect of each was analysed separately so that subsequent model comparison could be based on the same dataset. I evaluated the possible 32 models in terms of Pareto Smoothed Importance Sampling Leave-One-Out (PSIS-LOO) using the *loo* function in the *loo* package (Vehtari et al. 2018). PSIS-LOO is a method for measuring the predictive accuracy of models, as AIC does (Vehtari et al. 2018), and it can compare complex hierarchical models. I considered models with LOOIC – minLOOIC < 2 as the best set of models. For reasons of parsimony, I considered the inclusion of the null model in the best set as no positive support for including the effects. Model implementation and fitting was done using Stan 2.18.1 (Carpenter et al. 2017) and *rstan* 2.18.2 (Stan Development Team 2016). Fitting parameters were as follows: warmup = 70,000; iter = 20,000; thin = 2; and default values for other parameters except adapt_delta. adapt_delta was tuned between 0.95 to 0.97 accordingly to fitting results.

Lifetime reproductive success

To confirm whether or not survival becomes a proxy of fitness, the association between longevity and lifetime reproductive success (LRS) was analysed. Since 2002, members of the long-term research group have ringed nearly 600 fledglings of which we were able to follow the lifetime breeding activity of 22 (12 males, 10 females). Because the owls maintain year-round territories and use the same nests in successive years, the disappearance of a territory holder implies its death. If an individual was not found in two consecutive years, I considered the year in which the individual was last seen as the year of death. Lifetime was measured as the number of years from the year of birth to the year of death. The number of fledglings produced during an owl's lifetime was modelled with

sex and longevity by GLM (Poisson, log link). The effect of longevity was tested using the likelihood ratio test on a model with lifetime effect and a model without it. Overdispersion was tested on the final model using the *dispersiontest* function in *AER* (Kleiber and Zeileis 2008); no indication was found of overdispersion (Z = 0.76, P = 0.22).

Results

Mate choice test

I compared the actual values of the mean genetic index to the null distribution generated from a simulation of random mating by randomization test. None of the genetic indices, except $AAdist_{nonPBR}$ and $AAdist_{PBR}$ differed significantly between actual pairs and randomly simulated pairs (Table 7-5, Randomization test: all P > 0.050). Real pairs had significantly larger $AAdist_{nonPBR}$ (Table 7-5, Randomization test: P = 0.036) and $AAdist_{PBR}$ (Table 7-5, Figure 7-7, Randomization test: P = 0.004) than simulated pairs. The significance of $AAdist_{PBR}$ remained after FDR control (Table 7-5, q < 0.05).

I modelled the probability of a male being chosen by a female by GLMM with each genetic index as a predictor. Significant effects of Relatedness (Wald test: $\chi^2_1 = 8.185$, P = 0.004), MHCshare (Wald test: $\chi^2_1 = 4.469$, P = 0.035), $AAdist_{nonPBR}$ (Wald test: $\chi^2_1 = 5.262$, P = 0.022) and $AAdist_{PBR}$ (Wald test: $\chi^2_1 = 8.393$, P = 0.004) were found (Table 7-6). However, only the effects of Relatedness and $AAdist_{PBR}$ remained after FDR control (Table 7-6, q < 0.05). The negative regression coefficient of Relatedness (Table 7-6) indicated that a male with a low relatedness to the chooser was more likely to be chosen by a female. The positive regression coefficient of $AAdist_{PBR}$ (Table 7-6) indicated that a male with a large $AAdist_{PBR}$ for the chooser was more likely to be chosen by a female.

To examine the possibility that inbreeding avoidance might confound the mating bias of $AAdist_{PBR}$, I tested mate choice about $zzAAdist_{PBR}$. Irrespective of the analysis approach, the significance of MHC-based mating bias remained after controlling for the possible effect of Relatedness on $AAdist_{PBR}$ (Table 7-5, Randomization test, P = 0.044, Table 7-6, GLMM approach, $\chi^2_1 = 14.078$, P < 0.001). However, there was no significant correlation between relatedness and $AAdist_{PBR}$ (Mantel's r = 0.010, P = 0.340).

Direct benefit: analysis of own reproductive success

To examine the existence of a direct fitness benefit of the choice obtained during the present generation, Relatedness, $AAdist_{PBR}$ and $zzAAdist_{PBR}$ of pairs were correlated with reproductive success of the pairs. For Relatedness, the null model was the best for clutch size and number of fledglings (Table 7-7). Although the model with square of Relatedness was the best for presence of hatching failure, the null model was included in the best set of models (Table 7-7). For $AAdist_{PBR}$ (Table 7-8) and $zzAAdist_{PBR}$ (Table 7-9), the null model was the best for clutch size, number of fledglings and presence of hatching failure. Thus, although the square of Relatedness might contribute to hatching failure, there was statistically inadequate support for the direct benefit of the mate choice through

improvement in reproductive success.

Indirect benefit: analysis of offspring survival

To examine the existence of any indirect fitness benefit of the choice obtained through subsequent generations, I explored the effects of Relatedness, $AAdist_{PBR}$ and $zzAAdist_{PBR}$ of pairs on offspring survival. For all three indices, model selection based on PSIS-LOO included the null model in the best set of models (Table 7-10, 7-11, 7-12). However, models with genetic indices were also included in the best set of models. Thus, although parental genetic indices might provide some contribution to offspring survival rate, there was statistically inadequate support for indirect fitness benefit of the mate choice obtained through subsequent generations.

Lifetime reproductive success

There was a significant positive correlation between longevity and the number of fledglings produced (Figure 7-8, Estimate of regression coefficient of lifetime +SE = 0.552 +0.123; likelihood ratio test: $\chi^2_1 = 20.086$, $P < 0.001$).

Discussion

I detected support for MHC-based mate choice and inbreeding avoidance in the Ryukyu Scops Owl subspecies endemic to Minami-daito Island. Analysis of reproductive success and survival rate did not offer evidence that the mating bias had either direct and/or indirect fitness benefit. This is a rare attempt in which a correlation between parental MHC genotypes and offspring fitness components has been explored in a wild avian population. Simulations revealed low power and inflated type I errors of statistical tests used in MHC-based mate choice. I will first explain the mate choice in these owls then discuss the statistically inadequate support for the benefit of MHC-based mate choice. Finally, I will discuss the possible reasons for the low power and inflated type I errors of the mate choice test.

Mating bias towards a large $AAdist_{PBR}$ value suggests that the owls make MHC-based mate choices for genetic compatibility rather than for good genes. Under the good gene hypothesis, a specific male is attractive to all females (Mays Jr and Hill 2004). If such a mechanism works, then mating bias in terms of genetic indices that are defined only by the male genotype (MHCdiversity, MHCallele1, …, MHC allele6) would be expected. However, I did not observe such patterns. In contrast, under the genetic compatibility hypothesis, a male's attractiveness depends on the female making the choice, because females seek a good combination of maternal and paternal alleles (Mays Jr and Hill 2004). If such a mechanism works, then mating bias in terms of genetic indices that are defined for pairs (MHCshare, $AAdist_{nonPBR}$, $AAdist_{PBR}$) would be expected. This is the pattern that I detected.

I also detected a mating bias toward low Relatedness. This indicates that the owls avoid inbreeding while forming pairs. This raises the possibility that the detected mating

bias with respect to $AAdist_{PBR}$ is the result of inbreeding avoidance through MHC, because MHC-based mate choice is suggested to function as a mechanism of inbreeding avoidance (Tregenza and Wedell 2000). I think that this is a partial explanation because the P-value of the randomization test on $AAdist_{PBR}$ was increased by controlling for Relatedness (from 0.004 to 0.044). However, tests on $zzAAdist_{PBR}$ were still significant and there was a non-significant correlation between Relatedness and $AAdist_{PBR}$. These results indicate that MHC-based mate choice in this species has more of an immunological benefit over just avoiding inbreeding depression.

However, I was not able to provide statistically adequate support for any benefit of MHC-based mate choice. MHC-based mate choice for genetic compatibility is suggested to provide offspring with a "good" combination of MHC alleles and enhance their pathogenic resistance. This then increases the fitness of offspring and confers indirect benefit on the parents. The lack of a clear improvement in survival rate depending on parental genetic indices may be explained in three ways. First, there may be no actual effect of parental mate choice on the fitness of resultant offspring. Second, there really are effects of parental mate choice on the fitness of resultant offspring, but through fitness components other than survival. However, this seems unlikely because a correlation between longevity and LRS suggests that survival is a good predictor of fitness in this owl population. Third, there really are effects of parental mate choice on the fitness of resultant offspring, but I failed to detect them. Because our analysis of survival rate used a small dataset from 79 individuals from a single cohort, our sample size may be insufficient. Some of the models included in the best set might outcompete the null model if I was able to increase the sample size. Measuring the multiple fitness components of offspring using a large sample size will be an important theme of future study.

Finally, I discuss the statistical performance of mate choice tests. Simulation revealed the low power of traditional randomization-based mate choice tests. This may be due to the low genetic variation among potential mates. If potential mates have similar genotypes, then the genetic similarity of random-mating pairs and disassortative-mating pairs may not differ greatly. In the population concerned, the owls show an isolation-by-distance pattern at the microsatellite loci level (Sawada et al. 2018a), a situation indicating that potential mates have genetically similar genotypes. Simulation also revealed inflated type I errors in the GLMM approach, the cause of which may have been the assumption that each offspring was considered as the result of a single mate choice. This assumption implies that females choose a male every time they lay an egg. However, such a situation is unlikely for a species with a low rate of EPF. In such species, it is perhaps more appropriate to consider each brood as the result of a single mate choice. Therefore, at least for species with a low rate of EPF, the GLMM approach unreasonably increases the number of observations and overestimates the effect of predictors. However, this approach might allow the detection of small effects that cannot be detected by a randomization test due to its higher power than the randomization test. Considering the

above, I suggest that future studies of MHC-based mate choice should use both methods to complement low power and should evaluate validity through error rate analysis to consider the possibility of false positive results.

In conclusion, this study represents a rare attempt to test both direct and indirect benefits of MHC-based mate choice using trans-generational data in a wild bird population. The significance of this study is that it assessed the association between criteria of MHC-based mate choice in the parental generation and a fitness component in the resultant offspring generation. This approach can directly evaluate indirect benefits, compared with previous approaches that have assessed the association between own MHC genotype and own fitness component. Although I did not obtain statistically significant evidence of a fitness benefit of MHC-based mate choice in this study, reporting it is important for future research in order to extend our understanding of the evolutionary mechanism of MHC-based mate choice, by integrating results using meta-analysis (Kamiya et al. 2014).

Figure

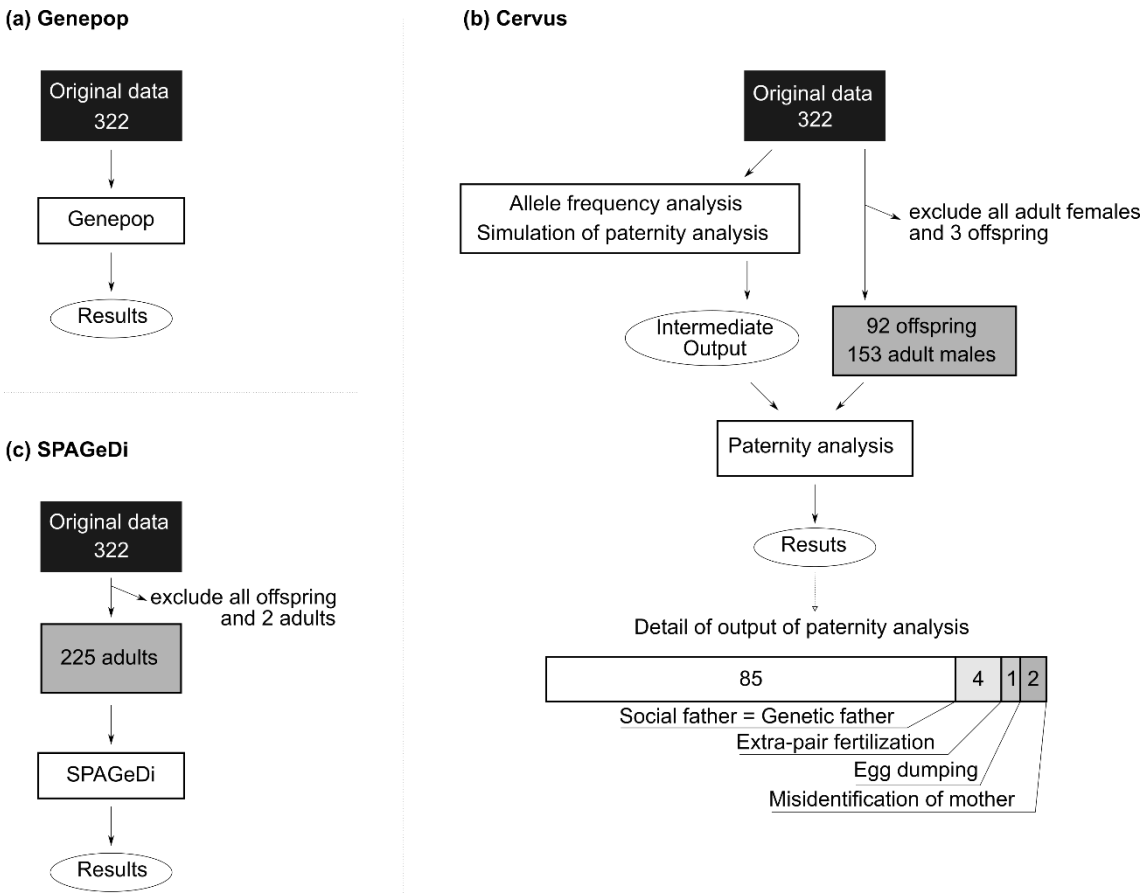


Figure 7-1

Data utilization for analyses on Genepop, SPAGeDi and Cervus. Black rectangle: original data of 322 individuals, grey rectangle: subset of data, white rectangle: analysis, white ellipse: output of analysis. (a) Genepop. All data were used. (b) Cervus. All females and three offspring which we do not have their maternal sample were excluded from a file containing data of offspring to be tested and their candidate fathers. Detail of paternity analysis is shown by bar chart. (c) SPAGeDi, relatedness was calculated from 255 adults after excluding all offspring and two adults. The two are misidentified mother and her mate.

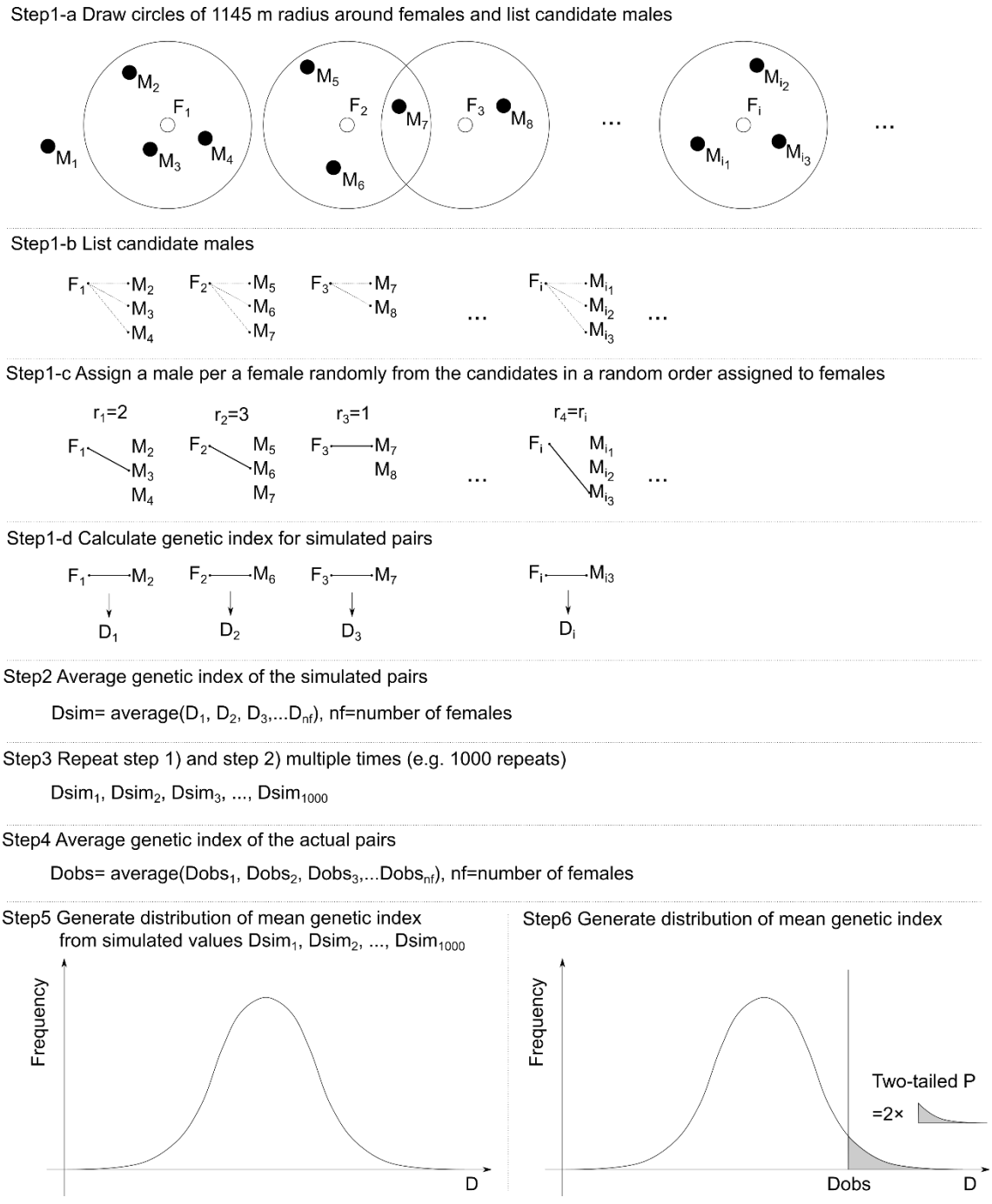


Figure 7-2

Detailed procedures of randomization test. Some notes for the steps are as follows. Step1-a: Males from the focal female dose not seems to become a pair with the female. To account for this in randomization test, males within 1145m were considered as potential mates. Step1-b: Females are assigned random order to choose a male from her candidates. By doing this, we can cope with a situation where multiple females share same males as their potential mate, as female F2 and F_3 share M_7 in the diagram. That is, if the female who can choose the male first choose the shared male, that male is remove from the

candidates of other females who choose male later. Because this procedure can sometimes remove all candidate males from some females, we assigned "Not Available" value, NA, to the female's mates and omit them from the following step1-c and step2.

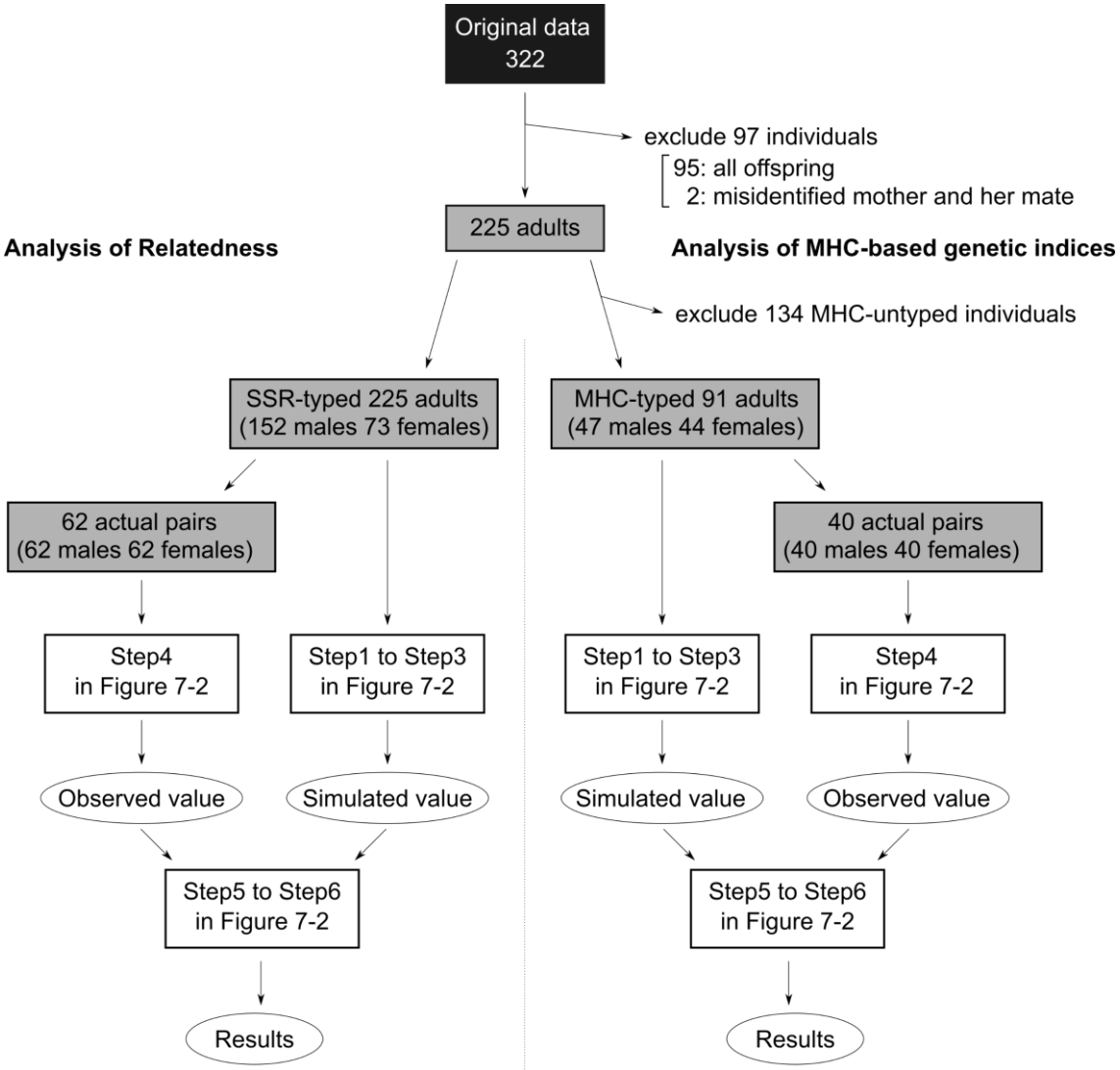
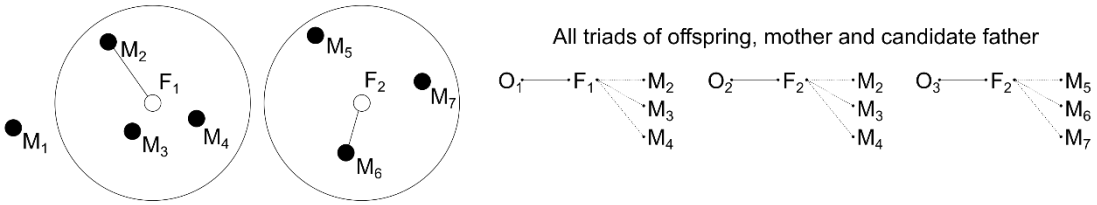


Figure 7-3
Data utilization in randomization test. Black rectangle: original data of 322 individuals, grey rectangle: subset of data, white rectangle: analysis, white ellipse: output of analysis

Step1-a For all offspring-mother diads, list candidate fathers
Candidates fathers are chosen based on georaphic distace between male and female as in step1-a and astep1-b of randomization test

e.g. O_1 and O_2 are offspring of Pair F_1 of M_2. O_3 is an offspring of pair F_2-M_6.



Step1-b Calculate genetic index for all mother-candidate father diads

Step1-c For all offspring-mother-candidate triads which reflect true social parents-offspring relationship, assign 1 to them, and the triads which do not, assign 0 to them

	Step1-a		Step1-b	Step1-c	
Offspring	Mother	Candidate Father	Genetic Index	True Father ?	Choice
O_1	F_1	M_2	D_{12}	Yes	1
O_1	F_1	M_3	D_{13}	No	0
O_1	F_1	M_4	D_{14}	No	0
O_2	F_1	M_2	D_{12}	Yes	1
O_2	F_1	M_3	D_{13}	No	0
O_2	F_1	M_4	D_{14}	No	0
O_3	F_2	M_5	D_{25}	No	0
O_3	F_2	M_6	D_{26}	Yes	1
O_3	F_2	M_7	D_{27}	No	0
⋮	⋮	⋮	⋮	⋮	⋮

Step2 Arrange this data into a data frame in R

OffspringID	MotherID	FatherID	GeneticIndex	Choice
1	1	2	D_{12}	1
1	1	3	D_{13}	0
1	1	4	D_{14}	0
2	1	2	D_{12}	1
2	1	3	D_{13}	0
2	1	4	D_{14}	0
3	2	5	D_{25}	0
3	2	6	D_{26}	1
3	2	7	D_{27}	0
⋮	⋮	⋮	⋮	⋮

Step3 Fit a GLMM model to the data frame using following formula

glmer(Choice ~ GeneticIndex +(1|MotherID)+(1|FatherID), family="binomial")

Figure 7-4

Detailed procedures of GLMM approach. Some notes for the steps are as follows. Step1-a: The way of listing candidate males (fathers) is the same as step1-a and step1-b in randomization test (males within 1145 m are considered as candidates). Step2: Each row

corresponds to an offspring-mother-candidate triad. Each row is a data points in the GLMM analysis in the next step. Step3: MotherID and FatherID are included into the model as random factors to account for non-independence of the data points due to sharing of parents between offspring.

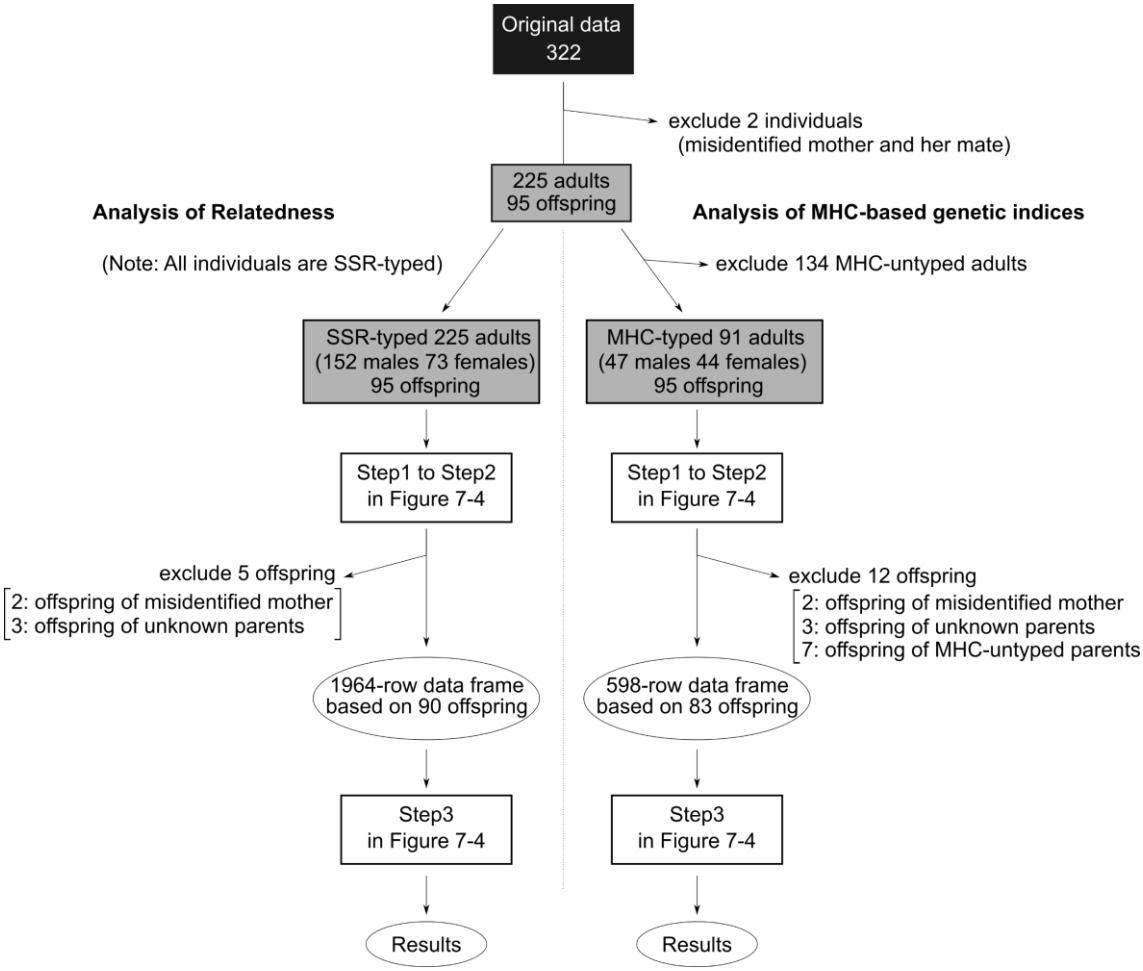


Figure 7-5

Data utilization in GLMM approach. Black rectangle: original data of 322 individuals, grey rectangle: subset of data, white rectangle: analysis, white ellipse: output of analysis.

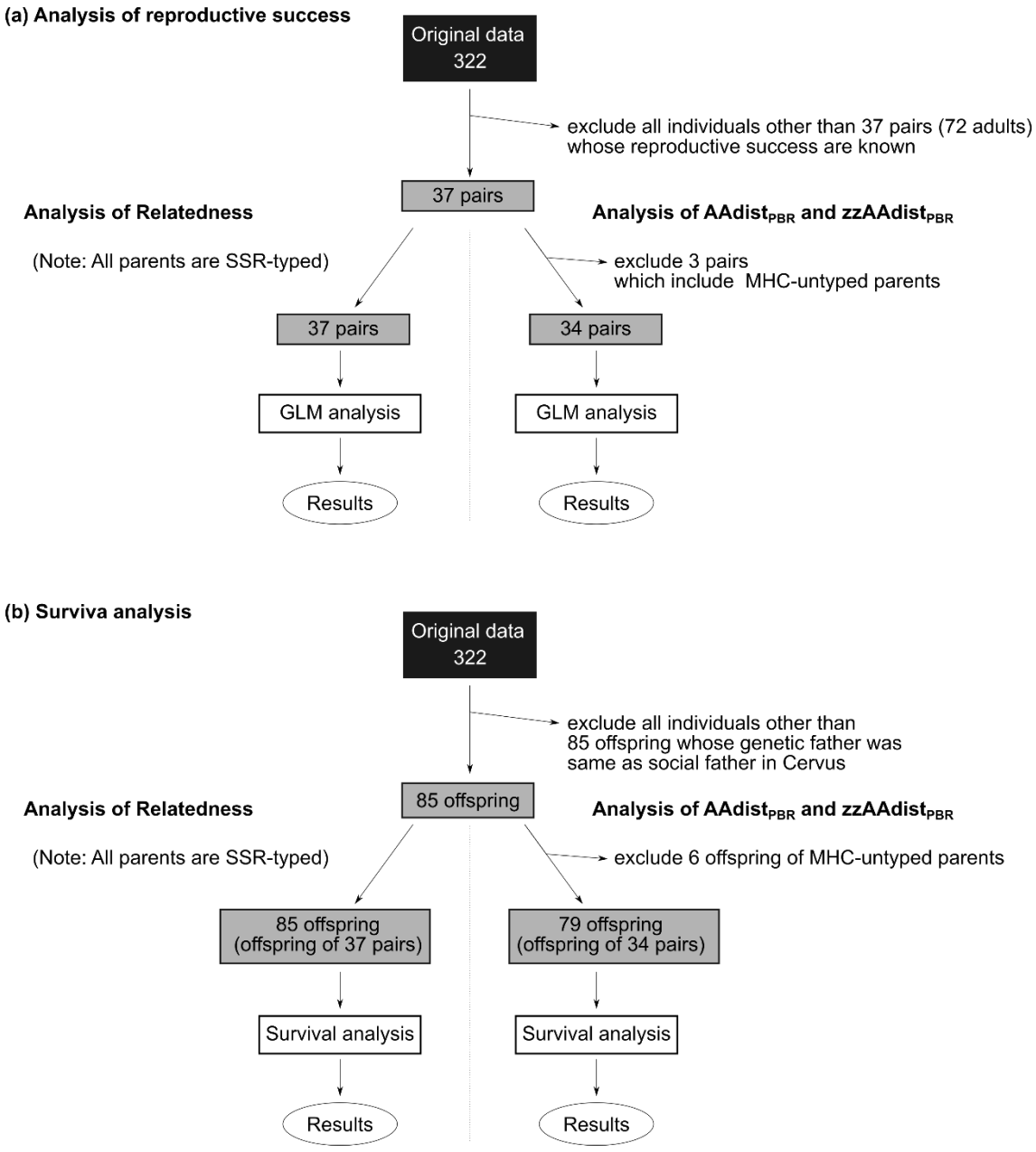


Figure 7-6

Data utilization in analyses to test benefit of mate choice. Black rectangle: original data of 322 individuals, grey rectangle: subset of data, white rectangle: analysis, white ellipse: output of analysis.

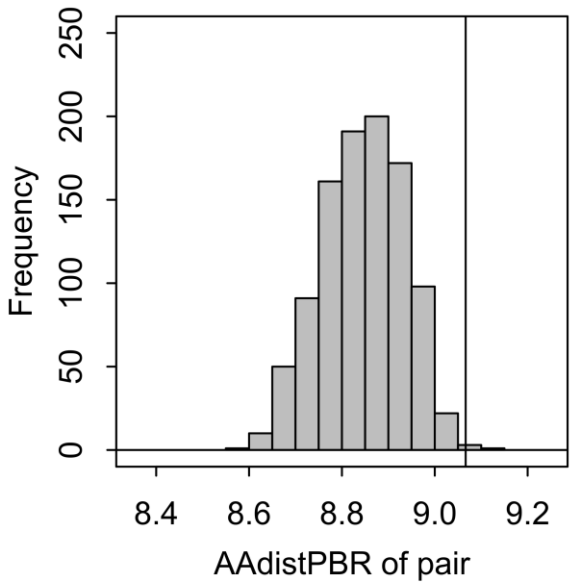


Figure 7-7
Result of randomization test with respect to $AAdist_{PBR}$. Observed value (solid line) deviated toward large value from a distribution expected under simulated random mating (histogram).

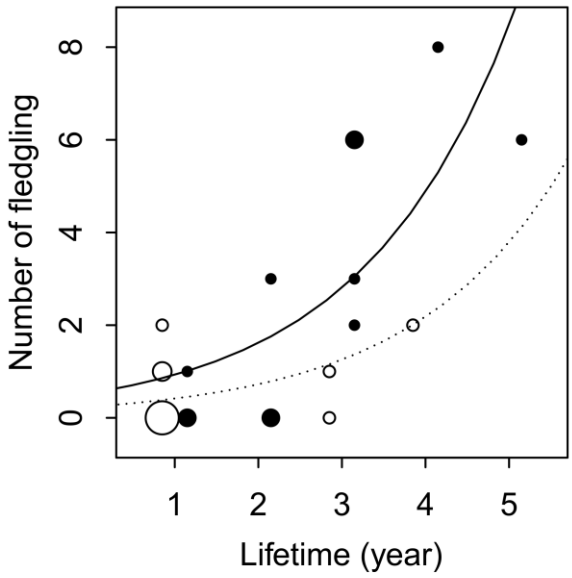


Figure 7-8
Correlation between longevity and number of fledglings produced during the lifetime. Dot size indicates sample size (black: male, white: female). Lines indicate mean number of fledglings estimated from the model (solid: male, dotted: female).

Table

Table 7-1 List of MID used in fusion primers

MID name	Sequence
Ion Xpress™ Barcode 1	CTAAGGTAACGAT
Ion Xpress™ Barcode 2	TAAGGAGAACGAT
Ion Xpress™ Barcode 3	AAGAGGATTCGAT
Ion Xpress™ Barcode 4	TACCAAGATCGAT
Ion Xpress™ Barcode 5	CAGAAGGAACGAT
Ion Xpress™ Barcode 6	CTGCAAGTTCGAT
Ion Xpress™ Barcode 7	TTCGTGATTCGAT
Ion Xpress™ Barcode 8	TTCCGATAACGAT
Ion Xpress™ Barcode 9	TGAGCGGAACGAT
Ion Xpress™ Barcode 10	CTGACCGAACGAT
Ion Xpress™ Barcode 11	TCCTCGAATCGAT
Ion Xpress™ Barcode 12	TAGGTGGTTCGAT
Ion Xpress™ Barcode 13	TCTAACGGACGAT
Ion Xpress™ Barcode 14	TTGGAGTGTCGAT
Ion Xpress™ Barcode 15	TCTAGAGGTCGAT
Ion Xpress™ Barcode 16	TCTGGATGACGAT
Ion Xpress™ Barcode 17	TCTATTCGTCGAT
Ion Xpress™ Barcode 18	AGGCAATTGCGAT
Ion Xpress™ Barcode 19	TTAGTCGGACGAT
Ion Xpress™ Barcode 20	CAGATCCATCGAT
Ion Xpress™ Barcode 21	TCGCAATTACGAT
Ion Xpress™ Barcode 22	TTCGAGACGCGAT
Ion Xpress™ Barcode 23	TGCCACGAACGAT
Ion Xpress™ Barcode 24	AACCTCATTCGAT

MID were selected from the sequence used in Ion Xpress™ Barcode

Table 7-2 Standard data on MHC alleles

Allele	Accession	N	Frequency	Length (bp)
Otel-DAB*01	LC340383	22	0.237	262
Otel-DAB*02	LC340384	45	0.484	262
Otel-DAB*03	LC340385	74	0.796	262
Otel-DAB*04	LC340386	61	0.656	262
Otel-DAB*05	LC340387	53	0.570	262
Otel-DAB*06	LC340388	23	0.247	262
Otel-DAB*07	LC340389	11	0.118	262
Otel-DAB*08	LC340390	6	0.065	262
Otel-DAB*09	LC340391	3	0.032	262
Otel-DAB*10	LC340392	2	0.022	262
Otel-DAB*12	LC340394	1	0.011	262

N: number of individuals with the allele; Frequency: proportion of individuals with

Table 7-3 Standard data on microsatellite alleles

Locus	N_A	H_E	H_O	F_{IS}	P
Oe085	7	0.750	0.755	-0.007	0.011
Oe022	9	0.819	0.811	0.011	0.094
Oe081	5	0.666	0.668	-0.003	0.934
Oe129	6	0.717	0.72	-0.005	0.009
Oe171	8	0.684	0.674	0.015	0.657
Oe084	11	0.811	0.755	0.070	0.052
Oe3-7	5	0.336	0.360	-0.073	0.195
Oe045	16	0.892	0.891	0.001	0.009
Oe029	3	0.641	0.627	0.022	0.761
Oe149	6	0.742	0.742	-0.001	0.058
Oe053	5	0.683	0.646	0.054	0.012
Oe0128	7	0.692	0.708	-0.023	0.017

N_A, Number of alleles; H_E, expected heterozygosity; H_O, observed heterozygosity; F_{IS}, individual inbreeding coefficient (Weir & Cockerham 1984); P, P-value calculated from exact tests of deviation from HWE, No P-values reached the significance threshold after Holm correction.

Table 7-4 Type I error and power of two tests of non-random mating (randomization test and the GLMM approach)

Test method	Genetic index	Type I error	Power
Randomization	Relatedness	0.059 (0.045, 0.073)	0.130 (0.110, 0.151)
	$AAdist_{PBR}$	0.056 (0.043, 0.072)	0.057 (0.043, 0.071)
	$zzAAdist_{PBR}$	0.056 (0.042, 0.071)	0.058 (0.043, 0.073)
GLMM	Relatedness	**0.209** (0.184, 0.224)	0.271 (0.244, 0.298)
	$AAdist_{PBR}$	**0.100** (0.083, 0.119)	0.162 (0.139, 0.186)
	$zzAAdist_{PBR}$	**0.259** (0.231, 0.287)	0.290 (0.262, 0.318)

95% CI of estimates are shown in parenthesis. Inflated type I errors are shown in bold font.

Table 7-5 Results of the randomization test

Genetic index	Obs (2.5th, 97.5th)	P	q
Relatedness	-0.019 (-0.034, 0.060)	0.158	0.385
MHCshare	0.475 (0.460, 0.579)	0.132	0.385
$AAdist_{nonPBR}$	5.617 (5.320, 5.609)	0.036	0.198
$AAdist_{PBR}$	9.067 (8.668, 9.003)	**0.004**	**0.044**
MHCdiversity	3.125 (3.045, 3.143)	0.210	0.385
MHCallele1	0.275 (0.233, 0.310)	0.776	0.948
MHCallele2	0.400 (0.366, 0.442)	0.680	0.935
MHCallele3	0.825 (0.786, 0.841)	0.364	0.572
MHCallele4	0.575 (0.535, 0.619)	0.958	0.958
MHCallele5	0.650 (0.581, 0.659)	0.176	0.385
MHCallele6	0.250 (0.209, 0.286)	0.866	0.953
$zzAAdist_{PBR}$	0.342 (-0.313, 0.335)	0.044	-

Obs: mean value of the genetic index of actual pairs, (2.5th, 97.5th): 2.5th and 97.5th points of distribution generated by simulation of random mating, from which Obs deviate indicates significance at alpha = 0.05, P: two-tailed P-value, q: q-value of FDR control. P-value lower than 0.05 with $q < 0.05$ are shown in bold font. FDR control was not applied to test on $zzAAdist_{PBR}$ because the test is an additional independent test after receiving multiple 11 tests on other indices.

Table 7-6 Results of the GLMM approach

Genetic index	Mean	SE	95% CI	Z	P	q
Relatedness	-1.667	0.583	(-2.845, -0.525)	-2.861	**0.004**	**0.023**
MHCshare	-0.857	0.405	(-0.961, -0.062)	-2.114	0.035	0.095
$AAdist_{nonPBR}$	0.207	0.090	(-1.947, 0.383)	2.294	0.022	0.080
$AAdist_{PBR}$	0.263	0.091	(-2.552, 0.441)	2.897	**0.004**	**0.023**
MHCdiversity	-0.151	0.164	(-0.340, 0.169)	-0.925	0.355	0.651
MHCallele1	0.163	0.259	(-1.595, 0.671)	0.631	0.528	0.726
MHCallele2	-0.232	0.244	(-1.437, 0.246)	-0.951	0.342	0.651
MHCallele3	-0.184	0.284	(-1.191, 0.372)	-0.649	0.517	0.726
MHCallele4	-0.075	0.239	(-1.429, 0.394)	-0.312	0.755	0.912
MHCallele5	0.053	0.243	(-1.485, 0.528)	0.216	0.829	0.912
MHCallele6	0.017	0.264	(-1.557, 0.535)	0.063	0.950	0.950
$zzAAdist_{PBR}$	0.296	0.079	(0.142, 0.451)	3.752	< **0.001**	-

Mean, standard error and 95% confidence interval of regression coefficient for the genetic index are given. Z and P: Wald statistic and corresponding P-value. q: q-value of FDR control. P-value lower than 0.05 with $q < 0.05$ are shown in bold font. FDR control was not applied to test on $zzAAdist_{PBR}$ because the test is an additional independent test after receiving multiple 11 tests on other indices.

Table 7-7 Analysis of reproductive success with Relatedness

Response variable	Predicter variable	AICc	Delta
Clutch size	Null	**114.46**	**0.00**
	Relatedness	**116.52**	**2.06**
	Lay	116.69	2.23
	Relatedness^2	116.69	2.24
	Relatedness + Relatedness^2	118.79	4.33
	Lay + Relatedness	118.89	4.43
	Lay + Relatedness^2	119.06	4.61
	Lay + Relatedness+ Relatedness^2	121.31	6.85
Number of fledglings	Null	**113.97**	**0.00**
	Relatedness^2	**115.05**	**1.07**
	Relatedness + Relatedness2	116.08	2.11
	Lay	116.09	2.12
	Relatedness	116.13	2.16
	Lay + Relatedness^2	117.36	3.39
	Lay + Relatedness	118.41	4.43
	Lay + Relatedness + Relatedness^2	118.60	4.63
Presence of hatching failure	Relatedness^2	**48.47**	**0.00**
	Null	**48.74**	**0.27**
	Relatedness	**49.02**	**0.55**
	Relatedness + Relatedness^2	**49.37**	**0.90**
	Lay + Relatedness^2	**49.98**	**1.52**
	Lay + Relatedness	**50.20**	**1.73**
	Lay	**50.35**	**1.88**
	Lay + Relatedness + Relatedness^2	**50.37**	**1.90**

Bold font: AICc – minAICc < 2

Table 7-8 Analysis of reproductive success with $AAdist_{PBR}$

Response variable	Predicter variable	AICc	Delta
Clutch size	Null	**105.48**	**0.00**
	$AAdist_{PBR}$	**107.30**	**1.82**
	$AAdist_{PBR}^2$	107.58	2.10
	Lay	107.74	2.25
	$AAdist_{PBR}$ + $AAdist_{PBR}^2$	109.68	4.19
	Lay + $AAdist_{PBR}$	109.70	4.21
	Lay + $AAdist_{PBR}^2$	109.97	4.49
	Lay + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	112.23	6.74
Number of fledglings	Null	**106.25**	**0.00**
	$AAdist_{PBR}$	**107.64**	**1.38**
	$AAdist_{PBR}^2$	**108.11**	**1.85**
	Lay	108.51	2.26
	$AAdist_{PBR}$ + $AAdist_{PBR}^2$	109.95	3.70
	Lay + $AAdist_{PBR}$	110.04	3.78
	Lay + $AAdist_{PBR}^2$	110.50	4.24
	Lay + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	112.50	6.25
Presence of hatching failure	Null	**44.93**	**0.00**
	$AAdist_{PBR}^2$	**45.21**	**0.28**
	Lay	**46.82**	**1.88**
	$AAdist_{PBR}$	47.18	2.25
	$AAdist_{PBR}$ + $AAdist_{PBR}^2$	47.38	2.45
	Lay+$AAdist_{PBR}^2$	47.45	2.52
	Lay + $AAdist_{PBR}^2$	49.21	4.28
	Lay + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	49.78	4.84

Bold font: AICc - minAICc < 2

Table 7-9 Analysis of reproductive success with $zzAAdist_{PBR}$

Response variable	Predicter variable	AICc	Delta
Clutch size	Null	**105.48**	**0.00**
	$zzAAdist_{PBR}$	**107.15**	**1.66**
	$zzAAdist_{PBR}^2$	**107.32**	**1.84**
	Lay	107.74	2.25
	$zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	109.34	3.86
	Lay + $zzAAdist_{PBR}$	109.56	4.07
	Lay + $zzAAdist_{PBR}^2$	109.73	4.24
	Lay + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	111.91	6.43
Number of fledglings	Null	**106.25**	**0.00**
	$zzAAdist_{PBR}^2$	**106.40**	**0.14**
	$zzAAdist_{PBR}$	**107.85**	**1.59**
	Lay	108.51	2.26
	$zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	108.62	2.37
	Lay + $zzAAdist_{PBR}^2$	108.80	2.55
	Lay+$zzAAdist_{PBR}$	110.26	4.01
	Lay + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	111.19	4.94
Presence of hatching failure	Null	**44.93**	**0.00**
	$zzAAdist_{PBR}$	**45.59**	**0.66**
	Lay	**46.82**	**1.88**
	$zzAAdist_{PBR}^2$	47.11	2.18
	Lay+$zzAAdist_{PBR}$	47.47	2.54
	$zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	47.98	3.05
	Lay + $zzAAdist_{PBR}^2$	49.14	4.21
	Lay + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	50.01	5.08

Bold font: AICc – minAICc < 2

Table 7-10 Results of survival analysis: models with Relatedness

Predicter	LOOIC
Order	**189.11**
Order + Relatedness^2	**189.11**
Order + Lay	**189.33**
Order + Relatedness	**189.46**
Null	**189.47**
Relatedness	**189.64**
Order + Relatedness + Relatedness^2	**189.84**
Relatedness + Relatedness^2	**190.16**
Relatedness^2	**190.23**
Order + Lay + Relatedness	**190.40**
Lay	**190.53**
Lay + Relatedness	**190.53**
Order + Lay + Relatedness + Relatedness^2	**190.68**
Sex + Order	**190.70**
Order + Lay + Relatedness^2	**190.91**
Lay + Relatedness + Relatedness^2	**190.93**
Lay + Relatedness^2	**191.04**
Sex + Order + Relatedness	191.13
Sex	191.16
Sex + Order + Lay + Relatedness	191.20
Sex + Relatedness	191.40
Sex + Order + Lay + Relatedness + Relatedness^2	191.60
Sex + Order + Relatedness + Relatedness^2	191.68
Sex + Order + Relatedness^2	191.78
Sex + Relatedness^2	191.90
Sex + Order + Lay	191.94
Sex + Lay	191.99
Sex + Relatedness + Relatedness^2	192.18
Sex + Lay + Relatedness	192.38
Sex + Lay + Relatedness + Relatedness^2	192.69
Sex + Order + Lay + Relatedness^2	192.72
Sex + Lay + Relatedness^2	192.87

LOOIC: looic values in output of loo function, Bold: LOOIC - minLOOIC < 2

Table 7-11 Results of survival analysis: models with $AAdist_{PBR}$

Predicter	LOOIC
$AAdist_{PBR}^2$	**169.18**
Order + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	**169.40**
Order + $AAdist_{PBR}^2$	**169.67**
Null	**169.71**
Sex + Order + Lay	**169.82**
$AAdist_{PBR}$ + $AAdist_{PBR}^2$	**170.12**
Lay	**170.18**
Order + $AAdist_{PBR}$	**170.57**
Order	**170.59**
Lay + $AAdist_{PBR}^2$	**170.62**
$AAdist_{PBR}$	**170.74**
Order + Lay + $AAdist_{PBR}^2$	**170.75**
Sex + $AAdist_{PBR}^2$	**170.86**
Sex + Order + $AAdist_{PBR}^2$	**170.97**
Order + Lay + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	**170.97**
Order + Lay + $AAdist_{PBR}$	**171.13**
Sex	171.20
Lay + $AAdist_{PBR}$	171.25
Lay + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	171.37
Order + Lay	171.37
Sex + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	171.74
Sex + Order + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	171.79
Sex + Lay	171.82
Sex + Order + $AAdist_{PBR}$	171.87
Sex + Order + Lay + $AAdist_{PBR}^2$	172.03
Sex + Order	172.12
Sex + Lay + $AAdist_{PBR}^2$	172.20
Sex + Order + Lay + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	172.26
Sex + $AAdist_{PBR}$	172.39
Sex + Lay + $AAdist_{PBR}$	172.74
Sex + Order + Lay + $AAdist_{PBR}$	172.74
Sex + Lay + $AAdist_{PBR}$ + $AAdist_{PBR}^2$	173.17

LOOIC: looic values in outputs of loo function, Bold: LOOIC – minLOOIC < 2

Table 7-12 Results of survival analysis: models with $zzAAdist_{PBR}$

Predicter	LOOIC
Sex + Lay	**163.54**
Null	**163.75**
$zzAAdist_{PBR}$	**163.93**
$zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	**163.97**
Lay	**164.04**
Lay + $zzAAdist_{PBR}$	**164.20**
$zzAAdist_{PBR}2$	**164.37**
Lay + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	**164.42**
Lay + $zzAAdist_{PBR}^2$	**164.53**
Order + Lay + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	**164.97**
Order + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	**165.04**
Order	**165.36**
Sex + Order + Lay	**165.38**
Sex	**165.40**
Order + $zzAAdist_{PBR}$	**165.51**
Sex + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	165.61
Sex + $zzAAdist_{PBR}$	165.69
Sex + $zzAAdist_{PBR}^2$	165.72
Order + Lay	165.88
Order + $zzAAdist_{PBR}^2$	165.92
Sex + Order + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	165.99
Sex + Lay + $zzAAdist_{PBR}$	166.01
Order + Lay + $zzAAdist_{PBR}$	166.12
Sex + Lay + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	166.23
Sex + Lay + $zzAAdist_{PBR}^2$	166.29
Order + Lay + $zzAAdist_{PBR}^2$	166.32
Sex + Order + Lay + $zzAAdist_{PBR}$ + $zzAAdist_{PBR}^2$	166.82
Sex + Order	166.94
Sex + Order + $zzAAdist_{PBR}$	167.08
Sex + Order + $zzAAdist_{PBR}^2$	167.49
Sex + Order + Lay + $zzAAdist_{PBR}$	167.89
Sex + Order + Lay + $zzAAdist_{PBR}^2$	168.18

LOOIC: looic values in output of loo function, Bold: LOOIC – minLOOIC < 2

Appendix

Parameter setting in AmpliSAS

In the genotyping analysis by AmpliSAS, we set *Maximum number of alleles per amplicon* = 20. This is determined so that it become larger than the largest "allele number per individual" of MHC class IIB in Strigidae (16 alleles in Blakiston's Fish Owl *Bubo blakistoni* (Kohyama et al. 2015)). Then we set *Minimum amplicon depth* = 100. *Minimum per amplicon frequency* for filtering parameters were set to 4.0% based on the result of AmpliCHECK following an example in the documentation of the pipeline (Sebastian 2018). AmpliCHECK preliminary analyse sequence data and calculates *minimum per amplicon frequency* for the variants which can be explained as sequencing errors or chimeras of the most abundant ones (Sebastian 2018). From this, we can obtain cut-off value for *minimum per amplicon frequency* to filter out the artefactual variants during the subsequent genotyping by AmpliSAS (Sebastian 2018). As we found cut-off value for minimum per amplicon frequency = 4.0% could exclude 99% of the artefactual variants in our dataset, we set Minimum per amplicon frequency = 4.0% in subsequent AmpliSAS analysis.

Parameter setting in parentage analysis

Annual survey up to 2007 (Takagi et al. 2007a; Takagi 2020) and after then (Sawada and Iwasaki unpublished) have detected about 200 to 250 males every year. Because their territories fill most part of forest in the island (Sawada et al. 2018a), we believe the number of non-detected males is not large. Hence, we considered 300 as a rough estimate of male population size. More accurate estimation by population dynamics model also supports this estimate (Sawada in preparation). Because there are some records of long distance dispersal within the island (Sawada et al. 2018a) which pose a possibility that females could be inseminated by all males in the island, we set Candidate fathers = 300 (i.e. number of all males in the island). Then, our sample contained 152 adult males. This is about 50% (152/300) of male population size. Thus, we set Prop. sampled = 0.50. Then we set Prop. loci mistyped = 0.0216, accordingly to the number of mismatches between mother and offspring in the following way. We firstly ran paternity analysis with arbitrary value for Prop. loci mistyped, and then we obtained "Mean observed error rate across loci" in the result of analysis as a value to use for Prop. loci mistyped. Because we could genotype all individuals for 12 loci of microsatellite, we arbitrary set Prop. loci typed = 0.99 and Minimum typed loci = 11.

Problem of small frequency of some MHC alleles

We used possession of MHC allele Otel-DAB*01, …, Otel-DAB*06 as binary variables MHCallele1, …, MHCallele6. Frequency of those alleles were larger than 25%.

On the other hand, we did not used possession of five MHC alleles Otel-DAB*07, …, Otel-DAB*10 and Otel-DAB*12 as such binary variables. Frequency of those alleles were lower than 12%.

As a preliminary analysis of randomization test, we used possession of all the 11 alleles as binary variables MHCallele1, …, MHCallele10 and MHCallele12 and, following procedures in the main text, we conducted randomization test on those 11 binary variables. That is, for each binary variable,

1) Randomly assign a male to each female to simulate random mating
2) Average the binary variable of the simulated pairs
3) Repeat step 1) and step 2) 1,000 times
4) Generate distribution of mean binary variable
5) Compare observed value of mean binary variable to the distribution and obtain P-values

In step 2), value of "the binary variable of the simulated pairs" means whether the male in the pair have that allele. Therefore, averaging this value over pairs yields proportion of pairs whose male has that allele. If there are small number of males who have that allele within population and number of pairs are also small, number of possible values for this average become small and null this distribution generated in step 4 become discrete. In such a situation P-values obtained by step 5 is imprecise.

In our dataset, such discretization of null distribution occurred for MHCallele7, …, MHCallele10 and MHCallele12 (i.e. Otel-DAB*07, …, Otel-DAB*10 and Otel-DAB*12) (Figure A7-1). We therefore decided to refrain from using them the final analysis.

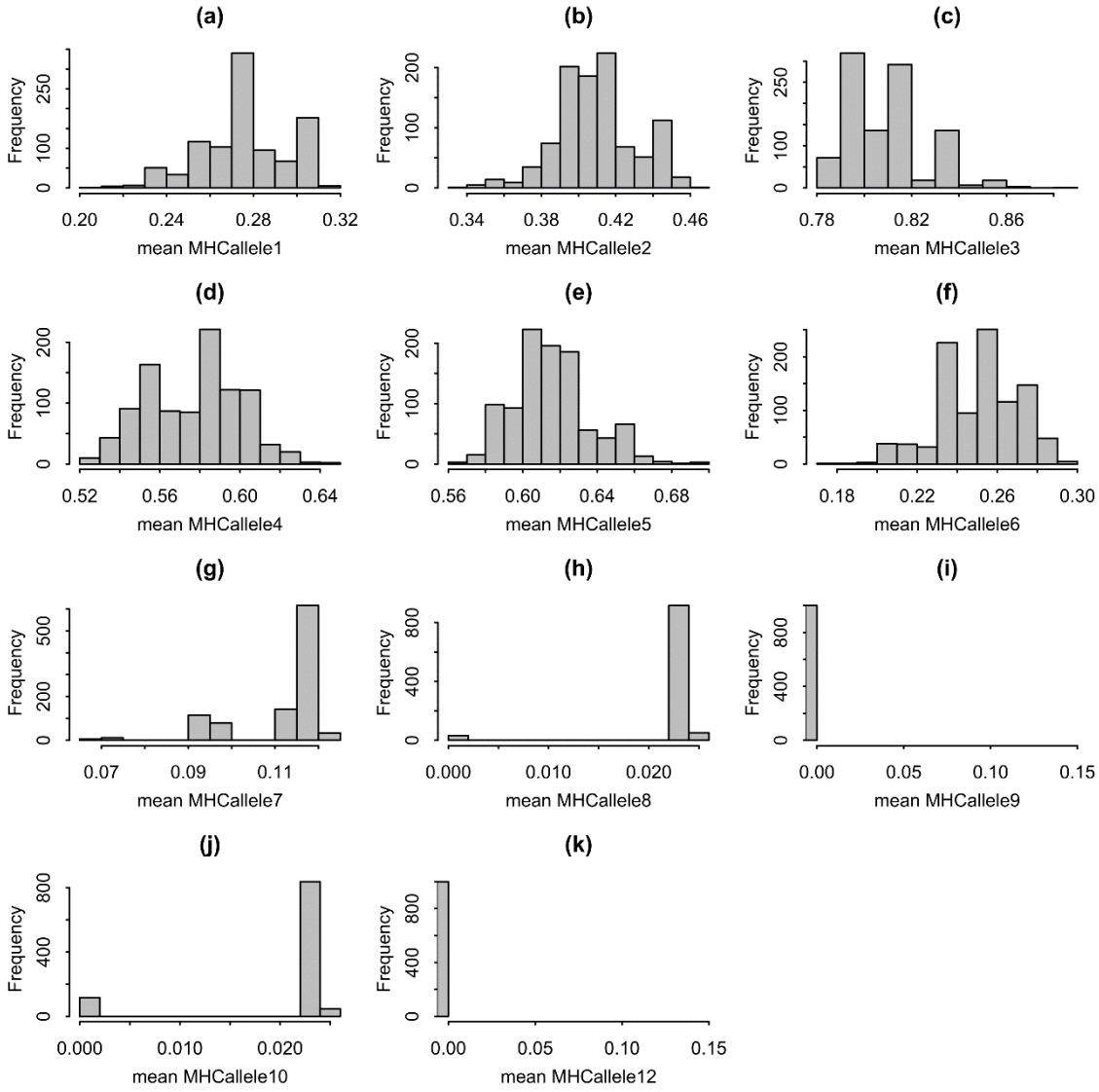


Figure A7-1

Null distribution of mean of MHCallele1, …, MHCallele12. These distributions correspond to the distribution depicted step5 in Figure 7-2.

Chapter 8

Natal and breeding dispersal kernel of the Ryukyu Scops Owl

Abstract
To discuss empirical studies on dispersal distance with theoretical basis, it is a good attempt for empiricists to focus on and estimate dispersal kernels. This study aims to offer a case study using a regression model with Weibull distribution which is a parametric distribution used as dispersal kernels. I analysed dispersal data of the Ryukyu Scops Owls obtained during 2012-2019. Although females and individuals fledged from late-breeding nest had short natal dispersal distance, no factors affected breeding dispersal significantly.

Introduction

Dispersal is an important process which appears across various biological disciplines (Bowler and Benton 2005; Ronce 2007). It is a behaviour of individuals which seeks resources in the context of behavioural ecology (Shaw and Kokko 2014). It is a demographic process which determines population dynamics in the context of population biology (Bjørnstad et al. 1999; Morales et al. 2010). It is a property of populations which determines gene flows across populations in the context of evolutionary biology (Bohonak 1999). Both empirical and theoretical studies have been elucidated existence and relevance of condition dependency of dispersal distances, such as sex, sex ratio, age and density (reviewd in Bowler & Benton 2005).

Empirical avian studies which analyse conditions affecting dispersal distance often use one or both of two approaches: 1) Drawing observed distribution of dispersal distance by histograms separately for categories (e.g. male and female), and comparing summary statistics (e.g. mean, median and kurtosis) of the distributions by the categories (e.g. Korpimaki & Lagerstrom 1988, Morton 1992). 2) Fitting linear model (including t-test and ANOVA) to the raw or transformed dispersal distance data and introducing possible effects as explanatory variables (e.g. Lahaye et al. 2001, Serrano et al. 2001, Szulkin & Sheldon 2008).

However, these ways of documentation of the dispersal distance does not necessarily conform to the treatment of the dispersal distance in theoretical studies. That is, theoreticians often describe and parametrize patterns of dispersal using parametric statistical distributions, that is, dispersal kernels (e.g. Clark 1998, Chave et al. 2002, Starrfelt & Kokko 2010). Dispersal kernel is a distribution of dispersal distance (Nathan et al. 2012), and is not necessarily normal distribution. By assuming the dispersal kernel to be specific distribution, various patterns of dispersal property are expressed freely by

varying the parameters of the distributions. To discuss empirical results with theoretical basis, it is a good attempt for empiricists to focus on and estimate dispersal kernels directly, additional to obtain summary statistics of observed histogram of dispersal distance. Note that linear models applying to raw dispersal data implicitly assume the dispersal distance follows normal distribution, hence, normal distribution as dispersal kernels.

This study aims to offer a case study analysing empirical data of dispersal distance with a regression model which uses Weibull distribution as error distribution. Weibull distribution is one of the common distributions used as dispersal kernels (Nathan et al. 2012).

Material and Methods

Dispersal data

This study uses dispersal data from 2012 to 2019 of a long-term monitoring population of the Ryukyu Scops Owl *Otus elegans* (Takagi et al. 2007a; Sawada et al. 2021a,b). The population is isolated on an oceanic island, Minami-daito Islnad, Japan (Akatani et al. 2011). A research group of which I am a member have been monitoring their breeding ecology since 2002. Nestlings were captured by hand at nests or mist net around nests, and ringed at 20-day old (Akatani et al. 2011; Sawada et al. 2020). The owl is strictly territorial and maintain year-round territory by monogamous pairs (Akatani et al. 2011). Whole island mark-recapture survey has been started in 2012 (Sawada et al. 2018a). From then, members of the research group walked along the forest area and recorded the identity of all territory holders and their geographic location in Universal Transversal Mercator coordinates system (Sawada et al. 2018a, 2021a,b). As many no-marked individuals as possible identified through this survey were also captured and ringed. Here, I defined the natal dispersal distance as the distance between natal nest and the location where the individuals identified while this territory survey in the next or after years. I defined the breeding dispersal distance as the distance between locations where an individual identified in a year and subsequent years. For the definition of breeding dispersal, because I do not completely know nests of all territorial individuals, I only considered dispersal event with the distance more than 2*129 = 258 m. 129 m is the mean radius when assuming the average-sized territory (5.2 ha) is a circle (Sawada et al. 2018a). Therefore, any two points observed across years within 2*129 m is likely to be the points in a same territory, that is, it implies that territory holder did not disperse.

Data of possible factors affecting dispersal distance

Sex of the individuals were determined by molecular method or by characteristic of hoot. Further information on the sex determination method are detailed in Sawada et al. (2021b) and Takagi (2020). Brood size at day 20, egg laying date and hatching order were determined by routine breeding monitoring. Further information on breeding monitoring method are detailed in Akatani et al. (2011) and Sawada et al. (2020).

Statistical analysis

I used regression model with Weibull distribution as an error distribution to estimate the dispersal kernel of the natal dispersal. Response variable is the dispersal distance *D* and *D* was assumed to follow Weibull distribution. Explanatory variables are: 1) *Sex*: binary variable (0: male, 1: female), 2) *Brood*: continuous variable, number of nestlings at day 20 (1 to 4), 3) *Lay*: continuous variable, egg laying date of natal nest. Here, raw laying date was firstly centred to mean of each year and the standardized values of this resultant centred laying dates were used (SD = 8.34 days). 4) *Order*: continuous variable, hatching order within a brood (1 to 4). I introduced the effect of these variables into shape parameter α, and scale parameter β of Weibull distribution using log-link functions:

$$log(\alpha) = \gamma_0 + \gamma_1 Sex + \gamma_2 Brood + \gamma_3 Lay + \gamma_4 Order$$
$$log(\beta) = \delta_0 + \delta_1 Sex + \delta_2 Brood + \delta_3 Lay + \delta_4 Order$$
$$D \sim Weibull(\alpha, \beta)$$

Then, I varied the combinations of explanatory variables in the model and searched for the best model in terms of pareto smoothed importance sampling leave one out (PSIS-LOO, Vehtari et al. 2017). Model fitting was conducted by statistical programming language Stan (Stan Development Team 2018) on R (R Core Team 2019) using *rstan* package (Stan Development Team 2019). Fitting parameters for Markov chain Monte Carlo (MCMC) procedures were as follows: warmup = 2,000; iter = 22,000; thin = 2. Model comparison was conducted by *loo* function in the *loo* package (Vehtari et al. 2018). To compare dispersal kernel with different values of explanatory variables, I calculated median of the dispersal kernel by $\beta\left(log\frac{1}{1-0.50}\right)^{\frac{1}{\alpha}}$ from the best model, while varying the values of explanatory variable. Posterior mean and 95% credible interval (CRI) were obtained.

Dispersal kernel of breeding dispersal was estimated just the same way as natal dispersal, but the explanatory variable was *Sex* only.

Results

From the surveys, I identified 152 cases (70 females and 82 males) of natal dispersal in which complete data of explanatory variables were available. Best model for the natal dispersal distance was the model including *Sex* and *Lay* (Table 8-1). Individuals fledged from later-breeding nest dispersed short distance (Figure 8-1). Median ±SD of the observed male dispersal distance was 630.98 ±1071.68 m. Median of the estimated dispersal kernel of males with *Lay* = -1, 0 and +1 were 905.27 m (95%CRI = 660.69, 1171.14), 790.14 m (95%CRI = 603.71, 1003.89) and 686.76 m (95%CRI = 491.74, 919.4), respectively (Figure 8-1a). Median ±SD of the observed female dispersal distance was 1263.11 ±1517.62 m. Median of the dispersal kernel of females with *Lay* = -1, 0 and +1 were 1402.08 m (95%CRI = 1061.87, 1790.67), 1232.91 m (95%CRI = 929.39, 1570.25) and 1081.15 m (95%CRI = 739.11, 1495.56), respectively (Figure 8-1b).

From the surveys, I identified 90 cases (44 females and 46 males) of breeding dispersal in which complete data of explanatory variables were available. Best model for the breeding dispersal distance was the null model (Table 8-1). Median ±SD of the observed dispersal distance was 653.26 ±1600.25. Median of the dispersal kernel was 1102.11 m (95%CRI = 849.04, 1383.6) (Figure 8-2).

Discussion

Females dispersed longer distances from natal nests than males, following a general pattern of avian species (Greenwood 1980). Sexual difference in the natal dispersal distance is often raised as a mechanism of inbreeding avoidance (E. Pusey 1987; Trochet et al. 2016). Therefore, this dispersal pattern might contribute to the inbreeding avoidance pattern in this population detected by Sawada et al. (2020). On the other hand, I did not find significant sexual difference in the breeding dispersal distance. Although small sample size and inability of accounting for other possible contributing factors (e.g. reproductive success, predation, divorce and quality of territory) may be the reason for non-significance, it may further support the role of their dispersal behaviour as just a mean of inbreeding avoidance, since sex-bias in natal dispersal seems to be more effective in the avoidance than in breeding dispersal. Because the owl maintains high population density for the island habitat (Takagi et al. 2007a; Sawada et al. 2018a, Sawada et al. 2021a), competition for territories is intense (Akatani et al. 2011). Therefore, once they establish a territory, leaving from there has high risk of losing opportunities of reproduction for their lifetime (Takagi unpublished data). If they leave, they may try to establish new territory anywhere possible irrespective of their sex.

Individuals from late-breeding nests dispersed shorter distances than those from early-breeding nests. This is contrary to the previous description in this population (Matsuo unpublished data). It is somewhat strange because the early fledged individuals seems to establish new territory near nest and the later fledged need more distance to find out unoccupied site, if competition is severe. However, some explanations are possible. First, individuals from late-breeding nests might have low survival rate or low detecting probability due to low settlement success, and thus long-distance dispersal is not accomplished or recorded by us. Second, individuals from early-breeding nest put weight on careful mate search, and individuals from late-breeding nest put weight more on early settlement because they do not have enough time to be choosy for mates.
This study used Bayesian estimation of Weibull regression model using Stan to estimate dispersal kernel of the natal and breeding dispersal in a population of an owl species. There are multiple advantages for this method. Firstly, using regression model circumvent separate analysis for each category of contributing factors, and hence avoid problems of reduced sample size and multiple testing. Secondly, fitting result can be used immediately as dispersal kernels in subsequent studies such as ones using probabilistic simulation. Thirdly, because the Weibull distribution is a commonly assumed dispersal kernel by theoreticians, results are used to test theoretical prediction

quantitatively. Fourthly, by obtaining MCMC samples of parameters, both point and interval estimates of any derived summary statistics of the kernel can be obtained. Collectively, I suggest fitting a regression model with error distributions which is used to describe dispersal kernel, is a natural and good way to bridge empirical result and theoretical prediction about ecological phenomena concerning dispersal.

Figure

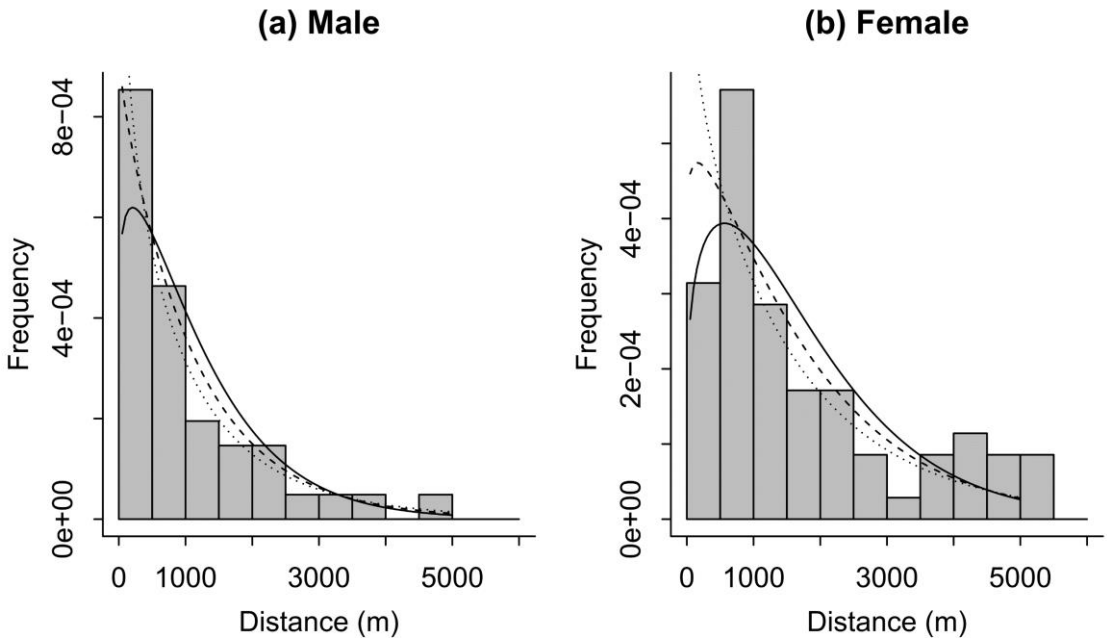


Figure 8-1

Observed distribution of the natal dispersal distance (histograms) and estimated natal dispersal kernel (lines). a: male, b: female. Solid line: *Lay* = -1, dashed line: *Lay* = 0, dotted line: *Lay* = 1. Unit of *Lay* amount to 8.34 days.

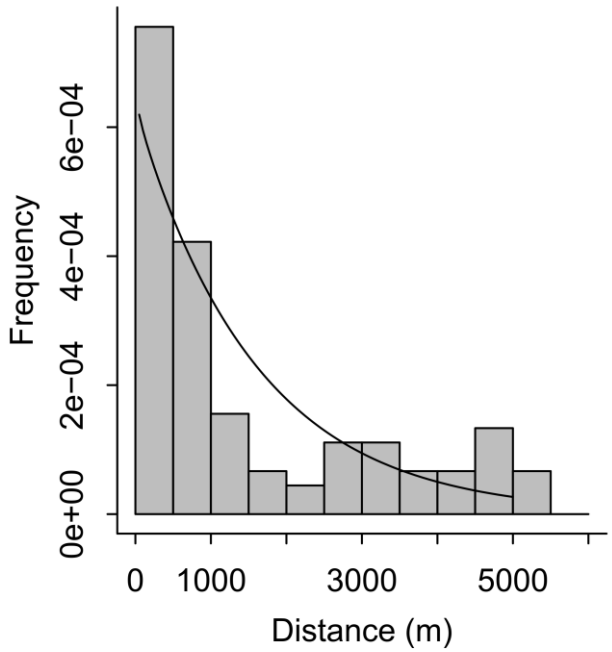


Figure 8-2
Observed distribution of the breeding dispersal distance (histograms) and estimated breeding dispersal kernel (lines).

Table

Table 8-1 Result of model comparisons

Response variable	Explanatory variable	LOOIC
Natal dispersal	Intercept + Sex + Lay	2501.24
	Intercept + Sex	2501.48
	Intercept + Lay	2502.23
	Intercept + Sex + Order	2504.08
	Intercept + Sex + Lay + Brood	2504.15
	Intercept + Sex + Lay + Order	2504.32
	Intercept + Lay + Order	2505.08
	Intercept + Sex + Brood	2505.21
	Intercept + Lay + Brood	2505.32
	Intercept	2507.34
	Intercept + Sex + Lay + Brood + Order	2507.70
	Intercept + Sex + Brood + Order	2508.18
	Intercept + Lay + Brood + Order	2508.63
	Intercept + Order	2509.73
	Intercept + Brood	2511.02
	Intercept + Brood	2511.02
Breeding dispersal	Intercept	1507.48
	Intercept + Sex	1510.68

LOOIC: looic values in output of loo function

Chapter 9

Fine-scale spatial genetic structure in the Minami-daito Island population of the Ryukyu Scops Owl

Abstract
Multiple factors can give rise to population genetic structure. Therefore, the generating process of genetic structure should be examined from multiple aspects simultaneously. I describe the fine-scale genetic structure of the Ryukyu Scops Owl *Otus elegans interpositus* population on Minami-daito Island and test isolation-by-distance, isolation-by-adaptation and assortative mating as candidates for its underlying mechanisms. Spatial principal component analysis detected a spatial autocorrelation structure for males, but not for females. Discriminant analysis of principal components and STRUCTURE analysis allowed us to classify the owl population into six genetically distinct groups. These clustering results were associated with relatedness. In addition, to these descriptive analyses, analyses of mechanisms preferred isolation-by-distance to others. Therefore, I inferred that isolation by distance and kinship structure are the most important underlying processes leading to their genetic structure.

Introduction

Even in highly volant animals, geographic distance is a key aspect for the formation of population genetic structure. Ornithologists have explicitly confirmed this by revealing sex-dependent spatial genetic structure consistent with sex-biased dispersal distance (Double et al. 2005; Temple et al. 2006; Van Dijk et al. 2015). More specifically, a strong isolation by distance (IBD, Wright 1943) pattern has been found in the sex which disperses the shorter distance.

However, other mechanisms can also give rise to population genetic structure. One of several well-established concepts is isolation by adaptation (IBA; Nosil et al. 2008, 2009). Local adaptation prevents gene flow between individuals inhabiting different environments. This results in a correlation between genetic differentiation at functional loci and ecological differentiation. It should be noted that, under IBA, we also expect an association between genetic differentiation at neutral loci and ecological distance among habitats, because local adaptation acts as a general barrier to neutral gene flow (Nosil et al. 2008, 2009). In addition, assortative mating also promotes reproductive isolation and genetic differentiation within a population (e.g. Huber et al. 2007; Elmer et al. 2009). The important point here is that these mechanisms work in combination, thus focusing on only one aspect may overlook other contributing mechanisms (Orsini et al. 2013).

Considering the above, genetic structure should be tested from multiple aspects to understand the processes that have generated it. Recent pioneering studies have practiced this. For example, Garroway et al. (2013) found associations between spatial genetic structure and environmental variables, which are known to be related to fitness components in the Great Tit (*Parus major*). Langin et al. (2015) detected spatial genetic structure in Island Scrub Jays (*Aphelocoma insularis*) with evidence of assortative mating based on bill morphology.

In this study, I explored the fine-scale genetic structure of the endemic subspecies of the Ryukyu Scops Owl *Otus elegans interpositus* on Minami-daito, an isolated oceanic island in the western Pacific, off Japan. Because of their sex-biased dispersal (see below), I expected a male specific IBD pattern. However, in order to consider the possibility that multiple processes may work together, I also tested IBA and assortative mating. Two main objectives were to: (1) describe their genetic structure, (2) address the mechanisms generating the structure.

Materials

The Ryukyu Scops Owl ranges from the northern Ryukyu Islands, Japan, to the northern islands of the Philippines (Ornithological Society of Japan 2012; Takagi et al. 2015; Gill and Donsker 2017). Subspecies *O. e. interpositus* is endemic to Minami-daito Island. The island is an uplifted coral atoll with an area of 32 km^2, situated approximately 360 km east of Okinawa Island (Figure 9-1). Most of the land area within the ring of the island's encircling hills consists of agricultural fields (sugarcane) and ponds. Small areas of forest interspersed amongst the fields, and wind-shelter belts mainly consisting of Fan Palm *Livistona chinensis* and Casuarina *Casuarina* spp., provide habitat used by the owls.

By tracking 46 fledglings using VHF radio telemetry, a previous study confirmed that females tend to disperse farther than males (male, n = 18, median = 583, range = 35–3570 m; female, n = 19, median = 1145, range = 0–2132 m, Matsuo & Takagi, unpublished data). The owls form long-term monogamous pairs and maintain year-round territories, although divorce and extra pair fertilizations have been observed occasionally (Iwasaki and Kubo unpublished data). Territory size is estimated to be 5.2 ha (Takagi et al. 2005). Further details on the breeding ecology of the owls have been described by Takagi et al. (2007b,a).

Sampling in the field

I used mist-nets and playback of hoots to capture owls at night during February to July in 2016. Unmarked individuals were newly marked and blood samples were obtained by brachial venepuncture. Samples were preserved in 99.5% ethanol at 4°C until DNA extraction. The locations of all individuals were recorded (using a handheld Garmin COLORADO 300 GPS) providing UTM (Universal Transverse Mercator) coordinates. Individuals were identified as paired by confirming their breeding activity or frequent

duet-call. Breeding activity was monitored by regularly checking their nests. Duet-calls were confirmed by walking around the entire island at night during February to July in 2016. Some owls marked previously (from 2002 to 2016) were also included in dataset as their existence was confirmed during the census.

Genotyping

DNA was extracted from blood samples using a DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA). All individuals were genotyped at 12 microsatellite loci, using markers Oe022, Oe085, Oe3-7, Oe084, Oe171, Oe128, Oe029, Oe53, Oe129, Oe081, Oe045 and Oe149 (Hsu et al. 2003, 2006b; Table 9-1). All loci were amplified in 10 µL reaction volume containing 10× Ex Taq Buffer (TaKaRa), 200 µM of each dNTP Mixture (TaKaRa), 0.5 µM of each primer (Supporting Information 1; Applied Biosystems), 0.25 units of Ex Taq (TaKaRa) and about 10 ng of genomic DNA. PCR conditions were 4 min at 94°C followed by 30 cycles of 30 sec at 94°C, 30 sec at primer specific annealing temperature (Table 9-1) and 30 sec at 72°C and finally 5 min at 72°C. PCR products were separated by capillary electrophoresis with an ABI PRISM 3730 Genetic Analyser (Applied Biosystems, Foster City, CA, USA) and fragment lengths were scored with Peak Scanner 2.0 (Applied Biosystems).

Standard population genetic analysis

For each locus, sample size, number of alleles, effective number of alleles, observed heterozygosity and expected heterozygosity were calculated using SPAGeDi (Hardy and Vekemans 2002). F_{IS} (Weir and Cockerham 1984) were calculated using GENEPOP 4.2 (Raymond and Rousset 1995). Null allele frequencies were estimated and their significance was tested by Bonferroni adjusted confidence intervals calculated from 1000 Monte Carlo simulations as implemented in Micro-checker (Van Oosterhout et al. 2004). Deviation from the Hardy Weinberg equilibrium (HWE) and the linkage disequilibrium (LD) was tested by exact tests implemented in GENEPOP. Markov chain parameters were set as follows: Dememorization number = 1000, Number of batches = 1000, Number of iterations per batch = 5000. P-value adjustments by Bonferroni correction were applied to multiple tests of HWE and LD.

Description of genetic structure

To identify fine-scale genetic structure within Minami-daito Island, I conducted three analyses: spatial principal component analysis (sPCA, Jombart et al. 2008), discriminant analysis of principal components (DAPC, Jombart et al. 2010) and structure analysis (STRUCTURE, Pritchard et al. 2000). sPCA does not assign individuals into subpopulations but can consider spatial information. Therefore, sPCA is considered suitable for describing structure originating from inherently spatial mechanisms such as IBD or IBA. In contrast, DAPC and STRUCTURE can assign individuals to subpopulations, but do not consider spatial information. Therefore, these analyses are expected to be suitable for describing group-like structure originating from

not necessarily spatial mechanisms such as assortative mating. All analyses below were conducted in R (R Core Team 2015), unless other software is referenced.

Firstly, I applied sPCA using the *spca* function implemented in the *adegenet* package (Jombart 2008). I analysed data from males and females separately so as to consider the effect of different dispersal distances between the sexes. I chose the 'neighbourhood by distance' option. Minimum distance between neighbours d_1 was set to zero. Maximum distance between neighbours d_2 was set to various values (1000, 2000, 3000, 4000 and 5000) to consider the above-mentioned dispersal range. sPCA was performed for each d_2 value. Because sPCA is a method to summarize variation and not a statistical test, results derived from sPCA do not allow judgement as to whether there is a 'significant' structure. *global.rtest* and *local.rtest* implemented in *adegenet* were used to decide which of the sPCA results to interpret. I refer to these tests as 'global test' and 'local test', respectively. These tests make this judgement. Roughly speaking, positive spatial autocorrelation structure is detected by the 'global test' and negative spatial autocorrelation structure by the 'local test'. Test parameters were set as follows: k = 3, nperm = 999. Significance level was set to 0.05. P-values were adjusted by progressive Bonferroni correction (Legendre and Legendre 1988).

To better interpret the sPCA results, I also applied the Mantel test (implemented in package *vegan* (Oksanen et al. 2017) to sPCA distance and environmental distance. sPCA distance was defined as Euclidian distance in three-dimensional space formed by the first three major axes of sPCA. A vegetation map and terrain data (available at biodiversity center of Japan, http://www.biodic.go.jp/, National Land Numerical Information, http://nlftp.mlit.go.jp/ksj/) were used to measure environmental dissimilarity. Seven variables (elevation, distance to the sea, areas of five categories of vegetation: Chinese Fan Palms, Casuarina, Chinese Banyans, agricultural fields and houses) were calculated using QGIS (QGIS Development Team 2018). Area was calculated within a 129 m radius of each sampling point. Radius was determined assuming that the average home range area of 5.2 ha is a circle (Takagi et al. 2005). After standardization of variables, Euclidian distance (in seven- dimensional space formed by seven environmental variables) was calculated as environmental distance.

Secondly, I applied DAPC using the find clusters and *dapc* functions implemented in *adegenet*. I determined the number of principal components (PCs) to construct the discriminant function using results from the cross-validation method described in Jombart and Collins (2015).

Thirdly, I applied STRUCTURE. Markov chain Monte Carlo calculations were carried out with 20,000 iterations after 10,000 iterations of burn-in. Cluster number k was set from 1 to 15, with 10 runs for each k. Best k value was determined based on delta k (Evanno et al. 2005) with Structure Harvester (Earl and VonHoldt 2012). Runs with the best k were averaged using CLUMPP (Jakobsson and Rosenberg 2007).

To better interpret clustering results, F_{ST} (Weir and Cockerham 1984) was calculated with SPAGeDi. As our samples contained related individuals (among 227 individuals,

60 parent-offspring pairs, 15 full-sibling pairs and six half-sibling pairs were included), a cluster might correspond to a group of relatives. To confirm this, correlation between relatedness (Queller and Goodnight 1989) computed using SPAGeDi and cluster distance was assessed by Mantel test. Cluster distance was defined as Euclidean distance in the k-dimensional space formed by k columns of Q matrix. Q matrix is an n × k matrix of assignment probability, where n and k are the numbers of individuals and clusters, respectively. If clusters correspond to relatives, cluster distance is expected to correlate with relatedness. I also applied AMOVA (Excoffier et al. 1992) to geographic distance and environmental distance with clustering results to test between-cluster differences in geographic locations and environmental features. Note that AMOVA is applicable to any type of distance data. The *adonis* function in *vegan* was used. The test would be significant if at least one cluster had a different geographic position or a different environmental feature from other clusters. As described in the results, I retained the same cluster number (k = 6) for DAPC and STRUCTURE. Therefore, I assessed consistency of clustering results between the two methods by H' value computed by CLUMPP, which varies from 0 to 1 depending on similarity between Q matrixes, while controlling for any label switching problems.

Tests for the generating mechanism of the genetic structure

I applied Mantel tests to establish whether the genetic structure is explained by IBD and/or IBA. Correlation between kinship coefficient (Loiselle et al. 1995) estimated with SPAGeDi and geographic distance was tested. Correlation between kinship coefficient and environmental distance was also tested. These two correlations are expected under IBD and IBA, respectively (Orsini et al. 2013). Note that the kinship coefficient can be used to test IBD and IBA based on individual data (ex. Ruiz-Gonzalez et al. 2015), just as pairwise F_{ST} is used in population-based analysis. To remove possible confounding effects of geographic distance with environmental distance in later tests, I also applied partial Mantel test implemented in vegan. I also performed Fisher's exact test to see whether genetic structure might be explained by assortative mating. I drew a contingency table in which rows and columns indicated the cluster number and the i, j elements indicate the frequency of pairs of a male from cluster i and a female from cluster j. Under assortative mating, frequency in the diagonal element should have a high value, which can be detected by Fisher's exact test on the contingency table.

Results

Sampling in the field

I collected blood samples from 70 unmarked individuals. The survival of 157 individuals marked before 2016 was confirmed. Among the total of 227 individuals, 63 breeding pairs were identified. The samples included 60 parent-offspring pairs, 15 full-sibling pairs and six half-sibling pairs.

Genotyping and population genetic analysis

All loci were genotyped for all 227 individuals. For the 12 loci, the number of alleles ranged from 3 to 16, effective number of alleles was 1.51 to 9.23, observed heterozygosity was 0.361 to 0.894 and expected heterozygosity was 0.336 to 0.892 (Table 9-2). Deviation from HWE was not found. I found significant LD for five loci pairs (Table 9-3). Because the inclusion of relatives in the samples could have caused the LD, I randomly selected an individual from each family and excluded other familial individuals from the data and tested LD again. Significant LD disappeared (Table 9-4), indicating that LD was due to family structure in the sample. Therefore, I did not exclude any loci from subsequent analysis. Sign of null alleles was detected in Oe053, although the estimated frequency was small (lower than 0.05).

Description of genetic structure

I performed sPCA on males and females separately. Global genetic structure was only supported for males (Global test; male, adjusted-P < 0.05 at 1000 m and 3000 m, adjusted-P > 0.05 at other distances; female, adjusted-P > 0.05 at all distances, Table 9-5). Local genetic structure was not supported for either sex (Local test; both sexes, adjusted-P > 0.05 at all distance, Table 9-5). I then focused on the first major axes of sPCA on male with d_2 = 1000 m and 3000 m. Note that these axes with a large positive eigenvalue correspond to a global structure. I hereafter call an individual's score for the first ith major axis as 'ith global score'. As the results for 1000 m and 3000 m were similar, I only show the results of 1000 m here (Figure 9-2). For the first global score, positive scores were relatively concentrated to the southeast and negative scores were to the northwest (Figure 9-3a). For the second global score, positive scores were concentrated to the southwest and negative scores were to the northeast (Figure 9-3b). For the third global score, positive scores were concentrated to the southwest and northeast, and negative scores were to the northwest and southeast (Figure 9-3c). These patterns seemed to capture actual genetic structure, because eigenvalues of the axes are more extreme than the others (Figure 9-3d). Correlation between sPCA distance and environmental distance was not significant (Mantel test; r = 0.008, P = 0.87, Table 9-6).

Before performing DAPC, k-means clustering found that the 227 individuals fell into six groups (BIC was minimum at k = 6, Figure 9-4). First, 20 PCs were retained to construct discriminant functions (Figure 9-4). Using the five discriminant functions, DAPC assigned all individuals to one of the six clusters. In each group, individuals were not biased to one place on the island, but were scattered throughout the island (Figure 9-5, 9-6). However, individuals that were assigned to the same cluster appeared to occupy closer positions. This pattern was observed in both sexes.

STRUCTURE analysis also found six clusters (delta k was maximum at k = 6, Figure 9-7). Results of 10 replicates for k = 6 were highly similar to each other (H' = 0.989).

Individuals assigned to the same cluster occupied closer positions on the island, however, they appeared to be more scattered than in DAPC (Figure 9-8).

Global F_{ST} between clusters was 0.091 in DAPC (pairwise F_{ST} = 0.075 to 0.123, Table 9-7) and 0.075 in STRUCTURE (pairwise F_{ST} = 0.057 to 0.096, Table 9-8). Cluster distance was significantly correlated with relatedness (Mantel test; DAPC, r = -0.386, P < 0.01; STRUCTURE, r = -0.481, P < 0.01, Table 9-6), indicating that clusters reflect kinship structure. AMOVA supported between-cluster differences in geographic location in both sexes (both sexes, both clustering methods, all P < 0.01, Table 9-9). AMOVA also detected differences in environmental features for both sexes (male, DAPC, P < 0.01, STRUCTURE, P < 0.05; female DAPC, P = 0.86, STRUCTURE, P < 0.05, Table 9-9). The assignments to clusters were not highly consistent between STRUCTURE and DAPC (H' = 0.491).

Tests for generating mechanisms of the genetic structure

Kinship coefficient and geographic distance were negatively correlated only for males (Mantel test; male, r = -0.038, P < 0.01; female, r = -0.012, P = 0.48, Table 9-6). Kinship coefficient and environmental distance were correlated with males (Mantel test; male, r = 0.013, P < 0.05, female, r = 0.023, P = 0.11, Table 9-6). After controlling for geographic distance, the correlation was diminished (partial Mantel test; male, r = -0.012, P = 0.06, female, r = -0.022, P = 0.09, Table 9-6). The tendency that paired individuals belong to the same cluster was significant for STRUCTURE (exact test, P < 0.01) but not for DAPC (exact test, P = 0.80).

Discussion

I revealed fine-scale spatial genetic structure in the population of the endemic subspecies of Ryukyu scops owl on Minami-daito Island. sPCA detected a spatial autocorrelation structure for males, but not for females. The owl population could be classified into six distinct groups by DAPC and STRUCTURE. I discuss possible explanations for these findings, considering the tests for the generating mechanism of the genetic structure.

The most plausible explanation for the sPCA results is that IBD occurred within an extremely small geographic scale, for the following reasons. Firstly, the structure is only supported in males, which is the sex that disperses the shorter distance (Matsuo & Takagi, unpublished data). This suggests that distance is an important factor generating the structure. Inconsistency between sexes prefers IBD to IBA, unless adaptation is sex dependent. Secondly, sPCA distance was not correlated with environmental distance. Structure described by sPCA is inherently spatially autocorrelated because of the rational of the method (Jombart et al. 2008). Provided environmental features have spatial autocorrelation, major axes of sPCA might represent variation occurring not only by IBD but also by IBA. The non-significant correlation between sPCA distance and environmental distance indirectly supports explanation by IBD. Thirdly, Mantel test of

kinship coefficient and geographic distance directly supported IBD in this population. In addition, IBA was not supported because the correlation between genetic distance and environmental distance became non-significant after controlling for relatedness.

My results are in accord with previous studies that have shown the shorter dispersal distance of males lead to a locally conspicuous genetic structure (Double et al. 2005; Woxvold et al. 2006; Van Dijk et al. 2015). I have confirmed that the owls on Minami-daito basically move along ring-shaped wind-shelter belts (Iwasaki et al. unpublished). The circumference of the wind-shelter belts is approximately 12 km, which is longer than the dispersal distance of the owls (range = 0–3570 m, Matsuo & Takagi, unpublished data). The tendency for short-distance dispersal within the wind-shelter belts might have encouraged IBD along the belts. Plotting sPCA scores on the island revealed such a pattern. This study may be an extremely rare example showing the effect of the direction of gene flow on fine-scale spatial genetic structure in an animal population (Dutech et al. 2005; Valverde et al. 2016).

There may be various explanations for the clustering results. The most plausible one is that clusters reflect kinship structure (Anderson and Dunham 2008; Goldberg and Waits 2010). Significant correlation between cluster distance and relatedness supports this idea. Taking IBD pattern into account, significant between-cluster differences in geographic position detected by AMOVA also supports clusters being groups of relatives. My samples include relatives because of the following properties: (1) The entire population consists of a relatively small number of individuals (estimated to be about 210 pairs; Takagi et al. 2007a); (2) I sampled as many individuals as I could from this small population; (3) Because their life span is 3 to 4 years and they breed every year, many familial individuals coexist in the population at the same time.

Another explanation is reproductive isolation by assortative mating, as individuals from the same cluster estimated by STRUCTURE tended to become breeding pairs. However, this is less likely than the explanation by family structure because linear habitat and shorter dispersal distance compared to the length of habitat increase the probability that individuals from the same clusters become pairs. The third explanation is that clusters correspond to groups that are adapted to different environments. That AMOVA detected between cluster differences in environmental features supports this idea. However, this also might be an implausible explanation because IBA was not supported by Mantel test.

In addition, differences in the assignment to clusters between two clustering methods might be explained by the inherent assumptions of the analysis. STRUCTURE assumes HWE and linkage equilibrium within a subpopulation (Pritchard et al. 2010), but DAPC does not (Jombart et al. 2010). I think that the assumption works as a kind of constraint when STRUCTURE searches for optimal assignment, compared to DAPC, which is free from the assumption. An important aspect of this study is that I addressed multiple hypotheses on genetic structure formation. Testing only IBD may overlook IBA if both IBD and IBA work in combination (Orsini et al. 2013). By simultaneously testing IBD,

IBA and assortative mating, I was able to estimate the most important likely generating mechanisms of the genetic structure of the owl population. That is, the fine scale genetic structure of Ryukyu scops owls was generated by IBD and kinship structure. Studies that have been able to evaluate the relative importance of multiple mechanisms are rare (Orsini et al. 2013). This study certainly contributes to increasing our knowledge of genetic structure formation and encourages subsequent studies.

Figure

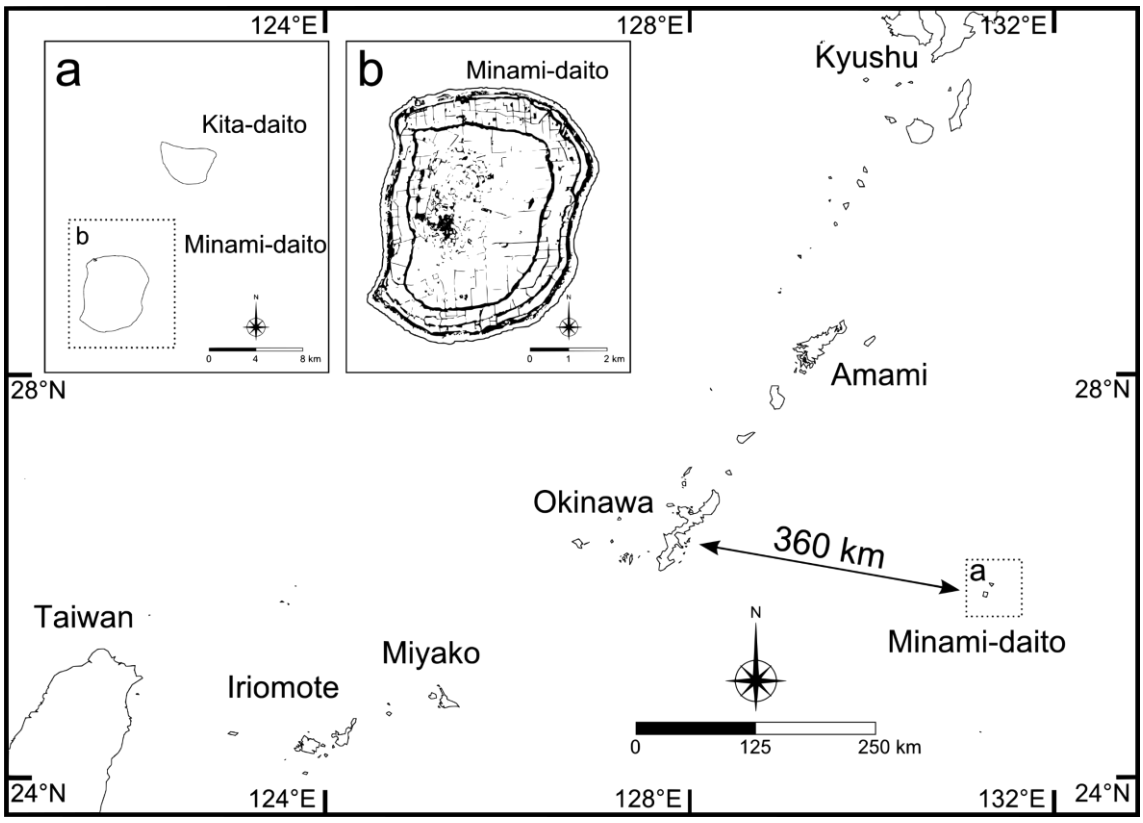


Figure 9-1
Minami-daito Island located ca. 360 km east of Okinawa Island. Enlarged details are shown in (a) and (b). Woods in map b are shown in grey. Circular wind-shelter belts can be recognized.

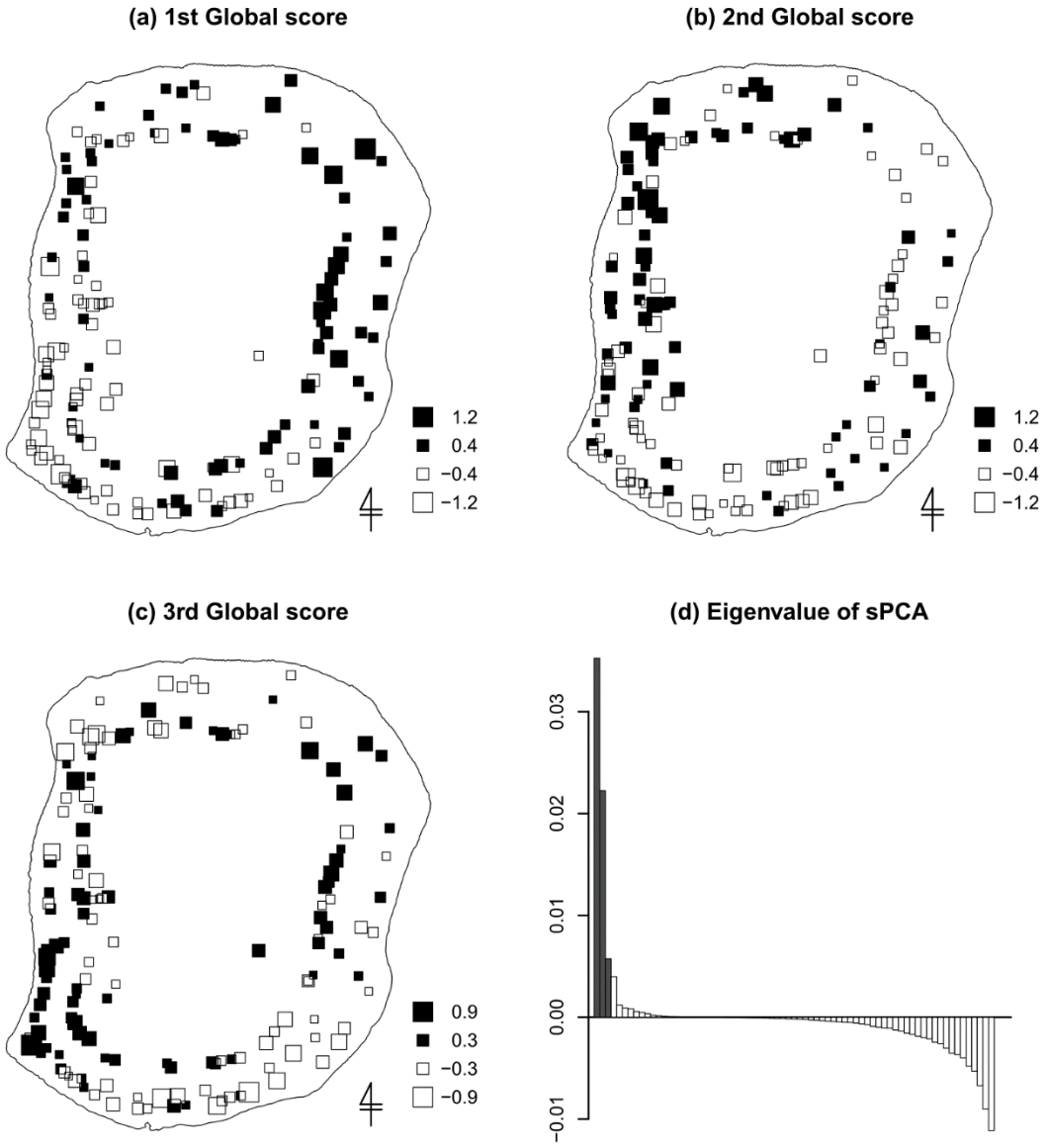


Figure 9-2

Results of sPCA for males with d_2 = 3000m. First (a), second (b), third (c) global scores of each individual are shown by the size and colour of markers on a map of Minami-daito Island. White indicates negative values and black dose positive values. Distribution of black and white resemble to those of 1000m (see Figure 9-3 in main text). Note that positive and white is reversed in second major axis between 1000 m and 3000 m. (d) Eigenvalues of each axis extracted by sPCA are shown as a bar plot. Eigenvalues of the first three major axes, which are interpreted in detail, are coloured dark grey.

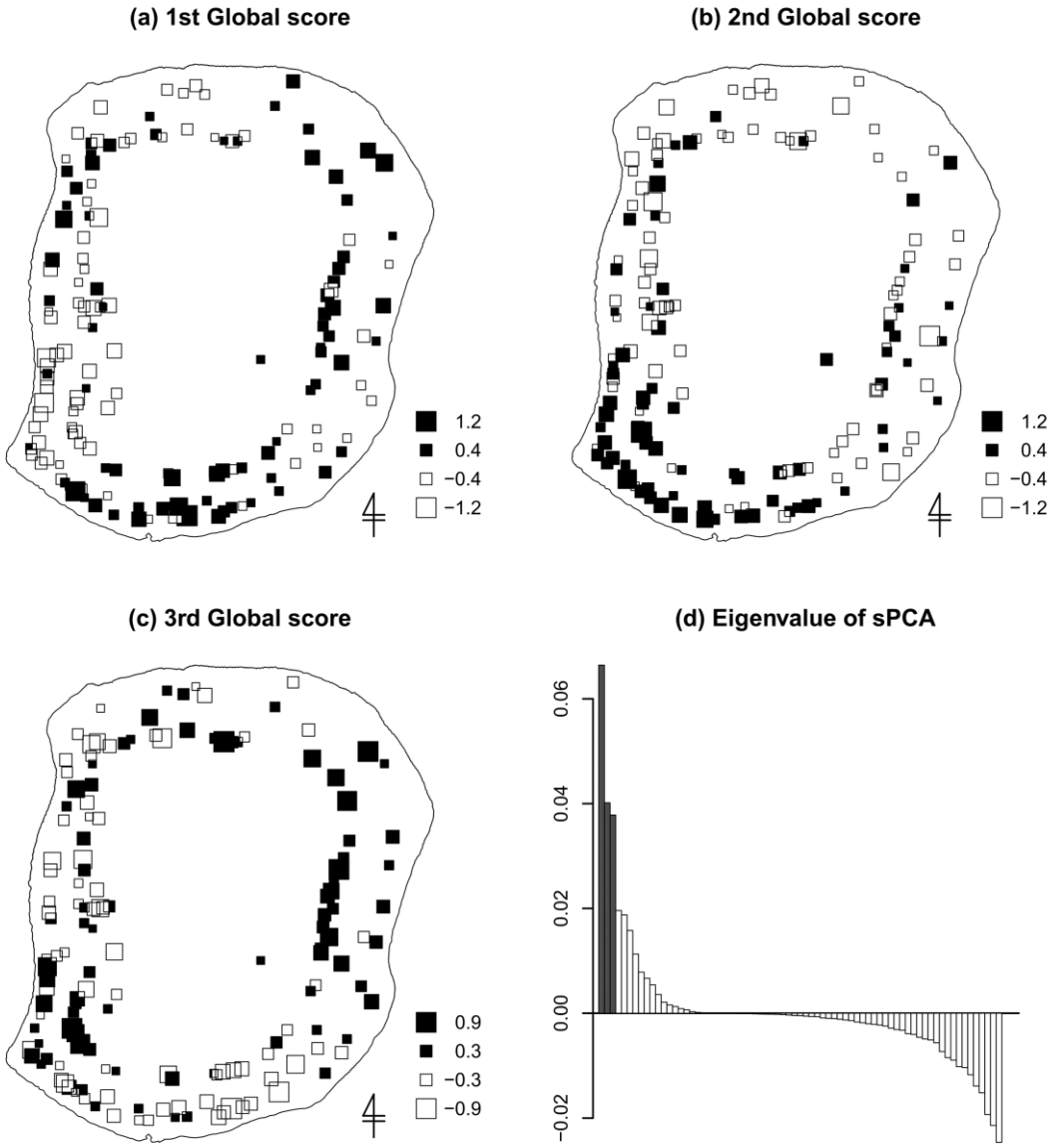


Figure 9-3

Results of sPCA for males with d_2 = 1000 m. First (a), second (b), third (c) global scores of each individual are shown by the size and colour of markers on a map of Minami-daito Island. White indicates negative values and black positive values. The position of markers indicates where each individual nested. (d) Eigenvalues of each axis extracted by sPCA are shown as a bar plot. Eigenvalues of the first three major axes, which are interpreted in detail, are coloured dark grey.

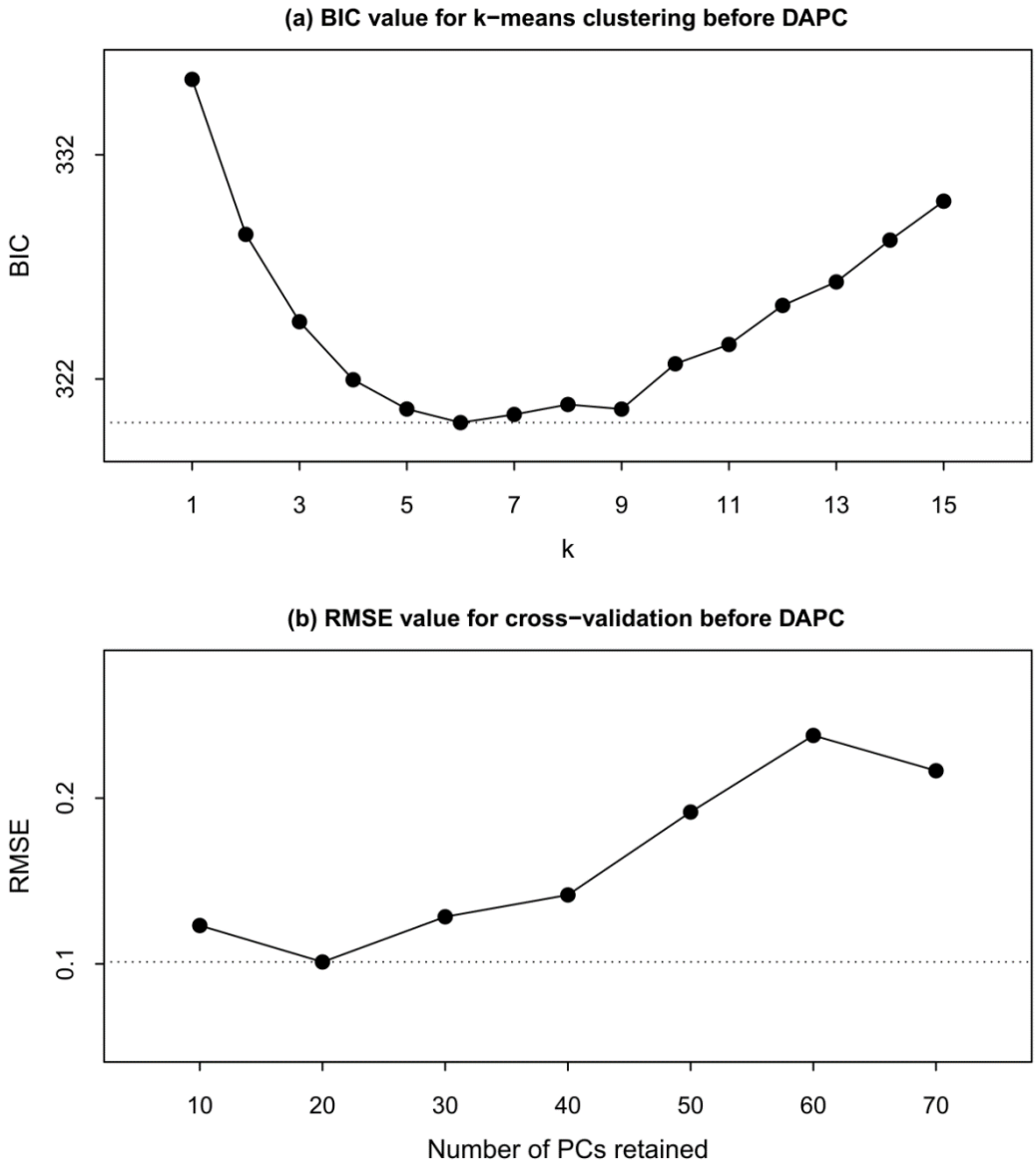


Figure 9-4

Results of analyses before DAPC. (a) BIC values computed by *find.cluster* are plotted against the number of clusters k. BIC was minimized at k = 6. (b) Root mean squared error (RMSE) values computed by *xvalDapc* are plotted against the number of PCs retained to compose discriminant function. Adopting the number which minimize root mean squared error (RMSE) is recommended by author of DAPC analysis (Jombart and Collins 2015)

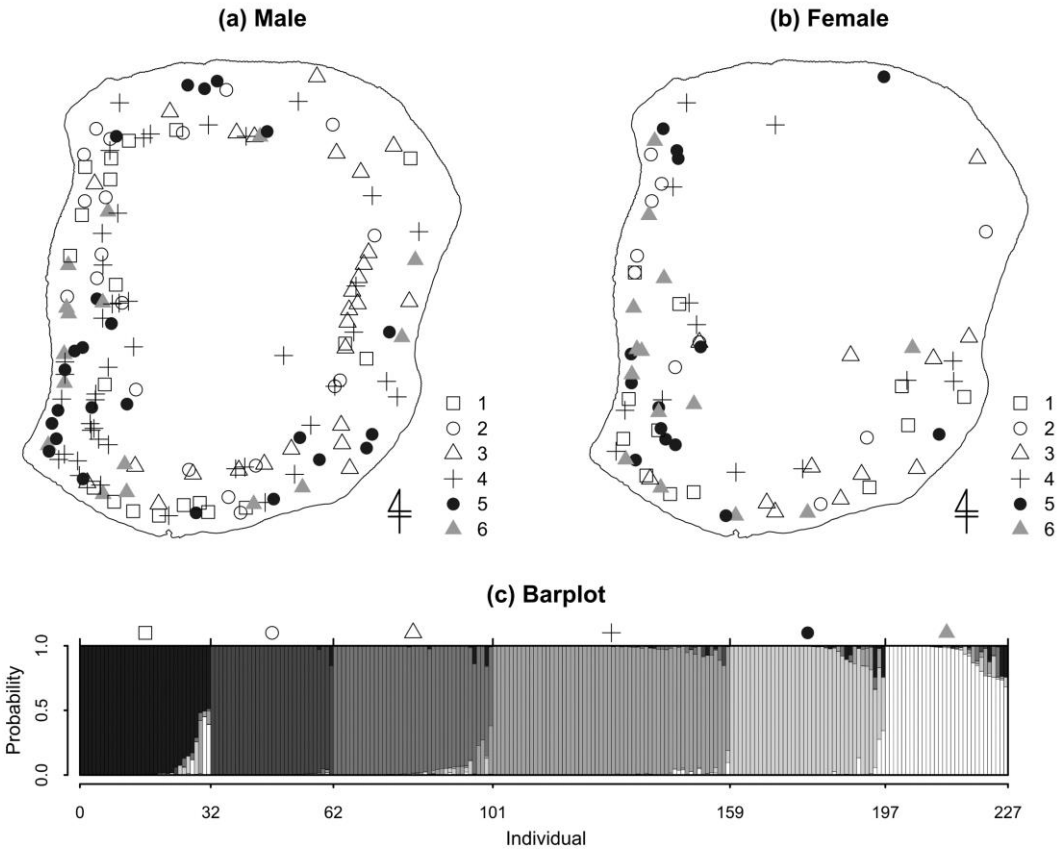


Figure 9-5

Results of DAPC. Clusters, to which each individual belongs, are shown by distinct markers on a map of Minami-daito Island: males (a) and females (b). (c) Assignment probabilities are visualized as a bar plot. Each bar represents an individual. Individuals are sorted by assignment probabilities. Proportions of each colour in each bar correspond to the assignment probability to each group. Markers above the bar plot accord with those in (a), (b).

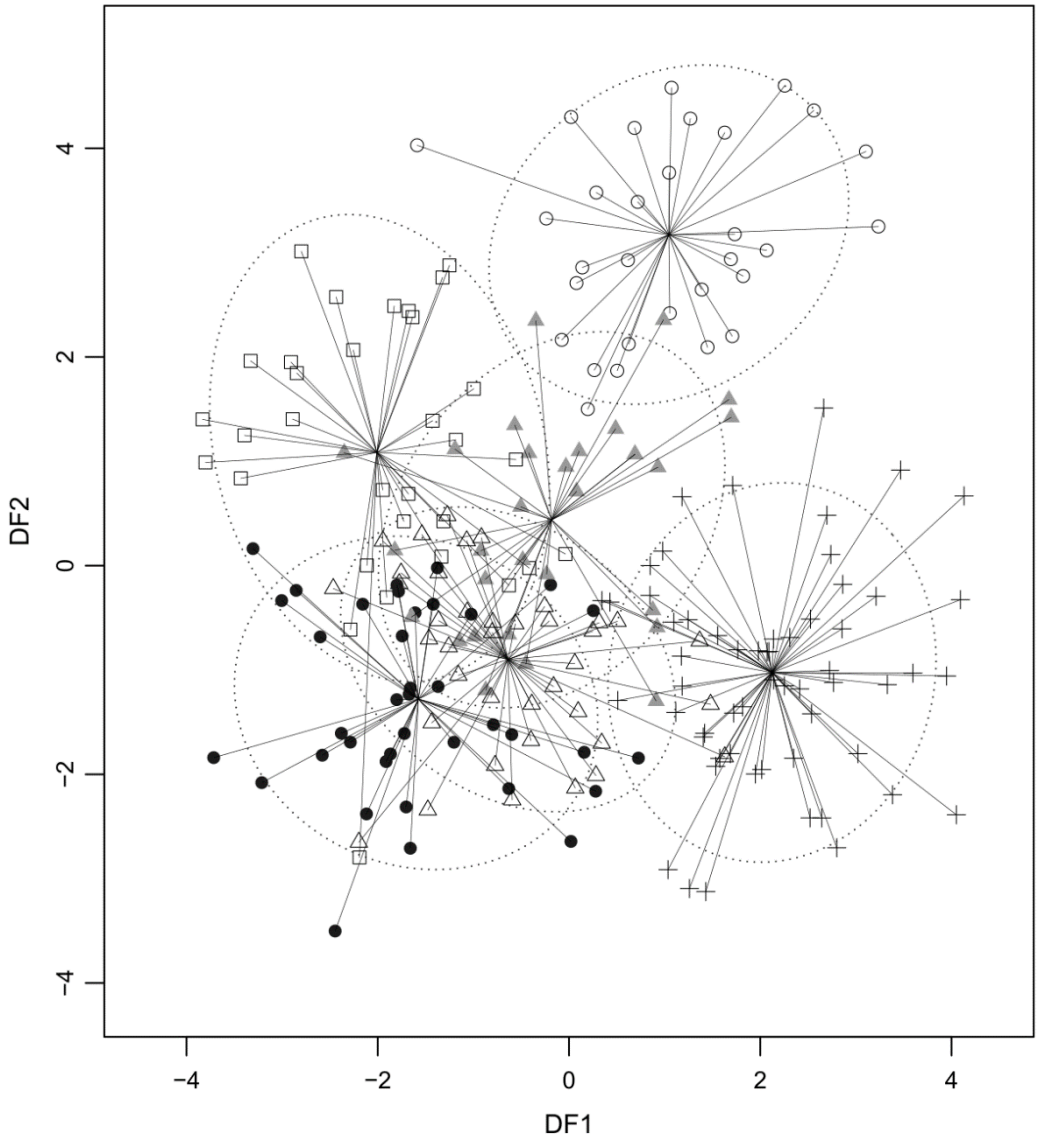


Figure 9-6

Scatter plot of the first two discriminant function score (DF1 and DF2). Each point represents an individual. Six genetically distinct groups are expressed by distinct marker types. 80 % probability ellipses are drawn for each cluster. Center of the lines indicate mean of the cluster. The markers in this plot corresponds to the marker in Figure 3 in the main text.

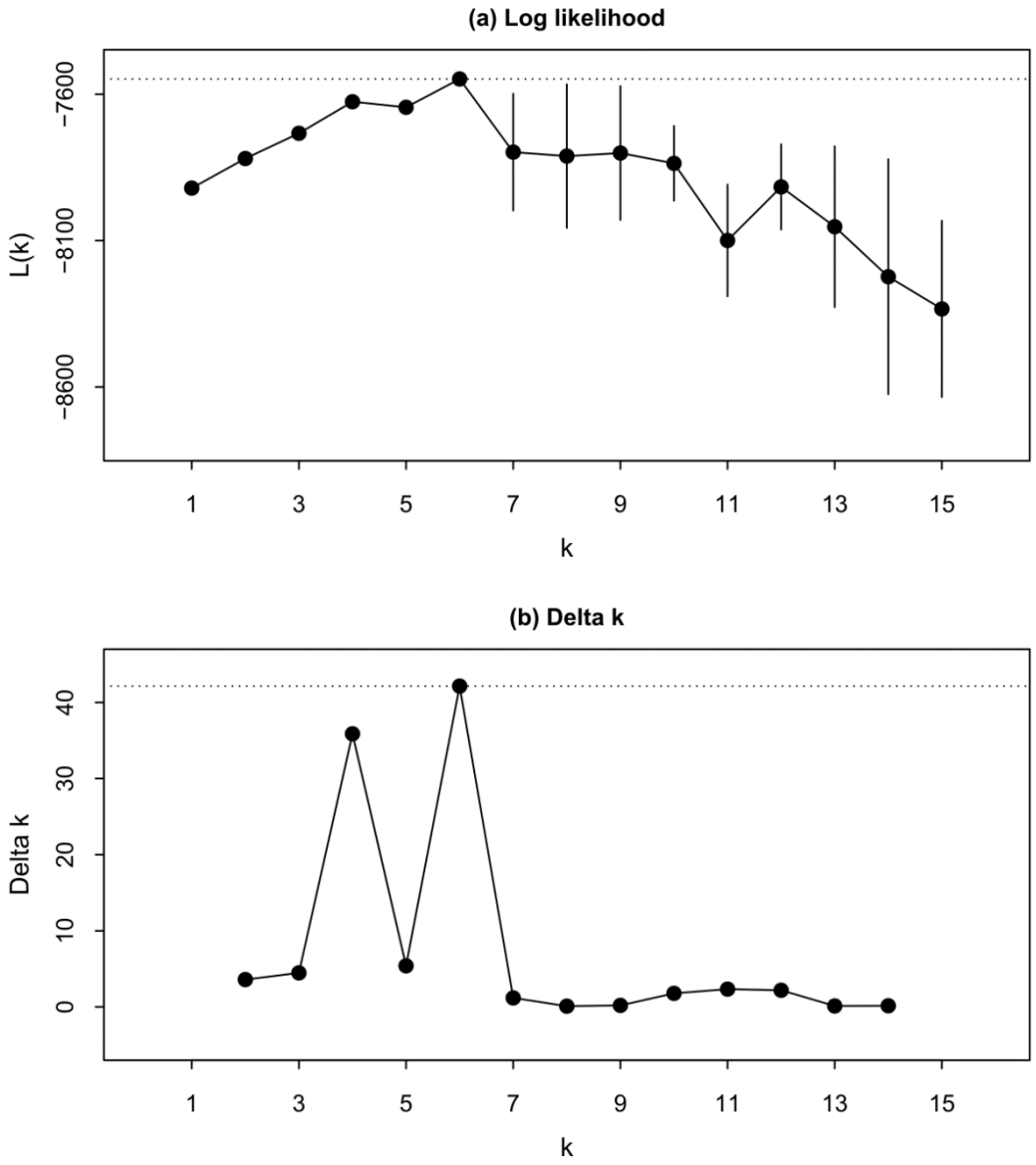


Figure 9-7

Results of analyses accompanying STRUCTURE. (a) Log likelihood L(*k*) are plotted against the number of clusters k. L(k) was minimized at k = 6. Error bars indicate standard errors. (b) Delta k values computed by Structure Harvester are plotted against the number of clusters *k*.

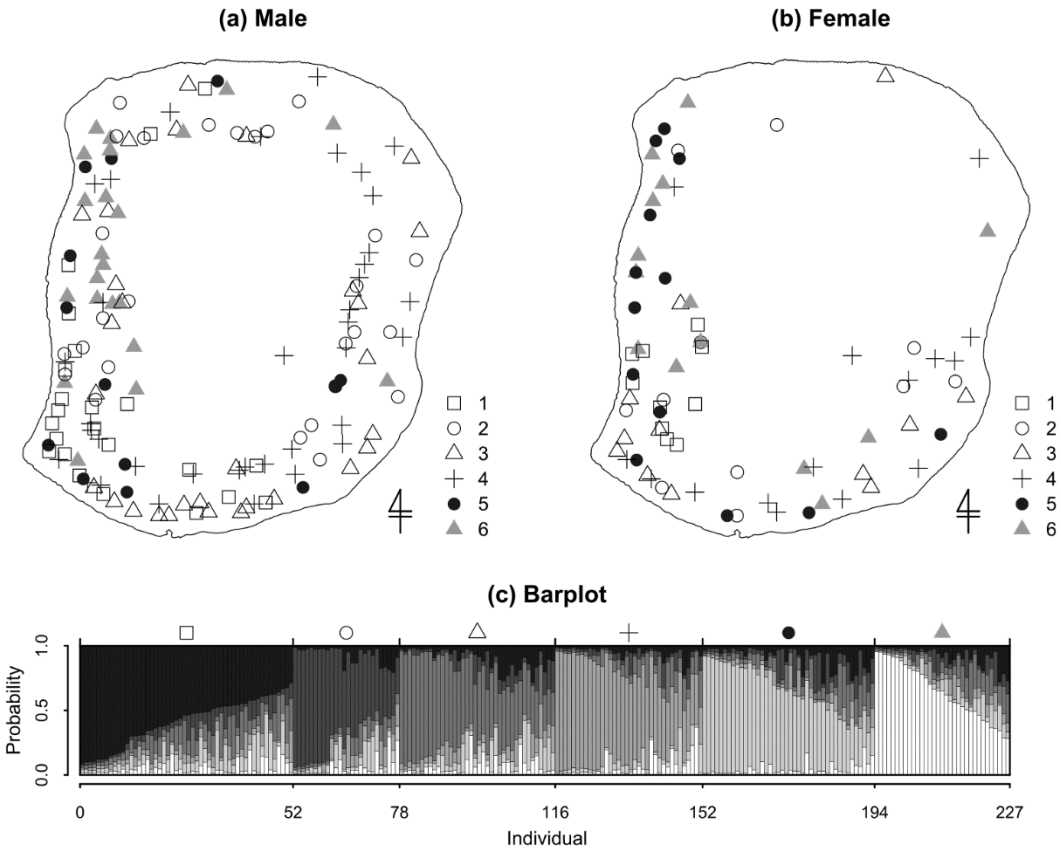


Figure 9-8

Results of STRUCTURE. Clusters to which each individual belongs are shown by distinct markers on a map of Minami-daito Island for male (a), for female (b). (c) Assignment probabilities are visualized by bar plot. Each bar represents an individual. Individuals are sorted by assignment probabilities. Proportions of each colour in each bar correspond to the assignment probability to each group. Markers above bar plot accord with those in (a), (b).

Table

Table 9-1 Information on primers of microsatellite markers

Locus	Repeated motif	Primer sequence (5'-3')	Ta (°C)	Label
Oe3-7	$(GATA)_{12}$	F-GTGGGTTTATTGCCCCCTCG	52	VIC
		R-CAGATGAATGAATGGATAGATGG		
Oe022	$(GATA)_{12}$	F-ATCTGATTCAGTGTCTCCATCCATG	64	6-FAM
		R-CCCAGGAATCTCTCCCAATGTT		
Oe045	$(GATA)_{13}GATTA(GATA)_{10}$	F-GTATGTTCTACGTTGGATTTCCA	58	HEX
		R-AAACCTGGCAAGTGCTGTT		
Oe029	$(GATA)_{12}$	F-TGTCCCAACTCCCCTGG	61	NED
		R-TTTCCAGAAGCAACCTG		
Oe081	$(GATA)_{14}$	F-GTAAGGGAAGTAGACGTCTGTTGG	61	HEX
		R-CAACTTTGTGTCATCTGAAAGG		
Oe084	$(GATA)_{15}$	F-GGGCATAGTTAGACCTTTGCAG	64	PET
		R-CACATCTGTTGTTCTCCGTGTTACC		
Oe085	$(GATA)_{12}$	F-TGCACAGAAATGAAGAAGAG	61	6-FAM
		R-GGGTTTCTCAAAACAGGCAGG		
Oe129	$(GATA)_{14}$	F-GTCACCTCTTGACATCCGAGTAGC	65	VIC
		R-GCTAAGAGTCCATTTGCCCATCTG		
Oe149	$(GATA)_{17}$	F-CACACATCCATTTTGGGGTGC	65	NED
		R-GGATGCTGGAACTGACCTGC		

Table 9-1 (continued)

Locus	Repeated motif	Primer sequence (5'-3')	Ta (°C)	Label
Oe053	$(GATA)_{13}$	F-CTCTGCATCTTAACGCACAGGAC	64	PET
		R-CCTCCAAGTGGACAGGAAAAGC		
Oe128	$(GATA)_{13}$	F-CGTTGTAAATGATGAATCGCCTAGTGC	64	PET
		R-ATGCATGTATACATACAAACCTGG		
Oe171	$(GATA)_{12}$	F-TTTTACAAACTACTAGTGCATGTCTCC	64	NED
		R-AGATGTTGTATTTCAGTGTCAG		

Ta, annealing temperature; Label, fluorescent-label bound to each reverse primer

Table 9-2 Basic population genetic statistics for microsatellite data

Locus	N	NA	NAe	AR	He	Ho	f_{null}	F_{IS}	P
Oe085	227	7	4.06	7	0.754	0.767	-0.009	-0.017	0.021
Oe022	227	9	5.46	9	0.817	0.802	0.008	0.018	0.564
Oe081	227	5	3.00	5	0.667	0.656	0.006	0.016	0.990
Oe129	227	5	3.55	5	0.718	0.744	-0.019	-0.037	0.338
Oe171	227	8	3.30	8	0.697	0.652	0.030	0.065	0.533
Oe084	227	11	5.36	11	0.813	0.762	0.031	0.063	0.062
Oe3-7	227	5	1.51	5	0.336	0.361	-0.065	-0.076	0.220
Oe045	227	16	9.23	16	0.892	0.894	-0.003	-0.003	0.220
Oe029	227	3	2.74	3	0.635	0.617	0.012	0.028	0.923
Oe149	227	6	3.81	6	0.738	0.718	0.013	0.027	0.301
Oe053	227	4	3.11	4	0.679	0.608	0.048	0.105	0.006
Oe128	227	6	3.28	6	0.695	0.705	-0.012	-0.014	0.179

N, number of individuals; NA, number of alleles; NAe, number of effective alleles (Nielsen et al. 2003); AR, Allelic richness (expected number of alleles among 454 gene copies); He, expected heterozygosity (Nei 1978); Ho, observed heterozygosity; f_{null}: null allele frequency estimated in Micro-checker with Oosterhout's algorithm; F_{IS}, F-statistics (Weir & Cockerham 1984); P, P-value calculated from exact tests of deviation from HWE, *: $P < 0.0045$ (Bonferroni correction of alpha = 0.05 for 12 simultaneous tests)

Table 9-3 P-values for exact tests of linkage disequilibrium

	Oe085	Oe022	Oe081	Oe129	Oe171	Oe084	Oe3-7	Oe045	Oe029	Oe149	Oe053	Oe128
Oe085	-				*							
Oe022	0.111319	-						*				
Oe081	0.248165	0.004864	-									
Oe129	0.206471	0.026049	0.826908	-								
Oe171	0.000194	0.019256	0.024886	0.667046	-			*				*
Oe084	0.030669	0.063274	0.147753	0.264610	0.323066	-				*		
Oe3-7	0.729672	0.005335	0.495476	0.824694	0.131264	0.013870	-					
Oe045	0.301547	0.000048	0.096050	0.252174	0.000164	0.011251	0.444911	-				
Oe029	0.493704	0.001412	0.569653	0.726810	0.339378	0.035594	0.215751	0.005852	-			
Oe149	0.008477	0.125398	0.166783	0.101772	0.024767	0.000000	0.056821	0.155408	0.003708	-		
Oe053	0.064223	0.030718	0.006995	0.189847	0.313565	0.060715	0.426996	0.189958	0.094026	0.308334	-	
Oe128	0.489909	0.050459	0.134926	0.020907	0.000547	0.002177	0.606796	0.676727	0.418591	0.062252	0.914785	-

P-value calculated from Exact tests of LD are below the diagonal. Significance codes are above the diagonal, *: P < 0.000758 (Bonferroni correction of alpha = 0.05 for 66 simultaneous tests)

Table 9-4 P-values for exact tests of linkage disequilibrium (after excluding family individual)

	Oe085	Oe022	Oe081	Oe129	Oe171	Oe084	Oe3-7	Oe045	Oe029	Oe149	Oe053	Oe128
Oe085	-											
Oe022	0.18254	-										
Oe081	0.65776	0.071685	-									
Oe129	0.086288	0.266171	0.605772	-								
Oe171	0.402942	0.252992	0.095699	0.154603	-							
Oe084	0.418232	0.029989	0.461811	0.0178	0.24834	-						
Oe3-7	0.553505	0.266132	0.529325	0.844782	0.378376	0.401825	-					
Oe045	0.274479	0.280318	0.479276	0.356754	0.016622	0.401494	0.885219	-				
Oe029	0.348793	0.085449	0.830958	0.575961	0.638899	0.337563	0.360543	0.878616	-			
Oe149	0.260239	0.736586	0.01426	0.889961	0.123311	0.077974	0.074752	0.586999	0.212471	-		
Oe053	0.043224	0.196287	0.34605	0.23631	0.011163	0.166274	0.802534	0.213927	0.326709	0.624264	-	
Oe128	0.371337	0.545492	0.142922	0.134883	0.134132	0.239113	0.160467	0.593526	0.02056	0.74893	0.662343	-

P-value calculated from Exact tests of LD are below the diagonal. Significance codes are above the diagonal, *: P < 0.000758 (Bonferroni correction of alpha = 0.05 for 66 simultaneous tests)

Table 9-5 Results of global test and local test on sPCA results

Test	Sex	Distance (m)	Test statistic	P	
Global	Male	1000	0.0318	0.026	*
		2000	0.0304	0.082	
		3000	0.0327	0.015	*
		4000	0.0314	0.049	
		5000	0.0334	0.057	
	Female	1000	0.0589	0.212	
		2000	0.0589	0.146	
		3000	0.0620	0.060	
		4000	0.0577	0.289	
		5000	0.0521	0.594	
Local	Male	1000	0.0304	0.698	
		2000	0.0310	0.545	
		3000	0.0307	0.580	
		4000	0.0307	0.554	
		5000	0.0345	0.436	
	Female	1000	0.0583	0.687	
		2000	0.0604	0.847	
		3000	0.0584	0.844	
		4000	0.0603	0.626	
		5000	0.0685	0.330	

Distance, radius within which two points are defined as neighbor (value for parameter d_2 in *spca* function); Test static, sum of highest three R^2 value (see documentation of *adegenet* ver 2.0.1); P, P-value; *: significance after progressive Bonferroni correction of P-value by Hewitt et al. (1997) for five distance classes: 1000, 2000, ..., 5000 m. (Test at distance i×1000 m was tested against alpha = 0.05/i)

Table 9-6 Results of Mantel test and partial Mantel tests

Sex	Distance A	Distance B	Distance C	r	P		Implication of test
Both	Cluster distance (DAPC)	Relatedness	-	-0.386	0.000	**	Interpretation of DAPC
	Cluster distance (STRUCTURE)	Relatedness	-	-0.481	0.000	**	Interpretation of
Male	sPCA distance (d_2 = 1000 m)	Environmental distance	-	0.008	0.866		Interpretation of sPCA
	sPCA distance (d_2 = 3000 m)	Environmental distance	-	-0.015	0.744		Interpretation of sPCA
	Kinship coefficient	Geographic distance	-	-0.038	0.000	**	Test of IBD
		Environmental distance	-	-0.013	0.034	*	Test of IBD and IBA
			Geographic distance	-0.012	0.055		Test of IBA
Female	Kinship coefficient	Geographic distance	-	-0.012	0.475		Test of IBD
		Environmental distance	-	0.023	0.111		Test of IBD and IBA
			Geographic distance	0.022	0.094		Test of IBA

Sex, Sex which analysis based on; Distance matrix A, B and C, correlation between A and B is computed, partial correlation is computed if C is provided; r, correlation coefficient; P, P-value *: $P < 0.05$, **: $P < 0.01$

Table 9-7 Pairwise F_{ST} of six clusters estimated by DAPC

	1	2	3	4	5	6
1	-	0.000	0.000	0.000	0.000	0.000
2	0.123	-	0.000	0.000	0.000	0.000
3	0.085	0.111	-	0.000	0.000	0.000
4	0.113	0.079	0.075	-	0.000	0.000
5	0.103	0.102	0.090	0.089	-	0.000
6	0.091	0.080	0.081	0.078	0.080	-

Below diagonal, pairwise F_{ST}; Above diagonal, P-value for null hypothesis H_0: $F_{ST} = 0$

Table 9-8 Pairwise F_{ST} of six clusters estimated by STRUCTURE

	1	2	3	4	5	6
1	-	0.000	0.000	0.000	0.000	0.000
2	0.067	-	0.000	0.000	0.000	0.000
3	0.087	0.071	-	0.000	0.000	0.000
4	0.078	0.058	0.060	-	0.000	0.000
5	0.096	0.073	0.062	0.072	-	0.000
6	0.084	0.057	0.096	0.088	0.095	-

Below diagonal, pairwise F_{ST}; Above diagonal, P-value for null hypothesis H_0: $F_{ST} = 0$

Table 9-9 Results of AMOVA

Sex	Distance	Cluster		df	SS	F	P	
Male	Geographic distance	DAPC	cluster	5	715×10^5	0.081	0.006	**
			residual	146	810×10^6			
			total	151	882×10^6			
		STRUCTURE	cluster	5	143×10^6	0.162	0.000	**
			residual	146	739×10^6			
			total	151	882×10^6			
	Environmental distance	DAPC	cluster	5	60	0.060	0.006	**
			residual	146	943			
			total	151	1003			
		STRUCTURE	cluster	5	56	0.056	0.014	*
			residual	146	948			
			total	151	1003			
Female	Geographic distance	DAPC	cluster	5	580×10^5	0.152	0.008	**
			residual	69	324×10^6			
			total	74	382×10^6			
		STRUCTURE	cluster	5	617×10^5	0.162	0.005	**
			residual	69	320×10^6			
			total	74	382×10^6			
	Environmental distance	DAPC	cluster	5	28	0.049	0.860	
			residual	69	543			
			total	74	571			
		STRUCTURE	cluster	5	58	0.102	0.042	*
			residual	69	513			
			total	74	571			

df, degree of freedom; SS, sums of squares; F, pseudo-F; P, P-value, *: $P < 0.05$, **: $P < 0.01$

Chapter 10

Missing piece of top predator-based conservation: demographic analysis of an owl population on a remote subtropical island

Abstract
Top predators are frequently the target of conservation programmes. Owls are such predators. However, previous studies of owls are biased to species occurring in temperate regions, whereas most owl species occur in tropical or subtropical regions and are understudied. Furthermore, owls are often endemic to islands and of unknown conservation status. Demographic data for such species are especially scarce although they are essential for initiating and promoting their conservation. As a case study of demographic analysis of owls in a tropical or subtropical area and on islands, I applied an integrated population model to seven-year monitoring data (2012-2018) of the Ryukyu Scops Owl population on Minami-daito Island, Japan. I used survival history data from 903 individuals, reproduction and sex ratio data from 213 broods, and count data of 2,526 individuals in total. Long-term averages of annual survival rates were 0.73 for adult females and 0.74 for adult males, although the sexual difference was not significant. Sex ratio estimates fluctuated annually and long-term averages were slightly skewed to males: 0.51 among fledglings, 0.54 among yearlings and 0.52 among adults. Long-term averages of population size were estimated to be 273.4 females and 296.8 males. The long-term average of population growth rate was 0.98, suggesting a slightly declining trend. It was fortunate to recognize the declining trend during the early phase. Considering the general lack of fundamental ecological data on owls of tropical or subtropical areas and on islands, it seems likely that many endangered owl populations await conservation efforts.

Introduction

Top predators are frequently the target of conservation programmes as they are expected to serve as keystone, indicator, umbrella, sentinel, or flagship species (Sergio et al. 2008). Although they may not always be surrogates of biodiversity (Bifolchi and Lodé 2005; Ozaki et al. 2006), there is no doubt that their role as sentinel or flagship species is important (Sergio et al. 2008). Taking advantage of their enormous fundraising potential (Sergio et al. 2008), focusing on such charismatic species allows the initiation of conservation efforts in areas such as forested tropical areas or on remote islands where research without financial support is especially difficult (Ando 2019).

To commence top-predator based conservation, fundamental information on the focal species is necessary for evidence-based conservation (Sutherland et al. 2004). However,

nocturnal predators are often difficult to study because their night time activity prevents direct observation and hampers the accumulation of fundamental ecological data (Duckworth 1998).

Owls represent such difficult to study nocturnal predators. They are often apex predators in nocturnal ecosystems (König and Weick 2008) and their presence may serve as a surrogate for biodiversity of the area (Sergio et al. 2005, 2008). The popularity of owls as pets in recent years has raised concerns about the need for their protection (Nijman and Nekaris 2017; Vall-Llosera and Su 2018). This increased interest in owls can be interpreted as indicating their great fundraising potential from a different perspective. Thus, the importance of owls and their potential value in conservation programmes is evident.

Some species of owls, such as the Eagle Owl *Bubo bubo* (Sergio et al. 2004; Schaub et al. 2010), Spotted Owl *Strix occidentalis* (Thomas 1990; Gutiérrez et al. 2017) and Burrowing Owl *Athene cunicularia* (Klute et al. 2003; Rebolo-Ifrán et al. 2017), have been important targets for conservation. However, most owl species occurring in tropical or subtropical regions and those endemic to islands, remain under studied (Warburton 2009; Sekercioglu 2010; Najmi-Hanis et al. 2016). Although not a few authors have pointed out the lack of information (Gerhardt and Gerhardt 1997; Severinghaus and Rothery 2001; Warburton 2009; Sekercioglu 2010), little attention continues to be paid to them. Their nocturnality and location in logistically inconvenient habitat seem to be the main reasons for the slow rate of data accumulation (Sekercioglu 2010). However, this does not reduce their importance and potential significance in conservation activities.

In order to conserve a species, demographic analysis features as a core aspect of any project because conservation aims to avoid extinction, in other words, to control the demographic process. Integrated population modelling is increasingly used to estimate demographic parameters (Schaub and Abadi 2010; Plard et al. 2019). Integrated population models (IPMs) are means of demographic analysis which include multiple sub models corresponding to multiple aspects of population dynamics (such as fecundity, survival and population size) in a single statistical model (Kery and Schaub 2011). Since this method models the system so that parameters in a sub model are also included in other sub models, parameter estimation is said to be improved compared with when sub models are fitted separately (Kery and Schaub 2011). Furthermore, even unobserved demographic parameters may be estimated by efficiently using multiple data (Plard et al. 2019). Therefore, IPM is a powerful tool for researchers wishing to conduct demographic analyses of long-term study populations (Kery and Schaub 2011). In most cases when applying an IPM, the total population size is estimated by assuming an even or specific value for sex ratio (Schaub et al. 2010; Abadi et al. 2016). However, IPM can separately estimate the population dynamics of females and males and hence the sex ratio (Mccaffery and Lukacs 2016; Plard et al. 2019). Estimating, not assuming, the sex ratio is clearly important, because small populations, which are common in island species or endangered species, are prone to stochastic variability of the sex ratio (Lande 1998) and

a skewed ratio can influence the fate of the population by decreasing the effective population size (Frankham 1995; Engen et al. 2003).

In this analysis — a case study of demographic analysis of an island population of a subtropical owl — I applied an IPM to a subspecific population of the Ryukyu Scops Owl *Otus elegans* without assuming the sex ratio. This subtropical species occurs from the Babuyan and Batanes Islands of the Philippines to Okinoshima Island, Japan (Warburton 2009; Ornithological Society of Japan 2012; Takagi et al. 2015; Gill et al. 2020). Four subspecies are known: nominate *elegans, interpositus, botelensis* and *calayensis* (Gill et al. 2020), all are resident and endemic to each island group (Hsu et al. 2006b; Warburton 2009; Ornithological Society of Japan 2012). All four subspecies feed mainly on insects and small vertebrates. This species is one of the top predators in the ecosystems of their home islands. I and members of the long-term study group have monitored the breeding ecology of *O. e. interpositus* on Minami-daito Island since 2002 (Takagi et al. 2007a; Sawada et al. 2018a; Takagi 2020), while a separate research group has monitored *O. e. botelensis* on Lanyu Island, Taiwan, since the 1980s (Severinghaus and Rothery 2001; Lee and Severinghaus 2004; Severinghaus 2007). Thus, the species is a rare, well-studied owl, not only in a non-temperate area but also on islands. The species provides a model or reference for subsequent conservation studies on owls in tropical or subtropical area and on islands.

Demographic analysis of *O. e. interpositus* is important in its own right for the species' conservation because it is categorized as "Near Threatened" in the IUCN red list, and subspecies *O. e. interpositus* is listed as "Vulnerable" in the Japanese red list (Ministry of the Environment of Japan 2019). Furthermore, description of its population dynamics can contribute to our understanding of island biology because the owl seems to play an important role in the persistence of the ecosystem on the island. Although two mammal species (Japanese Weasel *Mustela itatsi* and Domestic Cat *Felis catus*) have been introduced on Minami-daito Island, the owl was originally the top predator of the ecosystem on the island (Akatani 2011). As the species continues to predate many species of arthropods and geckos (Takagi and Akatani 2011), it is expected to regulate populations of its prey. This oceanic island is small and isolated (see Methods), and the simple and fragile nature of the ecosystem there is characteristic of such an island (Terborgh et al. 2001; Courchamp et al. 2003). The role of the owls on the island cannot be ignored when attempting to understand how the island ecosystem persists. The aims of this study were twofold: first, to describe the fundamental demographic status of *O. e. interpositus* by sex-explicit IPM; second, to provide standard and reference data for subsequent studies of owls in tropical or subtropical area or on remote islands.

Methods

Material

O. e. interpositus is endemic to Minami-daito Island (Takagi et al. 2007a), an isolated oceanic island lying 360 km east of Okinawa Island, Japan. Minami-daito Island has lost

four endemic avian populations (*Columba jouyi*, *Cettia diphone restricta*, *Parus varius*, *Corvus macrorhynchos*) since human colonization early in the 1900s (Anezaki 2012; Ornithological Society of Japan 2012). The climate of the island is subtropical with a mean annual temperature of 23.2˚C and a mean annual rainfall of 1618.5 mm (Japan Meteorological Agency, 1960–2019). The owls nest in natural cavities in Chinese Fan Palm *Livistona chinensis* and Australian Pine *Casuarina equisetifolia*, and in nest boxes (Takagi et al. 2007a). I and members of a long-term study group have provided 184 nest boxes on the island since the previous demographic survey by Takagi et al. (2007a). The owls raise one brood a year during their March to July breeding season. They lay clutches of one to four eggs from mid-March to mid-April. The incubation and nestling periods each last about one month. Further information on the population's breeding biology is available elsewhere (Takagi et al. 2005, 2007a; Akatani 2011; Akatani et al. 2011). As many adults as possible were captured by mist net during yearly censuses (see below) and nestlings were captured by hand at their nests (see below). All captured individuals were given metal rings, with unique combinations of reflective colour tapes wrapped around the rings so as to identify individuals without recapturing them (Takagi 2020).

Data collection

(a) Survival history and population size data

From February to July 2012 to 2018, I and members of the long-term study group walked through the island's forest for about 6 h after sunset while broadcasting owl hoots; research was conducted, almost every day except on rainy days (Takagi 2020). All individuals encountered, regardless of whether they were marked or unmarked, were noted according to their sex (from vocal characteristics), identity (from ring colours if marked) and location (by GPS receiver) (Sawada et al. 2018a). These data and their territories were recorded on a map of the island. Research walks were not decided randomly for logistical reasons. However, because we surveyed the same place at least twice during the survey season (February to July) each year, and because the owls are strictly territorial throughout the year, I believe that our censuses included all individuals on the island every year. From our surveys, I obtained two types of data. The first consisted of the presence or absence of each marked-individual in each year. These data, consisting of 1,652 presence records of 903 individuals, were used for the sub model of survival rate (see below). The second consisted of the number of males and females including unmarked individuals in each year, amounting to 1,523 males and 1,003 females. These data were used for the sub model of population size (see below). See Table 10-1 for detailed sample size.

(b) Fecundity data

I and members of the long-term study group visited all nest boxes and several natural nest cavities during daytime once every three to four days from late February every year (2012 to 2018). Since females occupy their nests from several days before egg-laying, regular

monitoring enabled us to record the beginning of breeding activity. For the nests where breeding initiation was confirmed, we then visited every day until clutch-completion. From about 26 days after the laying date of the first egg, we restarted visiting the nests every day to determine the hatching date and the number of hatchlings. After obtaining those data, we stopped visiting in order to minimize interference with breeding. We ringed the nestlings when they were 20 days old and collected blood samples by brachial venipuncture. The number of nestlings at that time, consisting of 487 nestlings from 213 broods, was used as a proxy for the number of fledglings and for fecundity data. The data were used for the sub model of fecundity (see below). See Table 10-2 for detailed sample size.

(c) Sex ratio data

I determined the sex of nestlings ringed when 20 days old in 2012 to 2018 by PCR amplification of the CHD gene (Fridolfsson and Ellegren 1999). Template DNA was extracted from blood samples collected during the above-mentioned routine survey. For the PCR-based sexing, we followed procedures detailed in Sawada et al. (2021b). The data were used for the sub model of sex ratio (see below). Because we failed to collect blood samples from one brood in 2014, those nestlings were excluded. Thus, the data consisted of 484 nestlings from 212 broods in total. See Table 10-2 for detailed sample size.

Demographic analysis

I used an IPM to estimate multiple demographic parameters of the owl population. Since the IPM consists of several sub models, each of which describes different aspects of population dynamics (Figure 10-1), I have described the sub models separately below. The IPM was implemented by Stan (Carpenter et al. 2017) and fitted by *rstan* package (Stan Development Team 2016) on R (R Core Team 2017). The parameters were as follows: iter = 25,000, warmup = 5,000, thin = 4. Convergence was confirmed based on *Rhat* diagnostic statistics and the output of *check_hmc_diagnostics* function in the *rstan* package.

(a) Sub model for survival history

To model the survival history of individual owls, I used the Cormack-Jolly-Sever model (CJS model, Lebreton et al. 1992). Observations of individuals during yearly censuses were arranged into an $n_i \times n_t$ matrix $\boldsymbol{Y}$ where n_i is the number of individuals and n_t is the number of years in which we conducted censuses. The element of the matrix, $Y_{i,t}$, is a binary variable which is one if individual i was observed in the census in year t and which is otherwise zero. From $\boldsymbol{Y}$, the CJS model estimates annual survival rate S and detection probability P. Here I assumed that survival rate S from year t to t+1 is dependent on Year (six-level categorical: “2012”, …, “2017”), Sex (0: female, 1: male) and Age (0: juvenile, 1: adult), and assumed that detection probability P is dependent

on the Researcher who conducted the census in the year (two-level categorical: "TI" in 2012 to 2015, "AS" in 2016 to 2018) and Sex (0: female, 1: male):

$$S_{i,t} = logit^{-1}\left[\alpha_0(t) + \alpha_{sex}Sex(i) + \alpha_{age}Age(i)\right]$$
$$P_{i,t} = logit^{-1}\left[\beta_0\left(Researcher(t)\right) + \beta_{sex}Sex(i)\right]$$

$S_{i,t}$ represents the survival rate of individual i from year t to year t+1. $P_{i,t}$ represents the detection probability of individual i in year t. α_0 is a year dependent intercept and β_0 is a researcher dependent intercept. α_{sex}, α_{age} and β_{sex} are regression coefficients. I included the effect of Sex in the detection probability because females react less strongly to broadcast owl hoots (Takagi et al. 2007a). The effect of Researcher was included because the effort to detect marked individuals was increased from 2016 onwards (when the researcher changed) aiming to conduct this capture-mark recapture analysis.

(b) Sub model for fecundity

To model the number of fledglings produced per reproductive female, I used a regression model using categorical distribution which describes the random variable that can take one of four possible outcomes (1 fledgling to 4 fledglings). I first assumed that the number of fledglings per nest recorded during routine breeding monitoring is dependent on Year (seven-level categorical: "2012", …, "2018"), Type (0: nest box, 1: natural cavity) and random effects of mother ID and father ID:

$$\boldsymbol{\theta}_{i,t} = softmax\left[\boldsymbol{\gamma}_0(t) + \boldsymbol{\gamma}_{nest}Type(i) + \boldsymbol{\gamma}_{motherID}(i) + \boldsymbol{\gamma}_{fatherID}(i)\right]$$
$$\boldsymbol{\gamma}_{mother}(i) \sim Multivariate\ Normal\left(0, \boldsymbol{\Sigma}_{Z,mother}\right)$$
$$\boldsymbol{\gamma}_{father}(i) \sim Multivariate\ Normal\left(0, \boldsymbol{\Sigma}_{Z,father}\right)$$
$$Z_{i,t} \sim Categorical\left(\boldsymbol{\theta}_{i,t}\right)$$

$\boldsymbol{\gamma}_0$ is a 4-dimensional vector corresponding to year dependent intercept. $\boldsymbol{\gamma}_{nest}$ is a 4-dimensional vector corresponding to fixed effect of nest type. $\boldsymbol{\gamma}_{motherID}$ and $\boldsymbol{\gamma}_{fatherID}$ are 4-dimensional vectors of random effects. $\boldsymbol{\Sigma}_{Z,mother}$ and $\boldsymbol{\Sigma}_{Z,father}$ are variance covariance matrixes. The Softmax function guarantees that the sum of the elements of the given vector becomes 1. Z takes a value from one to four with the probabilities specified by the four elements in the vector $\boldsymbol{\theta}$. We set the boundary (one and four) based on the minimum and maximum clutch size (Table 10-2). Before I fitted this model in the IPM, I fitted it separately to breeding monitoring data to validate the need for random factors, because including random factors made fitting the IPM difficult. I compared the predictive accuracy of the models with random effects to the model without random effects. Model comparison was based on Pareto-Smoothed-Importance-Sampling Leave One Out (PSIS-LOO, Vehtari et al. 2017) implemented in the *loo* package (Vehtari et al. 2018). The models including mother ID had the best predictive accuracy value (Table 10-3). Since the regression coefficients of type of nest $\boldsymbol{\gamma}_{nest}$ included zero in their 95% credible intervals (CRI), I dropped the effect and used the following model in the IPM:

$$\boldsymbol{\theta}_{i,t} = softmax[\boldsymbol{\gamma}_0(t) + \boldsymbol{\gamma}_{motherID}(i)]$$

$$\boldsymbol{\gamma}_{mother}(i) \sim Multivariate\ Normal\left(0, \boldsymbol{\Sigma}_{Z,mother}\right)$$
$$Z_{i,t} \sim Categorical\left(\boldsymbol{\theta}_{i,t}\right)$$

(c) Sub model for sex ratio

To model the sex ratio of offspring, I used a logistic regression model. The sex of nestlings was determined by molecular sexing; W was used as response variable (0: female, 1: male). The probability of a nestling being male Rn was assumed to depend on Year (seven-level categorical: "2012", …, "2018") and random effects of mother ID and father ID.

$$Rn_{i,t} = logit^{-1}\left[\delta_0(t) + \delta_{motherID}(i) + \delta_{fatherID}(i)\right]$$
$$\delta_{mother}(i) \sim Normal\left(0, \sigma_{,mother}\right)$$
$$\delta_{father}(i) \sim Normal\left(0, \sigma_{,father}\right)$$
$$W_{i,t} \sim Bernoulli\left(Rn_{i,t}\right)$$

δ_0 is a year dependent intercept. $\delta_{motherID}$ and $\delta_{fatherID}$ are random effects. For the same reason in the model of fecundity, I first evaluated the necessity for random effects by PSIS-LOO. As the inclusion of random factors was again not supported (Table 10-4), I used the following simple model without random factors in the IPM:

$$Rn_{i,t} = exp[\delta_0(t)]$$
$$W_{i,t} \sim Bernoulli\left(Rn_{i,t}\right)$$

(d) Sub model for population size

To model population dynamics, I used a matrix population model (Caswell 2001). Total population was divided into four classes by combinations of sex (male and female) and age class (yearling and adult). The population sizes of the classes: female yearling, female adult, male yearling and male adult, in year t, were denoted as $N_{Fy,t}$, $N_{Fa,t}$, $N_{My,t}$ and $N_{Ma,t}$, respectively. Assuming these represent the sizes before breeding, their inter year transition is represented by the following matrix model:

$$\begin{bmatrix} N_{Fy,t+1} \\ N_{Fa,t+1} \\ N_{My,t+1} \\ N_{Ma,t+1} \end{bmatrix} = \begin{bmatrix} S_{Fj,t}(1-Rn_t)F_tQ_t & S_{Fj,t}(1-Rn_t)F_tQ_t & 0 & 0 \\ S_{Fa,t} & S_{Fa,t} & 0 & 0 \\ S_{Fj,t}Rn_tF_tQ_t & S_{Fj}Rn_tF_tQ_t & 0 & 0 \\ 0 & 0 & S_{Ma,t} & S_{Ma,t} \end{bmatrix} \begin{bmatrix} N_{Fy,t} \\ N_{Fa,t} \\ N_{My,t} \\ N_{Ma,t} \end{bmatrix}$$

S, Rn, F and Q denote survival rate, sex ratio of fledglings, number of fledglings per reproducing female and proportion of reproducing females to overall females, respectively. Subscript F, M, j, a and t denote the dependency of the above parameters on Sex (two-level categorical: female (F), male (M)), Age (two-level categorical: juvenile (j), adult (a)) and Year (seven-level categorical: "2012", …, "2018"), respectively. I considered that S, Rn and F are written by the parameters which are included in the sub model a, b and c, respectively:

$$S_{Fj,t} = logit^{-1}[\alpha_0(t)]$$

$$S_{Fa,t} = logit^{-1}\left[\alpha_0(t) + \alpha_{age}\right]$$
$$S_{Mj,t} = logit^{-1}[\alpha_0(t) + \alpha_{sex}]$$
$$S_{Ma,t} = logit^{-1}\left[\alpha_0(t) + \alpha_{sex} + \alpha_{age}\right]$$
$$\boldsymbol{\theta}_t = (\theta_{t1}, \theta_{t2}, \theta_{t3}, \theta_{t4}) = softmax[\boldsymbol{\gamma}_0(t)]$$
$$F_t = \theta_{t1} + 2\theta_{t2} + 3\theta_{t3} + 4\theta_{t4}$$
$$Rn_t = exp[\delta_0(t)]$$

By linking model parameters in a sub model to other sub models, IPM improves parameter estimation (Plard et al. 2019).

Then, population size was assumed to be generated by stochastic processes based on the dynamics determined by the above matrix model and various latent processes. Firstly, I considered the latent parameter O_t, which denotes the number of total fledglings in year *t*. I assumed O_t to follow a Poisson distribution as follows:

$$O_t \sim Poisson\left(F_t Q_t\left(N_{Fy,t} + N_{Fa,t}\right)\right)$$

The mean of this distribution is the product of the number of females, the number of fledglings per reproductive female and the proportion of reproductive females Q_t. Secondly, additional latent parameters: number of females L_{ft} and males L_{mt} within O_t, were assumed to follow a binomial distribution:

$$L_{ft} \sim Binomial(O_t, 1 - Rn_t)$$
$$L_{mt} = O_t - L_{ft}$$

Thirdly, $N_{Fy,t+1}$ and $N_{My,t+1}$ were defined as the number of survivors of the offspring, L_{ft} and L_{mt}, respectively. $N_{Fa,t+1}$ and $N_{Ma,t+1}$ were defined as the number of survivors of the yearlings and adults, $N_{Fy,t} + N_{Fa,t}$ and $N_{My,t} + N_{Ma,t}$, respectively.

$$N_{Fy,t+1} \sim Binomial\left(L_{ft}, S_{fjt}\right)$$
$$N_{My,t+1} \sim Binomial\left(L_{Mt}, S_{Mjt}\right)$$
$$N_{Fa,t+1} \sim Binomial\left(N_{Fy,t} + N_{Fa,t}, S_{Fa,t}\right)$$
$$N_{Ma,t+1} \sim Binomial\left(N_{My,t} + N_{Ma,t}, S_{Ma,t}\right)$$

Finally, count data NC were assumed to be generated by random sampling from the population whose size was determined by the above processes. To describe them, we used a binomial distribution with a parameter P, which is the detection probability in the sub model for survival analysis:

$$NC_{F,t} \sim Binomial\left(N_{Fy,t} + N_{Fa,t}, P_{F,t}\right)$$
$$NC_{M,t} \sim Binomial\left(N_{My,t} + N_{Ma,t}, P_{M,t}\right)$$
$$P_{F,t} = logit^{-1}\left[\beta_0\left(Researcher(t)\right)\right]$$
$$P_{M,t} = logit^{-1}\left[\beta_0\left(Researcher(t)\right) + \beta_{sex}\right]$$

To implement these processes in the Stan, I used normal distribution approximation of discrete distributions. Normal distribution approximation has been used in the framework of IPM by Zhao et al. (2019), although the distribution they used was zero-truncated. A binomial distribution with size n and probability θ was substituted with a normal

distribution with a mean $n\theta$ and variance $n\theta(1-\theta)$. A Poisson distribution with mean λ was substituted with a normal distribution with mean λ and variance λ.

Summarizing demographic statistics

After fitting the IPM to the data, the mean and 95% CRI of the model parameters were obtained from MCMC samples. Although the method used here is Bayesian, I used "significant" when the CRI of the parameter did not include zero for convenience. In addition, several year-dependent demographic parameters were calculated from the same MCMC samples. Means and 95% CRI were also obtained. Firstly, total population size N_{tot}, population size of females N_f, population size of males N_m, population size of yearlings N_y, population size of adults N_a and breeding population size N_b were calculated as follows:

$$N_{tot,t} = N_{fy,t} + N_{fa,t} + N_{my,t} + N_{ma,t}$$
$$N_{f,t} = N_{fy,t} + N_{fa,t}$$
$$N_{m,t} = N_{my,t} + N_{ma,t}$$
$$N_{y,t} = N_{fy,t} + N_{my,t}$$
$$N_{a,t} = N_{fa,t} + N_{ma,t}$$
$$N_{b,t} = Q_t\left(N_{fy,t} + N_{fa,t}\right)$$

Secondly, population growth rate G was calculated as follows

$$G_{t+1} = \frac{N_{tot,t+1}}{N_{tot,t}}$$

Thirdly, yearling sex ratio Ry, adult sex ratio Ra and operational sex ratio Ro were calculated as a ratio of male population size over total population size:

$$Ry_{t+1} = \frac{N_{my,t}}{N_{y,t}}$$
$$Ra_{t+1} = \frac{N_{ma,t}}{N_{a,t}}$$
$$Ro_{t+1} = \frac{N_{m,t}}{N_{tot,t}}$$

Finally, long-term averages of survival rates, detection probabilities, number of fledglings, sex ratios, population sizes, proportion of reproductive females, and population growth rate, were obtained by averaging the corresponding parameters over years. Average estimates were taken for the period 2013 to 2018 because estimates for 2012 (which were based on data collected in the first year of the study) were less reliable than estimates for 2013 to 2018 (which were based on data from multiple years). Arithmetic means were used for the number of fledglings, detection probabilities, sex ratios, proportion of reproductive females, and population sizes. Geometric means were used for survival rates and population growth rates.

Checking goodness of fit of models

Although no statistically formal method of checking the goodness of fit of IPM is available at present, I checked the fit separately for each sub model in the IPM following Margalida et al. (2020). For the sub model for survival history, I used the *R2ucare* package (Gimenez et al. 2018). *R2ucare* implements mainly four statistical tests (test 2CT, test 3SR, test 2CL and test 3SM) for the CJS model, which tests basic assumptions of that model. Gimenez et al. (2018) recommended users to determine model structure based on which of the tests gave significance, and also recommended to apply tests separately for heterogeneous data (e.g. test male data and female data separately). Therefore, I applied the tests to male data and female data separately, and used a significance level of 0.00625 (= 0.05/8) because eight tests were conducted in total. For the sub model for fecundity, sex ratio and population size, I used a chi-square discrepancy measure and a posterior predictive check (Kery and Schaub 2011). In brief, for each MCMC step, two discrepancy measures D_1 and D_2 were calculated (D_1: between observed data and expected value from the model, D_2: between simulated data and expected value from the model) (Margalida et al. 2020). Then, D_2 was plotted against D_1. If the model fits the data well, then the plot scatters around the line of $D_2 = D_1$.

Life-stage simulation analysis

To determine which factors influenced variation in the population growth rate, I used life-stage simulation analysis (Wisdom et al. 2000). The coefficient of determination between the MCMC samples of population growth rate and the MCMC samples of other demographic parameters (survival rate S, fecundity F, sex ratio Rn, proportion of reproductive females Q) were calculated (Beissinger et al. 2008).

Results

Goodness of fit of models

For survival history of females, test 3SR reached significance (Table 10-5, P = 0.000) and a model with transience was recommended as model structure, according to Gimenez et al. (2018). For survival history of males, test 3SR reached significance (Table 10-5, P = 0.003) and a model with transience was recommended as model structure, according to Gimenez et al. (2018). I retained model structure unchanged because I considered that our CJS model already accounted for the source of the transience effect. As the owls are sedentary, most of the transient effect seemed to stem from the low survival rate of yearlings (Genovart and Pradel 2019). This effect was accounted for by including *Age* in survival rate. A posterior predictive check of the sub model for fecundity, sex ratio and population size did not find a significant lack of fit (Figure 10-2).

Estimates from IPM

(a) Survival rate

The effect of sex on survival rate was non-significant (α_{sex} = 0.05, CRI = [-0.13, 0.23]). Although CRI of α_{sex} included zero, the posterior probability of α_{sex} being larger than

zero, P (α_{sex} > 0), was 0.71 and suggested a slightly lower survival rate in females than males. In contrast, there was a significant effect of age on survival rate (α_{age}= -1.75, CRI = [-2.03, -1.48]) and juveniles had lower survival rates than adults. During our study period, the range of annual survival estimates was 0.23-0.46 for juvenile females, 0.63-0.83 for adult females, 0.24-0.47 for juvenile males, 0.65-0.83 for adult males (Figure 10-3ab, Table 10-6). The long-term average of annual survival estimates was 0.33 (CRI = [0.28, 0.38]) for juvenile females, 0.73 (CRI = [0.69, 0.77]) for adult females, 0.34 (CRI = [0.29, 0.39]) for juvenile males, and 0.74 (CRI = [0.71, 0.77]) for adult males.

(b) Detection probability

Females had a significantly smaller detection probability than males (Figure 10-3c, Table 10-7, β_{sex}= 1.31, CRI = [0.89, 1.76]). The probability also differed between researchers (Figure 10-3c, Table 10-7). Long-term averages of detection probability estimates were 0.62 (CRI = [0.56, 0.68]) for females and 0.86 (CRI = [0.81, 0.90]) for males.

(c) Fecundity

There was slight annual variation in the number of fledglings per reproductive female (Figure 10-4a). The range of estimate was 2.04-2.59 and the long-term average was 2.26 (CRI = [2.15, 2.36]) (Table 10-8).

(d) Proportion of reproductive females

The range of the proportion of reproductive females within the total female population was estimated to be 0.24-0.83 (Figure 10-4b, Table 10-9), while the long-term average was 0.65 (CRI = [0.52, 0.79]). The wide range of the interval estimate is because there were no direct data from which to estimate it thus the parameter was estimated indirectly from other demographic data.

(e) Sex ratio

There was annual variation and a slight skew in the sex ratio (Figure 10-4cdef). The range of estimates was 0.39-0.62 for the fledgling sex ratio, 0.40-0.64 for the yearling sex ratio, 0.48-0.55 for the adult sex ratio and 0.48-0.55 for the operational sex ratio (Table 10-10). The long-term average was 0.51 (CRI = [0.47, 0.56]) for the fledgling sex ratio, 0.54 (CRI = [0.48, 0.59]) for the yearling sex ratio, 0.52 (CRI = [0.48, 0.56]) for the adult sex ratio and 0.52 (CRI = [0.49, 0.55]) for the operational sex ratio (Table 10-10).

(e) Population size

Ranges of total, female and male population sizes were estimated to be 534.7-667.4, 242.7-347.2 and 276.9-323.6, respectively (Figure 10-5abc, Table 10-11). Long-term averages of the total, female and male population sizes were 570.2 (CRI = [539.6, 606.2]), 273.4 (CRI = [247.2, 305.5]) and 296.8 (CRI = [282.3, 314.1]), respectively. There was annual variation in population size (Figure 10-5de). The long-term average was 60.6 (CRI

= [47.9, 76.3]) for yearling females, 212.9 (CRI = [186.0, 244.2]) for adult females, 66.6 (CRI = [52.5, 87.6]) for yearling males and 230.2 (CRI = [205.6, 252.9]) for adult males. See Table 10-10 for the yearly estimates. The range of breeding population sizes was estimated to be 71.3-248.7 (Figure 10-5b, Table 10-11), and the long-term average was 177.3 (CRI = [141.0, 215.6]). The range of population growth rate was estimated to be 0.86-1.20 (Figure 10-5f, Table10-12), and the long-term average was 0.98 (CRI = [0.96, 1.00]).

Life-stage simulation analysis

Among the survival rate, sex ratio and fecundity estimates, survival rate of females had the largest effect on the population growth rate (Figure 10-6ab, adult, $R^2 = 0.063$; juvenile, $R^2 = 0.045$). However, survival rate of males had few effects (Figure 10-6cd, adult, $R^2 = 0.010$; juvenile, $R^2 = 0.006$). Sex ratio of fledgling had also a large effect (Figure 10-6e, $R^2 = 0.041$). Fecundity had the smallest effect among all parameters (Figure 10-6f, $R^2 = 0.000$). Proportion of reproductive females had an intermediate effect (Figure 10-6g, $R^2 = 0.028$).

Discussion

This is a rare study offering detailed, fundamental, demographic information for an owl population on a subtropical island. The results of this study may serve as a standard, providing reference data for subsequent research on owls in non-temperate areas and/or on remote islands.

Survival estimates were slightly higher for males than females, although the difference was not significant, and follows the general pattern of non-significant sexual differences in the survival rates of raptors (Newton et al. 2016). However, my results contrast with those of Severinghaus and Rothery (2001) whose survival rate estimates for conspecific *O. e. botelensis* on Lanyu Island were 7% higher for females than males. Although it is not clear which of the results from Lanyu Island and Minami-daito Island reflect the general demographic characteristics of this species, a possible mechanism exists that may lower female survival rate on Minami-daito Island.

On Minami-daito Island, introduced predators (Japanese Weasel *Mustela itatsi* and Domestic Cat *Felis catus*) may be the factor that lowers female survival rate especially during incubation and brooding until nestlings reach about 12 days old (Akatani 2011). Such predation has been observed during our research (Takagi et al. 2007a; Akatani and Takagi 2020). Field surveys designed to identify the attributes of individuals that tend to be predated are one future direction for the conservation of this owl population. The population may be driven towards extinction not only by predation per se but also by a skewed sex ratio resulting from sex-specific predatory pressures (Donald 2007).

Compared with other species, the survival rate of the Ryukyu Scops Owl seems to be relatively high for its body size. A recent review of the survival rate of raptors by Newton et al. (2016) reported a regression line to estimate survival rate from body mass of owls,

where survival rate = 0.030 + 0.121*log (body mass (g)). In the *O. e. interpositus* population, the average body masses of males and females are 86 g and 96 g, respectively (Sawada et al. 2021b). Fitting them into the regression yields an annual survival rate of 0.57 for males and 0.58 for females. Newton et al.'s (2016) regression is based mostly on continental populations in the temperate zone. Higher estimate, of nearly 0.75, may be a consequence of greater environmental stability in subtropical areas and on islands (Weigelt et al. 2013), such as Minami-daito.

The lower detection probability of females is due to two factors: their weaker responses to broadcast calls than males, and their withdrawal into their nest during most of the breeding season (Takagi et al. 2007a). Recognition of between-researcher variation in detection probability confirms the need to be cautious when comparing count data collected by different researchers.

The number of fledglings per female (among those that produced fledglings) was relatively stable and long-term estimate of 2.26 was very similar to a previous estimate of 2.3 (Akatani et al. 2011). The long-term estimate of the proportion of females that produce fledglings was about 66%. This is a lower boundary estimate of the proportion of breeding females, because some females fail to produce any fledglings. From this estimate and the female population size estimate, it transpires that an average of 177.3 nests produce fledglings each year. This is an important estimate because it indicates the proportion of breeding nests that we are recording by monitoring. It should be noted that I would have been unable to obtain this estimate without the strength of the IPM which facilitates the estimation of unobserved parameters (Plard et al. 2019).

Several points in relation to sex ratio estimates are of interest. First, is the increasing trend with age towards a male-biased sex ratio — whereas the ratio for fledglings was 0.51, the ratios were equal or more than 0.52 among yearlings and adults. This suggests that females have a lower survival rate than males (Donald 2007). As previously mentioned, females had a slightly lower survival estimate than males, although it did not reach significance. Female-biased dispersal and resultant emigration from the island is, in theory, also a possible mechanism contributing to male-biased sex ratios (Dale 2001). However, we have found no evidence of emigration of females from Minami-daito Island, and have never found (since 2002) the owl during annual surveys of neighbouring Kita-daito.

Second is temporal variation. Annual variation in the fledgling sex ratio may have several explanations, such as year-specific sexual differences in nestling survival rates until day 20 (the day on which we collect blood samples and determine the sex ratio), adaptive control of offspring sex depending on year-specific environment (Hipkiss and Hörnfeldt 2004; Sasvári and Nishiumi 2005) and demographic stochasticity due to the small population size (Lande 1998). I cannot tease these apart here, because our estimates do not include sex data from unhatched eggs nor from nestlings that died before being ringed on day 20. Apart from the causal explanations for the annual variation in the fledgling sex ratio, such variation can result in corresponding sex ratio variation during

subsequent life stages, and affect the operational sex ratio. Because the operational sex ratio influences the effective population size (Frankham 1995), obtaining knowledge of the sex ratio is one of the significant aspects of this study.

The long-term average population size estimate of 570.2 individuals was considerably higher than the previous estimate of 420 individuals (210 pairs) for the population just over a decade ago by Takagi et al. (2007a). There may be two explanations for this difference, the first of which is real population growth. A total of 184 nest boxes has been set up on the island since the previous survey by Takagi et al. (2007a) and these may have contributed to population growth. The second explanation is the difference in the method used for estimation between the two studies.

I observed fluctuation in the population size and a slight declining trend with a growth rate equal to or lower than 1.0. Since our analysis here is based on data from only seven years, it is not clear yet whether this temporal trend is short-term or not. Because of the small size of this population it may be highly vulnerable to inbreeding, demographic stochasticity and extinction (Frankham 1998). Life-stage simulation analysis revealed that female survival rate had the largest effect on the variation of the population growth rate. Therefore, programs intended to increase female survival seem to be a successful strategy for their conservation. Since their slightly smaller survival of females may be due to predation by introduced mammals as discussed above, monitoring those animals and assessing whether they predate upon specific types of owls (e.g. female or male, and yearling or adult) more than others are urgent tasks. Now that we have a fundamental population dynamics model, the possible effects of predation and its prevention can be evaluated with further analysis of population viability (I have not dealt with this here because it was beyond the scope of this study). The endemic *O. e. interpositus* subspecies of the Ryukyu Scops Owl on Minami-daito Island, an oceanic island in a subtropical area, exhibits unique morphology, vocal characteristics and genetic variation, underlying its conservation significance (Takagi et al. 2007a; Takagi 2011; Sawada et al. 2018b,a). Minami-daito Island has already lost four unique avian populations in the last hundred years (Anezaki 2012; Ministry of the Environment of Japan 2014). It is fortunate that we have been able to recognize this declining trend in the scops owl population allowing us to consider a conservation strategy for the future. I hope that this study will stimulate a stronger focus on understudied owl populations in tropical or subtropical areas and on islands that may be endangered or at risk. Considering the general lack of fundamental ecological data for such owls, there may be many endangered owl populations *awaiting conservation*.

Figure

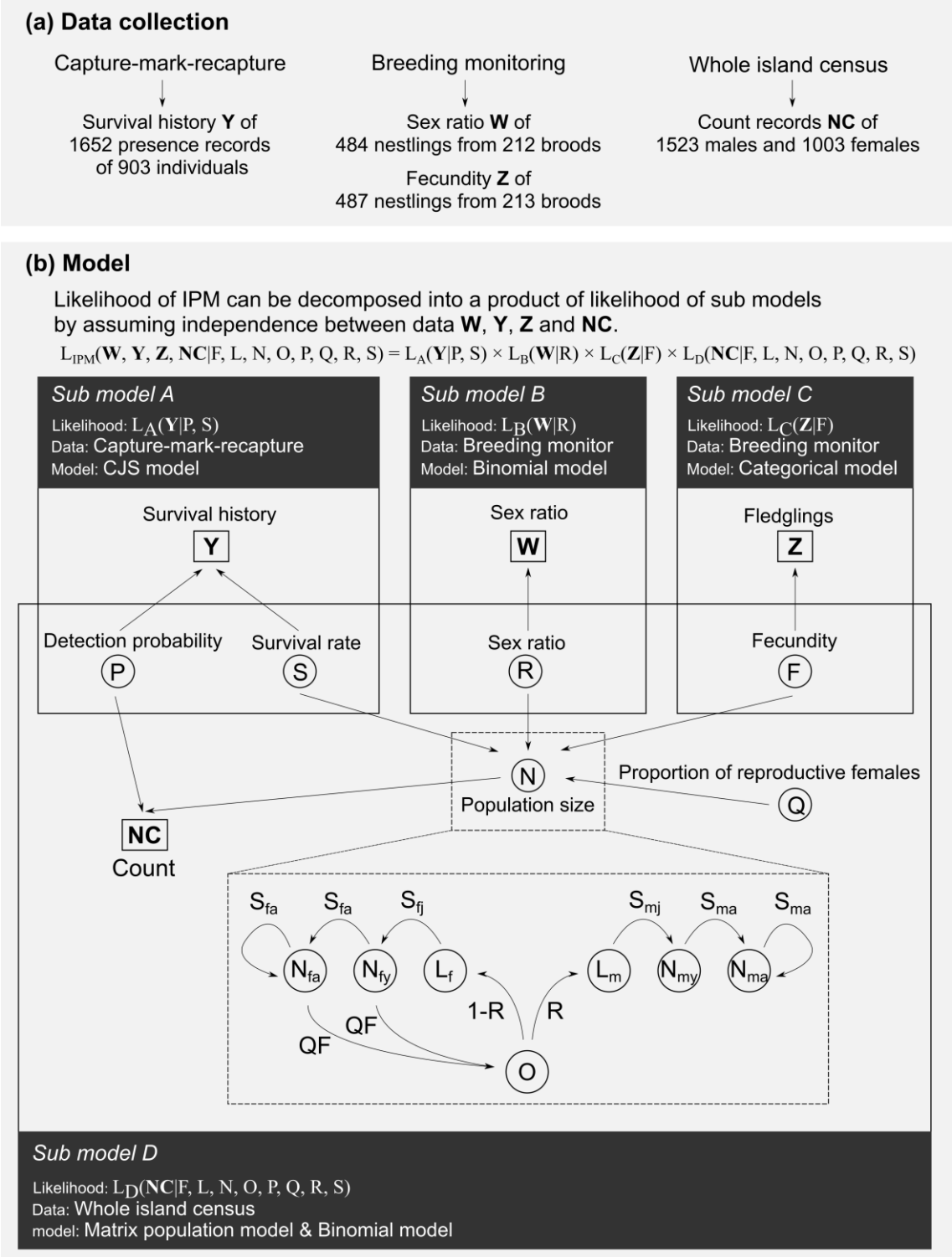


Figure 10-1

(a) Surveys, and data based on those surveys. (b) Model structure of the IPM used in this study. Characters enclosed by rectangles with solid lines are data, characters enclosed by

circles are model parameters. Four sub models are enclosed by frames. Subscripts of parameters used in the main text are partly dropped here for simplicity. P: detection probability, S: survival rate, Q: proportion of reproductive females that produced fledglings, R: sex ratio, F: number of fledglings per females that produced fledglings, N: population size. Relationships between parameters of the matrix population model are shown by a frame with dotted lines in the sub model D.

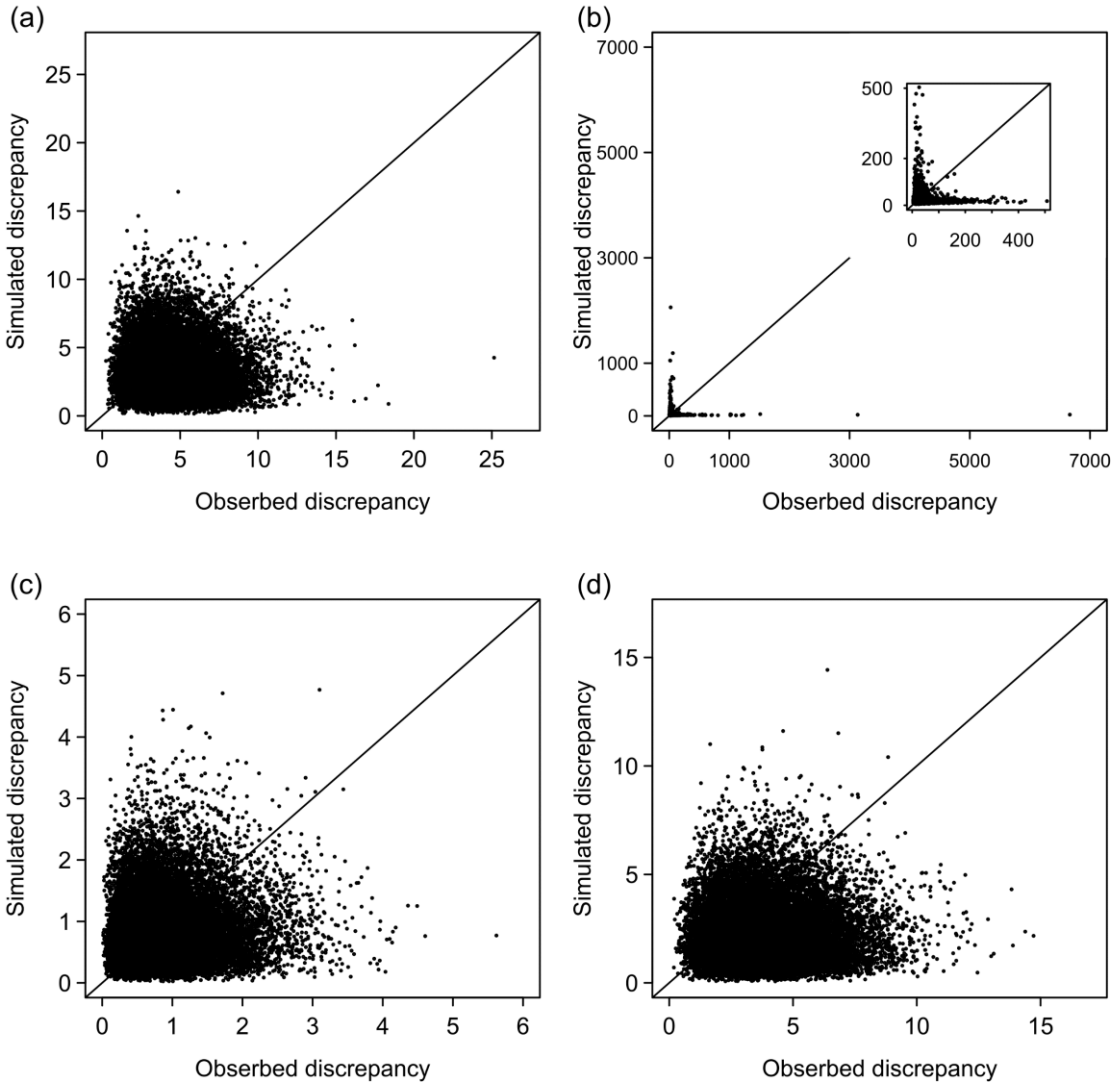


Figure 10-2

Results of posterior predictive check. (a) sex ratio, (b) fecundity, (c) male population, (d) female population. An additional plot on the plot (b) is the enlarged view of the plot.

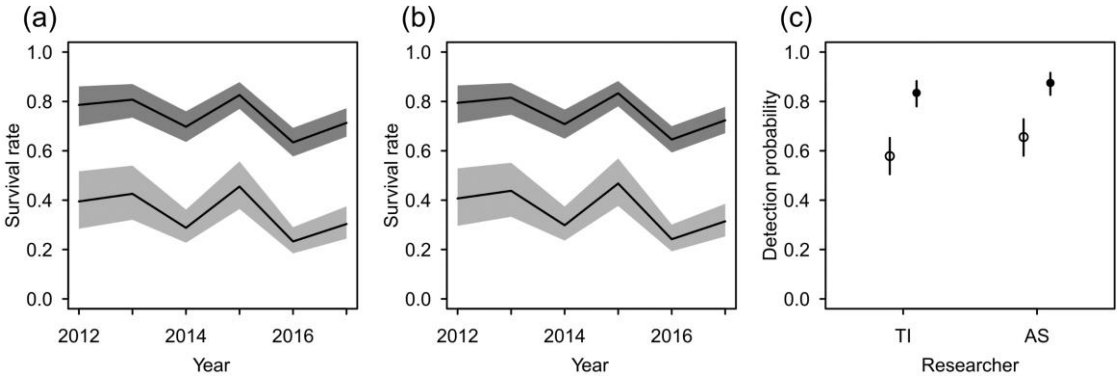


Figure 10-3

Survival rate of (a) females and (b) males, and (c) detection probability. Solid line with dark grey area: posterior mean and 95% CRI of adult survival rate. Solid line with pale grey area: posterior mean and 95% CRI of yearling survival rate. TI: main researcher from 2012 to 2015. AS: main researcher from 2016 to 2018. Open circle with a bar: posterior mean and 95% CRI of female detection probability. Filled circle with a bar: posterior mean and 95% CRI of male detection probability,

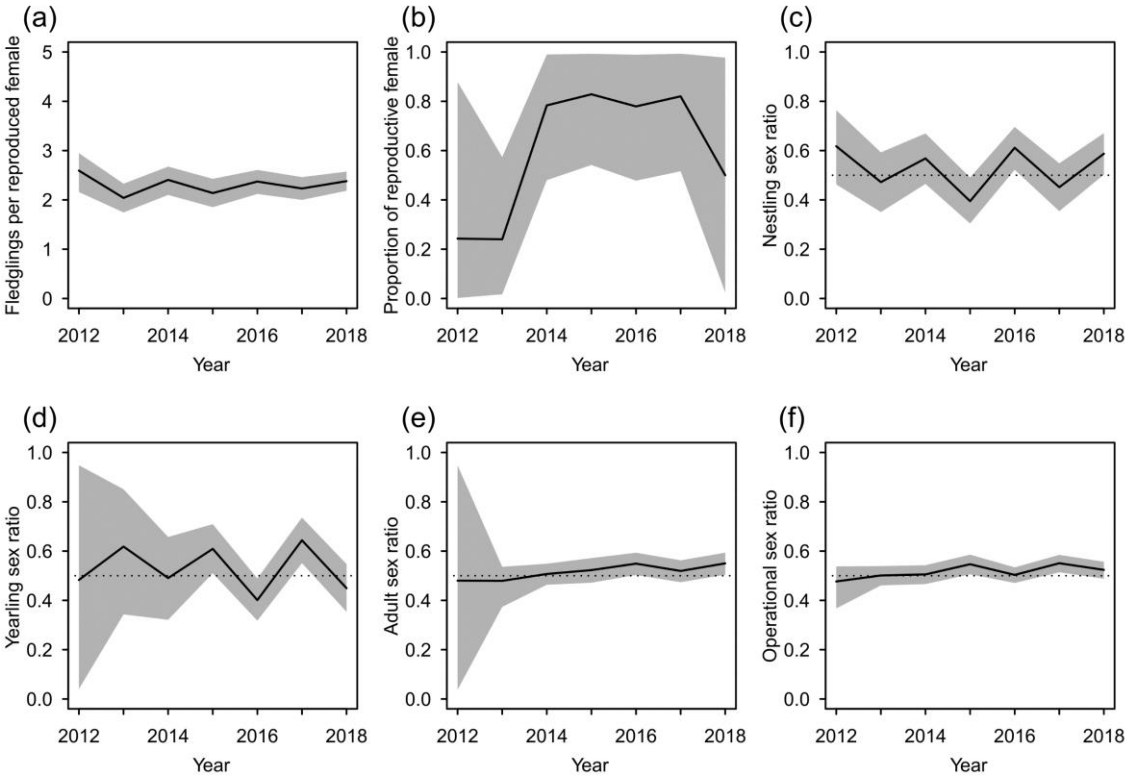


Figure 10-4

Fecundity and sex ratio. (a) number of fledglings per reproductive female that produced fledglings. (b) proportion of females that produced fledglings. Sex ratio of (c) fledgling, (d) yearling and (e) adult. (f) operational sex ratio. Solid line with pale grey area: posterior mean and 95% CRI. Dotted line: line of sex ratio = 0.5.

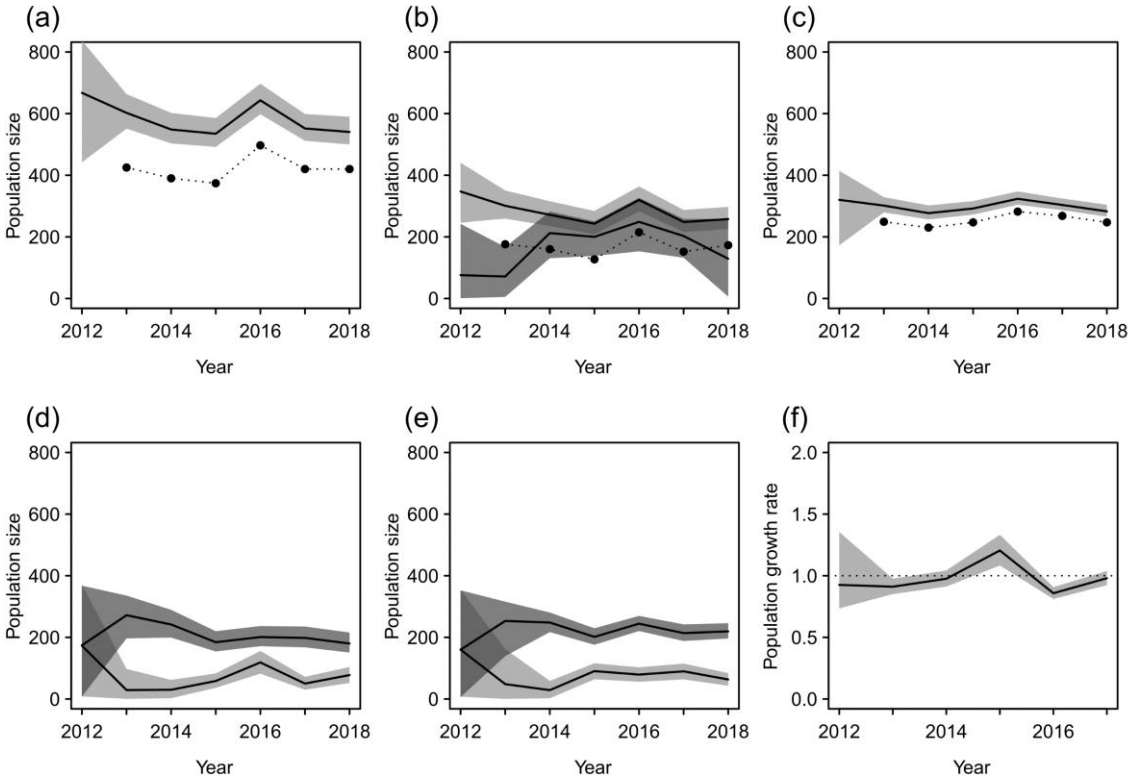


Figure 10-5

Population size and population growth rate. (a) Total population. (b) Female total population (pale grey) and reproductive female population (dark grey). (c) Male total population (pale grey). (d) Female yearling population (pale grey) and female adult population (dark grey). (e) Male yearling population (pale grey) and male adult population (dark grey). (f) Population growth rate. Solid line with grey area: posterior mean and 95% CRI. Solid line with black points: raw count data of (a) total population, (b) male total population and (c) female total population. Dotted line: line of growth rate = 1.0.

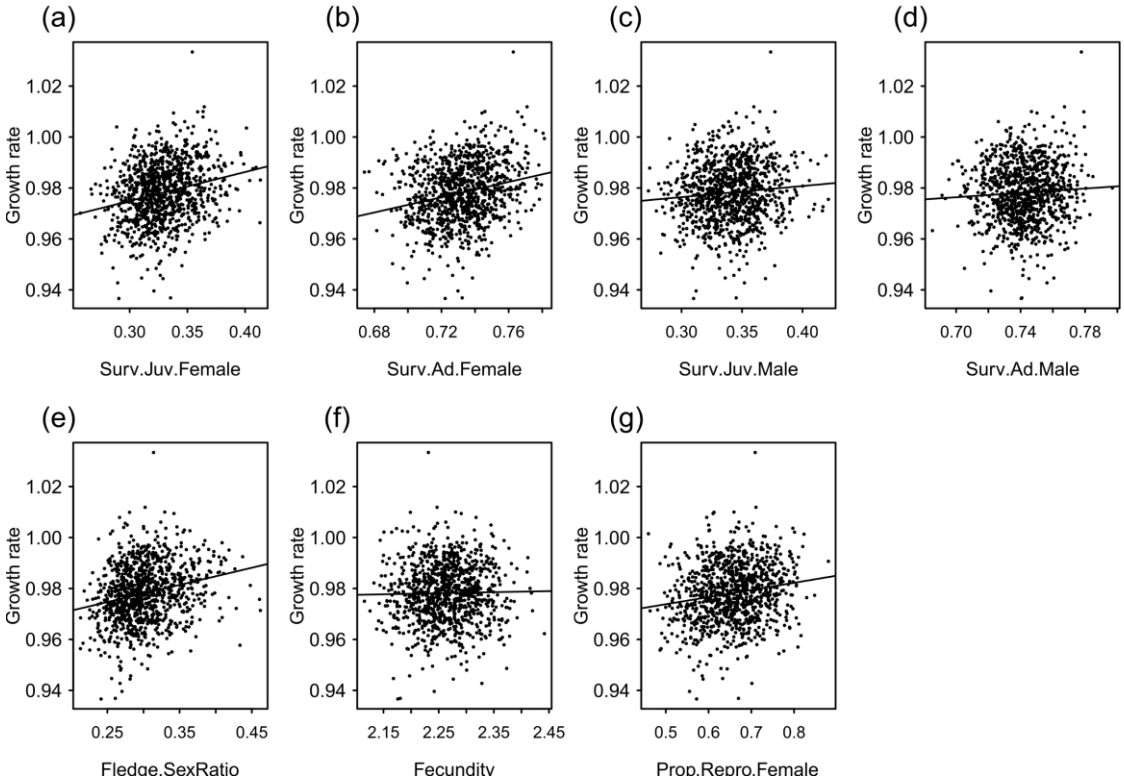


Figure 10-6

Results of life-stage simulation analysis. MCMC samples of the population growth rate are plotted against MCMC samples of other demographic parameters. (a) survival rate of juvenile female, (b) survival rate of adult female, (c) survival rate of juvenile male, (d) survival rate of adult male, (e) fledgling sex ratio, (f) fecundity, (g) proportion of reproductive females.

Table

Table 10-1 Sample size of survival history data and count data

	Survival history data[a]				Count data	
Year	Female nestling	Female adult	Male nestling	Male adult	Female	Male
2012	16	31	27	47		
2013	35	52	29	68	176	249
2014	33	50	31	86	160	230
2015	32	48	21	118	127	247
2016	42	75	52	151	215	282
2017	38	71	39	186	152	268
2018	0[b]	89	0[b]	185	173	247
Total	196	416	199	841	1003	1523

[a]: Figures are the number of individuals which we observed their presence in the year. [b]: Survival history data does not include nestlings in 2018 because their survival data can be obtained in 2019 or later.

Table 10-2 Sample size of fecundity data and sex ratio data

	Brood size				Nestling sex[a]	
Year	One-chick	Two-chick	Three-chick	Four-chick	Female	Male
2012	2	3	9	1	15	24
2013	9	10	10	0	32	27
2014	4	7	13	0	30	24
2015	5	11	7	0	29	19
2016	7	12	19	1	40	52
2017	4	16	10	0	34	32
2018	6	23	22	2	52	74
Total	37	82	90	4	232	252

[a]: A three-chick brood in 2014 whose sex data is incomplete is not included in the nestling sex data.

Table 10-3 Evaluation of including random effects into fecundity sub model

Random effect	LOOIC
MotherID	487.8
FatherID	492.5
No random effect	499.8

Table 10-4 Evaluation of including random effects into sex ratio sub model

Random effect	LOOIC
MotherID	675.9
FatherID	674.9
No random effect	674.5

Table 10-5 Results of test in R2ucare package

Sex	Test	Stat	df	P
Female	Test2CT	10.96	4	0.027
	Test3SR	24.94	5	0.000
	Test2CL	0.07	3	0.995
	Test3SM	10.06	4	0.039
Male	Test2CT	9.00	4	0.061
	Test3SR	17.67	5	0.003
	Test2CL	0.00	3	1.000
	Test3SM	14.17	4	0.007

Bold: significant at alpha = 0.00625 (= 0.05/8)

Table 10-6 Estimated survival rate

Year	Juvenile female	Adult female	Juvenile male	Adult male
2012 - 2013	0.39 (0.28, 0.52)	0.79 (0.70, 0.86)	0.41 (0.30, 0.53)	0.79 (0.71, 0.86)
2013 - 2014	0.43 (0.32, 0.54)	0.81 (0.73, 0.87)	0.44 (0.33, 0.55)	0.82 (0.75, 0.87)
2014 - 2015	0.29 (0.23, 0.36)	0.70 (0.64, 0.76)	0.30 (0.24, 0.37)	0.71 (0.65, 0.77)
2015 - 2016	0.46 (0.36, 0.56)	0.83 (0.77, 0.88)	0.47 (0.38, 0.57)	0.83 (0.78, 0.88)
2016 - 2017	0.23 (0.18, 0.29)	0.63 (0.58, 0.69)	0.24 (0.19, 0.30)	0.65 (0.59, 0.70)
2017 - 2018	0.30 (0.24, 0.37)	0.71 (0.66, 0.77)	0.31 (0.25, 0.39)	0.72 (0.67, 0.78)
Mean	0.33 (0.28, 0.38)	0.73 (0.70, 0.77)	0.34 (0.29, 0.39)	0.74 (0.71, 0.77)

Table 10-7 Estimated detection probability

Year	Researcher	Female	Male
2012	TI	0.58 (0.51, 0.65)	0.83 (0.78, 0.88)
2013	TI	0.58 (0.51, 0.65)	0.83 (0.78, 0.88)
2014	TI	0.58 (0.51, 0.65)	0.83 (0.78, 0.88)
2015	TI	0.58 (0.51, 0.65)	0.83 (0.78, 0.88)
2016	AS	0.66 (0.58, 0.73)	0.87 (0.83, 0.92)
2017	AS	0.66 (0.58, 0.73)	0.87 (0.83, 0.92)
2018	AS	0.66 (0.58, 0.73)	0.87 (0.83, 0.92)
Mean		0.62 (0.56, 0.68)	0.85 (0.81, 0.90)

Table 10-8 Estimated fecundity

Year	Fecundity
2012	2.59 (2.16, 2.95)
2013	2.04 (1.75, 2.33)
2014	2.41 (2.10, 2.68)
2015	2.14 (1.85, 2.43)
2016	2.37 (2.12, 2.61)
2017	2.23 (2.00, 2.46)
2018	2.38 (2.19, 2.57)
Mean	2.26 (2.15, 2.36)

Table 10-9 Estimated proportion of

Year	Proportion
2012	0.24 (0.00, 0.88)
2013	0.24 (0.02, 0.57)
2014	0.78 (0.48, 0.99)
2015	0.83 (0.54, 0.99)
2016	0.78 (0.48, 0.99)
2017	0.82 (0.52, 0.99)
2018	0.50 (0.03, 0.98)
Mean	0.66 (0.52, 0.79)

Table 10-10 Estimated sex ratio

Year	Fledgling sex ratio	Yearling sex ratio	Adult sex ratio	Operational sex ratio
2012	0.62 (0.46, 0.76)	0.48 (0.04, 0.95)	0.48 (0.04, 0.95)	0.48 (0.37, 0.54)
2013	0.47 (0.35, 0.59)	0.62 (0.34, 0.85)	0.48 (0.37, 0.54)	0.50 (0.46, 0.54)
2014	0.57 (0.46, 0.67)	0.49 (0.32, 0.66)	0.51 (0.46, 0.55)	0.51 (0.47, 0.54)
2015	0.39 (0.30, 0.49)	0.61 (0.51, 0.71)	0.52 (0.47, 0.57)	0.55 (0.51, 0.59)
2016	0.61 (0.52, 0.70)	0.40 (0.32, 0.49)	0.55 (0.50, 0.59)	0.50 (0.47, 0.53)
2017	0.45 (0.35, 0.55)	0.64 (0.55, 0.74)	0.52 (0.47, 0.56)	0.55 (0.51, 0.58)
2018	0.59 (0.50, 0.67)	0.45 (0.35, 0.55)	0.55 (0.50, 0.59)	0.52 (0.49, 0.56)
Mean	0.51 (0.47, 0.56)	0.54 (0.48, 0.59)	0.52 (0.48, 0.56)	0.52 (0.49, 0.55)

Table 10-11 Estimated population size

Year	Yearling female	Adult female	Female	Breeding female
2012	173.0 (8.3, 370.9)	174.3 (7.9, 367.7)	347.2 (246.2, 440.6)	75.8 (0.8, 242.2)
2013	28.9 (0.2, 97.3)	271.9 (196.7, 335.5)	300.8 (259.3, 350.5)	71.3 (5.2, 166.9)
2014	29.9 (2.4, 61.8)	241.7 (199.3, 289.3)	271.6 (235.3, 315.5)	212.3 (130.7, 281.8)
2015	58.4 (36.2, 83.0)	184.3 (154.2, 220.0)	242.7 (208.3, 283.9)	200.0 (138.1, 250.1)
2016	118.6 (82.3, 155.9)	201.0 (171.4, 236.7)	319.7 (283.2, 363.5)	248.7 (153.0, 326.6)
2017	50.0 (30.0, 71.9)	198.2 (167.6, 235.0)	248.2 (215.7, 287.4)	202.8 (132.2, 257.9)
2018	77.7 (52.2, 103.7)	179.9 (150.8, 215.8)	257.6 (225.2, 297.2)	128.8 (6.4, 258.8)
Mean	60.6 (47.9, 76.3)	212.9 (186.0, 244.2)	273.4 (247.2, 305.5)	177.3 (141.0, 215.6)

Table 10-11 (continued)

Year	Yearling male	Adult male	Male	Total
2012	160.2 (7.3, 353.7)	160.0 (6.7, 352.5)	320.2 (172.7, 414.3)	667.4 (442.1, 836.8)
2013	48.2 (0.3, 162.0)	253.3 (139.1, 315.8)	301.5 (279.3, 328.9)	602.3 (551.2, 663.2)
2014	28.8 (2.3, 58.6)	248.1 (217.1, 280.6)	276.9 (256.6, 302.0)	548.5 (503.3, 602.3)
2015	90.5 (64.0, 115.9)	201.6 (175.9, 229.4)	292.1 (272.1, 316.1)	534.7 (492.0, 585.6)
2016	79.1 (55.9, 102.7)	244.4 (220.5, 269.7)	323.6 (304.3, 347.3)	643.2 (597.9, 696.9)
2017	89.7 (63.6, 114.8)	213.9 (188.2, 242.1)	303.6 (286.7, 324.4)	551.8 (511.8, 598.7)
2018	63.3 (43.0, 83.9)	219.6 (196.4, 245.8)	282.9 (265.6, 304.4)	540.5 (499.9, 589.7)
Mean	66.6 (52.5, 87.6)	230.2 (205.6, 252.9)	296.8 (282.3, 314.1)	570.2 (539.6, 606.2)

Table 10-12 Estimated population growth rate

Year	Growth rate
2012-2013	0.93 (0.74, 1.36)
2013-2014	0.91 (0.85, 0.98)
2014-2015	0.98 (0.91, 1.04)
2015-2016	1.20 (1.08, 1.33)
2016-2017	0.86 (0.81, 0.91)
2017-2018	0.98 (0.92, 1.04)
Mean	0.98 (0.96, 1.00)

Chapter 11

General discussion

Target of mate choice

This study revealed tendencies of non-random mating with respect to genes (Chapter 7) and body size measures (Chapter 6). These tendencies were not accounted for by passive encounters of neighboring individuals and suggested contribution of active choice of mates to the occurrence of the tendencies. However, whether the genes and body sizes are the direct criteria which are used by the owls when choosing mate is unclear. Considering the fact that natural selections favor methods which mediate information efficiently (Endler 1992) and nocturnality of the owls, vocal characteristics are strong candidates which mediate the various information of potential mates. Developed vocal communication among owls also supports this idea (König and Weick 2008). Furthermore, because the owls are suggested that they do not learn vocalizations (Gahr 2000), the information is likely to be mediated honestly (Galeotti 1998; Gahr 2000; Redpath et al. 2000).

Especially, body size could be easily assessed through vocalization as body size often negatively correlate with the frequency of vocalizations (Ryan and Brenowitz 1985; Martin et al. 2017). Therefore, vocalization is the most likely candidate of direct target of body size-based mate choice. However, visual cue and physical contact are not ruled out. Not completely depending on acoustic signals, owls have large fore fronted eyes, which indicate their use of visual information even at low-light situations (König and Weick 2008). It may enable visual inspection of body size. Grooming among pairs offers opportunity to know body size and even more detailed information of mates (Soltis et al. 1997).

As for genetic make-up, not only vocal characteristics but also chemical cues may also mediate the information. Results on mammals and reptiles have suggested linkage between MHC genes and profile of body odor of individuals and suggested odor cues are the direct target of genetically based mate choice (e.g. Yamazaki et al. 1979; Olsson et al. 2003; Roberts et al. 2008). Longtime, birds have been believed to be anosmatic (Caro and Balthazart 2010). However, such notion has been changed these decades (Caro and Balthazart 2010; Avilés and Amo 2018). Some species especially of sea birds have preen wax of which differences in chemical compositions correlate genetic differences between individuals (Leclaire et al. 2014, 2017). One of the reasons why sea birds have developed olfaction skill is related to their need to find nest burrow at night (Bonadonna et al. 2003, 2004). Although owl is also a group of nocturnal birds, they are not treated in the field of avian olfaction. Males of the Ryukyu Scops Owl call and invite females into candidate nest cavities in the beginning of breeding season and female assess inside of the cavities (Sawada and Takagi unpublished data). Females might sense the smell of males remined in the cavity. From mark-recapturing of more

than 2000 individuals in the study, I have noticed the owls have weak but peculiar smells. Chemical analysis of preen wax is an interesting future direction to answer how they recognize genetic profiles of potential mates.

Evolution of mate preference

I studied how mate choice based on genes and body size affect individual's fitness, aiming to address an important problem of sexual selection: how mate preferences are evolved in the first place (Chapter 6, 7). For example, although Fisher's runaway process explains evolution of extreme traits such as long tail feathers in some bird species, this theory needs assuming prerequisite existence of heritable variation of the mate preference (Kirkpatrick and Ryan 1991). To address the problem, empiricists often seeks fitness benefit of the choosing behaviors.

Relationships between body size and number of recruits produced at a single reproduction event in males (Chapter 6), the fact that they reproduce multiple times in their lifetime and positive correlation between longevity and lifetime reproductive success (Chapter 7) suggest existence of fitness benefit of female's mate preferences with respect to male's body size. Then what is the proximate causes of the relationship between body size and the number of recruits? Increased foraging efficiency due to increased agility and maneuverability of small males may have an advantage in breeding season and producing healthy offspring (Mueller 1986). Low-energy demand may also prefer small males in the subtropical island where strong typhoons sometime severely damage the environment on which they feed (Takagi et al. 2007b).

Contrary to body size, I did not find significant fitness benefit for choosing mate based on MHC genes. However, I think this is probably due to low power of analyses which is derived from small number of individuals, small number of years I tracked the owls and use of only single cohort (Chapter 7). Because prognosis after fledging is an outcome of accumulating annual effects, survival history of fledglings can considerably vary between cohorts (Grant and Grant 2014). More intensive analyses exploiting data of multiple cohorts and multiple SNP genotypes along whole genomes, which is already started, would reveal fitness benefit of genetically based mate choice.

Sexual size dimorphism and body size-based mate choice

A series of analyses showed existence of reversed sexual size dimorphism (Chapter 2), emergence of the dimorphism at growing period (Chapter 3), advantage of small males (Chapter 6) and existence of size assortative mating (Chapter 6). From these results, importance of jointly discussing sexual size dimorphism and size assortative mating would be stressed. One of the classic explanations for evolution of reversed sexual size dimorphism in raptors assumes natural selection for small males due to good foraging skills (as discussed above). However, if females preferers small males because they are good food provider for their offspring, sexual selection is also responsible for the small male advantage (Møller and Jennions 2001). Although teasing apart the effect of these

two selection pressures is difficult (Mueller 1986), recognizing it is important to lead reasonable interpretation of results.

There was also an advantage of smallness in females with respect to survival rate (Chapter 6). Long-living individuals were expected to have large lifetime reproductive success (Chapter 7), probably due to increased number of opportunities for reproduction. These results suggest selection pressure prefers small individuals also in females. From the fact that females have larger size than males, this suggests there are some counter balancing selection pressure keeping females being larger than males. Identifying the pressure is a problem to be solved in the future study.

Inbreeding avoidance and sex-biased dispersal

There were signs of inbreeding avoidance (Chapter 7), sex-biased dispersal (Chapter 8) and sex-dependent spatial genetic structures (Chapter 9). Since the sexual difference in dispersal distance is a most widely accepted proximate mechanism leading inbreeding avoidance (E. Pusey 1987; Szulkin and Sheldon 2008; Lebigre et al. 2010), sex-biased dispersal seems to be the mechanism of the owl's inbreeding avoidance. On the other hand, I suggest this causal relationship can be reversed. As already discussed, genetically based mate choice may be mediated by recognition of odor profiles. Therefore, under the existence of isolation by distance pattern in genetic profiles of males and needs of early territory establishment in males, female's dispersal while rejecting genetically similar males can result in longer dispersal distance in females than males even without inherent tendency of sex-biased dispersal (Hardouin et al. 2015). Therefore, causal relationships between inbreeding avoidance and sex-biased dispersal is not as simple as often discussed.

Mate choice and population process

This dissertation documented results from fundamental description of traits (Chapter 2, 3, 4, 5) to results from fitting of population dynamics model (Chapter 10), while considering the fact that mate choice behavior of individuals relates to various aspect of a population. Demographic analysis in the Chapter 10 used integrated population model (Schaub and Abadi 2010; Plard et al. 2019). This is a statistical method which jointly estimates multiple demographic processes in a statistical model. Although I here included only fundamental processes (population size, reproduction and survival), there are room for development. For examples, processes of mate choice modelled in the Chapter 7 and processes of dispersal modelled in the Chapter 8 can be accommodated in the integrated population model. This extension enables to estimate how such the mate choice behavior and the dispersal behavior for mate search influence the processes at population scale and even enables to estimate feedback relationships between the processes (Plard et al. 2019). This is a promising future research which I have already get started.

Significance of long-term study of island population

Without a research basis of a long-term study population, comprehensive works for mate choice cannot be realized. In the history of ecology and evolution, pioneering forefront knowledge are often provided by researches on long-term study populations. For examples, contributions of Darwin's Finches in Galapagos Islands (Grant and Grant 2014), Great Tis in Wytham Woods (Perrins 1965; McCleery et al. 2004) and Red Deer on the Isle of Rum (Kruuk et al. 1999; Slate et al. 2000) cannot be overestimated. Because such populations accumulate fundamental ecological data for decades, researchers are able to test various theories of ecology and evolution at their will. Among the long-term study populations, island populations especially offer good properties for ecological researches such as an evident boundary of population, simple ecological systems and variations in environment and geological history (Whittaker and Fernandez-Palacios 2007).

A population of the Ryukyu Scops Owls on Minami-daito island is one of the rare long-term study populations in East Asia. Ongoing study is accumulating their fundamental data on the isolated oceanic island. As the conspecific populations occur through the islands of the Ryukyu Archipelago (Ornithological Society of Japan 2012), the owls have a promising potential to extend eco-evolutionary studies on a population to multiple populations.

On the other hand, the population on Minami-daito Island have a problem to note as a model population for evolutionary studies. That is, intensive deforestation after human colonization in the early 1900s and altered ecosystem by many introduced species have definitely changed selection pressures on the owls, making it difficult to lead discussion on their evolutionary history. First, records of the colonist described that the island was entirely covered by dense forest (Minami-daito Village 1990). This is quite different from current circular wind shelter belts planted by humans (Takagi et al. 2007b). This probably have altered the selection pressures on spatial distributions of individuals and dispersal strategies. Second, although casuarina is a main tree species which is used as nest by the owls, it is a species introduced by humans (Akatani et al. 2011). Therefore, casuarinas have undoubtedly contributed to maintain the damaged population after deforestation. Third, wild cats and Japanese weasel are now predators of the owls, although any mammalian predators have not been present before human colonization. Despite these problems, I believe the population has still worth studying because these weak points can be overcome or even become strong point depending on researchers' skill and idea. Development of genomics may be used to infer recent demography after human colonization. Simple structure of wind shelter belts and territories line up in a row on the wind shelter belts (Takagi et al. 2007a; Sawada et al. 2018a) is a setting just like the ones assumed in theoretical studies. Introduction of species can be viewed as experiment of evolutionary biology if we properly collect and analyze their data. My hope is that the long-term study of the owls on Minami-daito Island which I have undertaken these five years will last for decades to come and continue to contribute to

our understanding of evolutionary biology with nonconventional ingenuity of far-sighted researchers.

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References

Abadi, F., C. Barbraud, and O. Gimenez. 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile Emperor Penguins. Glob. Chang. Biol. 23:1353–1359.

Abel, R. L., C. R. Laurini, and M. Richter. 2012. A palaeobiologist's guide to 'virtual' micro-CT preparation. Palaeontol. Electron. 15:1–16.

Adams, D. C., and E. Otárola-Castillo. 2013. Geomorph: An r package for the collection and analysis of geometric morphometric shape data. Methods Ecol. Evol. 4:393–399.

Akatani, K. 2011. Ryukyu Scops Owl Ryukyu-konohazuku (Jpn) *Otus elegans*. Bird Res. News 8:4–5.

Akatani, K., T. Matsuo, and M. Takagi. 2011. Breeding ecology and habitat use of the Daito Scops Owl (*Otus elegans interpositus*) on an oceanic island. J. Raptor Res. 45:315–323.

Akatani, K., and M. Takagi. 2020. Remigial and rectricial molt sequences in a captive Ryukyu Scops-Owl. Wilson J. Ornithol. 131:828–833.

Alcaide, M., S. V Edwards, and J. J. Negro. 2007. Characterization, polymorphism, and evolution of MHC Class II B genes in birds of prey. J. Mol. Evol. 65:541–554.

Anderson, E. C., and K. K. Dunham. 2008. The influence of family groups on inferences made with the program Structure. Mol. Ecol. Resour. 8:1219–1229.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, NJ.

Andersson, M., and R. Å. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biol. J. Linn. Soc. 15:105–130.

Andersson, M., and L. W. Simmons. 2006. Sexual selection and mate choice. TRENDS Ecol. Evol. 21:296–302.

Ando, H. 2019. Genetic and ecological conservation issues for oceanic island birds, revealed by a combination of the latest molecular techniques and conventional field work. Ecol. Res. 34:255–264.

Anezaki, S. 2012. Avifauna of Kita-daito Island and Minami-daito Island before World War II. J. Yamashina Inst. Ornithol. 43:105–151.

Appleby, B. M., and S. M. Redpath. 1997. Indicators of male quality in the hoots of Tawny Owls (*Strix aluco*). J. Raptor Res. 31:65–70.

Avilés, J. M., and L. Amo. 2018. The evolution of olfactory capabilities in wild birds: a comparative study. Evol. Biol. 45:27–36.

Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends Ecol. Evol. 17:369–378.

Bai, M. L., and L. L. Severinghaus. 2012. Disentangling site and mate fidelity in a monogamous population under strong nest site competition. Anim. Behav. 84:251–259.

Banks, S. C., J. Dubach, K. L. Viggers, and D. B. Lindenmayer. 2010. Adult survival and microsatellite diversity in possums: effects of major histocompatibility complex-linked microsatellite diversity but not multilocus inbreeding estimators. Oecologia 162:359–370.

Banner, K. M., and M. D. Higgs. 2017. Considerations for assessing model averaging of regression coefficients: assessing MA for regression coefficients. Ecol. Appl. 27:78–93.

Barton, K. 2019. MuMIn: Multi-Model Inference, Version 1.43.6. 1–75.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67:1–48.

Bateson, Z. W., S. C. Hammerly, J. A. Johnson, M. E. Morrow, L. A. Whittingham, and P. O. Dunn. 2016. Specific alleles at immune genes, rather than genome-wide heterozygosity, are related to immunity and survival in the critically endangered Attwater's Prairie-chicken. Mol. Ecol. 25:4730–4744.

Becker, P. H., and M. Wink. 2003. Influences of sex, sex composition of brood and hatching order on mass growth in Common Terns *Sterna hirundo*. Behav. Ecol. Sociobiol. 54:136–146.

Beissinger, S. R., J. M. Wunderle, J. M. Meyers, B. E. Saether, and S. Engen. 2008. Anatomy of a bottleneck: diagnosing factors limiting population growth in the Puerto Rican Parrot. Ecol. Monogr. 78:185–203.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B 57:289–300.

Bernatchez, L., and C. Landry. 2003. MHC studies in nonmodel vertebrates: what have we learned about natural selection in 15 years? J. Evol. Biol. 16:363–377.

Bhullar, B.-A. S., J. Marugán-Lobón, F. Racimo, G. S. Bever, T. B. Rowe, M. A. Norell, and A. Abzhanov. 2012. Birds have paedomorphic dinosaur skulls. Nature 487:223–226.

Bhullar, B. A. S., Z. S. Morris, E. M. Sefton, A. Tok, M. Tokita, B. Namkoong, J. Camacho, D. A. Burnham, and A. Abzhanov. 2015. A molecular mechanism for the origin of a key evolutionary innovation, the bird beak and palate, revealed by an integrative approach to major transitions in vertebrate history. Evolution. 69:1665–1677.

Bifolchi, A., and T. Lodé. 2005. Efficiency of conservation shortcuts: an investigation with otters as umbrella species. Biol. Conserv. 126:523–527.

Bildstein, K. L., and F. Hamerstrom. 1980. Age and sex differences in the size of Northern Harriers. J. F. Ornithol. 51:356–360.

Birkhead, T. R., L. Atkin, and A. P. Møller. 1987. Copulation behaviour of birds. Behaviour 101:101–138.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends Ecol. Evol. 14:427–432.

Blanchard, R., and L. Ellis. 2001. Birth weight, sexual orientation and the sex of preceding siblings. J. Biosoc. Sci. 33:451–467.

Blanckenhorn, W. U. 2000. The evolution of body size: what keeps organisms small? Q. Rev. Biol. 75:385–407.

Bohonak, A. J. 1999. Dispersal, gene flow, and population structure. Q. Rev. Biol. 74:21–45.

Bolnick, D. I., and B. M. Fitzpatrick. 2007. Sympatric speciation: models and empirical evidence. Annu. Rev. Ecol. Evol. Syst. 38:459–487.

Bonadonna, F., F. Hesters, and P. Jouventin. 2003. Scent of a nest: discrimination of own-nest odours in Antarctic Prions, *Pachyptila desolata*. Behav. Ecol. Sociobiol. 54:174–178.

Bonadonna, F., M. Villafane, C. Bajzak, and P. Jouventin. 2004. Recognition of burrow's olfactory signature in Blue Petrels, *Halobaena caerulea*: an efficient discrimination mechanism in the dark. Anim. Behav. 67:893–898.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. Camb. Philos. Soc. 80:205–225.

Bright, J. A., J. Marugán-lobón, S. N. Cobb, and E. J. Rayfield. 2016. The shapes of bird beaks are highly controlled by nondietary factors. Proc. Natl. Acad. Sci. 113:5352–5357.

Brommer, J. E., P. Karell, T. Pihlaja, J. N. Painter, C. R. Primmer, and H. Pietiäinen. 2003. Ural Owl sex allocation and parental investment under poor food conditions. Oecologia 137:140–147.

Brouwer, L., I. Barr, M. van de Pol, T. Burke, J. Komdeur, and D. S. Richardson. 2010. MHC-dependent survival in a wild population: evidence for hidden genetic benefits gained through extra-pair fertilizations. Mol. Ecol. 19:3444–3455.

Brown, J. H., T. S. Jardetzky, J. C. Gorga, L. J. Stern, R. G. Urban, J. L. Strominger, and D. C. Wiley. 1993. Three-dimensional structure of the human class II histocompatibility antigen HLA-DR1. Nature 364:33–39.

Candolin, U. 2003. The use of multiple cues in mate choice. Biol. Rev. 78:575–595.

Caro, S. P., and J. Balthazart. 2010. Pheromones in birds: myth or reality? J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 196:751–766.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. J. Stat. Softw. 76.

Caswell, H. 2006. Matrix population models: construction, analysis, and interpretation. Second. Sinauer Associates, Sunderland, Massachusetts.

Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. Am. Nat. 159:1–23.

Christiansen, O. B., B. Pedersen, H. S. Nielsen, and A.-M. N. Andersen. 2004. Impact of the sex of first child on the prognosis in secondary recurrent miscarriage. Hum.

Reprod. 19:2946–2951.
Cignoni, P., M. Corsini, and G. Ranzuglia. 2008. MeshLab: an open-source 3D mesh processing system. ERCIM News 73:47–48.
Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. Am. Nat. 152:204–224.
Class, B., and J. E. Brommer. 2018. Shared environmental effects bias phenotypic estimates of assortative mating in a wild bird. Biol. Lett. 14:20180106.
Clegg, S. M., and I. P. F. Owens. 2002. The "island rule" in birds: medium body size and its ecological explanation. Proc. Biol. Sci. 269:1359–1365.
Consuegra, S., and C. Garcia De Leaniz. 2008. MHC-mediated mate choice increases parasite resistance in salmon. Proc. R. Soc. B Biol. Sci. 275:1397–1403.
Courchamp, F., J. L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. Biol. Rev. Camb. Philos. Soc. 78:347–383.
Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Inc, Sunderland, Massachusetts.
Crespi, B. J. 1989. Causes of assortative mating in arthropods. Anim. Behav. 38:980–1000.
Currie, D., A. C. Mateman, C. M. Lessells, and R. Fanchette. 2002. Sexual size dimorphism in the critically endangered Seychelles Scops Owl *Otus insularis*. Ringing Migr. 21:16–18.
Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. OIKOS 92:344–356.
Darwin, C. 1874. The descent of man, and selection in relation to sex. 2nd ed. John Murray.
de Almeida Borghezan, E., K. da Silva Pinto, J. Zuanon, and T. H. da Silva Pires. 2019. Someone like me: size-assortative pairing and mating in an Amazonian fish, Sailfin Tetra *Crenuchus spilurus*. PLoS One 14: e0222880.
Donald, P. F. 2007. Adult sex ratios in wild bird populations. Ibis. 149:671–692.
Dormann, C. F., J. M. Calabrese, G. Guillera-Arroita, E. Matechou, V. Bahn, K. Bartoń, C. M. Beale, S. Ciuti, J. Elith, K. Gerstner, J. Guelat, P. Keil, J. J. Lahoz-Monfort, L. J. Pollock, B. Reineking, D. R. Roberts, B. Schröder, W. Thuiller, D. I. Warton, B. A. Wintle, S. N. Wood, R. O. Wüest, and F. Hartig. 2018. Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecol. Monogr. 88:485–504.
Double, M. C., R. Peakall, N. R. Beck, and A. Cockburn. 2005. Dispersal, philopatry, and infidelity: dissecting local genetic structure in Superb Fairy-wrens (*Malurus cyaneus*). Evolution. 59:625–635.
Dray, S., D. Bauman, G. Blanchet, D. Borcard, S. Clappe, G. Guenard, T. Jombart, G. Larocque, P. Legendre, N. Madi, and H. H. Wagner. 2020. adespatial: multivariate multiscale spatial analysis. R package version 0.3-8. https://cran.r-project.org/package=adespatial

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Modell. 196:483–493.

Duckworth, J. W. 1998. The difficulty of estimating population densities of nocturnal forest mammals from transect counts of animals. J. Zool. 246:466–468.

Dutech, C., V. L. Sork, A. J. Irwin, P. E. Smouse, and F. W. Davis. 2005. Gene flow and fine-scale genetic structure in a wind-pollinated tree species, *Quercus lobata* (Fagaceaee). Am. J. Bot. 92:252–261.

E. Pusey, A. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol. Evol. 2:295–299.

Earhart, C. M., and N. K. Johnson. 1970. Size dimorphism and food habits of north American owls. Condor 72:251–264.

Earl, D. A., and B. M. VonHoldt. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv. Genet. Resour. 4:359–361.

Eising, C. M., C. Eikenaar, H. Schwabl, and T. G. G. Groothuis. 2001. Maternal androgens in Black-headed Gull (*Larus ridibundus*) eggs: consequences for chick development. Proc. R. Soc. London. Ser. B Biol. Sci. 268:839–846.

Eizaguirre, C., S. E. Yeates, T. L. Lenz, M. Kalbe, and M. Milinski. 2009. MHC-based mate choice combines good genes and maintenance of MHC polymorphism. Mol. Ecol. 18:3316–3329.

Elmer, K. R., T. K. Lehtonen, and A. Meyer. 2009. Color assortative mating contributes to sympatric divergence of neotropical cichlid fish. Evolution. 63:2750–2757.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton.

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. Am. Nat. 139:S125–S153.

Engen, S., R. Lande, and B. E. Sæther. 2003. Demographic stochasticity and Allee effects in populations with two sexes. Ecology 84:2378–2386.

Erlandsson, J., and E. Rolán-Alvarez. 1998. Sexual selection and assortative mating by size and their roles in the maintenance of a polymorphism in Swedish *Littorina saxatilis* populations. Hydrobiologia 378:59–69.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol. Ecol. 14:2611–2620.

Excoffier, L., P. E. Smouse, and J. M. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491.

Fargallo, J. A., J. Martínez-Padilla, A. Toledano-Díaz, J. Santiago-Moreno, and J. A. Dávila. 2007. Sex and testosterone effects on growth, immunity and melanin coloration of nestling Eurasian Kestrels. J. Anim. Ecol. 76:201–209.

Fernández-Juricic, E., M. D. Gall, T. Dolan, V. Tisdale, and G. R. Martin. 2008. The

visual fields of two ground-foraging birds, House Finches and House Sparrows, allow for simultaneous foraging and anti-predator vigilance. Ibis. 150:779–787.
Frankham, R. 1997. Do island populations have less genetic variation than mainland populations? Heredity. 78:311–327.
Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: a review. Genet. Res. 66:95–107.
Frankham, R. 1998. Inbreeding and extinction: island populations. Conserv. Biol. 12:665–675.
Fridolfsson, A.-K., and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. J. Avian Biol. 30:116–121.
Gahr, M. 2000. Neural song control system of hummingbirds: comparison to swifts, vocal learning (songbirds) and nonlearning (suboscines) passerines, and vocal learning (budgerigars) and nonlearning (dove, owl, gull, quail, chicken) nonpasserines. J. Comp. Neurol. 426:182–196.
Galeotti, P. 1998. Correlates of hoot rate and structure in male Tawny Owls *Strix aluco*: implications for male rivalry and female mate choice. J. Avian Biol. 29:25–32.
Galeotti, P. R., B. M. Appleby, and S. M. Redpath. 1996. Macro and microgeographical variations in the “hoot” of Italian and English Tawny Owls (*Strix aluco*). Ital. J. Zool. 63:57–64.
Galipaud, M., L. Bollache, and F. X. Dechaume-Moncharmont. 2013. Assortative mating by size without a size-based preference: the female-sooner norm as a mate-guarding criterion. Anim. Behav. 85:35–41.
Garroway, C. J., R. Radersma, I. Sepil, A. W. Santure, I. De Cauwer, J. Slate, and B. C. Sheldon. 2013. Fine scale genetic structure in a wild bird population: the role of limited dispersal and environmentally based selection as causal factors. Evolution. 67:3488–3500.
Gelman, A. 2020. Prior choice recommendations. https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations
Genovart, M., and R. Pradel. 2019. Transience effect in capture-recapture studies: the importance of its biological meaning. PLoS One 14:e0222241.
Gerhardt, R. P., and D. M. Gerhardt. 1997. Size, dimorphism, and related characteristics of ciccaba owls from Guatemala. Pp. 190–196 *in* J. R. Duncan, D. H. Johnson, and T. H. Nicholls, eds. Biology and conservation of owls of the Northern Hemisphere 2nd International symposium. Saint Paul, USA.
Gil, D., E. Bulmer, P. Celis, and I. López-Rull. 2008. Adaptive developmental plasticity in growing nestlings: sibling competition induces differential gape growth. Proc. R. Soc. B Biol. Sci. 275:549–554.
Gill, F., and D. Donsker. 2017. IOC World Bird List (v 7.1).
Gill, F., and D. Donsker. 2019. IOC World Bird List (v 9.1).
Gill, F., D. Donsker, and P. Rasmussen. 2020. IOC World Bird List (v 10.2).
Gimenez, O., R. Choquet, J. Lebreton, and R. Pradel. 2018. R2ucare: An R package to

perform goodness-of-fit tests for capture-recapture models. 9:1749–1754.
Godin, J. J., and S. E. Briggs. 1996. Female mate choice under predation risk in the Guppy. Anim. Behav. 51:117–130.
Goldberg, C. S., and L. P. Waits. 2010. Quantification and reduction of bias from sampling larvae to infer population and landscape genetic structure. Mol. Ecol. Resour. 10:304–313.
Goodall, C. 1991. Procrustes methods in the statistical analysis of shape. J. R. Stat. Soc. B 53:285–339.
Goodship, N. M., and K. L. Buchanan. 2006. Nestling testosterone is associated with begging behaviour and fledging success in the Pied Flycatcher, *Ficedula hypoleuca*. Proc. R. Soc. B Biol. Sci. 273:71–76.
Goymann, W., B. Kempenaers, and J. Wingfield. 2005. Breeding biology, sexually dimorphic development and nestling testosterone concentrations of the classically polyandrous African Black Coucal, *Centropus grillii*. J. Ornithol. 146:314–324.
Grant, P. R., and B. R. Grant. 2014. 40 years of evolution: Darwin's Finches on Daphne Major Island. Princeton University Press, Princeton, NJ.
Grant, P. R., and B. R. Grant. 2008. Pedigrees, assortative mating and speciation in Darwin's Finches. Proc. R. Soc. B Biol. Sci. 275:661–668.
Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's Finches. Science. 296:707–711.
Green, D. M. 2019. Rarity of size-assortative mating in animals: assessing the evidence with anuran amphibians. Am. Nat. 193:279–295.
Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28:1140–1162.
Groothuis, T. G. G., and H. Schwabl. 2008. Hormone-mediated maternal effects in birds: mechanisms matter but what do we know of them? Philos. Trans. R. Soc. B Biol. Sci. 363:1647–1661.
Gutiérrez, R. J., P. N. Manley, and P. A. Stine. 2017. The California Spotted Owl: current state of knowledge. Gen. Tech. Rep. PSW-GTR-254. Albany, CA US Dep. Agric. For. Serv. Pacific Southwest Res. Stn. 254.
Hakkarainen, H., V. Koivunen, and E. Korpimäki. 1997. Reproductive success and parental effort of Tengmalm's Owls: effects of spatial and temporal variation in habitat quality. Ecoscience 4:35–42.
Hakkarainen, H., and E. Korpimäki. 1991. Reversed sexual size dimorphism in Tengmalm's Owl: is small male size adaptive? Oikos 61:337–346.
Hakkarainen, H., K. Lahti, P. Lundvall, J. Wiehn, E. Huhta, T. Mappes, and P. Tolonen. 1996. A test of male mating and hunting success in the Kestrel: the advantages of smallness? Behav. Ecol. Sociobiol. 39:375–380.
Hamilton, W., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? Science. 218:384–387.
Han, C. S., P. G. Jablonski, B. Kim, and F. C. Park. 2010. Size-assortative mating and

sexual size dimorphism are predictable from simple mechanics of mate-grasping behavior. BMC Evol. Biol. 10:359.

Hardouin, A., V. Bretagnolle, P. Tabel, C. Bavoux, G. Burneleau, and D. Reby. 2009. Acoustic cues to reproductive success in male owl hoots. Anim. Behav. 78:907–913.

Hardouin, L. A., P. Legagneux, Y. Hingrat, and A. Robert. 2015. Sex-specific dispersal responses to inbreeding and kinship. Anim. Behav. 105:1–10.

Hardy, O. J., and X. Vekemans. 2002. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Mol. Ecol. Notes 2:618–620.

Heesy, C. P. 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. Anat. Rec. - Part A Discov. Mol. Cell. Evol. Biol. 281:1104–1110.

Hendry, A. P., and T. Day. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. Mol. Ecol. 14:901–916.

Herrel, A., V. Schaerlaeken, J. J. Meyers, K. A. Metzger, and C. F. Ross. 2007. The evolution of cranial design and performance in squamates: consequences of skull-bone reduction on feeding behavior. Integr. Comp. Biol. 47:107–117.

Hipkiss, T., and B. Hörnfeldt. 2004. High interannual variation in the hatching sex ratio of Tengmalm's Owl broods during a vole cycle. Popul. Ecol. 46:263–268.

Hirons, G. J. M., A. R. Hardy, and P. I. Stanley. 1984. Body weight, gonad development and moult in the Tawny Owl (*Strix aluco*). J. Zool. 202:145–164.

Hogan, F., C. Burridge, R. Cooke, and J. Norman. 2007. Isolation and characterization of microsatellite loci to DNA fingerprint the Powerful Owl (*Ninox strenua*). Mol. Ecol. Notes 7:1305–1307.

Hogg, D. A. 1980. A re-investigation of the centres of ossification in the avian skeleton at and after hatching. J. Anat. 130:725–743.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6:65–70.

Hsu, B. Y., B. Doligez, L. Gustafsson, and S. Ruuskanen. 2019. Transient growth-enhancing effects of elevated maternal thyroid hormones at no apparent oxidative cost during early postnatal period. J. Avian Biol. 50: e01919.

Hsu, Y. C., S. H. Li, Y. S. Lin, M. T. Philippart, and L. L. Severinghaus. 2006a. High frequency of extra-pair copulation with low level of extra-pair fertilization in the Lanyu scops owl *Otus elegans botelensis*. J. Avian Biol. 37:36–40.

Hsu, Y. C., S. H. Li, Y. S. Lin, and L. L. Severinghaus. 2006b. Microsatellite loci from Lanyu Scops Owl (*Otus elegans botelensis*) and their cross-species application in four species of strigidae. Conserv. Genet. 7:161–165.

Hsu, Y. C., L. L. Severinghaus, Y. S. Lin, and S. H. Li. 2003. Isolation and characterization of microsatellite DNA markers from the Lanyu Scops Owl (*Otus elegans botelensis*). Mol. Ecol. Notes 3:595–597.

Huber, S. K., L. F. De Leon, A. P. Hendry, E. Bermingham, and J. Podos. 2007. Reproductive isolation of sympatric morphs in a population of Darwin's Finches. Proc. R. Soc. B Biol. Sci. 274:1709–1714.

Hunt, J., R. Brooks, and M. D. Jennions. 2005. Female mate choice as a condition-dependent life-history trait. Am. Nat. 166:79–92.

Indykiewicz, P., P. Podlaszczuk, A. Surmacki, K. Kudelska, J. Kosicki, M. Kamiński, and P. Minias. 2017. Scale-of-choice effect in the assortative mating by multiple ornamental and non-ornamental characters in the black-headed gull. Behav. Ecol. Sociobiol. 71:183.

Inoue, T., M. Matsumoto, T. Yoshida, and I. Washitani. 2019. Spatial patterns of the Ryukyu Scops Owl's Otus elegans breeding success and forest landscape factors on Amami-Ōshima Island. Japanese J. Ornithol. 68:19–28.

Jakobsson, M., and N. A. Rosenberg. 2007. CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806.

Jiang, Y., D. I. Bolnick, and M. Kirkpatrick. 2013. Assortative mating in animals. Am. Nat. 181:E125–E138.

Jombart, T. 2008. adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405.

Jombart, T., and C. Collins. 2015. A tutorial for discriminant analysis of principal components (DAPC) using adegenet 2.0.0. Imp. Coll. London MRC Cent. Outbreak Anal. Model.

Jombart, T., S. Devillard, and F. Balloux. 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet. 11:94.

Jombart, T., S. Devillard, A.-B. Dufour, and D. Pontier. 2008. Revealing cryptic spatial patterns in genetic variability by a new multivariate method. Heredity. 101:92–103.

Jones, A. G., and N. L. Ratterman. 2009. Mate choice and sexual selection: what have we learned since Darwin? Proc. Natl. Acad. Sci. 106:10001–10008.

Jordan, W. C., and M. W. Bruford. 1998. New perspectives on mate choice and the MHC. Heredity. 81:239–245.

Jouventin, P., B. Lequette, and F. S. Dobson. 1999. Age-related mate choice in the Wandering Albatross. Anim. Behav. 57:1099–1106.

Juola, F. A., and D. C. Dearborn. 2012. Sequence-based evidence for major histocompatibility complex-disassortative mating in a colonial seabird. Proc. R. Soc. B Biol. Sci. 279:153–162.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol. Ecol. 16:1099–1106.

Kamiya, T., K. O'Dwyer, H. Westerdahl, A. Senior, and S. Nakagawa. 2014. A quantitative review of MHC-based mating preference: the role of diversity and

dissimilarity. Mol. Ecol. 23:5151–5163.
Karaman, E., E. Kaya, D. Narinc, and M. Z. Firat. 2014. Bayesian hierarchical modeling of growth via Gompertz model: an application in poultry. Pp. 105–107 *in* E. Lanzarone and F. Ieva, eds. The Contribution of Young Researchers to Bayesian Statistics.
Kery, M., and M. Schaub. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, London, U.K.
Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. Nature 350:33–38.
Kleiber, C., and A. Zeileis. 2008. Applied econometrics with R. Springer, New York.
Klingenberg, C. P. 2013. Cranial integration and modularity: insights into evolution and development from morphometric data. Hystrix 24:43–58.
Klute, D. S., L. W. Ayers, M. T. Green, W. H. Howe, S. L. Jones, J. A. Shaffer, S. R. Sheffield, and T. S. Zimmerman. 2003. Status assessment and conservation plan for the Western Burrowing Owl in the United States. US Department of Interior, Fish and Wildlife Service, Biol Tech Publ FWS/BTP-R6001-2003, Washington, DC.
Kohyama, T. I., K. Omote, C. Nishida, T. Takenaka, K. Saito, S. Fujimoto, and R. Masuda. 2015. Spatial and temporal variation at major histocompatibility complex class IIB genes in the endangered Blakiston's Fish Owl. Zool. Lett. 1:13.
Kokko, H., R. Brooks, M. D. Jennions, and J. Morley. 2003. The evolution of mate choice and mating biases. Proc. R. Soc. London B Biol. Sci. 270:653–664.
Kokko, H., M. D. Jennions, and A. Houde. 2007. Evolution of frequency-dependent mate choice: keeping up with fashion trends. Proc. R. Soc. B Biol. Sci. 274:1317–1324.
König, C., and F. Weick. 2008. Owls of the World. Yale University Press, London.
Korpimäki, E. 1990. Body mass of breeding Tengmalm's Owls *Aegolius funereus*: seasonal, between-year, site and age-related variation. Ornis Scand. 21:169–178.
Korpimaki, E., and M. Lagerstrom. 1988. Survival and natal dispersal of fledglings of Tengmalm' s Owl in relation to fluctuating food conditions and hatching date. J. Anim. Ecol. 57:433–441.
Korpimaki, E., and K. Norrdahl. 1991. Numerical and functional responses of Kestrels, Short-Eared Owls, and Long-Eared Owls to vole densities. Ecology 72:814–826.
Korpimeki, E., and K. Norrdahl. 1989. Predation of Tengmalm' s Owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. Oikos 54:154–164.
Kristan, D. M., R. J. Gutiérrez, and A. B. Franklin. 1996. Adaptive significance of growth patterns in juvenile Spotted Owls. Can. J. Zool. 74:1882–1886.
Krüger, O. 2005. The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. Evol. Ecol. 19:467–486.
Kruuk, L. E. B., T. H. Clutton-Brock, S. D. Albon, J. M. Pemberton, and F. E.

Guinness. 1999. Population density affects sex ratio variation in Red Deer. Nature 399:459–461.

Kulemeyer, C., K. Asbahr, P. Gunz, S. Frahnert, and F. Bairlein. 2009. Functional morphology and integration of corvid skulls – a 3D geometric morphometric approach. 6:2.

Kumar, S., G. Stecher, and K. Tamura. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Mol. Biol. Evol. 33:1870–1874.

Kuroda, N. 1923. Descriptions of new forms of birds from the Borodino Islands. Bull. Br. Ornithol. Club 43:120–123.

Lack, D. 1947. The significance of clutch-size. Ibis. 89:302–352.

Lahaye, W. S., R. J. Gutiérrez, and J. R. Dunk. 2001. Natal dispersal of the spotted owl in southern California: dispersal profile of an insular population. Condor 103:691–700.

Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. OIKOS 83:353–358.

Landry, C., D. Garant, P. Duchesne, and L. Bernatchez. 2001. "Good genes as heterozygosity": the major histocompatibility complex and mate choice in Atlantic Salmon (*Salmo salar*). Proc. R. Soc. B Biol. Sci. 268:1279–1285.

Langin, K. M., T. S. Sillett, W. C. Funk, S. A. Morrison, M. A. Desrosiers, and C. K. Ghalambor. 2015. Islands within an island: repeated adaptive divergence in a single population. Evolution. 69:653–665.

Le Galliard, J.-F., M. Massot, M. M. Landys, S. Meylan, and J. Clobert. 2006. Ontogenic sources of variation in sexual size dimorphism in a viviparous lizard. J. Evol. Biol. 19:690–704.

Lebigre, C., R. V. Alatalo, and H. Siitari. 2010. Female-biased dispersal alone can reduce the occurrence of inbreeding in black grouse (*Tetrao tetrix*). Mol. Ecol. 19:1929–1939.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62:67–118.

Leclaire, S., M. Strandh, J. Mardon, H. Westerdahl, and F. Bonadonna. 2017. Odour-based discrimination of similarity at the major histocompatibility complex in birds. Proc. R. Soc. B Biol. Sci. 284:20162466.

Leclaire, S., W. F. D. Van Dongen, S. Voccia, T. Merkling, C. Ducamp, S. A. Hatch, P. Blanchard, É. Danchin, and R. H. Wagner. 2014. Preen secretions encode information on MHC similarity in certain sex-dyads in a monogamous seabird. Sci. Rep. 4:6920.

Lee, Y.-F., and L. L. Severinghaus. 2004. Sexual and seasonal differences in the diet of Lanyu Scops Owls based on fecal analysis. J. Wildl. Manage. 68:299–306.

Legendre, P., and L. Legendre. 1988. Numerical Ecology, Volume 24 (Developments in Environmental Modelling). Elsevier, Amsterdam.

Lehmann, L., L. F. Keller, and H. Kokko. 2007. Mate choice evolution, dominance effects, and the maintenance of genetic variation. J. Theor. Biol. 244:282–295.

Loiselle, B. A., V. L. Sork, J. Nason, and C. Graham. 1995. Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). Am. J. Bot. 82:1420–1425.

Loonstra, A. H. J., M. A. Verhoeven, and T. Piersma. 2018. Sex-specific growth in chicks of the sexually dimorphic Black-tailed Godwit. Ibis. 160:89–100.

Ludwig, S. C., and P. H. Becker. 2008. Supply and demand: causes and consequences of assortative mating in Common Terns *Sterna hirundo*. Behav. Ecol. Sociobiol. 62:1601–1611.

Luo, S. 2017. Assortative mating and couple similarity: patterns, mechanisms, and consequences. Soc. Personal. Psychol. Compass 11: e12337 .

Lykou, A., and I. Ntzoufras. 2011. WinBUGS: a tutorial. Wiley Interdiscip. Rev. Comput. Stat. 3:385–396.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, Massachusetts.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209–220.

Margalida, A., J. Jiménez, J. M. Martínez, J. A. Sesé, D. García-Ferré, A. Llamas, M. Razin, M. Colomer, and B. Arroyo. 2020. An assessment of population size and demographic drivers of the Bearded Vulture using integrated population models. Ecol. Monogr. 90:e01414.

Marti, C. D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. Auk 107:246–254.

Martin, G. R. 2014. The subtlety of simple eyes: the tuning of visual fields to perceptual challenges in birds. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 369:20130040.

Martin, G. R. 2007. Visual fields and their functions in birds. J. Ornithol. 148:S547–S562.

Martin, G. R., and T. Piersma. 2009. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. Proc. R. Soc. Biol. Sci. Ser. B 276:437–445.

Martin, K., M. A. Tucker, and T. L. Rogers. 2017. Does size matter? Examining the drivers of mammalian vocalizations. Evolution. 71:249–260.

Massemin, S., E. Korpimäki, and J. Wiehn. 2000. Reversed sexual size dimorphism in motors: evaluation of the hypotheses in kestrels breeding in a temporally changing environment. Oecologia 124:26–32.

Matsui, H., G. R. Hunt, K. Oberhofer, N. Ogihara, K. J. McGowan, K. Mithraratne, T. Yamasaki, R. D. Gray, and E. Izawa. 2016. Adaptive bill morphology for enhanced tool manipulation in New Caledonian Crows. Sci. Rep. 6:22776.

Matthews, T., and A. du Plessis. 2016. Using X-ray computed tomography analysis tools to compare the skeletal element morphology of fossil and modern frog

(Anura) species. Palaeontol. Electron. 19:1T.
Mays Jr, H. L., and G. E. Hill. 2004. Choosing mates: good genes versus genes that are a good fit. TRENDS Ecol. Evol. 19:554–559.
Mccaffery, R., and P. M. Lukacs. 2016. A generalized integrated population model to estimate Greater Sage-grouse population dynamics. Ecosphere 7: e01585.
McCleery, R. H., R. A. Pettifor, P. Armbruster, K. Meyer, B. C. Sheldon, and C. M. Perrins. 2004. Components of variance underlying fitness in a natural population of the Great Tit *Parus major*. Am. Nat. 164:E62–E72.
McDonald, P. G., P. D. Olsen, and A. Cockburn. 2005. Sex allocation and nestling survival in a dimorphic raptor: does size matter? Behav. Ecol. 16:922–930.
McGillivray, W. B. 1985. Size, sexual size dimorphism, and their measurement in Great Horned Owls in Alberta. Can. J. Zool. 63:2364–2372.
Milinski, M. 2006. The major histocompatibility complex, sexual selection and mate choice. Annu. Rev. Ecol. Evol. Syst. 37:159–186.
Miller, C. W., and A. J. Moore. 2007. A potential resolution to the lek paradox through indirect genetic effects. Proc. R. Soc. B Biol. Sci. 274:1279–1286.
Minami-daito Village. 1990. Minami-daito Sonshi (The history of Minami-daito village) (In Japanese). The village office of Minami-daito.
Ministry of the Environment of Japan. 2019. Japanese Red Lists 2019.
Ministry of the Environment of Japan. 2014. Threatened wildlife of Japan -Red Data Book Vol. 2 Aves. Gyosei, Tokyo.
Mitteroecker, P., and P. Gunz. 2009. Advances in Geometric Morphometrics. 36:235–247.
Mitteroecker, P., P. Gunz, S. Windhager, and K. Schaefer. 2013. A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. Hystrix 24:59–66.
Mock, D. W., and G. A. Parker. 1998. The evolution of sibling rivalry. Oxford University Press, New York.
Møller, A., and M. Jennions. 2001. How important are direct fitness benefits of sexual selection? Naturwissenschaften 88:401–415.
Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philos. Trans. R. Soc. B Biol. Sci. 365:2289–2301.
Morton, M. L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the Mountain White-crowned Sparrow. Condor 94:117–133.
Mueller, H. C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bull. 98:387–406.
Mueller, H. C., and D. D. Berger. 1967. Observations on migrating Saw-Whet Owls. Bird-Banding 38:120–125.

Müller, W., T. G. G. Groothuis, and C. Dijkstra. 2007. Consequences of sex-specific growth on sibling competition in Black-headed Gulls: a sexually-size dimorphic species with scramble competition. J. Ornithol. 148:495–502.

Najmi-Hanis, Z., C. L. Puan, M. Zakaria, and B. Azhar. 2016. Home range and activity patterns of Sunda Scops Owl in peninsular Malaysia. Raffles Bull. Zool. 64:28–32.

Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol. Rev. 85:935–956.

Narinç, D., N. Öksüz Narinç, and A. Aygün. 2017. Growth curve analyses in poultry science. Worlds. Poult. Sci. J. 73:395–408.

Nathan, R., E. Klein, J. J. Robledo-Arnuncio, and E. Revilla. 2012. Dispersal kernels: review. Pp. 187–210 *in* Dispersal ecology and evolution. Oxford University Press, Oxford.

Newton, I., M. J. Mcgrady, and M. K. Oli. 2016. A review of survival estimates for raptors and owls. Ibis. 158:227–248.

Nielsen, H. S., L. Mortensen, U. Nygaard, O. Schnor, O. B. Christiansen, and A. M. N. Andersen. 2008. Brothers and reduction of the birth weight of later-born siblings. Am. J. Epidemiol. 167:480–484.

Nijman, V., and K. A. I. Nekaris. 2017. The Harry Potter effect: the rise in trade of owls as pets in Java and Bali, Indonesia. Glob. Ecol. Conserv. 11:84–94.

Nilsson, J.-A., and M. Svensson. 1996. Sibling competition affects nestling growth strategies in Marsh Tits. J. Anim. Ecol. 65:825–836.

Nogueira, B. R. F., M. P. Reis, A. C. Carvalho, E. A. C. Mendoza, B. L. Oliveira, V. A. Silva, and A. G. Bertechini. 2019. Performance, growth curves and carcass yield of four strains of broiler chicken. Brazilian J. Poult. Sci. 21:4.

Nosil, P., S. P. Egan, and D. J. Funk. 2008. Heterogeneous genomic differentiation between walking-stick ecotypes: “isolation by adaptation” and multiple roles for divergent selection. Evolution. 62:316–336.

Nosil, P., D. J. Funk, and D. Ortiz-Barrientos. 2009. Divergent selection and heterogeneous genomic divergence. Mol. Ecol. 18:375–402.

Odom, K. J., and D. J. Mennill. 2012. Inconsistent geographic variation in the calls and duets of Barred Owls (*Strix varia*) across an area of genetic introgression. Auk 129:387–398.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. Mcglinn, P. R. Minchin, R. B. O’hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs, and H. Wagner. 2017. vegan: community ecology package. https://CRAN.R-project.org/package=vegan.

Olsson, M., T. Madsen, J. Nordby, E. Wapstra, B. Ujvari, and H. Wittsell. 2003. Major histocompatibility complex and mate choice in sand lizards. Proc. R. Soc. B Biol. Sci. 270:S254–S256.

Ornithological Society of Japan. 2012. Check-list of Japanese Birds, 7th revised edn. The Ornithological Society of Japan, Sanda.

Orsini, L., J. Vanoverbeke, I. Swillen, J. Mergeay, and L. De Meester. 2013. Drivers of population genetic differentiation in the wild: isolation by dispersal limitation, isolation by adaptation and isolation by colonization. Mol. Ecol. 22:5983–5999.

Ottinger, M. A., S. Pitts, and M. A. Abdelnabi. 2001. Steroid hormones during embryonic development in Japanese Quail: plasma, gonadal, and adrenal levels. Poult. Sci. 80:795–799.

Owens, I. P. F., and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proc. R. Soc. B Biol. Sci. 265:397–407.

Ozaki, K., M. Isono, T. Kawahara, S. Iida, T. Kudo, and K. Fukuyama. 2006. A mechanistic approach to evaluation of umbrella species as conservation surrogates. Conserv. Biol. 20:1507–1515.

Pande, S., and N. Dahanukar. 2012. Reversed sexual dimorphism and differential prey delivery in Barn Owls (*Tyto alba*). J. Raptor Res. 46:184–189.

Paterson, S., K. Wilson, and J. M. Pemberton. 1998. Major histocompatibility complex variation associated with juvenile survival and parasite resistance in a large unmanaged ungulate population. Proc. Natl. Acad. Sci. U. S. A. 95:3714–3719.

Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. Philos. Trans. R. Soc. B Biol. Sci. 364:1483–1489.

Peng, R. D. 2008. simpleboot: simple bootstrap routines. R package version 1.1-3.

Penn, D. J., and W. Potts. 1999. The evolution of mating preferences and major histocompatibility complex genes. Am. Nat. 153:145–164.

Penteriani, V. 2002. Variation in the function of Eagle Owl vocal behaviour: territorial defence and intra-pair communication? Ethol. Ecol. Evol. 14:275–281.

Pérez-Camacho, L., G. García-Salgado, S. Rebollo, S. Martínez-Hesterkamp, and J. M. Fernández-Pereira. 2015. Higher reproductive success of small males and greater recruitment of large females may explain strong reversed sexual dimorphism (RSD) in the Northern Goshawk. Oecologia 177:379–387.

Pérez-Camacho, L., S. Martínez-Hesterkamp, S. Rebollo, G. García-Salgado, and I. Morales-Castilla. 2018. Structural complexity of hunting habitat and territoriality increase the reversed sexual size dimorphism in diurnal raptors. J. Avian Biol. 49: e01745 .

Perrins, C. . M. . 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34:601–647.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, New York.

Pincheira-Donoso, D., and J. Hunt. 2017. Fecundity selection theory: concepts and evidence. Biol. Rev. 92:341–356.

Plard, F., R. Fay, M. Kéry, A. Cohas, and M. Schaub. 2019. Integrated population models: powerful methods to embed individual processes in population dynamics models. Ecology 100: e02715 .

Podos, J. 2010. Acoustic discrimination of sympatric morphs in Darwin’s Finches: a

behavioural mechanism for assortative mating? Philos. Trans. R. Soc. B Biol. Sci. 365:1031–1039.

Podos, J., and P. S. Warren. 2007. The evolution of geographic variation in birdsong. Adv. Study Behav. 37:403–458.

Pomiankowski, A. 1987. The costs of choice in sexual selection. J. Theor. Biol. 128:195–218.

Potts, W. K., C. J. Manning, and E. K. Wakeland. 1994. The role of infectious disease, inbreeding and mating preferences in maintaining MHC genetic diversity: an experimental test. Philos. Trans. R. Soc. London B Biol. Sci. 346:369–378.

Potts, W. K., and E. K. Wakeland. 1990. Evolution of diversity at the major histocompatibility complex. Trends Ecol. Evol. 5:181–187.

Pratt, H. D. 2005. The Hawaiian Honeycreepers. Oxford University Press, Oxford.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Pritchard, J. K., X. Wen, and D. Falush. 2010. Documentation for structure software: version 2 . 3.

Pusey, A., and M. Wolf. 1996. Inbreeding avoidance in animals. Trends Ecol. Evol. 11:201–206.

Puurtinen, M., T. Ketola, and J. S. Kotiaho. 2009. The good-genes and compatible-genes benefits of mate choice. Am. Nat. 174:741–752.

QGIS Development Team. 2018. QGIS Geographic Information System. - Open Source Geospatial Foundation Project.

Queller, D. C., and K. F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution. 43:258–275.

R Core Team. 2015. R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

R Core Team. 2019. R: a language and environment for statistical computing.

R Core Team. 2017. R: a language and environment for statistical computing.

Raymond, M., and F. Rousset. 1995. An exact test for population differentiation. Evolution. 49:1280–1283.

Rebolo-Ifrán, N., J. L. Tella, and M. Carrete. 2017. Urban conservation hotspots: predation release allows the grassland-specialist burrowing owl to perform better in the city. Sci. Rep. 7:3527.

Redpath, S. M., B. M. Appleby, and S. J. Petty. 2000. Do male hoots betray parasite loads in Tawny Owls? J. Avian Biol. 31:457–462.

Reimchen, T. E., and P. Nosil. 2004. Variable predation regimes predict the evolution of sexual dimorphism in a population of Threespine Stickleback. Evolution. 58:1274–1281.

Richardson, D. S., J. Komdeur, T. Burke, and T. von Schantz. 2005. MHC-based patterns of social and extra-pair mate choice in the Seychelles Warbler. Proc. R. Soc. B Biol. Sci. 272:759–767.

Rickard, I. J. 2008. Offspring are lighter at birth and smaller in adulthood when born after a brother versus a sister in humans. Evol. Hum. Behav. 29:196–200.

Roberts, S. C., L. M. Gosling, V. Carter, and M. Petrie. 2008. MHC-correlated odour preferences in humans and the use of oral contraceptives. Proc. R. Soc. B Biol. Sci. 275: 2715–2722.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu. Rev. Ecol. Evol. Syst. 38:231–253.

Royle, N. J., I. R. Hartley, I. P. F. Owens, and G. A. Parker. 1999. Sibling competition and the evolution of growth rates in birds. Proc. R. Soc. London. Ser. B Biol. Sci. 266:923–932.

Ruiz-Gonzalez, A., S. A. Cushman, M. J. Madeira, E. Randi, and B. J. Gómez-Moliner. 2015. Isolation by distance, resistance and/or clusters? Lessons learned from a forest-dwelling carnivore inhabiting a heterogeneous landscape. Mol. Ecol. 24:5110–5129.

Ryan, M. J., and E. A. Brenowitz. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. Am. Nat. 126:87–100.

Saitoh, T., N. Sugita, S. Someya, Y. Iwami, S. Kobayashi, H. Kamigaichi, A. Higuchi, S. Asai, Y. Yamamoto, and I. Nishiumi. 2015. DNA barcoding reveals 24 distinct lineages as cryptic bird species candidates in and around the Japanese Archipelago. Mol. Ecol. Resour. 15:177–186.

Santos, A. M. C., R. Field, and R. E. Ricklefs. 2016a. New directions in island biogeography. Glob. Ecol. Biogeogr. 25:751–768.

Santos, P. S. C., A. Courtiol, A. J. Heidel, O. P. Höner, I. Heckmann, M. Nagy, F. Mayer, M. Platzer, C. C. Voigt, and S. Sommer. 2016b. MHC-dependent mate choice is linked to a trace-amine-associated receptor gene in a mammal. Sci. Rep. 6:38490.

Santos, P. S. C., F. U. Michler, and S. Sommer. 2017. Can MHC-assortative partner choice promote offspring diversity? A new combination of MHC-dependent behaviours among sexes in a highly successful invasive mammal. Mol. Ecol. 26:2392–2404.

Sardell, R. J., B. Kempenaers, and E. H. Duval. 2014. Female mating preferences and offspring survival: testing hypotheses on the genetic basis of mate choice in a wild lekking bird. Mol. Ecol. 23:933–946.

Sasvári, L., and I. Nishiumi. 2005. Environmental conditions affect offspring sex-ratio variation and adult survival in Tawny Owls. Condor 107:321–326.

Sawada, A., H. Ando, and M. Takagi. 2020. Evaluating the existence and benefit of major histocompatibility complex-based mate choice in an isolated owl population. J. Evol. Biol. 33:762–772.

Sawada, A., T. Iwasaki, C. Inoue-Kawai, K. Nakaoka, T. Nakanishi, N. Aso, S. Nagai, H. Ono and M. Takagi. 2021a. Missing piece of top predator-based conservation: demographic analysis of an owl population on a remote subtropical island. Pop.

Ecol. In press.
Sawada, A., T. Iwasaki, T. Matsuo, K. Akatani, and M. Takagi. 2021b. Reversed sexual size dimorphism in the Ryukyu Scops Owl *Otus elegans* on Minami-daito Island. Ornithol. Sci. 20:15–26.
Sawada, A., T. Iwasaki, and M. Takagi. 2018a. Fine-scale spatial genetic structure in the Minami-daito Island population of the Ryukyu Scops Owl *Otus elegans*. J. Zool. 307:159–166.
Sawada, A., T. Yamasaki, Y. Iwami, and M. Takagi. 2018b. Distinctive features of the skull of the Ryukyu Scops Owl from Minami-daito Island, revealed by computed tomography scanning. Ornithol. Sci. 17:45–54.
Scandolara, C., M. Caprioli, R. Lardelli, G. Sgarbi, D. Rubolini, R. Ambrosini, and N. Saino. 2014. Brothers and sisters are stabbing each other in the back: long-term effects of sex of siblings on Barn Swallow offspring. Anim. Behav. 87:187–193.
Schaub, M., and F. Abadi. 2010. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. 152: S227–S237.
Schaub, M., A. Aebischer, O. Gimenez, S. Berger, and R. Arlettaz. 2010. Massive immigration balances high anthropogenic mortality in a stable Eagle Owl population: lessons for conservation. Biol. Conserv. 143:1911–1918. Elsevier Ltd.
Schlager, S. 2015. Morpho: calculations and visualisations related to geometric morphometrics. R package version 2.3.1.
Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9:671–675.
Schoenjahn, J., C. R. Pavey, and G. H. Walter. 2020. Why female birds of prey are larger than males. Biol. J. Linn. Soc. 129:532–542.
Sebastian, A. 2018. AmpliSAT Manual Amplicon Sequencing Analysis Tools. http://evobiolab.biol.amu.edu.pl/amplisat
Sebastian, A., M. Herdegen, M. Migalska, and J. Radwan. 2016. Amplisas: a web server for multilocus genotyping using next-generation amplicon sequencing data. Mol. Ecol. Resour. 16:498–510.
Sekercioglu, C. H. 2010. The mystery of nocturnal birds in tropical secondary forests. Anim. Conserv. 13:12–13.
Sepil, I., R. Radersma, A. W. Santure, I. D. E. Cauwer, J. Slate, and B. C. Sheldon. 2015. No evidence for MHC class I-based disassortative mating in a wild population of Great Tits. J. Evol. Biol. 28:642–654.
Sergio, F., J. Blas, M. G. Forero, J. A. Donázar, and F. Hiraldo. 2007. Size-related advantages for reproduction in a slightly dimorphic raptor: opposite trends between the sexes. Ethology 113:1141–1150.
Sergio, F., T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh, and F. Hiraldo. 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. Annu. Rev. Ecol. Evol. Syst. 39:1–19.

Sergio, F., L. Marchesi, P. Pedrini, M. Ferrer, and V. Penteriani. 2004. Electrocution alters the distribution and density of a top predator, the Eagle Owl *Bubo bubo*. J. Appl. Ecol. 41:836–845.

Sergio, F., I. Newton, and L. Marchesi. 2005. Top predators and biodiversity. Nature 436:192–192.

Serrano, D., J. L. Tella, M. G. Forero, and J. A. Donázar. 2001. Factors affecting breeding dispersal in the facultatively colonial Lesser Kestrel: individual experience vs. conspecific cues. J. Anim. Ecol. 70:568–578.

Servedio, M. R., and R. Lande. 2006. Population genetic models of male and mutual mate choice. Evolution. 60:674–685.

Severinghaus, L. L. 2007. Cavity dynamics and breeding success of the Lanyu Scops Owl (*Otus elegans*). J. Ornithol. 148:407–416.

Severinghaus, L. L. 2000. Territoriality and the significance of calling in the Lanyu Scops Owl *Otus elegans botelensis*. Ibis. 142:297–304.

Severinghaus, L. L., and P. Rothery. 2001. The survival rate of Lanyu Scops Owls *Otus elegans botelensis*. Ibis. 143:540–546.

Shaw, A. K., and H. Kokko. 2014. Mate finding, Allee effects and selection for sex-biased dispersal. J. Anim. Ecol. 83:1256–1267.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64:419–461.

Shine, R., and M. Fitzgerald. 1995. Variation in mating systems and sexual size dimorphism between populations of the Australian python Morelia spilota (Serpentes: Pythonidae). Oecologia 103:490–498.

Slade, J. W. G., M. J. Watson, T. R. Kelly, G. B. Gloor, M. A. Bernards, and E. A. Macdougall-Shackleton. 2016. Chemical composition of preen wax reflects major histocompatibility complex similarity in songbirds. Proc. R. Soc. B Biol. Sci. 283:20161966.

Slate, J., L. E. B. Kruuk, T. C. Marshall, J. M. Pemberton, and T. H. Clutton-Brock. 2000. Inbreeding depression influences lifetime breeding success in a wild population of Red Deer (*Cervus elaphus*). Proc. R. Soc. B Biol. Sci. 267:1657–1662.

Slice, D. E. 2007. Geometric morphometrics. Annu. Rev. Anthropol. 36:261–281.

Sofaer, H. R., P. L. Chapman, T. S. Sillett, and C. K. Ghalambor. 2013. Advantages of nonlinear mixed models for fitting avian growth curves. J. Avian Biol. 44:469–478.

Soltis, J., F. Mitsunaga, K. Shimizu, Y. Yanagihara, and M. Nozaki. 1997. Sexual selection in Japanese Macaques I: female mate choice or male sexual coercion? Anim. Behav. 54:725–736.

Stan Development Team. 2016. RStan: the R interface to Stan. R package version 2.14.1.

Stan Development Team. 2019. RStan: the R interface to Stan. R package version

2.19.2. 016.
Stan Development Team. 2018. Stan modeling language users guide and reference manual, version 2.18.0.
Starrfelt, J., and H. Kokko. 2010. Parent-offspring conflict and the evolution of dispersal distance. Am. Nat. 175:38–49.
Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford.
Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19:305–308.
Szulkin, M., and B. C. Sheldon. 2008. Dispersal as a means of inbreeding avoidance in a wild bird population. Proc. R. Soc. B Biol. Sci. 275:703–711.
Szulkin, M., K. V. Stopher, J. M. Pemberton, and J. M. Reid. 2013. Inbreeding avoidance, tolerance, or preference in animals? Trends Ecol. Evol. 28:205–211.
Taborsky, B., L. Guyer, and M. Taborsky. 2009. Size-assortative mating in the absence of mate choice. Anim. Behav. 77:439–448.
Takagi, M. 2013. A typological analysis of the hoot of the Ryukyu Scops Owl across island populations in the Ryukyu Archipelago and two oceanic islands. Wilson J. Ornithol. 125:358–369.
Takagi, M. 2011. Vicariance and dispersal in the differentiation of vocalization in the Ryukyu Scops Owl *Otus elegans*. Ibis. 153:779–788.
Takagi, M. 2020. Vocalizations of the Ryukyu Scops Owl *Otus elegans*: individually recognizable and stable. Bioacoustics 29:28–44.
Takagi, M., and K. Akatani. 2011. The diet of Ryukyu Scops Owl *Otus elegans* interpositus owlets on Minami-daito Island. Ornithol. Sci. 10:151–156.
Takagi, M., K. Akatani, and S. Matsui. 2005. Conservation biology of the isolated population of the Daito Scops Owl on Minami-daito island. 14th Rep. Pro- Nat. Found. 3–10.
Takagi, M., K. Akatani, S. Matsui, and A. Saito. 2007a. Status of the Daito Scops Owl on Minami-daito Island, Japan. J. Raptor Res. 41:52–56.
Takagi, M., K. Akatani, A. Saito, and S. Matsui. 2007b. Drastic decline of territorial male Daito Scops Owls on Minami-daito Island in 2006. Ornithol. Sci. 6:39–42.
Takagi, M., T. Saitoh, N. Yamaguchi, H. Okabe, I. Nishiumi, and M. Takeishi. 2015. A breeding record of the Ryukyu Scops Owl on Okinoshima, in northernmost Fukuoka, Japan. Ornithol. Sci. 14:53–59.
Tanabe, A. S., and H. Toju. 2013. Two new computational methods for universal DNA barcoding: a benchmark using barcode sequences of bacteria, archaea, animals, fungi, and land plants. PLoS One 8:e76910.
Temple, H. J., J. I. Hoffman, and W. Amos. 2006. Dispersal, philopatry and intergroup relatedness: fine-scale genetic structure in the White-breasted Thrasher, *Ramphocinclus brachyurus*. Mol. Ecol. 15:3449–3458.
Terborgh, J., L. Lopez, P. V. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros,

R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science. 294:1923–1926.

Terry, A. M. R., T. M. Peake, and P. K. McGregor. 2005. The role of vocal individuality in conservation. Front. Zool. 2:10.

Thomas, J. W. 1990. A conservation strategy for the Northern Spotted Owl. Interagency Scientific Committee.

Thoß, M., P. Ilmonen, K. Musolf, and D. J. Penn. 2011. Major histocompatibility complex heterozygosity enhances reproductive success. Mol. Ecol. 20:1546–1557.

Tornberg, R., M. Mönkkönen, and M. Pahkala. 1999. Changes in diet and morphology of Finnish Goshawks from 1960s to 1990s. Oecologia 121:369–376.

Tregenza, T., and N. Wedell. 2000. Genetic compatibility, mate choice and patterns of parentage: invited review. Mol. Ecol. 9:1013–1027.

Trochet, A., E. A. Courtois, V. M. Stevens, M. Baguette, A. Chaine, D. S. Schmeller, and J. Clobert. 2016. Evolution of sex-biased dispersal. Q. Rev. Biol. 91:297–320.

Vall-Llosera, M., and S. Su. 2018. Trends and characteristics of imports of live CITES-listed bird species into Japan. Ibis. 161:590–604.

Valverde, J., J. M. Gómez, C. García, T. F. Sharbel, M. N. Jiménez, and F. Perfectti. 2016. Inter-annual maintenance of the fine-scale genetic structure in a biennial plant. Sci. Rep. 6:37712.

Van Dijk, R. E., R. Covas, C. Doutrelant, C. N. Spottiswoode, and B. J. Hatchwell. 2015. Fine-scale genetic structure reflects sex-specific dispersal strategies in a population of Sociable Weavers (*Philetairus socius*). Mol. Ecol. 24:4296–4311.

Van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol. Ecol. Notes 4:535–538.

Vehtari, A., J. Gabry, Y. Yao, and A. Gelman. 2018. loo: efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.0.0.

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27:1413–1432.

Verboven, N., P. Monaghan, D. M. Evans, H. Schwabl, N. Evans, C. Whitelaw, and R. G. Nager. 2003. Maternal condition, yolk androgens and offspring performance: a supplemental feeding experiment in the Lesser Black-backed Gull (*Larus fuscus*). Proc. R. Soc. B Biol. Sci. 270:2223–2232.

Wagner, R. H. 1999. Sexual size dimorphism and assortative mating in Razorbills (*Alca torda*). Auk 116:542–544.

Walsh, B., and M. Lynch. 2018. Evolution and selection of quantitative traits. Oxford University Press, New York.

Wang, D., W. Forstmeier, M. Valcu, N. J. Dingemanse, M. Bulla, C. Both, R. A. Duckworth, L. M. Kiere, P. Karell, T. Albrecht, and B. Kempenaers. 2019. Scrutinizing assortative mating in birds. PLoS Biol. 17: e3000156.

Warburton, T. 2009. The Philippine owl conservation programme: why is it needed?

Ardea 97:429–438.
Warkentin, I. G., R. H. M. Espie, D. J. Lieske, and P. C. James. 2016. Variation in selection pressure acting on body size by age and sex in a reverse sexual size dimorphic raptor. Ibis. 158:656–669.
Warkentin, I. G., P. C. James, and L. W. Oliphant. 1992. Assortative mating in urban-breeding Merlins. Condor 94:418–426.
Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. J. Mach. Learn. Res. 11:3571–3594.
Wegner, K. M., M. Kalbe, J. Kurtz, T. B. H. Reusch, and M. Milinski. 2003. Parasite selection for immunogenetic optimality. Science. 301:1343-1343.
Weigelt, P., W. Jetz, and H. Kreft. 2013. Bioclimatic and physical characterization of the world's islands. Proc. Natl. Acad. Sci. U. S. A. 110:15307–15312.
Weir, B. S., and C. C. Cockerham. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution. 38:1358–1370.
Wetton, J. H., R. E. Carter, D. T. Parkin, and D. Walters. 1987. Demographic study of a wild House Sparrow population by DNA fingerprinting. Nature 327:147–149.
Whittaker, R. J., and J. M. Fernandez-Palacios. 2007. Island biogeography: ecology, evolution, and conservation. second edi. Oxford University Press, Oxford.
Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). Ardea 55:1–92.
Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.
Wojczulanis-Jakubas, K., S. M. Drobniak, D. Jakubas, M. Kulpińska-Chamera, and O. Chastel. 2018. Assortative mating patterns of multiple phenotypic traits in a long-lived seabird. Ibis. 160:464–469.
Wong, B. B. M., and U. Candolin. 2005. How is female mate choice affected by male competition? Biol. Rev. Camb. Philos. Soc. 80:559–571.
Woxvold, I. A., G. J. Adcock, and R. A. Mulder. 2006. Fine-scale genetic structure and dispersal in cooperatively breeding apostlebirds. Mol. Ecol. 15:3139–3146.
Wright, S. 1943. Isolation by Distance. Genetics 28:114–138.
Yamazaki, K., and G. K. Beauchamp. 2007. Genetic basis for MHC-dependent mate choice. Adv. Genet. 59:129–145.
Yamazaki, K., M. Yamaguchi, L. Baranoski, J. Bard, E. A. Boyse, and L. Thomas. 1979. Recognition among mice. Evidence from the use of a Y-maze differentially scented by congenic mice of different major histocompatibility types. J. Exp. Med. 150:755–760.
Ydenberg, R. C., and S. Forbes. 1991. The survival-reproduction selection equilibrium and reversed size dimorphism in raptors. OIKOS 60:115–120.
Zárybnická, M., J. Riegert, L. Brejšková, J. Šindelář, M. Kouba, J. Hanel, A.

Popelková, P. Menclová, V. Tomášek, and K. Šťastný. 2015. Factors affecting growth of Tengmalm's Owl (*Aegolius funereus*) nestlings: prey abundance, sex and hatching order. PLoS One 10:e0138177.

Zelano, B., and S. V Edwards. 2002. An MHC component to kin recognition and mate choice in birds: predictions, progress, and prospects. Am. Nat. 160:S225–S237.

Zhao, Q., T. W. Arnold, J. H. Devries, D. W. Howerter, R. G. Clark, and M. D. Weegman. 2019. Land-use change increases climatic vulnerability of migratory birds: insights from integrated population modelling. J. Anim. Ecol. 88:1625–1637.

Ziegler, A., H. Kentenich, and B. Uchanska-Ziegler. 2005. Female choice and the MHC. Trends Immunol. 26:496–502.

Zou, G. Y. 2007. Toward using confidence intervals to compare correlations. Psychol. Methods 12:399–413.

Zusi, R. L. 1993. Patterns of diversity in the avian skull. P. 1993 *in* J. Hanken and B. K. Hall, eds. The skull, volume 2: patterns of structural and systematic diversity. University of Chicago Press, London.

List of publication

Sawada, A., H. Ando, and M. Takagi. 2020. Evaluating the existence and benefit of major histocompatibility complex-based mate choice in an isolated owl population. J. Evol. Biol. 33:762–772.

Sawada, A., T. Iwasaki, T. Matsuo, K. Akatani, and M. Takagi. 2021. Reversed sexual size dimorphism in the Ryukyu Scops Owl *Otus elegans* on Minami-daito Island. Ornithol. Sci. 20: 15-26.

Sawada, A., T. Iwasaki, and M. Takagi. 2018. Fine-scale spatial genetic structure in the Minami-daito Island population of the Ryukyu Scops Owl *Otus elegans*. J. Zool. 307:159–166.

Sawada, A., T. Yamasaki, Y. Iwami, and M. Takagi. 2018. Distinctive features of the skull of the Ryukyu Scops Owl from Minami-daito Island, revealed by computed tomography scanning. Ornithol. Sci. 17:45–54.

Sawada, A., K. Akatani, and M. Takagi. 2021. Growth curve of Ryukyu Scops Owl nestlings, an owl species with asynchronous hatching and reversed sexual dimorphism. Ardea. In press.

Sawada, A., T. Iwasaki, C. Inoue-Kawai, K. Nakaoka, T. Nakanishi, N. Aso, S. Nagai, H. Ono and M. Takagi. 2021. Missing piece of top predator-based conservation: demographic analysis of an owl population on a remote subtropical island. Pop. Ecol. In press.