HOKKAIDO UNIVERSITY

Title	Paternal roles on the facultative multiple breeding of Japanese tit
Author(s)	乃美, 大佑
Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	甲第12671号
Issue Date	2017-03-23
DOI	https://doi.org/10.14943/doctoral.k12671
Doc URL	https://hdl.handle.net/2115/65572
Type	doctoral thesis
File Information	Daisuke_Nomi.pdf

Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

Paternal roles on the facultative multiple breeding of Japanese tit



Daisuke Nomi

A Ph.D. Dissertation Submitted to Division of Biosphere Science,
Graduate school of Environmental Science, Hokkaido University

March 2017

Table of contents

Summary……...3

Chapter 1……6

General introduction

Chapter 2……..17

Facultative multiple breeding as a female conditional strategy in Japanese tits: partner's quality affects the initiation of second clutches

Chapter 3……..35

Male contribution in feeding facilitate female multiple breeding in Japanese tits

Chapter 4……..55

General discussion

Acknowledgements……..65

References……67

Summary

Life history theory predicts that individuals should allocate reproductive effort in current and future reproduction to maximize fitness. One way to increase annual reproductive success for short-lived species is to produce more than one clutch or litter per season, known as multiple breeding. Although multiple breeding always appears to be advantageous, the co-existence of single and multiple breeders is observed within species or even within populations and within individuals (i.e. facultative multiple breeding). Elucidating the mechanisms producing facultative multiple breeding would significantly contribute to the better understanding of a complex life history in wild populations. In this thesis, I present the studies of reproductive ecology of Japanese tits (*Parus minor*) in Tomakomai, Hokkaido during 2009-2010 and 2012-2015 seasons in order to elucidate the mechanism of producing facultative multiple breeding. The Japanese tit is a closely related to and recently separated from the Great tit (*Parus major*), which has been a subject for a great number of ecological, behavioral, and evolutionary studies and considered as one of the most studied wild birds in the world. This species is suitable for this study for its abundance and willingness to use nestboxes to breed, and numerous past studies for reference and comparison.

In chapter 2, I considered facultative multiple breeding as female alternative reproductive tactics (ARTs) and examined the factors affecting the reproductive decisions. ARTs have been investigated mostly in males and their own condition. In many bird species, however, both parents raise their offspring and, therefore, partner's condition may also

affect ARTs. I analyzed 6 years of data on multiple breeding in Japanese tits in northern Japan, where nearly half of breeding pairs reproduce multiple times within breeding seasons. I found that the hatching date was negatively correlated to the probability of multiple breeding, and male, but not female age was negatively correlated to the timing of breeding. I did not find a negative relationship between multiple breeding and female survival. Rather, multiple breeders exhibited higher return rates than single breeders. These results suggested that single brooded females may be using the best of a bad job strategy, which is predicted from the theories of ARTs. I also demonstrated the partner's role on the initiation of later breeding.

In chapter 3, I examined further roles of male parents on annual reproductive success. Parental food provisioning is thought to be the most energetically costly behavior than any other parental care in breeding. Therefore, not only female but also male contribution in feeding to chicks should be important for their reproductive success. However, few studies have investigated the effects of male contribution on multiple breeding. One of the hypotheses why males continue parental care after copulation is that male assistance may decrease female workload and consequently females can achieve higher frequency of reproduction (enhanced fecundity hypothesis). Multi-brooded species or population is suitable for testing this hypothesis as consecutive breeding attempts occur in a short period. I assessed male contribution in feeding and found that female parents with high contributed males in the first breeding were more likely to initiate second breeding, probably due to the reduced work load in feeding.

Chapter 4 briefly integrates the findings of the entire studies to draw general conclusions. Firstly, I suggest the possible mechanism of the evolution of male parental care. Secondly, I also suggest a possible structure of the male and female alternative reproductive tactics and their interactions in facultative multiple breeding. Finally, I will present future prospects for the studied population of Japanese tits.

Chapter 1

General introduction



Life history theory is a framework to explain the complex diversity of reproductive strategies and life cycles in organisms (Stearns 1992). The theory has been used to understand how natural selection can shape different life cycles and reproductive strategies at both inter and intra specific levels (Stearns 1992). Such understanding also enables us to make predictions on how species and individuals will respond to fluctuating environmental conditions such as rapid climate change (Winkler et al. 2002, Visser et al. 2006) or decreased food availability (Pascual and Peris 1992).

Individuals can adjust the number of offspring they produce in one season by changing either the number of offspring per breeding attempt or the number of breeding attempts per season (Stearns 1992). A wide range of species, especially mammals and birds, raises only one brood per year because the reproduction and caring offspring are costly and the period of suitable environmental conditions for breeding is too short to permit another breeding attempt. In contrast, some small bodied mammals and birds raise more than one litter or brood per year, known as multiple breeding. In such species, however, the number of breeding attempts in a season often varies annually in multi-brooded species (i.e. facultative multiple breeding, Verhulst et al. 1997, Verhulst 1998). The term "facultative multiple breeding" can be also applied to individual level because whether the individuals reproduce once or more in a season is plastic as female conditions are known to affect the propensity of multiple breeding (Geupel and DeSante 1990, Jacobs et al. 2013). Although many studies showed that multiple breeding can considerably increase annual or life time reproductive success compared with single breeding (Weggler 2006, Carro et al. 2014, Hoffmann et al. 2015), why single and multiple breeders coexists within populations is still

unclear (Hoffmann et al. 2015). Therefore, elucidating the mechanisms producing single and multiple breeders would significantly contribute to the better understanding of a complex life history in wild populations.

In this thesis, I will add two novel perspectives on facultative multiple breeding. First, I propose facultative multiple breeding as a conditional strategy with alternative reproductive tactics (ARTs). ARTs are discontinuous distribution of reproductive traits between individuals of the same sex, which evolve when disruptive natural or sexual selection favors these discrete traits (Taborsky et al. 2008). In conditional strategy, tactics are plastic and can be switched within individuals in response to ecological conditions or individual quality (condition or age) (Taborsky et al. 2008, Candolin and Vlieger 2013). In fact, probability of multiple breeding often varies annually within population and depends on individual conditions (e.g. Hoffman et al. 2015). The advantage to use the framework of conditional strategy is to consider fitness of alternative tactics explicitly. In previous studies, the costs of multiple breeding relative to single breeding have been investigated (e.g. Verhulst 1998), which implicitly assumes overall equal fitness between ARTs. Most of such studies have found little evidence on the costs of multiple breeders, suggesting that multiple breeding is always a better strategy. Conditional strategy framework clearly explains the case why different phenotypes coexist even when the fitness differs (Taborsky and Brockmann 2010).

Second, I will demonstrate the importance of males on facultative multiple breeding. Since females are the ones who produce offspring, it is generally (but not explicitly)

assumed that only females can decide whether they reproduce once or more. However, males can significantly affect reproductive success especially for species with parental care. Surprisingly, few studies have examined the effects of males on the probability of multiple breeding.

Facultative multiple breeding has been studied mostly in bird species. Many studies have reported causal factors affecting multiple breeding at the population level (annual variation), individual level, or both (Table 1-1). The most influential factor for multiple breeding is the timing of first breeding (Table 1-1); early breeders are more likely to produce second clutches because the breeding season is limited. However, although the timing of breeding itself is often determined by the quality of both male and female parents (Harvey 1979, Auld et al. 2013), previous studies have rarely considered the roles of male parents (Table 1-1). This is probably because the female is assumed to control the initiation of the second clutch. In species with bi-parental care, such as most bird species, the reproductive output should be a result of both male and female investment. Because males substantially affect reproductive success directly (e.g., feeding of nestlings, Møller 2000, Stodola et al. 2010) or indirectly (e.g., incubation feeding of female, Nilsson and Smith 1988, Cantarero et al. 2014), the effects of male quality on multiple breeding and on the timing of breeding should be examined.

Multiple breeding significantly affects annual fledging number (Hoffman et al. 2015) and, therefore, the probability of multiple breeding affects population growth (Podolsky et al. 2007) and species sensitivity to environmental change (Jiguet et al. 2007). Therefore, to

study the causes and consequences of multiple breeding will be important not only from life a history perspective but also conservation perspective (Husby et al. 2009). Moreover, male roles on population dynamics have been stressed relatively recently (Rankin and Kokko 2007). In this sense, male's roles on the probability of multiple breeding would deserve attentions.

In this thesis, I investigated the factors differentiating the ARTs in females focusing on the roles of male parents on multiple breeding, using Japanese tits (*Parus minor*) as a model species. The Japanese tit is a closely related to and recently separated from the Great tit (*Parus major*) (Päckert et al. 2005), which has been a subject for a great number of ecological, behavioral, and evolutionary studies and considered as one of the most studied wild birds in the world. Particularly, their individual based reproductive ecology and behavior have been intensively studied with detailed research ongoing for almost a hundred years (Clutton-Brock and Sheldon 2010). This is attributed to several characteristics of the species. Probably the most important characteristic of the great tit and Japanese tit is their willingness to breed in artificial nestboxes. This allows researchers to study their reproductive ecology in details with sufficient sample size. Another important characteristic is its popularity. As mentioned above, the great knowledge of its ecology and methods for scientific studies can provide opportunities for studies of greater scales and for profound understandings, which are comparable to past and future studies. In terms of multiple breeding, some populations breed only once but others do twice or more (Verboven et al. 2001). Also, variations within populations and individuals among years have been reported (Verboven et al. 2001). Such great variations within and among populations enable deep

understanding of why different reproductive tactics have been produced and maintained. They rarely change partners (i.e., divorce) within breeding seasons and the same partners tend to breed in the next year when both the male and female survive (Saitou and Asakawa 2009).

The study population of Japanese tits is situated in a deciduous secondary forest in Tomakomai Experimental forest (TOEF) on the island of Hokkaido, Japan (42° 40'N, 141° 36' E, 50-100m a.s.l., Fig. 1-3). The forest is owned by Hokkaido University since 1904 and has been established as a field of research and education for over 30 years. The field sites of the present study are located in the southern and eastern parts of TOEF (Fig. 1-1). The area is surrounded by a natural broad-leaved deciduous forest with some conifer plantations. In the fall of 2008, 150 wooden nestboxes were set in the two study plots (300 in total, Yuta and Koizumi 2012). All nestboxes are regularly set 50 m apart from each other in a grid (Fig. 1-2). This thesis is based on the Japanese tits' reproductive ecology investigated in 2009-2010, and 2012-2015 seasons.

Thesis overview

In chapter 2, I investigated causes and consequences of multiple breeding in Japanese tits. I considered facultative multiple breeding is a result of female alternative reproductive tactics (ARTs) and examined the factors affecting the reproductive decisions. ARTs have been investigated mostly in males and their own condition. In many bird species, however, both parents raise their offspring and, therefore, partner's condition may also affect ARTs. I hypothesized that both male and female quality affects the probability of multiple breeding.

In chapter 3, I investigated further roles of male parents on annual reproductive success. Parental provisioning is thought to be the most energetically costly behavior than any other parental care in breeding. Therefore, not only female but also male contribution in feeding to fledglings is important for their reproductive success. However, few studies have conducted on the effect of male contribution on multiple breeding. I hypothesized that female parents with high contributed males in the first breeding may be more likely to initiate second breeding due to reduced work load in feeding.

In chapter 4, I briefly integrated the findings of the entire studies to draw general conclusions about facultative multiple breeding. Finally, I will present future prospects for the studied population of Japanese tits.

Table 1-1 List of studies that examined the factors affecting multiple breeding in birds. Only significant factors detected are shown.

Species	Factors affecting multiple breeding	Experimental or observational	Reference
American Dipper	timing (–) (residents earlier than migrants)	observational	Morrissey 2004
Barn Owl	timing (–), number of offsring raised in males (+)	observational	Béziers and Roulin 2015
Black Noddy	timing (–)	observational	Gauger 2000
Black Redstart	timing (–), female age (+)	observational	Weggler 2006
Black Throated Blue Warbler	annual variation in food availability (+), timing of predation (–), male age (+)	observational	Holmes et al. 1992
Black Throated Blue Warbler	food availability (+)	experimental	Nagy and Holmes 2005a
Black Throated Blue Warbler	food availability (+), nestling body weight (+), number of fledglings (+)	observational	Nagy and Holmes 2005b
Blue Tit	number of fledglings (–)	experimental	Parejo and Danchin 2006
Cassin's Auklet	timing (–), female age (+), upwelling (+), interaction between female age and upwelling (–)	observational	Johns et al. 2017
Coal Tit	timing (–)	observational	Sanz et al. 1993
Common Tern	food availability (+)	observational	Moore and Morris 2005
Crested Caracara	timing (–)	observational	Morrison 1998
Eastern Bluebird	number of fledglings (–)	experimental	Siefferman and Hill 2008
Eurasian Hoopoe	timing (–), female age (+), number of fledglings (+)	observational	Hoffmann et al. 2015
European Coot	timing (–)	experimental	Brinkhof et al. 2002
Great Tit	timing (–)	experimental	Barba et al. 1995
Great Tit	weight loss of female (–)	observational	De Leat and Dhondt 1987
Great Tit	diffrence between hatching date and peak of catapillar abundance (–)	observational	Husby et al. 2009
Great Tit	female age (+), habitat (+), density (–)	observational	Kluijver 1951
Great Tit	number of fledglings (–)	experimental	Smith et al. 1987
Great Tit	timing (–), number of fledglings (–)	experimental	Timbergen 1987
Great Tit	food availability (+)	observational	Van Balen 1973
Great Tit	timing (–), number of fledglings (–), nestling body weight (–)	experimental	Verboven and Vehulst 1996
Great Tit	timing (–)	observational	Verboven and Visser 1998
Great Tit	diffrence between hatching date and peak of catapillar abundance (–)	observational	Verboven et al. 2001
Great Tit	timing (–)	experimental	Verhulst et al. 1995
Hooded Warbler	timing (–)	observational	Ogden and Stutchbury 1996
Little Penguin	timing (–)	observational	Agnew et al. 2014
Little Swift	timing (–), female age (+)	observational	Hotta 1996
Louisiana Waterthrush	timing (–)	observational	Mulvihill et al. 2009
Mountain Bluebird	interaction with female quality and timing (+)	experimental	O'Brien and Dawson 2012
Prothonotary Warbler	timing (–), female age (+)	observational	Bulluck et al. 2013
Red-necked Grebe	timing (–)	observational	Kloskowski 2001
Southern House Wren	timing (–), rainfall (+)	observational	Carro et al. 2014
Tree Sparrow	timing (–)	observational	Garcia-Navas and Sanz 2012
Western Bluebird	temperature (+), timing (–), female weight (+)	observational	Jacobs et al. 2013
Wrentit	timing (–), female age (+)	observational	Geupel and DeSante 1990

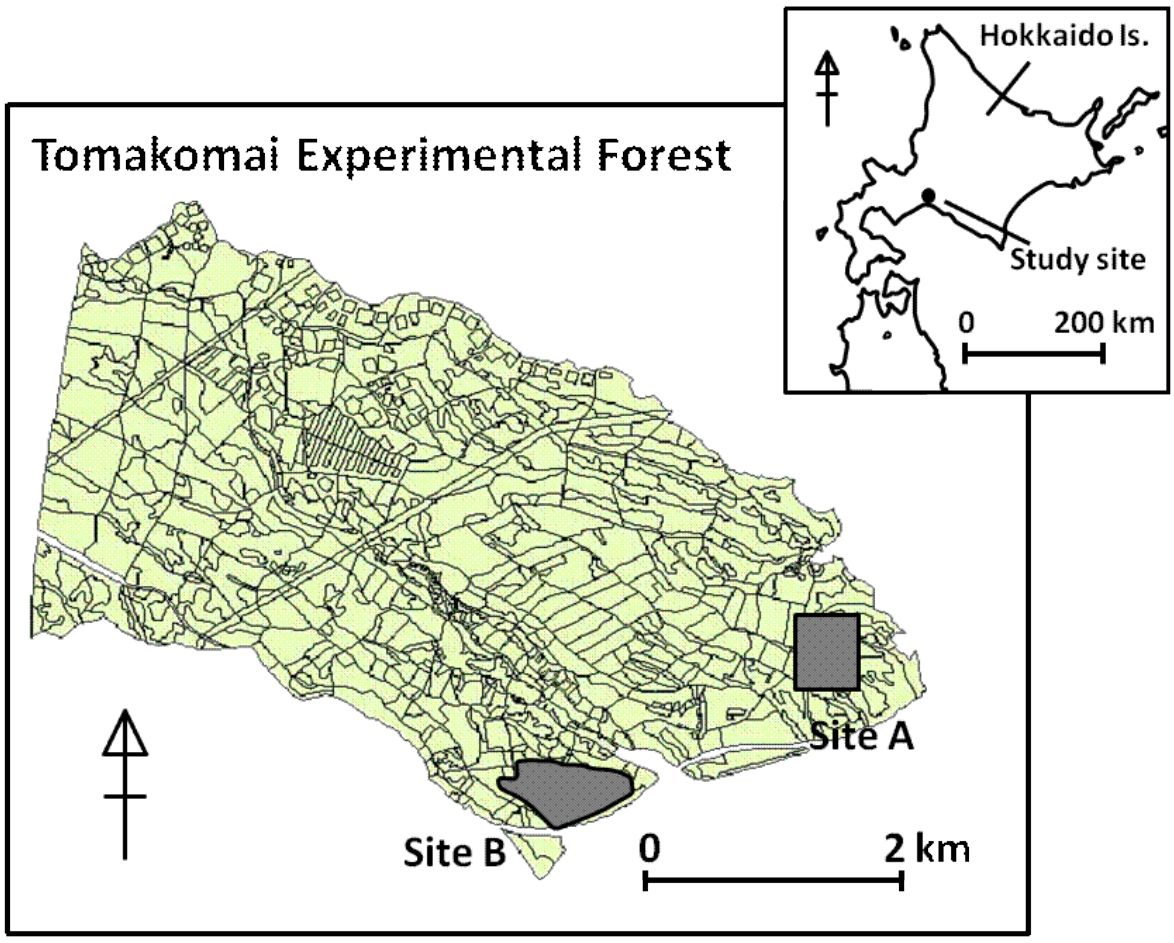

Fig. 1-1 Map showing the location of the study area.

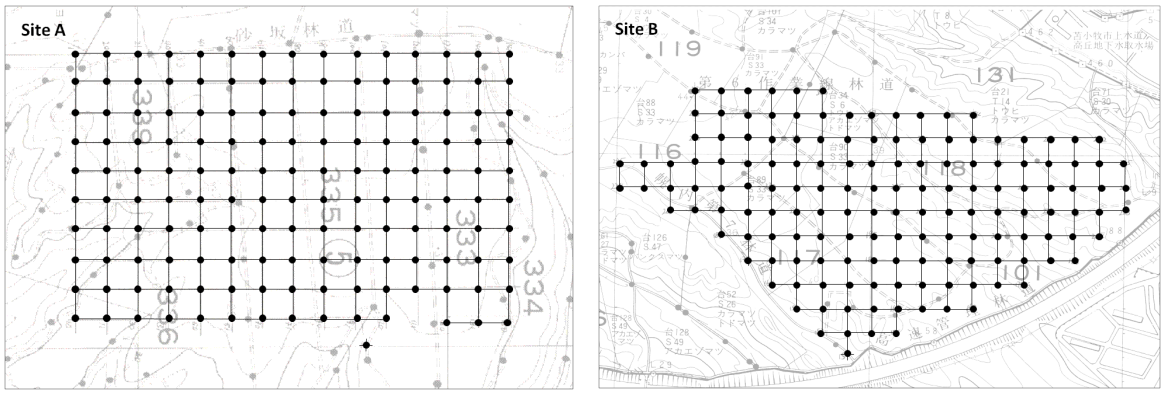

Fig. 1-2 Map showing distribution of nestboxes (represented by black circles) in two sites. All nestboxes are 50m away from each other, and Site A and Site B are 2.5 km apart.

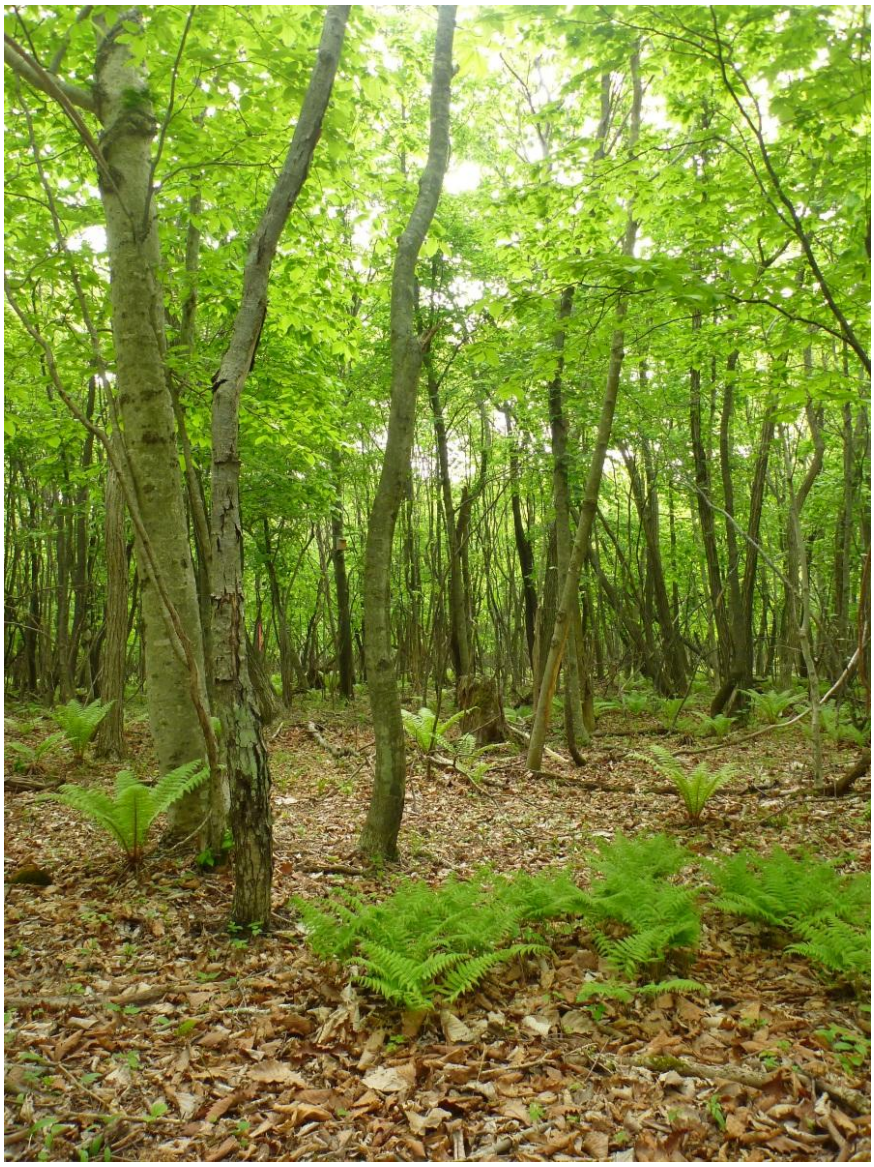

Fig. 1-3 Tomakomai experimental forest (TOEF).

Chapter 2

Facultative multiple breeding as a female conditional strategy in Japanese tits: partner's quality affects the initiation of second clutches





Introduction

Alternative reproductive tactics (ARTs) are phenotypic variations in a population characterized by a discontinuous distribution of reproductive traits between individuals of the same sex (Brockmann et al.2008). Such divergent phenotypes include behavioral, morphological, physiological and life history differences, and may evolve when disruptive natural or sexual selection favors these discrete traits (Taborsky and Brockmann et al. 2010). ARTs generally occur under the competition for mates, such as fighters and sneakers (Gross 1996). In some cases, tactics are fixed in each individual throughout their life when determined genetically (Lank et al. 1995, Neff and Lister 2007). Under this alternative strategy, different tactics are maintained through frequency-dependent selection and the average fitness of each tactic (Gross 1996). In other cases, tactics are plastic and can be switched within individuals in response to ecological conditions or individual quality (condition or age) (Taborsky et al. 2008, Candolin and Vlieger 2013). This conditional strategy is more common in natural populations compared to alternative strategy. Fitness generally differs between tactics under conditional strategy: individuals that have higher competitive ability (condition or age) usually employ better tactic whereas those with bad conditions do the best of the bad job choosing and alternative tactic (Gross 1996).

ARTs have been studied mostly in males because intra-sexual, competition is much

stronger, resulting in more diverse reproductive tactics among males (Brockmann et al. 2008). However, strong reproductive competition could also exist among females (Clutton-Brock 2009), especially when the opportunity of gaining high quality males is limited. Moreover, when reproductive costs and benefits vary with the amount of resources available among individuals, conditional strategy of females can be expected (Johnson and Brockmann 2012). Therefore, it is worth examining female ARTs more explicitly to understand the coexisting of different reproductive behaviors (Brockmann et al. 2008).

Facultative multiple breeding (FMB) is a good candidate for studying female ARTs. FMB represents the co-existence of single and multiple breeders within populations or the situation where the number of breeding attempts in a season is not fixed within populations (Verhulst et al. 1997, Verhulst 1998). Since females primarily decide initiation of the second litter or clutch, the coexistence of different tactics can be considered as female ARTs. FMB is a common reproductive strategy in various taxa especially among short-lived species (Verhulst et al. 1997, Bennett and Owens 2002, Carro et al. 2014). The term FMB can be also applied to individual level because whether the individuals reproduce once or more in a season is plastic as female conditions are known to affect the propensity of multiple breeding (Geupel and DeSante 1990, Jacobs et al. 2013). This also suggests that FMB is a conditional strategy rather than alternative strategy. FMB has been widely studied among bird species (e.g., Hoffmann et al. 2015), but

surprisingly, few studies have examined FMB within a framework of conditional strategy.

Another important point is that mate quality could also influence ARTs (Johnson and Brockmann 2012). In FMB, most previous studies have investigated the effects of female's quality, as well as environmental factors, on the likelihood of multiple breeding (Husby et al. 2009, Bulluck et al. 2013, Carro et al. 2014). This is likely because the females are assumed to control the initiation of the second breeding. Since most passerine birds are socially monogamous with biparental care, male quality can also be an ecological condition for female parents to initiate second breeding. The most influential factor reported so far is the timing of breeding; early breeders are more likely to produce second clutches because the length of the breeding season is limited (Hoffmann et al. 2015, and references therein). Importantly, the timing of breeding itself is often determined by the quality of both male and female parents (Harvey 1979, Jankowiak and Wysocki 2015, Whelan et al. 2016). Thus, studies on FMB including mate quality may provide important implications for understanding ARTs.

Alternative phenotypes may reflect different decisions of resource allocation associated with tradeoffs between reproduction and survival (Taborsky and Brockmann 2010). Therefore, understanding fitness costs and benefits of alternative tactics is important to elucidate the mechanisms producing ARTs. Multiple breeding has apparent benefits in terms of the number of offspring they can produce within a single season: it can be just multiplied. The major cost is

generally considered reduced survival rate. However, there are still equivocal results among studies on the survival cost of multiple breeding (e.g, costly; Bryant 1979, Brinkhof et al. 2002, not costly; Geupel and DeSante 1990, Nagy and Holmes 2005, Cornell and Williams 2016). If single breeding has fitness benefits, the trade-off between reproduction and survival may exist. If there is no tradeoff, single brooded females are considered to have lower fitness but employ the tactic that gains higher fitness under those conditions.

This study aimed to elucidate the determinants of female ARTs in a facultative multi-brooded population. I analyzed 6 years of breeding data of facultative multi-brooded Japanese Tits (*Parus minor*). First, I assessed the importance of candidate factors affecting multiple breeding included the timing of breeding as well as male and female individual quality. Second, I examined whether multiple breeding affects annual reproductive success and parental survival.

Methods

Study Species, Study Area, and Field Procedures

The Japanese tit is a small (ca. 14 g) cavity nesting passerine that readily uses nest boxes for breeding. The Japanese tit is short-lived (male: 2.6 years, female: 2.0 years, Saitou and Asakawa 2009), socially monogamous species with bi-parental care. The study population has been monitored for 6 years during the breeding seasons in 2009–2010 and 2012–2015 seasons in

Tomakomai Experimental Forest (TOEF, 42.40°N, 141.36°E, 5–90 m.a.s.l.), Hokkaido, Japan (Yuta and Koizumi 2012, Nomi et al. 2015, in press). The study area consists of natural broad-leaved deciduous forests with some conifer plantations. The dominant canopy trees are oaks and maples. I established two study sites within the forest (ca. 30 ha each) in autumn, 2008. At each site, approximately 150 nest boxes were hung up on trees with a distance of 50 m between the boxes. The environment of the two sites is similar (Yuta and Koizumi 2016), and the reason for establishing two sits was merely due to the lack of enough space to set 300 nest boxes in a single site. Thus, I considered the two as a spatial replicate. The nest boxes were cleaned every year after the breeding season.

I checked all nest boxes weekly from late April to late August, and recorded basic breeding parameters such as laying date and clutch size. Hatching date and fledging date were confirmed by daily visits. Parents were caught, measured and ringed with both colored rings and numerical ones for individual identification when nestlings were 5–7 days old. Numeric ones were attached to the offspring when 13 days old. Body mass was measured using an electronic balance (accuracy: 0.1 g). Tarsus length was measured using a digital caliper to the nearest 0.01 mm. I used the presence or absence of a color ring when captured and size-corrected body mass (body mass divided by tarsus length) for the indicators of individual quality. I could not determine the age for most of the parents because of low recapture rate of parents and

recruitment of fledglings. However, the presence of color rings can be a proxy of age because only breeding parents were attached with color rings the year before. Thus, color-ringed parents are over 2 years old, whereas individuals without rings consisted mostly of first year adults with some older ones who immigrated from other areas. As a result, this indicator is slightly conservative when looking at the effect of age because putative young adults (i.e. without color ring) included some older individuals. Size-corrected body mass has often been used as a body condition index (reviewed in Labocha and Hayes 2012).

Statistical Analysis

Factors affecting the probability of multiple breeding.

For the analysis of factors affecting the probability of multiple breeding, I used a generalized linear mixed model (GLMM) with a logit-link and binomial error distribution. The dependent variable was whether each female initiated a second clutch or not (1 and 0, respectively). The independent variables in the full model included hatching date of the first successful clutch, number of fledglings, male and female size-corrected body mass and presence or absence of a color ring (1 and 0, respectively) in males and females. I included male and female ID, site and year as random effects. In this analysis, I used the 2010 and 2013-2015 seasons (4 years of data) because I did not survey in 2008 and 2011 seasons and parents had no or few color rings in the 2009 and 2012 seasons. I used only successful nests (i.e. nests in which at least one nestling

fledged) in the first clutches in the analysis. Replacement clutches (i.e. nests after the first clutch with no offspring fledged) were excluded from the analysis, because pairs who failed their first clutch might have already paid substantial costs in the first clutch, which can affect the probability of multiple breeding.

To examine the impact of male and female quality on hatching date, I additionally ran LMM for hatching date as a dependent variable and the presence of color ring and size-corrected body mass for both male and female as independent variables in the full model. I included male and female ID, site and year as random effects.

Annual reproductive success and survival cost of multiple breeding.

I used t-test to examine the difference of annual reproductive success between single and multiple breeders. Annual reproductive success was defined as the number of total fledglings produced annually. I used 6 years of data for this analysis, but only used the data of individuals who had succeeded (i.e. at least one nestling fledged) in the first clutch.

For the analysis of parental survival, I used GLMM with a logit-link and binomial error distribution. The dependent variable was whether parents bred the next year or not (1and 0, respectively). Because I did not have data for the 2011 breeding season, we used the recapture data of parents from the 2009–2010, 2012–2013, 2013–2014, and 2014–2015 seasons. The independent variables included the number of breeding attempts (single breeder: 0, multiple

breeder: 1), and size-corrected body mass. Female ID, site and year were included as random effects. We used only the data of individuals who had succeeded (i.e. at least one nestling fledged) in the first clutch in single breeders and individuals who had succeeded in both the first and second clutches for multiple breeders. Because return rates in consecutive years includes true survival, site fidelity or breeding propensity, return rates must be carefully interpreted (Siefferman and Hill 2008). During the 6 years, there was only one individual that disappeared one year and bred again in the following year, indicating that detection rate is high within the study sites. However, I cannot distinguish breeding dispersal and death if any individuals have emigrated from the study sites permanently. I treated return rates as apparent survival.

All analyses were performed using the statistical software R 2.15.3 (R Development Core Team). All GLMMs were implemented by package "lme4". Multicollinearity of independent variables was tested before analysis using the variance inflation factor (VIF) and was not detected (i.e. VIF < 2). The results of the GLMMs are presented with Wald chi-squared tests.

Results

General characteristics of multiple breeding

Of the 81 females with first clutches that successfully fledged at least one nestling, 39 females initiated a second clutch (48.1%). For individuals that breed multiple years, six females changed

the alternative tactics across years (single to multiple: 2, multiple to single: 4), whereas 7 females did not (single to single: 2, multiple to multiple: 5). For males, 6 individuals changed the tactics (single to multiple: 3, multiple to single: 3), whereas 6 did not (single to single: 2, multiple to multiple: 4). Although no statistical evaluation was performed due to small sample size, no apparent tendency for sexual bias or direction of tactic shift was observed. This individual flexibility confirmed the ARTs are not an alternative strategy.

Factors affecting the probability of multiple breeding

I analyzed the effects of hatching date, male and female quality, and number of fledglings on the probability of multiple breeding (2010 and 2013-2015 seasons combined). Only hatching date was significantly correlated to the probability of multiple breeding (Table 2-1). Pairs who started their first breeding earlier were more likely to initiate second breeding (Table 2-1, Fig. 2-1). Notably, probability of multiple breeding decreased from approximately 60% before the hatching date around June 15 to 10% after (Fig. 2-1), indicating the strong effect of time constraints on the number of breeding attempts in this population.

I also analyzed the effects of individual quality on the hatching date. However, the only significant variable was the presence of color ring of males (Table 2-1). Hatching date of females paired with color ringed males was earlier than non-color ringed males (Fig. 2-2).

Importantly, male and female presence of color rings was not correlated (Pearson's correlation coefficient, $n = 92$, $r = 0.125$, $P = 0.235$). Similarly, no significant correlation was observed for body weight, body condition, wing lengths or tarsus lengths between breeding pairs (Pearson's correlation coefficient, $n = 92$, $r = -0.073$-0.054, $P = 0.487$-0.934), indicating that little possibility of assortative mating.

Annual reproductive success and survival cost of multiple breeding

During the 6 years, annual reproductive success was approximately 1.7 times higher in multiple breeders than single breeders (mean number of total fledglings; single: 9.17, multiple: 15.46, t-test; $n = 134$, df = 102.345, $p < 0.001$).

Of the 73 females that had succeeded with their first clutch (4 years; 2009, 2012-2014 seasons combined), 18 individuals returned the next year to breed. I analyzed the impact of multiple breeding on apparent survival. Both number of breeding attempts and size-corrected mass were positively correlated with female survival (Table 2-1), indicating that multiple breeders had higher apparent survival than single breeders (Fig. 2-3).

Discussion

I investigated both causes and consequences of multiple breeding to elucidate what factors

differentiate female ARTs. The probability of multiple breeding was largely determined by the timing of breeding, corresponding to the previous studies (e.g,, Hoffmann et al. 2015). However, the timing was partly explained by male quality. In addition, I found no apparent negative influence of multiple breeding on parental survival. Rather, multiple breeders had higher apparent survival than single breeders, indicating the large difference in fitness between the tactics. Females who paired with older males could initiate breeding earlier and gain more fitness benefits through multiple breeding. Single brooded females may be "making the best of a bad job" strategy by avoiding the cost of reproduction in unfavorable environments.

The most important finding is that male, but not female, quality was an ecological condition for females to choose alternative tactics. Because the timing of breeding is ultimately determined by females (i.e. egg laying), it seems intriguing that male quality is more important than female quality for the timing of breeding. Even young or small females who mate with older males can gain higher reproductive success. Although the mechanism behind the male age determining the timing of breeding is still unclear, a possible explanation is age-mediated territory quality. Since the territory size of adult males is larger than that of juveniles (Dhondt 1971), females paired with older males may have access to better resources, thereby facilitating an early initiation of breeding. Another possibility is that male songs or male presence stimulates female reproductive activity (reviewed in Davies and Deviche 2014). Older males

generally produce better quality singing (Kipper and Kiefer 2010) so that they might be able to induce female activity earlier than younger males regardless of the territory quality.

Multiple breeding significantly improved the annual reproductive success without apparent costs on female survival. The results of previous studies examining the survival costs of multiple breeding remain equivocal. Same as the present study, most observational studies reported no relationship or even a positive relationship between multiple breeding and survival (e.g., Geupel and DeSante 1990, Nagy and Holmes 2005b, Cornell and Williams 2016). Even in experimental studies, few detected survival cost of multiple breeding (costly: Verhulst 1998, not costly: Boer-Hazewinkel 1987, Siefferman and Hill 2008). Verhulst (1998) showed that females of experimentally removed second clutches showed higher survival, but this only occurred in the years of poor food availability in winter, suggesting that survival cost of multiple breeding depends on environmental conditions of the non-breeding season. This may be a reason why most studies failed to detect survival cost of multiple breeding.

Alternative explanation is that survival cost of reproduction on multiple breeders might be mitigated by their partner. In bi-parental care species, reproductive costs of one parent may involve not only their own effort, but also the effort of its partner (Winkler 1987). I did not assess a reproductive effort of each parent in the present study, but there may be a partner's

effect on the parental survival (see chapter 3).

Many studies have investigated multiple breeding on birds, yet no one discussed about female FMB within a framework of ARTs. In this study, I present new idea for understanding the mechanism producing FMB. Although studies on FMB are limited in birds, multiple breeding has been reported in a variety of taxa, including many mammals (Bronson 1985), reptiles (Breedveld et al. 2017), amphibians (Morrison and Hero, 2003), fishes (Evans and Magurran, 2000), insects (Fritz, Stamp and Halverson 1982) and even plants (Paige and Whitham 1987). Therefore, I suggest that considering FMB as ARTs can be general idea applicable to many organisms. In addition to this, this study underscores partner's roles on decision-making in conditional strategies. Despite numerous studies have documented ARTs (reviewed in Taborsky and Brockmann 2010), surprisingly few study reported the roles of mate on ARTs. In FMB in socially monogamous birds, mate quality can also be applied to male conditional strategies because males can also have the opportunity to choose single or multiple breeding. Many studies reported that males increase or decrease their reproductive effort according to female quality (e.g., plumage attractiveness; Mahr et al. 2012, egg quality; Walters et al. 2014, nest size; Cantarero et al. 2016). Therefore, males may also decide single or multiple breeding based on female quality.

Table 2-1 Summary of the result of GLMMs. Significance of variables was assessed using Wald chi-squared tests.

Variable	β	SE	*df*	χ2	*P*
Probability of multiple breeding *n* = 81					
Intercept	8.299	9.587	1	0.750	0.387
Hatching date	– 0.179	0.055	1	10.634	0.001
Male presence of color ring	0.997	0.739	1	1.823	0.177
Male body condition	5.486	10.359	1	0.281	0.596
Female presence of color ring	–0.973	0.761	1	1.633	0.201
Female body condition	–1.836	8.319	1	0.049	0.825
Number of fledglings	0.100	0.123	1	0.669	0.413
Hatching date *n* = 92					
Intercept	35.230	19.249	1	3.349	0.067
Male presence of ring	– 3.315	1.282	1	6.687	0.010
Male size-corrected body mass	36.077	19.728	1	3.345	0.067
Female presence of ring	– 2.326	1.364	1	2.907	0.088
Female size-corrected body mass	10.088	16.488	1	0.374	0.540
Female apparent survival *n* = 73					
Intercept	–28.316	9.566	1	8.762	0.003
Number of breeding attempts	1.706	0.808	1	4.456	0.035
Size-corrected body mass	35.770	12.855	1	7.745	0.005

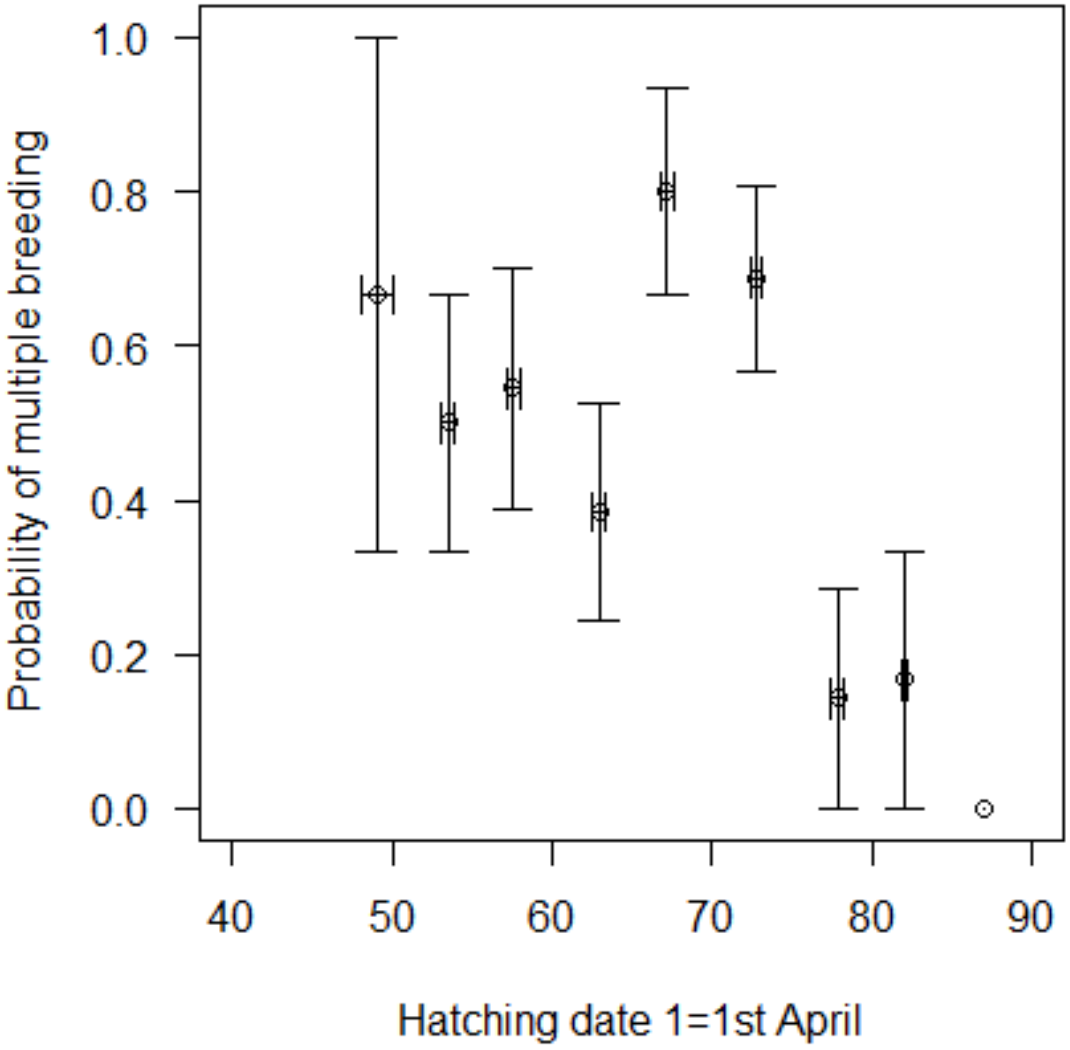

Fig. 2-1 Probability of multiple breeding in relation to hatching date. Probability of multiple breeding was averaged every 5 days. Arrows showed standard errors.

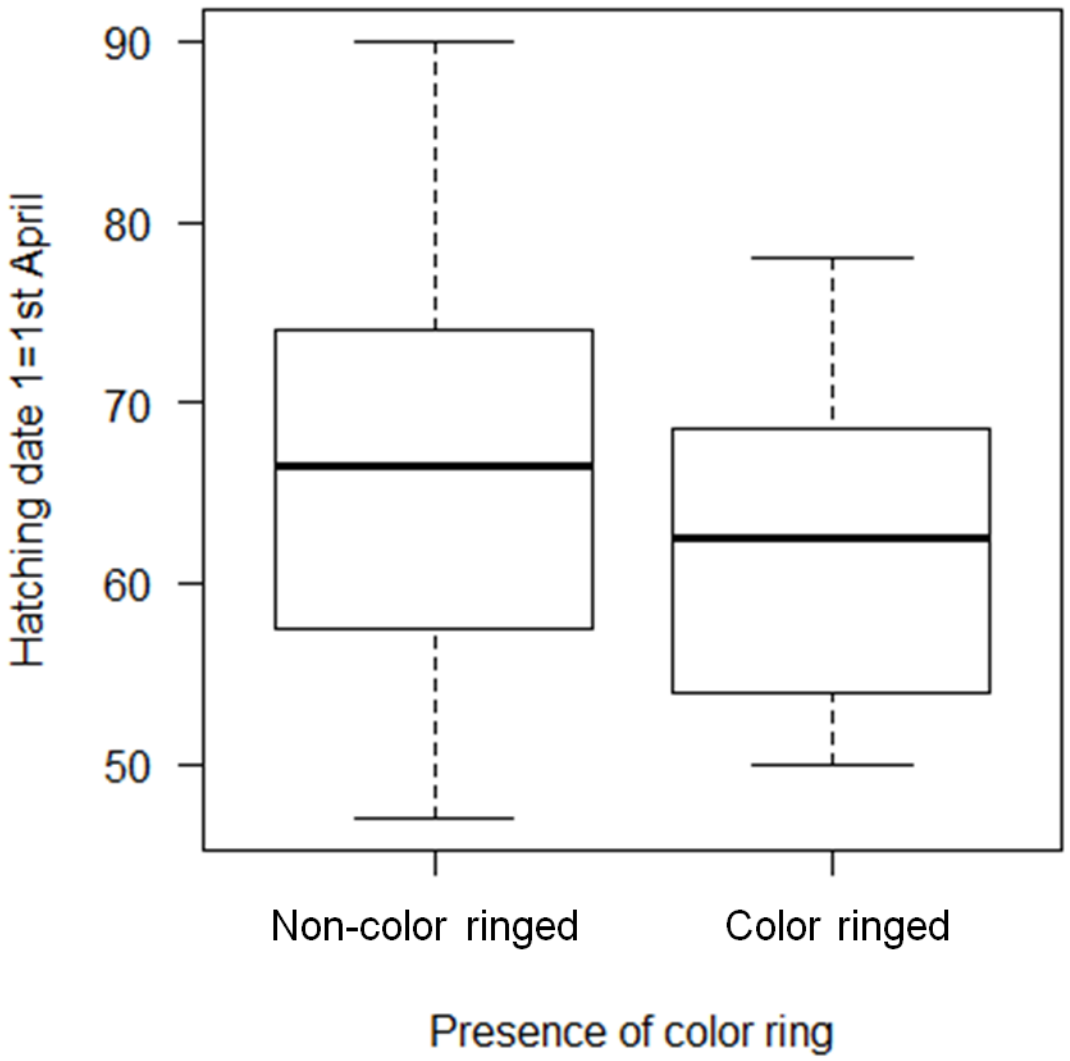

Fig. 2-2 Boxplot of hatching date between color-ringed and non-color ringed males.

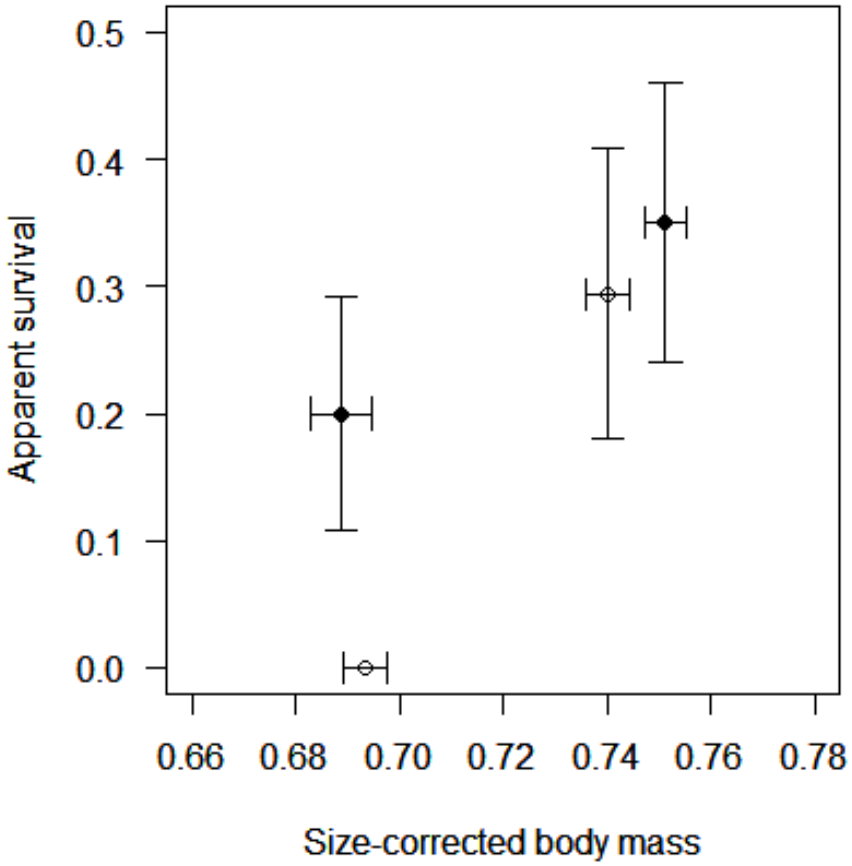

Fig. 2-3 The relationship between the size-corrected mass and female survival. Open circles represent single breeders and closed circles represent multiple breeders. Plots and bars represent mean value and standard errors which are calculated by dividing the data into 2 rank categories starting from the lowest value of size-corrected mass (single breeders: 17, 16 samples, multiple breeders: 20, 20 samples).

Chapter 3

Male contribution in feeding facilitate female multiple breeding in Japanese tits



Introduction

Understanding parental care is still a central research area in evolutionary behavioral ecology (Royle et al. 2012). One of the main questions is which sex provides parental care (Royle et al. 2012). In species with internal fertilization, such as birds and mammals, males choose whether to remain or desert offspring, and paternity is often uncertain. Therefore, males are more likely to seek out new females rather than to continue care of their offspring (Trivers 1972, Dawkins and Carlisle 1976, Gross and Shine 1981, Queller 1997). More generally, males are less likely to provide care whenever males compete for females. This situation is common because males produce gametes faster than females, and this difference in potential reproductive rates biases the operational sex ratio toward males (Clutton-Brock and Parker 1992, Fromhage and Jennions 2016). Despite such theoretical predictions, males remain with and care for their offspring in many species, especially in birds (Royle et al. 2012).

Why don't males desert their partners after mating? Parental care reduces survival and future mating opportunities of parents and, thus, is costly to their fitness (Royle et al. 2012). Therefore, the benefits of care, such as enhanced offspring survival, should outweigh the costs. Notably, the importance of male assistance, such as direct provisioning of food or defense, on reproductive success has frequently been shown in male removal or manipulation experiments (Lyon et al. 1987, Robertson 1998, Moreno et al. 1999). However, many such experimental

studies have failed to find a direct link between male removal and predicted reduction of reproductive success: females often compensated for the removal and raised offspring equally well (Gowaty 1983, Martin et al. 1985, Bart and Tornes 1989). If male assistance is not essential for reproductive success, why do males continue care at the expense of future mating opportunities? It has been hypothesized that that they remain with and care for offspring because they cannot be polygamous due to competition with paired males or because the aggressive behavior of females to other females makes it difficult to mate with second females (reviewed in Davies et al. 2012).

Another reason why males continue parental care may be that paternal care contributes both to the reproductive success of the current breeding and to future mating opportunities. This situation could occur when male parental care reduces female reproductive efforts and consequently females can achieve higher reproductive rates (enhanced fecundity hypothesis: Tallamy 2000, load-lightening hypothesis: West and Capellini 2016). This hypothesis has been empirically tested in some insects, mammals, and cooperative breeding birds (Jenkins et al. 2000; West and Capellini 2016); however, at present, few studies have been conducted on socially monogamous, non-cooperative breeding birds, which include the majority of avian species (e.g. Wolf et al. 1991).

Species producing more than one brood or litter per season (known as multiple breeding)

are suitable for testing this hypothesis because consecutive breeding attempts occur in a short period (Wolf et al. 1991, Jenkins et al. 2000). Multiple breeding is a common reproductive strategy in various taxa, especially in short-lived species (Verhulst et al. 1997). In fact, within a species, multiple breeders have higher annual and lifetime reproductive success compared with single breeders (Hoffmann et al. 2015, Cornell and Williams 2016).

Studies of multiple breeding have been conducted mostly in birds, and many have reported that timing of the first breeding and female quality (such as age) are main factors for multiple breeding (e.g. Hoffmann et al. 2015). However, previous studies have rarely considered the roles of male parents on multiple breeding (e.g. Wolf et al. 1991). This is most likely because the female is assumed to control the initiation of the second breeding. However, males may substantially affect reproductive success, such as improving nestling body weight by provisioning (Stodola et al. 2010) or female body condition by incubation feeding (Nilsson and Smith 1988, Cantarero et al. 2014). Moreover, post-fledging care of the first brood is mainly a male role (Verhulst and Hut 1996). Therefore, a highly contributing male may reduce female reproductive effort and, consequently, the female is more likely to initiate a second breeding.

In this chapter, I investigated the importance of male feeding contributions on the annual reproductive success of Japanese tits *Parus minor*, which are facultative multiple breeders (Yuta and Koizumi 2012). Specifically, I predicted females with a high male feeding contribution

would have a better condition and be more likely to initiate a second breeding than those without. I also examined the impact of male contribution on fledging success and nestling weight, which are important indices of reproductive success.

Methods

Study species, study area, and field procedures

The Japanese tit is a small (ca. 14 g), hole-nesting passerine that readily accepts nest boxes for breeding. This species is a short-lived (lifespan: ca. 2 years; Saitou and Asakawa 2009), socially monogamous species with biparental care. In the studied population, most nestlings could fledge (> 80 % in the first and second broods) throughout the breeding season (Yuta and Koizumi 2012, Nomi et al. in press). Therefore, multiple breeding should significantly increase annual reproductive success.

The study was conducted over 3 years (2013–2015) in the Tomakomai Experimental Forest (TOEF, 42.40°N, 141.36°E, 5–90 m.a.s.l.), Hokkaido, Japan. The study area is mostly covered with natural broad-leaved deciduous forests with some conifer plantations. In the autumn of 2008, I established two study sites in the forest (ca. 30 ha each) (Yuta and Koizumi 2012). In each site, approximately 150 nest boxes were hung up in a regular 50 m grid. Nest boxes were cleaned every year after breeding season.

I checked all the nest boxes weekly from late April to early August and recorded breeding parameters, such as laying date and clutch size. Hatching date and fledging date were confirmed by daily visits. Parents were caught and ringed for individual identification when nestlings were 5–7 days old, and body mass and tarsus length were measured at the same time. Nestlings were caught at 13-days-old and the same body traits were measured. Body mass was measured using an electronic balance (accuracy: 0.1 g), and tarsus length was measured using a digital caliper to the nearest 0.01 mm.

Video recording and observation of feeding

For the observation of feeding behavior, I used GZ-E225 video cameras with BN-VG138 batteries (JVC KENWOOD Corporation, Kanagawa, Japan) attached to tripods that were placed 2–3 meters from the nest-boxes. Basically, video recordings were conducted for 3–5 hours in the morning (08:00–13:00) with various nestling ages (2-17 age) and I counted the number of male and female feedings from the video data. However, I used only data when nestling age was 10 because the male feeding contribution changes as the nestlings become older (Fig.A4). Moreover, I avoided recording on rainy days because weather conditions affect feeding behavior (Radford et al. 2001). Therefore, I used data when the nestling age was 9 to 12-days-old.

Statistical analyses

Male contribution on multiple breeding

For the analysis of male contribution on the initiation of second breeding, I used a generalized linear mixed model (GLMM) with a logit-link and binomial error distribution. The response variable was whether the female initiates a second brood or not (1 and 0, respectively). The explanatory variables in the full model included male feeding contribution (number of male feedings/total number of feedings) as the main effect and hatching date, number of fledglings, and female body condition as covariates. For the male contribution, I used the relative proportion (i.e., number of male feedings / number of male + female feedings) rather than the absolute value (i.e., male feeding attempts) because the requirements of food for fledglings substantially depended on the timing of hatching and, therefore, the relative proportion should be a better indicator (Appendix). Body condition was calculated as body mass divided by the tarsus length, which is a method that has often been used in previous studies (reviewed in Labocha and Hayes 2012).

I included female ID as a random effect to account for pseudo-replication, as some individuals bred several times in the study years. I also included year as a random effect to account for differences in the probability of multiple breeding among years. Study site was also included as random effect to account for differences in the probability of multiple brooding among sites. For this analysis, I used only successful nests (i.e. nests in which at least one nestling fledged) in the first broods. I excluded nests where male contribution was both 0 (only

female feeds nestlings) and 1 (only male feeds nestlings) for the analysis because either the male or female may have deserted these nests.

Male contribution on fledging success, nestling weight, and female body condition

I also constructed a similar GLMM with a logit-link function with a binomial error distribution for the analysis of male feeding contribution on fledging success. The response variable was the number of fledglings per number of hatchlings in each nest. The explanatory variables included male feeding contribution as the main effect, and hatching date, number of hatchlings, and female body condition as covariates. For the analysis of male feeding contribution on nestling weight, I used LMM. The response variable was mean nestling weight per brood. The explanatory variables included male feeding contribution as the main effect and hatching date, number of nestlings in a brood, and male/female body weights (for controlling genetic effect) as covariates.

For the analysis of male feeding contribution on female body condition, I also used LMM. The explanatory variables included male feeding contribution as the main effect and hatching date and number of nestlings in a brood as covariates. In the three analyses, individual ID, sites and years were again included as random effects. I used the data of all broods including first, replacement, and second broods in these analyses.

For all analyses, I used the statistical software R 2.15.3 (R Development Core Team) with package "lme4" for GLMMs and selected the best model using AIC_c (AIC corrected for small

sample size, Burnham and Anderson 2002) with package "MuMIn." Then, I used likelihood ratio test to assess the significance of each variable in the best model and other models with $\Delta AIC_c < 2$, which are considered to be statistically equivalent (Burnham and Anderson 2002). The multicollinearity of explanatory variables was tested using the variance inflation factor (VIF) and was not detected (i.e. VIF < 2).

Results

The mean laying date of the first breeding was May 16 (range: April 25–June 10) for the three years studied. The second breeding begin approximately one week after the successful nesting (at least one nestling fledged) of the first broods. The probability of second breeding attempts (proportion of females) was 44 % (range: 25–64 %). Only a few pairs changed their mates in the second broods (ca. 5 %). I observed the feeding behavior of 89 nests, and the total observation time was 435 hours.

Effects of male contribution on multiple breeding

Of the 55 pairs that successfully fledged at least one nestling in the first breeding, 23 pairs initiated a second breeding. I examined the effects of male feeding contribution during the first brood on the propensity of multiple breeding. The best model included male contribution, hatching date, and number of fledglings (Table 3-1a), and all parameters were significantly

associated with probability of multiple breeding (Table 3-2a). Pairs with a high male feeding contribution were more likely to initiate a second brood (Fig. 3-1). The second model, which included female body condition, also showed $\Delta AIC_c < 2$, but the parameter was not significant (Likelihood-ratio test, $\chi^2 = 0.92$, $P = 0.337$).

Effects of male contribution on fledging success, nestling weight, and female body condition

Male contribution did not significantly affect fledging success; the best model included only hatching date, and the ΔAIC_c of the second best model included male contribution and was > 2 (Table 3-1b). However, male contribution had a positive effect on nestling weight. The best model included male contribution and male weight (Table 3-1c), and both parameters were significantly correlated nestling weight (Table 3-2c, Fig. 3-2). The second model, which included female weight, showed $\Delta AIC_c < 2$ and the parameter was also significant (Likelihood-ratio test, $\chi^2 = 5.85$, $P = 0.016$). In contrast, female body condition was not affected by male contribution; the best model included only random effects and the ΔAIC_c of the second model, which included male contribution, was > 2 (Table 3-1d).

Discussion

The results supported the hypothesis that pairs with a higher male feeding contribution were more likely to begin a second breeding and to have heavier nestlings. This illustrates the significance of

male roles on annual reproductive success, which has been an underrated factor in previous studies of multi-brooded birds. More importantly, the results may provide a clue to understanding why biparental care is widespread among birds, even though in many species females managed to successfully fledge their nestlings when males were absent (Møller 2000). Annual reproductive success may eventually lead to high lifetime reproductive success because birds are short-lived and annual reproductive success may be directly linked to their fitness. Moreover, a recent study found that annual reproductive success affects pair-bond duration and female return rate to the same territory next year (Middleton et al. 2006). Pair bond duration affects the survival (Culina et al. 2015) and reproductive success of the next year (Van De Pol et al. 2006; Sánchez-Macouzet et al. 2014). Therefore, in terms of future breeding opportunities and successes, male contribution may have an important role in the maintenance of the biparental care.

To date, few studies have examined the importance of male roles on multiple breeding. Wolf et al. (1991) examined the male removal effect on reproductive success, but did not detect a significant effect on the probability of multiple breeding. The difference between the present study and Wolf et al. (1991) may be in the reproductive cost of each breeding attempt. Wolf et al. (1991) used a species with a small brood size (1–4) and naturally high frequency of multiple breeding (91 %). In those species, male parental care may be less significant than for species with a large brood size in a single breeding attempt. Since males have several roles in breeding, such

as territory acquisition and territory quality (e.g. food availability, Tschumi et al. 2014), I suggest that further research should be focused on male quality or some other variables relevant to male quality and on multiple breeding as well as the timing of breeding.

Why don't all males contribute by feeding to prompt multiple breeding if male contribution greatly increases their annual reproductive success? In contrast to females, males have more choices for increasing their fitness, such as extra-pair mating (Møller 2000) or nest defense (Kryštofková et al. 2011). Therefore, low contributing males may engage in extra-pair mating in the first brood and sneaking in the second breeding, or concentrate on nest defense or vigilance to predators. Further research is needed in multi-brooded species to examine if there are any tradeoffs between male feeding contribution and other behaviors contributing to fitness.

Male contribution also increased nestling growth (Fig. 3-2). This may be because prey items or sizes were different between males and females. This study did not investigate prey item or size quantitatively, but several other studies in birds have reported differences in prey items or sizes between males and females due to a size-related difference in bill size or foraging ability (Ishikawa and Watanuki 2002, Fernàndez and Lank 2008). Males may be able to return higher quality prey items or larger prey than females; therefore, pairings with high contributing males may have heavier nestlings.

Contrary to the prediction, male contribution was not positively correlated to female body

condition, nor was female body condition correlated to the propensity of multiple breeding. I assumed that female body condition would affect multiple breeding because a previous study on Great tits showed a significant difference in female weight loss between single and double breeders during the first breeding (De Laet and Dhondt 1989). Females might have assessed male quality by feeding ability and decided whether to initiate a second breeding. Male provisioning is important, not only in pre-fledging care (Stodola et al. 2010), but also for post-fledging care (Verhulst and Hut 1996). Thus, female multiple breeding may be a result of differential allocation in relation to male quality, if male contribution indicates his quality (Sheldon 2000), regardless of female body condition. An alternative explanation is simply that the timing of measuring parent's body traits might have affected the results. I captured and measured parents when nestlings were 5–7 days old and there may not be large difference in body condition between single and multi-brooded females during this period.

Do contributing males always contribute? This question is important because consistency in parental care can be a key factor for subsequent mate choice (Nakagawa et al. 2007). In this chapter, I found a positive relationship in individual feeding rate (feeding rate per chick per hour) between the first and second broods (Pearson's correlation coefficient, $n = 39$, $r = 0.534$, $P < 0.001$). Moreover, the proportion of male feedings is consistent between the first and second breeding (Pearson's correlation coefficient, $n = 18$, $r = 0.473$, $P = 0.047$), indicating that the

contributions of each parent are consistent as long as the pair remains.

Recently, some studies have shown that parental provisioning is influenced by individual personality and/or male and female compatibility (Barnett et al. 2012, Mutzel et al. 2013, David et al. 2015). Individual feeding rates may be determined by offspring demand, food availability, and the combination of male and female personalities, which may affect the mate choice or the subsequent reproductive actions of females. More studies are needed to clarify the determinant of individual feeding rate, the combination of male and female provisioning, and their consequences.

Table 3-1 Model selection of the GLMMs for the probability of multiple breeding, fledging success, mean nestling weight, and female body condition in relation to male contribution in feeding and other covariates. ΔAIC_c is the difference in AIC_c values between the given model and the model with the lowest AIC_c. Weight indicates the Akaike's weights showing the support for each model relative to other models, in which the sum is1. Only top models ($\Delta AIC_c < 4$) and null models (only random effects included) are shown.

Model	df	ΔAIC_c	Weight
a. Proportion of multiple breeding *n* = 55			
Male contribution + hatching date + number of fledglings	7	0.00	0.421
Male contribution + hatching date + female body condition + number of fledglings	8	1.56	0.193
Hatching date + number of fledglings	7	2.02	0.154
Male contribution + hatching date	8	3.49	0.074
Null	4	11.54	0.001
b. Fledging success *n* = 89			
Hatching date	5	0.00	0.520
Hatching date + male contribution	6	2.10	0.182
Hatching date + female body condition	6	2.21	0.173
Null	4	6.99	0.011
c. Nestling weight *n* = 89			
Male weight + male contribution	7	0.00	0.390
Female weight + male weight + male contribution	8	0.30	0.335
Male contribution	6	2.84	0.094
Female weight + male contribution	7	4.26	0.046
Male weight	8	4.62	0.039
Null	5	12.65	0.001
d. Female body condition *n* = 89			
Null	5	0.00	0.913
Male contribution	6	4.73	0.086

7 **Table 3-2** Parameter estimates and *P* values of the best models of GLMMs.

Parameter	Estimate	SE	df	$\chi 2$	*P*
a. Probability of multiple breeding					
Intercept	–12.154	4.215	1	9.10	0.003
Male contribution	7.578	3.574	1	4.65	0.031
Hatching date	–0.277	0.087	1	13.29	< 0.001
Number of fledglings	0.769	0.307	1	6.12	0.013
b. Fledging success					
Intercept	4.831	0.457	1	18.31	< 0.001
Hatching date	–0.035	0.012	1	9.24	0.002
c. Mean nestling weight					
Intercept	9.523	1.353	1	26.44	< 0.001
Male contribution	1.947	0.491	1	14.39	< 0.001
Male weight	0.257	0.088	1	8.54	0.003

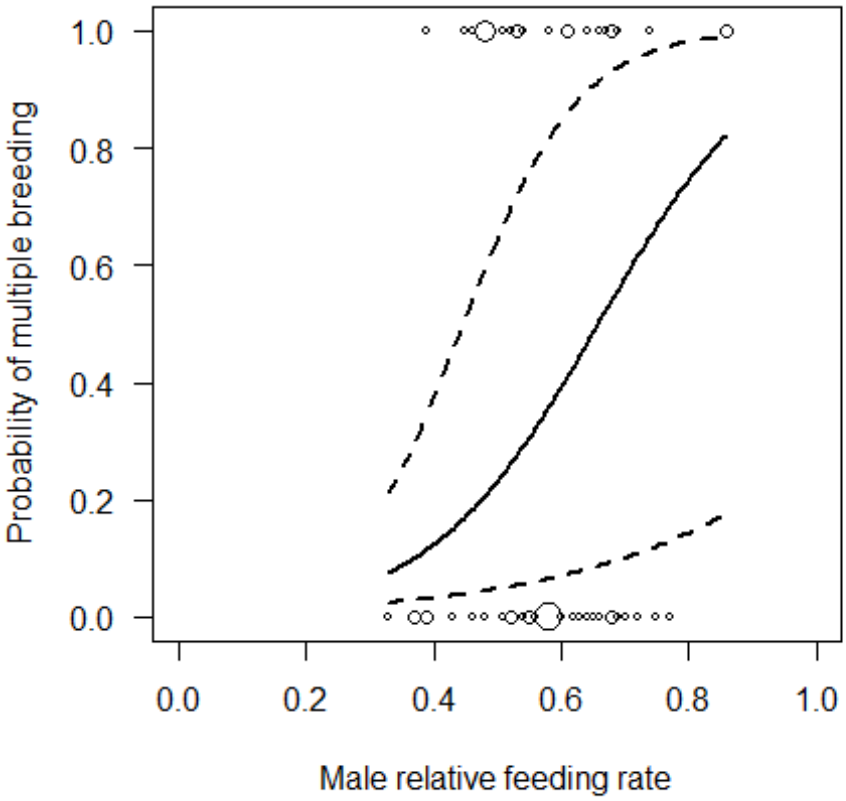

Fig. 3-1 The relationship between male feeding contribution and probability of multiple breeding. Parameters were estimated using the generalized linear mixed model shown in Table 3-1a. Lines are predicted values (±SE). Circle size represents sample size.

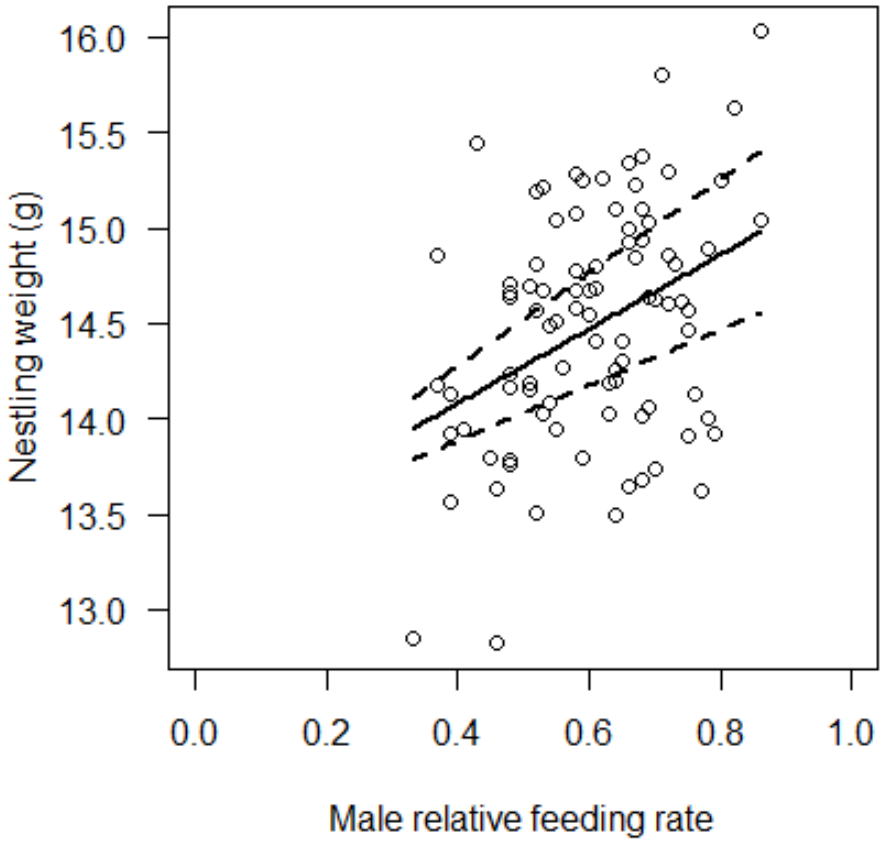

Fig. 3-2 The relationship between male feeding contribution and mean nestling weight. Parameters were estimated using the generalized linear mixed model shown in Table 3-2c. Lines are predicted values (±SE).

Appendix Factors affecting parental food provisioning behavior

In this appendix I describe the factors affect parental food provisioning behavior. First I investigated provisioning behavior of each nest with various nestling ages (day 2-17) using LMMs. Response variable was log-transformed feeding rate per hour. Explanatory variables included standardized hatching date (difference between the hatching date and mean hatching date of first brood each year), brood size at recording, and nestling age. Nest ID, pair ID, recording date, and year were included as random effects. Significance of each variable was examined by likelihood ratio tests. The LMMs showed that hatching date, brood size at recording, and nestling age were all significantly correlated to feeding rate (n=138, all; $P < 0.001$). Standardized hatching date was negatively (partial coefficient; -0.011 ± 0.002) and the number of nestlings at recording and nestling age were positively correlated with feeding rate (partial coefficient; 0.086 ± 0.019, 0.044 ± 0.009 each).

Secondly, I analyzed the factors affecting the male contribution using GLMM with binomial error distribution. Response variable was the number of male and female nest visits. Explanatory variables included standardized hatching date, brood size at recording, and nestling age. Nest ID, pair ID, recording date, and year were also included as random effects. Standardized hatching date, brood size were not significantly correlated with male contribution (n = 119, partial coefficient; -0.006 ± 0.003, -0.048 ± 0.041; *P* –value; 0.096, 0.238, each). However, nestling age was negatively correlated with male contribution (partial coefficient; -0.093 ± 0.015, $P < 0.001$, Fig.A4).

The first analysis indicated that necessary feeding effort for each nest was considerably different depending on breeding timing, number of nestlings and nestling ages. The relationship between breeding timing and provisioning rate might be due to the phenology of prey species (caterpillar abundance may be low). Therefore, I considered that the absolute value for food provisioning was less reliable to represent male contribution compared to the relative value. However, the second analysis showed that male contribution varied in relation to nestling age. Therefore, I used only the data of 9-12

nestling age for the analyses of male contribution on the propensity of multiple breeding, fledging success, and nestling weight.

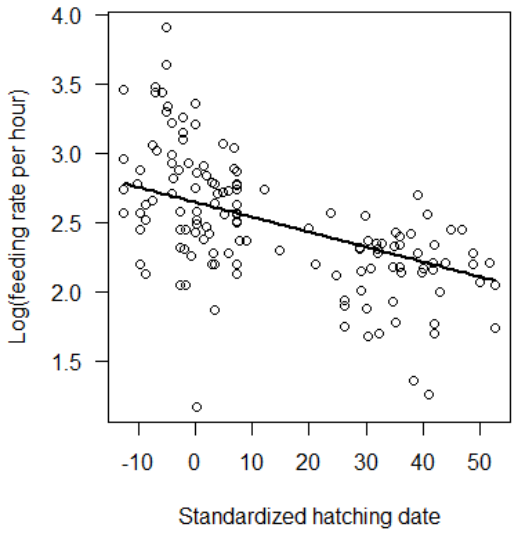

Fig.A1

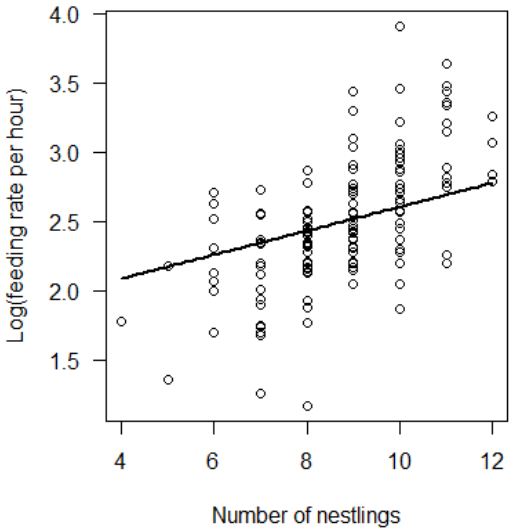

Fig.A2

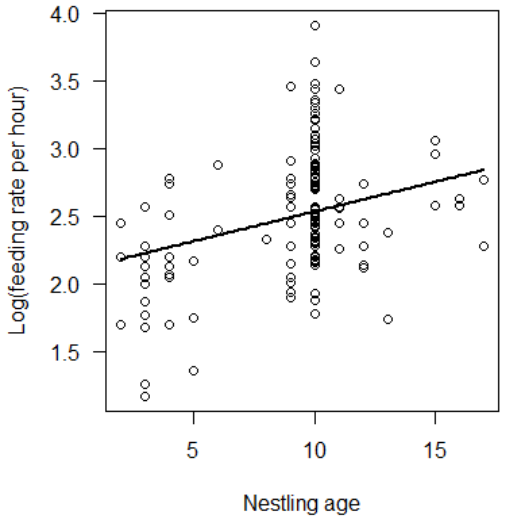

Fig.A3

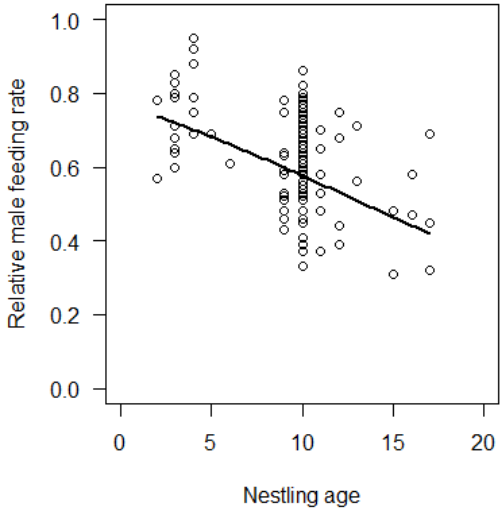

Fig.A4

Chapter 4

General discussion



In this thesis, I investigated the reproductive ecology of Japanese tits focusing on multiple breeding. In chapter 2, the paternal role of facultative multiple breeding in Japanese tits was presented and causal factors for the probability of multiple breeding and survival probability of single and multiple breeders was analyzed. I found that facultative multiple breeding is a result of female conditional strategy in relation to male quality; females mated with older males started breeding early in the season and consequently showed better performance in annual reproduction. These results imply the significance of male quality on annual reproductive success, which has been an underrated factor in previous studies on multiple breeding. In chapter 3, I investigated further roles of male parents on annual reproductive success and found that female parents with high contributed males in the first breeding were more likely to initiate second breeding.

Male roles on annual reproductive success and life time reproductive success

Fig. 4-1 shows the overview of the results in the thesis. In this thesis I found that male age and male feeding contribution affected the probability of female multiple breeding, and that multiple breeding had a positive, not negative, effect on female survival. These results indicate that males indirectly affect females' survival. Male survival was not negatively affected by the number of breeding attempts in the season (unpublished data). In Japanese tits, most males and females (70-80%) re-mates in the next year if they survive (Saitou and Asakawa 2009). Therefore, there may be a positive feedback to male fitness; contributing males and older males might enhance female survival and this means that both male and female have higher chances to breed next year together when they breed multiple times in

the season. Thus, males may have important roles for both male and female reproductive success of the next year leading to a higher lifetime reproductive success.

The effect of reproductive success and pair-bond on survival probability

Here, I propose that the positive relationship between multiple breeding and survival may be due to the enhanced pair bond by the fledgling success. The relationship between reproductive success and pairbond or divorce has been well documented in avian studies (Culina et al. 2014). However, evidence of the effect of pair bond on survival probably was only recently found (Culina et al. 2015, and references therein). Differences in survival linked to pairing choices might be especially important in species where pair members overwinter together, and where associating with a partner might confer a higher rank in a competitive winter environment (Ekman 1990, Lemmon et al. 1997). Some studies have suggested that retaining partner assistance reduces survival costs (Ekman 1990, Pampus et al. 2005). Although the mechanism is still unclear, individuals may be more likely to obtain sufficient food by cooperative behavior and survive in harsh winter if they remain with their mates. This fitness feedback may further drive male contribution in feeding (Fig. 4-1), and thus lead to the evolution of male parental care.

Is facultative multiple breeding a result of "male" alternative reproductive tactics?

The results of this thesis demonstrated that facultative multiple breeding is a female conditional strategy; females mating with high quality males showed better performance in reproduction. However, facultative multiple breeding can also be considered as a male conditional strategy (Fig. 4-2). Since males also have an opportunity to choose single or

multiple breeding, they can make decision by assessing the value of second breeding based on the female quality or their own condition. However, in the studied 6 years, there were no males who changed their mate for the second brood in the season while some females changed their mate (within season divorce, ca. 5% of females, unpublished data). This indicates that active divorce within the season may be conducted only by females and some floater males early in the season were selected by females in the second breeding. Therefore, male opportunity of second breeding is limited by female reproductive decision (Fig. 4-2).

Males, however, may still be able to decide multiple breeding indirectly (Fig. 4-2). In chapter 3, I demonstrated the importance of male feeding contribution to multiple breeding. Therefore, if males recognize their partner's quality and own situation during the first breeding or earlier, they should allocate more efforts to food provisioning than other activities, such as seeking extra-pair mating opportunity. In addition to facultative multiple breeding, to cooperate with females and concentrate on offspring care versus to seek for extra-pair mating can also be considered as a male alternative reproductive tactics (ARTs). What is important is that both males and females can significantly affect the decision of ARTs for the opposite sex in socially monogamous species (Fig. 4-2). This complex interaction has not been taken into consideration for the framework of conditional strategy, which would contribute to the understanding of evolution of complex life histories.

Proximate factors for the initiation of breeding

Since the timing of breeding is the most influential factor for multiple breeding in avian species (this study, and Table 1-1), how the initiation of breeding is determined is crucial. Because females have a final decision on breeding (egg laying) and timing of breeding each year is largely influenced by spring temperature, effects of male quality on timing of breeding have rarely been considered. However, there is accumulating evidence of male effects on the timing of breeding, for example, in domesticated female canaries (*Serinus canaries*), male songs stimulates the nest building activity of females (Hinde and Steel, 1976). More recently, Wingfield et al. (1997) found in the Pacific White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*), that captive females responded to elevated ambient temperature by developing a brood patch and ovarian follicles, but only when males were in the same room. Moreover, in the Zebra Finch (*Taeniopygia guttata*), exposing females to vocalizations of their mate and playback from a colony other than their own stimulates early laying (Waas et al. 2005). However, these previous studies were mostly conducted in captivity and this may be due to the difficulty in controlling many factors in field studies. More studies are required to elucidate male roles on breeding timing in wild populations.

When the female decision made?

I initially considered that the female decision is made after the first brood nestlings fledged. In fact, most multi-brooded pairs start second breeding after fledging. However, some pairs started second breeding (egg laying) *before* fledging (1-3 days, unpublished. data). It seems that these females already knew the best timing of second breeding. Perhaps some females such as older or experienced females might have planned to breed multiple times before the

first breeding and decide to initiate the second breeding or not according to their own condition and/or male contribution in the end of the first breeding. In multi-brooded population, if they had already evolved to breed multiple times, all individuals may have the *ability* to breed more than once per season. Physiological or endocrinological analysis may be needed to understand when female decide to initiate second breeding.

Future prospective studies for the Japanese tits in TOEF

Lastly, I would like to discuss prospective researches on the Japanese tit population in Tomakomai experimental forest (TOEF), Hokkaido, Japan. During the six year survey, fieldwork methodology and techniques on the population have been established. The population of Japanese tits and the field site has potentials for further extensive and systematic researches on ecological and evolutionary biology. By continuing to monitor the breeding biology of this species, we would be able to do long term individual based studies which may answer many questions in ecological and evolutionary biology (Clutton-Brock and Sheldon 2010).

The study site is also suitable for field experiments. The site has been divided into two plots with 150 nestboxes in each site that are 2km apart. Therefore, these sites can be used as a large-scale experimental site of reproductive traits and a control site, which offers monitoring of natural reproduction like many excellent study systems in Europe (Clutton-Brock and Sheldon 2010). For example, in 2012 season, we studied individual based behaviors and their plasticity of extra- pair behavior by an experimental manipulation (Yuta 2013).

As already shown in this thesis, this study population has unique characteristics in breeding biology especially for the high frequency of multiple breeding. Regardless of whether correlative or experimental, multi-brooded population has been a useful characteristic to examine the plasticity of individual behavior, which have contributed greatly to understanding the ecology and evolution of natural populations. In this sense, this population has many possibilities.

In terms of characteristics of the study site, I must remember another characteristic that other bird species such as coal tits (*Periparus ater*), marsh tits (*Poecile palustris*), varied tits (*Poecile varius*), Eurasian nuthatches (*Sitta europea*) also frequently used nestboxes for breeding (Nomi et al. in press). Although, numerous studies have done in this taxonomic group, few studies or study sites used multiple species breeding in sympatry. Future works should focus and further utilize the characteristics unique to the population.

Another possibility is that we would be able to make more collaborative studies, since the species and closely related great tit have been used for many studies by many researchers. For example, by comparing ecology of other populations of this species such as variation in clutch size (Møller et al. 2014), or by genetic analysis among population (Laine et al. 2016), we can understand variation in the strength and form of natural selection and also the evolutionary history and process of adaptive population differentiation in the Japanese tit.

In terms of collaborative studies, TOEF itself may be a good place. The forest is used by many researchers with a variety of research areas, and collaborative studies have already

been undertaken (e.g. Nakano and Murakami 2001, Fukui et al. 2006). By collaborating with other researchers and/or using the knowledge gained from past studies, this study site has potential for more integrative ecological studies.

I hope that the Japanese tit and this field site will be used by more researchers and produce more fascinating studies.

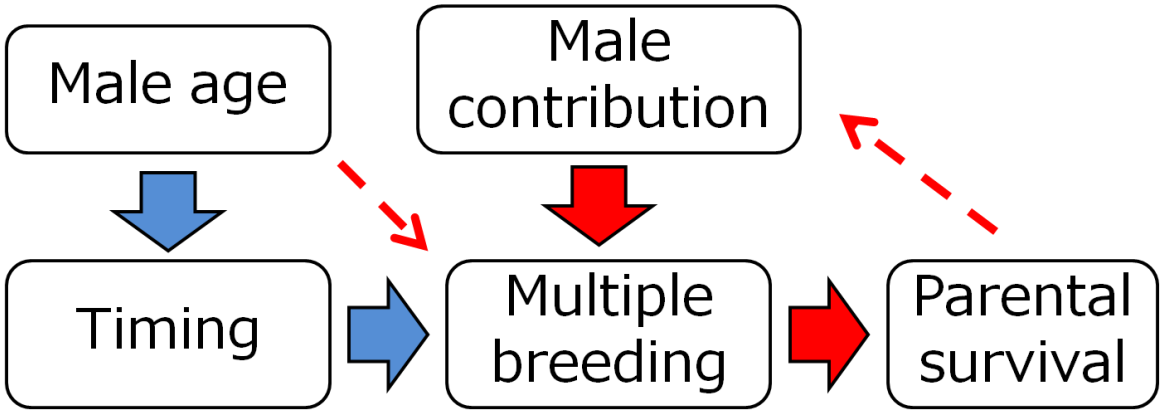

Fig. 4-1

Schematic overview of the results of the thesis. Blue arrow shows a negative effect and red arrow shows a positive effect. Red dashed line represents a positive indirect effect.

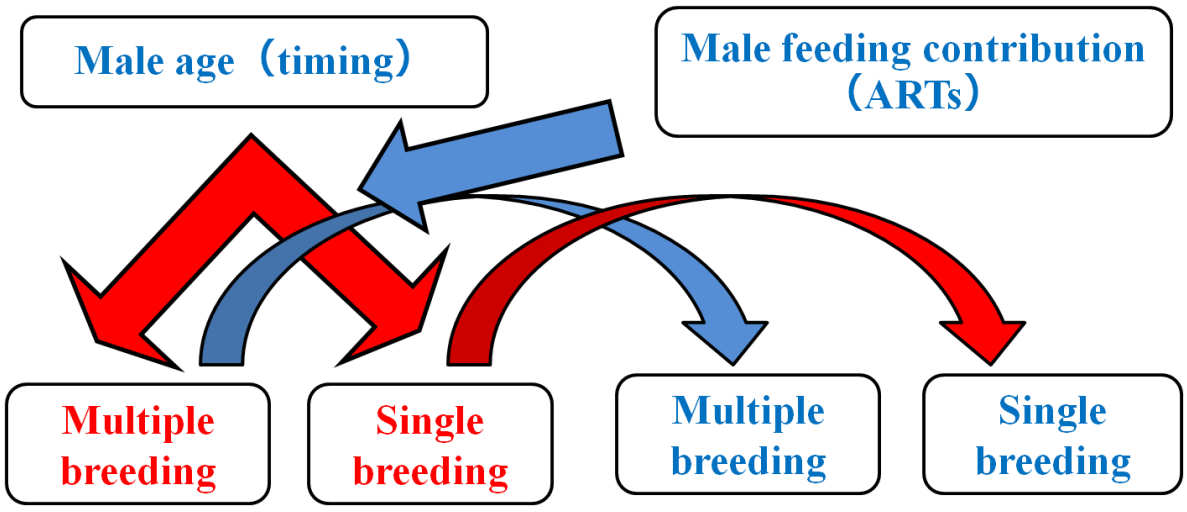

Fig. 4-2

Schematic overview of the interactions between male and female ARTs. Blue arrows show male decisions and red arrows show female decisions. Females decide whether they breed multiple times according to the timing of breeding which is influenced by male age and male feeding contribution (female ARTs). Male feeding contribution can be considered as male ARTs and male ARTs indirectly affect female ARTs. After females chose multiple breeding, males may still have the opportunity to desert their partner or clutches (though I consider this possibility is low). Therefore, I drew a blue arrow from the female multiple breeding (red) and male multiple breeding (blue). When females choose single breeding, males may be forced to be single breeders because operational sex ratio may be male-biased later in the breeding seasons, and this may limit the chances of obtaining new females.

Acknowledgements

Many people contributed to my studies. I do not name all of them here because there are so many people who supported me in many ways. None of the work I have presented could have been done without them.

Firstly, I need to thank my supervisor, Itsuro Koizumi, for his consistent support, guidance, and encouragement. I thank him for his intellectual input into my research, teaching me how to improve my writing. I also thank Professors Takashi Noda and Takenori Takada for their time and effort of reading and for constructive comments to improve my thesis.

Of course I need to thank Teru Yuta; the teacher of my field work. During the first year of my master course I learned many things from him not only field works. The field work he taught was very intensive. The breeding season of Japanese tits at TOEF lasts for four months from May to August. During this period, I was out and walked in the woods with stepladders from dawn to dusk every day. Although I found something new every day in the field, I was also continuously fighting with weariness of daily routines when I was alone. I was fortunate to have many people coming and help field work. I also greatly thank stuffs in TOEF for their supports in field work assistance. The laboratory work on genetic analyses was also required much efforts and boring as well as the fieldwork. However, new discoveries from the work made me forget the efforts.

The last five years at Hokkaido University have been exciting and a lot of fun thanks to all of the members of animal ecology lab, and Sapporo and Tomakomai FSC labs. I have been lucky to be surrounded by many kind people. Thank you for all of you supporting my studies.

I would also like to thank my family for their supports throughout my student life. I cannot express my gratitude in words. Finally, I would like to thank all those Japanese tits and other species of birds for their patience to cooperate to my studies. I dedicate this thesis to them.

Daisuke Nomi

References

Agnew, P., D. Houston, C. Lalas, J. Wright (2014). Variation in reproductive performance of little penguins (*Eudyptula minor*) attributable to double brooding. Journal of Ornithology 155:101−109.

Auld, J. R., C. M. Perrins, and A. Charmantier (2013). Who wears the pants in a mute swan pair? Deciphering the effects of male and female age and identity on breeding success. Journal of Animal Ecology 82:826–835.

Barba, E., J. Gil-Delgado, and J. S. Monros (1995). The costs of being late: consequences of delaying great tit *Parus major* first clutches. Journal of Animal Ecology 64:642–651.

Barnett, C. A., C. F. Thompson, and S. K. Sakaluk (2012). Aggressiveness, boldness and parental food provisioning in male house wrens (*Troglodytes aedon*). Ethology 118:984–993.

Bart, J., A. Tornes (1989). Importance of monogamous male birds in determining reproductive success: evidence for house wrens and a review of male-removal studies. Behavioral Ecology and Sociobiology 24:109–116.

Bennett, P. M., and I. P. Owens (2002). Evolutionary Ecology of Birds-Life histories, Mating Systems and Extinction. Oxford University Press, Oxford.

Béziers, P., and A. Roulin (2016). Double brooding and offspring desertion in the barn owl (*Tyto alba*). Journal of Avian Biology 47:235–244.

Boer-Hazewinkel, D. (1987). On the cost of reproduction: parent survival and production of second clutches in the Great Tit. Ardea 75:99–110.

Brinkhof, M. W. G., A. J. Cave, S. Daan, and A. C. Perdeck (2002). Timing of current reproduction directly affects future reproductive output in European Coots. Evolution 55:400–411.

Brockmann, H. J., R. Oliveira, and M. Taborsky (2008). Integrating mechanisms and function: prospects for future research. In Alternative Reproductive Tactics: An Integrative Approach (R. F. Oliveira, M. Taborsky, and H. J. Brockmann Editors). Cambridge University Press, Cambridge, UK. pp. 471–489.

Bryant, D. M. (1979). Reproductive costs in the House Martin (*Delichon urbica*). Journal of Animal Ecology 48:655–675.

Bulluck, L., S. Huber, C. Viverette, and C. Blem (2013). Age-specific responses to spring temperature in a migratory songbird: older females attempt more broods in warmer springs. Ecology and Evolution 3:3298–3306.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: a Practice Information-Theoretic Approach. Springer, Berlin, Germany.

Candolin, U., and L. Vlieger (2013). Should attractive males sneak: the trade-off between current and future offspring. PLoS One 8:e57992.

Cantarero, A., J. López-Arrabé, A. Palma, A. J. Redondo, and J. Moreno (2014). Males respond to female begging signals of need: a handicapping experiment in the pied flycatcher, *Ficedula hypoleuca*. Animal Behaviour 94:167–173.

Cantarero, A., J. López-Arrabé, M. Plaza, I. Saavedra-Garcés, and J. Moreno (2016). Males

feed their mates more and take more risks for nestlings with larger female-built nests: an experimental study in the Nuthatch *Sitta europaea*. Behavioral Ecology and Sociobiology 70:1141–1150.

Carro, M. E., M. E. Mermoz, and G. J. Fernández (2014). Factors affecting the probability of double brooding by Southern House Wrens. Journal of Field Ornithology 85:227–236.

Clutton-Brock, T. H., G. A. Parker (1992). Potential reproductive rates and the operation of sexual selection. Quarterly Review of Biology 67:437–456.

Clutton-Brock, T. (2009). Sexual selection in females. Animal Behaviour 77:3–11.

Clutton-Brock, T., and B.C. Sheldon (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562–573.

Cornell, A., and T. D. Williams (2016). Individual quality and double-brooding in a highly synchronous songbird population. The Auk: Ornithological Advances 133:251–260.

Culina, A., R. Radersma, and B. C. Sheldon (2014). Trading up: fitness consequences of divorce in monogamous birds. Biological Reviews 90:1015–1034.

Culina, A., S. Lachish, and B. C. Sheldon (2015). Evidence of a link between survival and pair fidelity across multiple tit populations. Journal of Avian Biology 46:507–515.

Davies, S., and P. Deviche (2014). At the crossroads of physiology and ecology: food supply and the timing of avian reproduction. Hormones and Behavior 66:41–55.

Dhondt, A. A. (1971). Some factors influencing territory in the Great tit, *Parus major*

Gerfaut 61:125–135.

De Laet, J. F., and A. A. Dhondt (1989). Weight loss of the female during the first brood as a factor influencing second brood initiation in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. Ibis 131:281–289.

Ekman, J. (1990). Alliances in winter flocks of willow tits; effects of rank on survival and reproductive success in male–female associations. Behavioral Ecology and Sociobiology 26:239–245.

Evans, J. P., and A. E. Magurran (2000). Multiple benefits of multiple mating in guppies. Proceedings of the National Academy of Sciences of the United States of America 97:10074–10076.

Fernàndez, G., and D. B. Lank (2008). Foraging behaviour of non-breeding western sandpipers *Calidris mauri* as a function of sex, habitat and flocking. Ibis 150:518–526.

Fritz, R. S., N. E. Stamp, and T. G. Halverson (1982). Iteroparity and semelparity in insects. American Naturalist 120:264–268.

Fromhage, L. and M. D. Jennions (2016). Coevolution of parental investment and sexually selected traits drives sex-role divergence. Nature Communications 7.

Fukui, D. A. I., M. Murakami, S. Nakano, and T. Aoi (2006). Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75:1252–1258.

Garcia-Navas, V., and J. J. Sanz (2012). Yearly and seasonal variation of breeding parameters in a declining multi-brooded passerine, the Tree Sparrow. Ardea 100:79–88.

Gauger ,V. H. (2000). Double brooding in the black noddy (*Anous minutus*): incidence and effect of an unusual seabird reproductive strategy. PhD dissertation, Universtiy of Hawaii, Manoa, Honululu, HI

Geupel, G. R., and D. F. Desante (1990). Incidence and determinants of double brooding in Wrentits. The Condor 92:67–75.

Gowaty, P. A. (1983). Male parental care and apparent monogamy among eastern bluebirds (*Sialia sialis*). American Naturalist 121:149–157.

Gross, M. R., and R. Shine (1981). Parental care and mode of fertilization in ectothermic vertebrates. Evolution 35:775–793.

Gross, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology & Evolution 11:92–98.

Harvey, P. H., P. J. Greenwood, C. M. Perrins, and A. R. Martin (1979). Breeding success of Great tits *Parus major* in relation to age of male and female parent. Ibis121:216–219.

Hill, D. L., N. Pillay, and C. Schradin (2015). Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitarily than communally. Journal of Animal Ecology 84:1497–1508.

Hinde, R.A., and E. Steel (1976). The effect of male song on an estrogen-dependent behavior pattern in the female canary (*Serinus canarius*). Hormones and Behavior 7: 293–304.

Hoffmann, J., E. Postma, and M. Schaub (2015). Factors influencing double brooding in Eurasian Hoopoes *Upupa epops* Ibis 157:17–30.

Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit (1992). Multiple brooding and productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens),* in an unfragmented temperate forest. The Auk 109:321–333.

Hotta, M. (1996). Timing of Laying in Multiple-brooded Little Swifts *Apus affinis*. Japanese Journal of Ornithology 45:23–30.

Husby, A., L. E. B. Kruuk, and M. E. Visser (2009). Decline in the frequency and benefits of multiple brooding in Great Tits as a consequence of a changing environment. Proceedings of the Royal Society of London, Series B 276:1845–1854.

Ishikawa, K., and Y. Watanuki (2002). Sex and individual differences in foraging behavior of Japanese cormorants in years of different prey availability. Journal of Ethology 20:49–54.

Jacobs, A. C., L. L. Reader, and J. M. Fair (2013). What determines the rates of double brooding in the Western Bluebird? The Condor 115:386–393.

Jankowiak, Ł., and D. Wysocki. (2015). Do individual breeding experience and parental effort affect breeding season length in blackbirds? Behavioral Ecology 27:829–834.

Jenni, L., and M. Kéry (2003). Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society London, Series B 270:1467–1471.

Jenkins, E. V., C. Morris, and S. Blackman (2000). Delayed benefits of paternal care in the burying beetle *Nicrophorus vespilloides*. Animal Behavior 60:443–451.

Johns, M. E., P. Warzybok, R. W. Bradley, J. Jahncke, M. Lindberg, and G. A. Breed (2017). Age, timing, and a variable environment affect double brooding of a long-lived seabird. Marine Ecology Progress Series 564:187–197.

Johnson, S. L., and H. J. Brockmann (2012). Alternative reproductive tactics in female horseshoe crabs. Behavioral Ecology 23:999–1008.

Kipper, S., and S. Kiefer (2010). Age-related changes in birds' singing styles: on fresh tunes and fading voices? Advances in the Study of Behavior 41:77–118.

Klomp, H. (1970). The determination of clutch-size in birds a review. Ardea 58:1–124.

Kloskowski, J. (2001). Double-brooding in Red-necked Grebes. Waterbirds 24:121–124.

Kluijver, H. N. (1951). The population ecology of the Great Tit, *Parus m. major* L. Ardea 39:1–135.

Kryštofková, M., M. Haas, and A. Exnerová (2011). Nest defense in blackbirds *Turdus merula*: effect of predator distance and parental sex. Acta Ornithologica 46:53–61.

Labocha, M. K., and J. P. Hayes (2012). Morphometric indices of body condition in birds: a review. Journal of Ornithology 153:1–22.

Laine, V. N., T. I. Gossmann, K. M. Schachtschneider, C. J. Garroway, O. Madsen, K. J. Verhoeven, ... and R. P. Crooijmans (2016). Evolutionary signals of selection on cognition from the great tit genome and methylome. Nature communications 7.

Lank, D. B., C. M. Smith, O. Hanotte, T. Burke, and F. Cook (1995). Genetic polymorphism for alternative mating behavior in lekking male ruff, *Philomachus pugnax*. Nature 20:137–145.

Lemmon, D., M. L. Withiam, and C. P. L. Barkan (1997). Mate protection and winter pair-bonds in black-capped chickadees. Condor 99:424–433.

Lyon, B, R. D. Montgomerie, and L. D. Hamilton (1987). Male parental care and monogamy in snow buntings. Behavioral Ecology and Sociobiology 20:377–382.

Mahr, K., M. Griggio, M. Granatiero, and H. Hoi (2012). Female attractiveness affects paternal investment: experimental evidence for male differential allocation in blue tits. Frontiers in zoology 9:1.

Martin, K., F. G. Cooch, R. F. Rockwell, and F. Cooke (1985). Reproductive performance in lesser snow geese: are two parents essential? Behavioral Ecology and Sociobiology 17:257–263.

Middleton, H. A., C. A. Morrissey, and D. J. Green (2006). Breeding territory fidelity in a partial migrant, the American dipper *Cinclus mexicanus*. Journal of Avian Biology 37:169–178.

Møller, A. P. (2000). Male parental care, female reproductive success and extra-pair paternity. Behavioral Ecology 11:161–168.

Møller, A. P., F. Adriaensen, A. Artemyev, J. Bańbura, E. Barba, C. Biard, ... and F. Cecere (2014). Clutch-size variation in Western Palaearctic secondary hole-nesting passerine birds in relation to nest box design. Methods in Ecology and Evolution 5:353–362.

Moore, D. J., and R. D. Morris (2005). The production of second clutches in the common tern: proximate effects of timing and food supply. Waterbirds 28:458–467.

Moreno, J., J. P. Veiga, and P. J. Cordero (1999). Effects of paternal care on reproductive success in the polygynous spotless starling *Sturnus unicolor*. Behavioral Ecology and Sociobiology 47:47–53.

Morrison, J. L. (1998). Effects of double brooding on productivity of Crested Caracaras. The Auk 115:979–987.

Morrison, C., and J. M. Hero (2003). Geographic variation in life-history characteristics of amphibians: A review. Journal of Animal Ecology 72:270–279.

Morrissey, C. A. (2004). Effect of altitudinal migration within a watershed on the reproductive success of American dippers. Canadian Journal of Zoology 82:800–807.

Mulvihill, R. S., S. C. Latta, and F. L. Newell (2009). Temporal constraints on the incidence of double brooding in the Louisiana Waterthrush. The Condor 111:314–348.

Mutzel, A., N. J. Dingemanse, Y. G. Araya-Ajoy, and B. Kempenaers (2013). Parental provisioning behaviour plays a key role in linking personality with reproductive success. Proceeding of Royal Society London series B 280:20131019.

Nagy, L. R., and R. T. Holmes (2005a). Food limits annual fecundity of a migratory songbird: an experimental study. Ecology 86:675–681.

Nagy, L. R., and R. T. Holmes (2005b). To double-brood or not? Individual variation in the reproductive effort in Blackthroated Blue Warblers (*Dendroica caerulescens*). The Auk 122:902–914.

Nakagawa, S., D. O. J. Gillespie, B. J. Hatchwell, and T. Burke (2007). Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. Journal of Evolutionary Biology 20:1674–1681.

Nakano, S., and M. Murakami (2001). Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98:166–170.

Nilsson, J.-Å., and H. G. Smith (1988). Incubation feeding as a male tactic for early hatching. Animal Behaviour 36:641–647.

Nomi, D., T. Yuta, and I. Koizumi (2015). Offspring sex ratio of Japanese Tits *Parus minor* is related to laying date and clutch size only in the first clutches. Acta Ornithologica 50:213–220.

Nomi, D., T. Yuta, and I. Koizumi (In press). Breeding biology of four sympatric tits in northern Japan. The Wilson Journal of Ornithology

Neff, B. D., and J. S. Lister (2007). Genetic life history effects of juvenile survival in bluegill. Journal of Evolutionary Biology 20:517–525.

O'Brien, E. L., and R. D. Dawson (2012). Experimental dissociation of individual quality, food and timing of breeding effects on double-brooding in a migratory songbird. Oecologia 172:689–699.

Ogden, L. J. E., and B. J. M. Stutchbury (1996). Constraints on double brooding in a Neotropical migrant, the Hooded Warbler. The Condor 98:736–744.

Päckert, M., J. Martens, S. Eck, A. A. Nazarenko, O. P. Valchuk, B. Petri, and M. Veith (2005). The great tit (*Parus major*) - a misclassified ring species. Biological Journal of Linnaean Society 86:153–174.

Paige, K. N., and T. G. Whitham (1987). Flexible life history traits: Shifts by scarlet gilia in response to pollinator abundance. Ecology 68:1691–1695.

Pampus, M., K. H. Schmidt, and W. Wiltschko (2005). Pair bond and breeding success in blue tits *Parus caeruleus* and great tits *Parus major*. Ibis 147:92–108.

Parejo, D., and E. Danchin (2006). Brood size manipulation affects frequency of second clutches in the Blue Tit. Behavioral Ecology & Sociobiology 60:184–194.

Partridge, L., and P. H. Harvey (1988). The ecological context of life history evolution. Science 241:1449–1455.

Pascual, J. A., and S. J. Peris (1992). Effects of forest spraying with two application rates of cypermethrin on food supply and on breeding success of the Blue Tit (*Parus caeruleus*). Environmental Toxicology & Chemistry 11:1271–1280.

Podolsky, A. L., T. R. Simons, and J. A. Collazo (2007). Modeling population growth of the ovenbird (*Seiurus aurocapilla*) in the southern Appalachians. The Auk 124:1359–1372.

Queller, D. C. (1997). Why do females care more than males? Proceedings of Royal Society London series B Biological Sciences 264:1555–1557.

Radford, A. N., R. H. McCleery, R. J. W. Woodburn, and M. D. Morecroft (2001). Activity patterns of parent great tits *Parus major* feeding their young during rainfall. Bird Study 48:214–220.

Rankin, D., and H. Kokko (2007). Do males matter? The role of males in population dynamics. Oikos 116:335–348.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Robertson, I. C. (1998). Paternal care enhances male reproductive success in pine engraver beetles. Animal Behavior 56:595–602.

Royle, N. J., P. T. Smiseth, and M. Kolliker (2012). The evolution of parental care. Oxford University Press, Oxford

Saitou, T., and M. Asakawa (2009). Breeding Population of the Great Tit *Parus major*. Yamashina Institute of Ornithology 40:104–116. (in Japanese with English summary).

Sánchez-Macouzet, O., C. Rodríguez, and H. Drummond (2014). Better stay together: pair bond duration increases individual fitness independent of age-related

variation. Proceeding of Royal Society London, Series B 281:20132843.

Sanz, J. J., J. Moreno, and M. M. Pancorbo (1993). The significance of double broods in the Coal Tit *Parus ater* breeding in a montane coniferous forest in central Spain. Ardeola 40:155–161.

Sheldon, B. C. (2000). Differential allocation: tests, mechanisms and implications. Trends in Ecology & Evolution 15:397–402.

Siefferman, L., and G. E. Hill (2008). Sex-specific costs of reproduction in eastern bluebirds *Sialia sialis*. Ibis 150:32–39.

Smith, H. G., H. Källander, and J. Å. Nilsson (1987). Effect of experimentally altered brood size on frequency and timing of second clutches in the great tit. The Auk 104:700–706.

Stearns, S. C. (1992). The Evolution of Life Histories. Oxford University Press, Oxford.

Stodola, K. W., E. T. Linder, D. A. Buehler, K. E. Franzreb, D. H. Kim, and R. J. Cooper (2010). Relative influence of male and female care in determining nestling mass in a migratory songbird. Journal of Avian Biology 41:515–522.

Taborsky, M., R. F. Oliveira, and H. J. Brockmann (2008). The evolution of alternative reproductive tactics: concepts and questions. In Alternative Reproductive Tactics: An Integrative Approach (R. F. Oliveira, M. Taborsky, and H. J. Brockmann Editors). Cambridge University Press, Cambridge, UK. pp. 1–21.

Taborsky, M., and H. J. Brockmann (2010). Alternative reproductive tactics and life history phenotypes. In Animal behaviour: evolution and mechanisms. Springer, Berlin,

Germany. pp. 537–586.

Tallamy, D. W. (2000). Sexual selection and the evolution of exclusive paternal care in arthropods. Animal Behavior 60:559–567.

Tinbergen, J. M. (1987). Costs of reproduction in the Great Tit: intraseasonal costs associated with brood size. Ardea 75:111–122.

Trivers, R. L. (1972). Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man. Aldine, Chicago, pp136–179.

Tschumi, M, M. Schaub, and R. Arlettaz (2014). Territory occupancy and parental quality as proxies for spatial prioritization of conservation areas. PLoS ONE 9: e97679.

Van Balen, J. H. (1973). A comparative study of the breeding ecology of the Great tit *Parus major* in different habitats. Ardea 61:1–93.

Van De Pol, M., D. Heg, L. W. Bruinzeel, B. Kuijper, and S. Verhulst (2006). Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oystercatchers (*Haematopus ostralegus*). Behavior Ecology 17:982–991.

Verhulst, S., and R. A. Hut (1996). Post-fledging care, multiple breeding and the costs of reproduction in the great tit. Animal Behavior 51:957–966.

Verboven, N., and S. Verhulst (1996) Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. Journal of Animal Ecology 65:264–273.

Verboven, N., and M. E. Visser (1998). Seasonal variation in local recruitment of great tits: the importance of being early. Oikos 81:511–524.

Verboven, N., J. M. Tinbergen, and S. Verhulst (2001). Food, reproductive success and multiple breeding in the Great Tit, *Parus major*. Ardea 89:387–406.

Verhulst, S., J. H. van Balen, and J. M. Tinbergen (1995). Seasonal decline in reproductive success of the great tit: variation in time or quality? Ecology 76:2392–2403.

Verhulst, S., J. M. Tinbergen, and S. Daan (1997). Multiple breeding in the Great Tit. A trade-off between successive reproductive attempts?. Functional Ecology11:714–722.

Verhulst, S. (1998). Multiple breeding in the Great Tit: The costs of rearing a second clutch. Functional Ecology 12:132–140.

Visser, M. E., L. J. M. Holleman, and P. Gienapp (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172.

Waas, J.R., P. W. Colgan, and P. T. Boag (2005). Playback of colony sound alters the breeding schedule and clutch size in zebra finch (*Taeniopygia guttata*) colonies. Proceeding Royal Society London series B 272:383–388.

Walters, L. A., N. Olszewski, and K. Sobol (2014). Male House Wrens provide more parental provisioning to nests with a brighter artificial egg. The Wilson Journal of Ornithology 126: 508–515.

Weggler, M. (2006). Constraints on, and determinants of, the annual number of breeding attempts in the multi-brooded black redstart *Phoenicurus ochruros*. Ibis 148:273–284.

West, H. E., and I. Capellini (2016). Male care and life history traits in mammals. Nature

communications 7, 11854 doi:10.1038/ncomms11854.

Whelan, S., D. Strickland, J. Morand-Ferron, and D. R. Norris (2016). Male experience buffers female laying date plasticity in a winter-breeding, food-storing passerine. Animal Behaviour 121:61–70.

Wingfield, J. C., T. P. Hahn, M. Wada, and S. J. Schoech (1997). Effects of day length and temperature on gonadal development, body mass, and fat depots in white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. General and Comparative Endocrinology 107:44–62.

Winkler, D. W. (1987). A general model for parental care. American Naturalist 130:526–543.

Winkler, D. W., P. O. Dunn, and C. E. McCulloch (2002). Predicting the effects of climate change on avian life-history traits. Proceedings of the National Academy of Sciences of the USA 99:13595–13599.

Wolf, L., E. D. Ketterson, and V. Jr. Nolan (1991). Female condition and delayed benefits to males that provide care: a removal study. Auk 108:371–380.

Yuta, T., and I. Koizumi (2012). Long breeding season and high frequency of multiple brooding in Great tits in northern Japan. Ardea 100:197–201.

Yuta, T. (2013). Reproductive ecology of Japanese great tits focusing on extra-pair paternity. Ph.D. dissertation in Graduate school of Environmental Science, Hokkaido University.

Yuta, T., and I. Koizumi (2016). Does nest predation risk affect the frequency of extra-pair paternity in a socially monogamous passerine?. Journal of Avian Biology 47:153–158.