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Title	Testing the roles of visual preference in the evolution of white dot plumage patterns in Estrildid finches (Family Estrildidae)
Author(s)	,
Citation	. ( ) 15309
Issue Date	2023-03-23
DOI	10.14943/doctoral.k15309
Doc URL	http://hdl.handle.net/2115/91621
Type	theses (doctoral)
File Information	Ayumi_Mizuno.pdf

Doctoral Dissertation

Testing the roles of visual preference in the evolution of white dot plumage patterns in Estrildid finches (Family Estrildidae)

（カエデチョウ科鳥類の羽装の白い水玉模様と視覚選好の進化関係）

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A thesis submitted for the degree of

Doctor of Life Science

March 2023

学 位 論 文 内 容 の 要 旨

博士の専攻分野の名称　博士（生命科学）　氏 名 水野 歩

学 位 論 文 題 名

Testing the roles of visual preference in the evolution of white dot plumage patterns in Estrildid finches
(Family Estrildidae)
（カエデチョウ科鳥類の羽装の白い水玉模様と視覚選好の進化関係）

第1章　序論

　動物において，同種あるいは異種間での情報伝達をになう行動や形態は信号形質とよばれる．水玉模様は，代表的な信号形質の一つである．水玉模様とは，複数の丸い色パッチが規則正しく配置された模様を指し，捕食回避のための警告信号や，種内コミュニケーション信号（性的/社会的信号）として機能することがある．特に鳥類では，目立つ水玉模様は幅広い分類群の羽装にみられ，性的/社会的信号として使用する種もいる．羽装の水玉模様の進化に関しては，その機能的側面に過去の研究は焦点をあてており，進化的起源は不明である．本学位論文は，鳥類の羽装の水玉模様という信号形質の起源とその進化の解明に向け，感覚バイアス仮説に着目する．この仮説は，主に自然淘汰によってもたらされた感覚特性や選好（感覚バイアス）が，信号形質の起源にかかわると予測する．すなわち，採餌や捕食回避等のために特定の刺激への反応性を雌がもともと持っていた場合，その反応性を刺激する雄の性的信号の進化が促される．この仮説を支持する知見の多くは魚類において得られており，雄が体表に餌と似た模様を持つことで雌を惹きつけると報告されている．従来の感覚バイアス仮説では，雄が持つ信号形質に対する雌の感覚バイアスの関与が注目されてきた．しかし，自然淘汰によって進化した感覚特性は雌雄共通であり，雌雄相互的に機能する信号もあることから，感覚バイアス仮説は雌雄に共有される信号形質の進化をも説明できると期待される．

　カエデチョウ科鳥類は全体の約1/4種以上が雌雄とも羽装に白い水玉模様を持ち，一部の種では実際に信号として機能することが示されている．加えて本科は羽装の水玉模様と視覚特徴の似た餌を食性に持つ．本研究はカエデチョウ科の羽装における白い水玉模様の進化に対する採餌由来の視覚選好の寄与に焦点を当て，行動実験と系統種間比較を行う．第2章では食性と羽装の白い水玉模様の進化関係を系統種間比較により検討する．第3章では本科の1種コモンチョウ *Neochmia ruficauda* の行動実験により，水玉模様への視覚選好を調査する．第4章では白い水玉模様への視覚選好が羽装の水玉模様の進化に先行することを予測し，カエデチョウ科の鳥種網羅的な行動実験に系統種間比較解析をあてはめ推定する．

第2章　羽装の白い水玉模様とシロアリ食の進化関係

　羽装の白い水玉模様が採餌に起因する視覚特性と関連して進化したと予測した．カエデチョウ科の一部は，シロアリのような白くて粒状の無脊椎動物を好んで採餌する．この食性と白い水玉模様の進化関係を，系統関係を考慮した種間比較解析により検討した．文献資料に基づき，カエデチョウ科全種に関するシロアリ食性（シロアリやアリの卵・蛹・幼虫を食べるか），羽装の水玉模様の有無と直径を解析に用いた．その結果，水玉模様とシロアリ食性は非独立に進化しており，

水玉模様を羽装に持つ種はシロアリ食性に進化しやすく，持たない種はシロアリ食性に進化しにくいことが明らかとなった．なお，この傾向は雌雄でほぼ一貫していた．このことからカエデチョウ科の雌雄でみられる羽装の白い水玉模様の進化とシロアリ食性は進化的に関連しており，それは白い粒状の視覚刺激に対する選好に促された可能性がある．

第3章　コモンチョウの白い水玉模様に対する視覚選好
　カエデチョウ科鳥類は白い水玉模様に対して視覚選好を持つ可能性がある．特に，第2章の知見とその羽装の白い水玉模様をふまえ，コモンチョウ *Neochmia ruficauda* では特に，水玉選好が顕著であると期待される．視覚選好の検討のため，黒地に白い水玉模様あるいは縞模様が印刷された刺激（水玉刺激と縞刺激）を対呈示する行動実験を実施した．視覚選好が採餌とかかわる可能性が高いため，餌なし条件と，それに続く餌あり条件とをもうけ，両刺激への選好注視反応を計測した．その結果，コモンチョウは両条件下で白い水玉刺激に対して高い視覚選好を示した．すなわち，先行する餌なし条件で水玉刺激が餌ではないと学習する機会があったにもかかわらず，餌あり条件でも，水玉刺激に対して強烈な視覚選好をコモンチョウは呈したことになる．あわせて餌なし条件では，水玉刺激への採餌様行動もみられた．これらは，水玉選好が即時的経験に上書きされない内在的傾向であり，かつ，採餌欲求によって強化されることを示唆している．なお，一連の水玉刺激への選好注視反応には，雌雄で大きな違いは確認されなかった．

第4章　共通祖先形質としての白い水玉模様への視覚選好
　感覚バイアス仮説に基づくならば，白い水玉模様への視覚選好は羽装の水玉模様の進化に先行して存在すると考えられる．すべてのカエデチョウ科鳥類は穀類食であることから，穀類採餌に由来する白い水玉模様への視覚選好をこれらの種の共通祖先種は持ち，その視覚選好が本科の雌雄共通な信号形質である羽装模様の進化に寄与した可能性がある．あるいはそうではなく，共通祖先種にはなかった視覚選好が，シロアリ食性や水玉羽装を持つ特定の現生種のみで進化した可能性もある．そこで羽装に水玉模様を持つ種・持たない種，シロアリ食性である種・ない種を含むカエデチョウ科12種に対し，第3章と同じ手法で白い水玉模様への視覚選好を計測した．得られた行動データを系統関係を考慮した種間比較によって解析し，信号形質の進化に選好の存在が先立つかを検討した．結果は白い水玉模様への共通祖先種が持っていたことを裏付けるものであった．全体的な傾向として，餌なし条件下では縞刺激よりも水玉刺激を好んで注視し，明らかな性差は存在しなかった．また，水玉刺激への選好注視反応はシロアリ食性や羽装の水玉模様による正・負どちらの影響も受けていなかった．その一方，餌あり条件では刺激間での反応差は認められなかった．これらの結果は，カエデチョウ科の雌雄に共通する水玉模様の進化に関し，感覚バイアス仮説を支持する．

第5章　結論
　感覚バイアス仮説はさまざまな信号形質の進化を説明してきたが，本研究によって初めて，鳥類の羽装模様への援用可能性が示された．得られた知見から，本来ならば採餌のための視覚選好が，副次的効果としてカエデチョウ科鳥類の羽装の白い水玉模様の進化を促したと考えられる．従来の感覚バイアス仮説では，雄の性的信号と雌の感覚バイアスの進化関係ばかり着目されてきた．しかし本研究は，雌雄共通な信号の進化についても感覚バイアス仮説から説明しうることを示した．鳥類は羽の色にも模様にも著しい種間多様性がみられる．その進化に関し本研究は，これまで議論されてこなかった羽装模様の進化的起源に光をあて，新たな視座を与えた．

CONTENTS

GENERAL INTRODUCTION

Animals use a wide variety of signalling traits, such as bright colours and conspicuous patterns, to convey information to others (Andersson 1994; Hebets and Papaj 2005; Osorio and Vorobyev 2008; Laidre and Johnstone 2013; Hutton et al. 2015; Caro and Allen 2017; Cuthill et al. 2017). Dot patterns are one of the most widespread signalling traits in living things as either aposematic signals in interspecific interaction (Lev-Yadun 2009; Stevens and Ruxton 2012) or sexual/social signals in intraspecific communication, such as mate choice or social dominance (reviewed in Pérez-Rodríguez et al. 2017). This means that dot patterns can evoke aversion or attraction depending on the context, and the species of the signaller and receiver of dot signals. For example, dot patterns covering the entire body are known to function as warning signals against predators in ladybugs *Coccinella septempunctata* (Průchová et al. 2014) or in poison frogs *Dendrobates pumilio* (Siddiqi et al. 2004; Darst et al. 2006; Maan and Cummings 2012), whereas polymorphic dot patterns also contribute to individual recognition and mate choice in poison frogs (Summers et al. 1999; Siddiqi et al. 2004; Reynolds and Fitzpatrick 2007; Maan and Cummings 2008, 2009; Crothers et al. 2011). However, the functions of dot patterns have been studied in limited species compared with the vast numbers and diversity of animal species displaying dot patterns, leaving their evolution unresolved. In particular, it remains unclear why dot patterns have evolved as attractive social signals.

In birds, plumage dot patterns are very common (Somveille et al. 2016; Mason and Bowie 2020), and some of them are known to function as signals both under sexual/social contexts (Alatalo et al. 1992; Roulin 1999; Crowhurst et al. 2012; Zanollo et al. 2012; Soulsbury et al. 2016; Soma and Garamszegi 2018). Individual birds with more conspicuous dot patterns (e.g., larger number of dots, or higher reflectance dots) can gain higher mating success (barn owls *Tyto alba*, Roulin 1999) or social dominance

GENERAL INTRODUCTION

(diamond firetails *Stagonopleura guttata*, Crowhurst et al. 2012; Fig. I-1a), suggesting that dot patterns, like other ornamental traits, evolved as signals as they reflect the quality of individuals owing to the production costs (Zahavi 1975, 1977; Andersson 1986; Grafen 1990). However, the cost associated with plumage dots is puzzling. Dot patterns usually appear as either achromatic spots on melanin-based feathers or melanin spots on whitish feathers. White plumage is known to require some maintenance cost to avoid bacterial growth, parasites (Kose and Møller 1999; Ruiz-de-Castañeda et al. 2012) or abrasion (Griggio et al. 2011), while melanin-pigmented plumage also incurs production and maintenance cost (McGraw et al. 2002; Galván and Alonso-Alvarez 2008; Piault et al. 2012; Guindre-Parker and Love 2014; Roulin 2016). Therefore, these traits can reflect immune challenges (Hanssen et al. 2008), hormone levels (Moreno and López-Arrabé 2021) or diets of individuals (McGlothlin et al. 2007). Even so, it is not clear whether having dots on plumage is more costly than total white or black plumage. Presumably, white spots may save resources for pigment production (Prum et al. 1999), but that does not explain why colourless parts take a particular shape (e.g., circle) and the same could be said for melanin spots as well.

As an alternative to the condition dependence mechanisms, which explain signalling traits have evolved as indicators of individual quality, the sensory bias hypothesis (Ryan and Keddy-Hector 1992; Endler and Basolo 1998; Ryan 1998; Rodríguez and Snedden 2004; Fuller et al. 2005; see details Appendix) could possibly explain the evolution of dot patterns as signals. This hypothesis attempts to explain why specific traits evolved as mating signals, by focusing on female sensory preferences shaped under natural selection (Ryan and Keddy-Hector 1992; Endler and Basolo 1998; Ryan 1998; Rodríguez and Snedden 2004; Fuller et al. 2005; Fuller and Endler 2018). If particular characteristics are detected easily and perceived clearly by females, they can more likely be used as mate choice criteria than other less detectable/perceivable traits (Endler 1992; Ryan 1998). The hypothesis posits that signallers derive reproductive

benefits from attracting the pre-existing sensory bias of receivers, originally shaped for foraging or predator avoidance (Ryan 1990, 1998; Ryan and Keddy-Hector 1992; Endler and Basolo 1998; Rodríguez and Snedden 2004). Typically, if males have traits that mimics food, they become successful in mating by attracting females that have a sensory bias for the food that is being mimicked. In this way, males may have evolved sexual traits that attract the attention of females by stimulating pre-existing sensory systems of females (Ryan 1990, 1998; Endler and Basolo 1998). For example, in water mites *Neumania papillator*, males send vibratory signals that mimic those from their prey species to solicit female hunting response, leading to successful spermatophore transfer (Proctor 1991, 1992). A similar scenario can explain the evolution of colour pattern of body surface in some fish, such as guppies Poecilia reticulata, several Goodeinae species or African cichlids, where males attract females by having colour patterns that resemble foods that they prefer (Rodd et al. 2002; Garcia and Ramirez 2005; Egger et al. 2011). However, in birds, the idea that sexual ornament traits evolved from diet-related preferences has not been well tested. Exceptionally in bowerbirds (Ptilonorhynchidae), the colour of the decorations of these birds used for male courtship was claimed to match with female colour preference when foraging (Madden and Tanner 2003; but see also Borgia and Keagy 2006). In addition, in male jungle fowls *Gallus gallus*, their wattle ornamentations function for enhancing food-related visual displays (Schenkel 1958; Stokes and Williams 1971; Smith et al. 2009).

The sensory bias hypothesis yields the following three main predictions. First, signal features can be explained in the light of sensory system properties of signal receivers, i.e., females (e.g., Ryan et al. 1993; Endler and Basolo 1998; Fuller and Endler 2018; Rosenthal 2018). Second, such signals can readily draw attention of females (e.g., Ryan and Cummings 2013). Finally, females should prefer to mate with males bearing such signal traits (e.g., Basolo 1990a, 1990b; Ryan and Rand 1990; Rodd et al. 2002; Garcia and Ramirez 2005). Although these predictions are usually applied to

explain the evolution of male signalling traits via female mate choice, the same explanations could be possible for the evolution of social signals that are used in social situations like group foraging, or sexual signals that are used for mutual mate choice. Considering that males and females evolved to have similar sensory systems, both sexes may show similar sensory preference towards particular stimuli, which can facilitate the signal evolution in any social contexts, including dominance interaction or individual identification.

Estrildid finches (family Estrildidae) are good subjects to test the idea that diet-related sensory bias contributed to the evolution of plumage colour patterns. Estrildid finches are gregarious socially monogamous songbirds with varying degrees of coloniality and plumage dichromatism (Goodwin 1982). In over 25% of Estrildid species, both males and females have white dot plumages, which have been suggested to have served a signalling function (Soma and Garamszegi 2018; see examples in Fig. I-1). Specifically, they show social and sexual displays in a close distance, often on the same perch (Goodwin 1982; Soma and Garamszegi 2015), where dots on the flank (Fig. I-1) could serve as a clue for individual identification or social/sexual signals. Supporting this idea, a species of Estrildid finch, diamond firetails *S. guttata* (Fig. I-1a), has white dot patterns on its flank, and the number of dots is associated with its physical condition (Zanollo et al. 2012) and social dominance in females (Crowhurst et al. 2012).

Aims

As a first attempt to understand the evolutionary relationships between foraging-related visual preference and plumage dot patterns in birds, I aimed to investigate the possible role of sensory bias in the evolution of plumage patterns in Estrildid finches. The phrase "sensory bias" has two meanings: species have high sensitivity to a particular stimulus, or species pay attention to a particular stimulus (Fuller et al. 2005). In this thesis, I

focused on this second facet and tested whether Estrildid finches have visual attention or visual preference (sensory bias) for white dot patterns. Chapter 1 examined the evolutionary relationship between diet and white dot plumage patterns using phylogenetic comparative approaches, predicting that the visual bias that helps foraging is responsible for plumage pattern evolution. In Chapter 2, I tested the visual preference for white dot patterns by conducting preferential-looking tests using star finches *Neochmia ruficauda* (Fig. 2-2a) with conspicuous white dot plumage patterns, a species of Estrildid finches. In Chapter 3, I conducted behaviour experiments using the same protocols used in Chapter 2 and phylogenetic comparative analyses to examine whether the visual preference for white dot patterns is a pre-existing sensory bias.
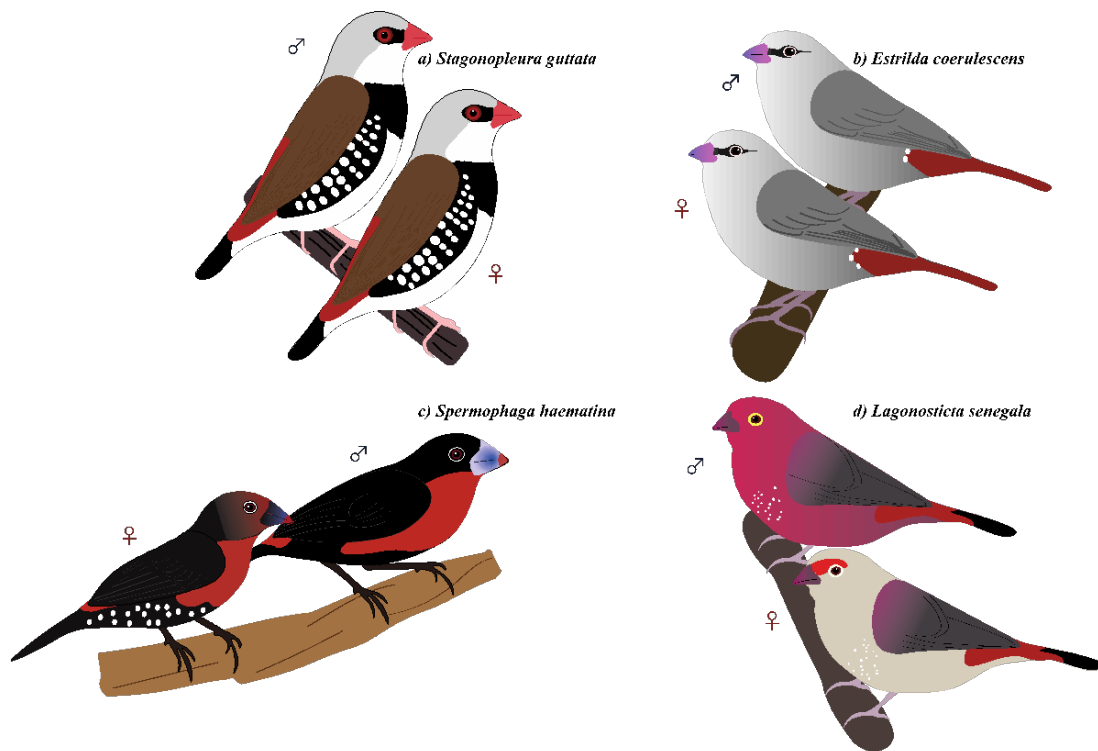
Figure I-1. Examples of interspecific variations and sexual differences in plumage patterns of Estrildids (a-d). (a) In diamond firetails *S. guttata*, females have more white dots than males (Crowhurst et al. 2012), where the number of dots reflects the physical condition (Zanollo et al. 2012) and social dominance of females (Crowhurst et al. 2012). (b) In lavender waxbills *Estrilda coerulescens*, both males and females have only a few white spots on their under tail-coverts. (c) In western bluebills *Spermophaga haematina*, females have white dot patterns. (d) In red-billed fire finches *Lagonosticta senegala*, although the body colour is greatly different between males and females, both sexes have almost invisible white dots along their flank and chest.

CHAPTER 1 The evolutionary relationships between termite-eating and white dot plumage patterns

Introduction

Birds are characterised by conspicuous or cryptic plumage patterns, which are likely to have evolved for intraspecific communications or as a result of predator-prey interactions, respectively (Roulin 1999; Bortolotti et al. 2006; Gluckman 2014; Marshall and Gluckman 2015; Soma and Garamszegi 2018). The signalling function of patterns is often explained in light of honest indicator mechanisms, which propose that vivid colours or distinct patterns are possessed by individuals with better conditions as honest signals of an individual's quality. Supporting this view, in zebra finches *Taeniopygia guttata*, black and white stripes on the chest of the males represent early nestling diets (Birkhead et al. 1999), and females prefer males with symmetric chest stripes (Swaddle and Cuthill 1994). Similarly, in common waxbills *Estrilda astrild*, the regularity of barred plumage reflects body condition, especially in adult males (Marques et al. 2016).

What has remained a mystery until now is why a particular type of plumage patterns (e.g., colour combinations or shape of the pattern motif, such as dots) evolved in each species. In order to gain an evolutionary understanding of the plumage colour patterns of different birds, it would be of help to investigate the role of foraging-related sensory bias. Prey-like colour patterns are known to have evolved in fish (Rodd et al. 2002; Garcia and Ramirez 2005), which could be explained by deception mechanisms that predict male signal traits exploit female sensory systems and females suffer costs, and can also solely be attributed to shared visual mechanisms beneficial for the detection of foods and the identification of conspecifics (sensory bias). Male traits explained by the sensory bias hypothesis may even evolve as honest indicators (Garcia

and Ramirez 2005). Having sensitivity for a particular colour may contribute to the successful foraging of food and the identification of conspecifics in the same colour. For a similar reason, being able to see or pay attention to small dots or stripes (higher visual acuity) can help in both the visual detection of small/thin prey items and the identification of finely patterned conspecific individuals. Therefore, here, I predict that a sensory bias for termite-eating may have caused the evolution of white dot patterns in Estrildids.

I hypothesised that these white dot patterns evolved due to a sensory bias that facilitates foraging behaviour for whitish small round prey often found in swarms, such as termites and ant larvae or eggs. Actually, red-headed finches *Amadina erythrocephala* are known to take harvester termites *Hodotermes mossambicus*, and star finches *Neochmia ruficauda* eat giant northern termites *Mastotermes darwiniensis* (Goodwin 1982). Uraeginthus spp. also eat Odontotermes (Hamed and Evans 1984) or Macrotermes (Yamashina 2014). In captivity, western bluebills *Spermophaga haematina* eat house fly maggots *Musca domestica* (Goodwin 1982). These prey are regularly consumed in some Estrildid species, as they ensure the protein intake needed for the breeding season is met. However, Estrildid finches are generally grain-eaters.

In this chapter, I tested my hypothesis that white dot patterns in Estrildid finches evolved in species foraging small, round, white gregarious insects by using phylogenetic comparative approaches. First, I performed ancestral state reconstruction on white dot patterns and eating termites (including other gregarious round invertebrates) to determine whether foraging preceded the evolution of sexual characteristics, as is often depicted in notable examples of sensory bias (e.g., Ryan 1998). Second, I examined the correlation between the evolution of white dot patterns and termite-eating using phylogenetic regression models. Finally, I tested the evolutionary transition between the two traits (i.e., termite-eating and white dots).

Materials and methods

Data collection

The diet of 134 Estrildid species was collected using information from "Estrildid Finches of the World" (Goodwin 1982) and "Handbook of the Birds of the World, Vol. 15" (Payne 2010). I verified whether each species feeds on whitish round gregarious forms of invertebrates, which included termites and the eggs, larvae, and pupae of ants, but did not include winged-termites because of their colour, shape, and mobility. For convenience, those species that were found to feed on round invertebrates will be denoted as termite-eaters hereafter. Furthermore, to consider the alternative possibility, that the invertebrate protein diet influences the plumage patterns regardless of the colour and shape of the prey, I checked whether each species feeds on any invertebrates, which included ants, spiders, caterpillars, and worms (referred to as invertebrate-eaters, hereafter). Each Estrildid species was categorised as a termite-or non-termite eater, and an invertebrate-or non-invertebrate eater, wherein invertebrate-eating species encompassed all termite-eating species. I was unable to add specific information about each species, such as species variation and sex/individual differences in feeding behaviour and seasonality, due to the limited amount of information provided in the literature. It should also be noted that the above categorisations (i.e., termite-eater and invertebrate-eater) included only those species regularly consuming each diet. In other words, such species consume these small invertebrates frequently enough to be listed in the literature that describes the diet of Estrildids.

I collected data on the presence/absence of white dot patterns in 134 species of Estrildid finches based on the descriptions of the above two books (Goodwin 1982; Payne 2010). Dot patterns were defined as white dots appearing regularly and repeatedly on plumage, as the members of this family of birds do not ever have black or red dots. I scored the presence and absence of these dot patterns as 1 and 0, respectively.

**CHAPTER 1 The evolutionary relationships between termite-eating
and white dot plumage patterns**

The plumage of males and females within a species was checked separately since some species have plumage dichromatism. Additionally, I scored the conspicuousness of dots by taking the diameter of the dots (in cm) in both males and females based on the data obtained from Soma and Garamszegi (2018), in which the diameter was scored as 0 for species without dots. The dot diameter was chosen as the representative of conspicuousness because it is positively correlated with the area of body surfaces where plumage patterns exist (Soma and Garamszegi 2018). Although some Estrildids have UV vision (Ödeen and Håstad 2003), there was no pattern in the nonvisible part of the spectrum that was apparent only under UV light (Soma and Garamszegi 2018). As males and females can differ with respect to the presence of white dot patterns, I repeated the analyses for male and female datasets, which scored the presence of dots in males or females of each species respectively. The same analyses were also carried out for the species dataset used to score for the presence of dots on either or both sexes.

Phylogeny

For the phylogenetic comparative analyses, I used multiple alternative trees from https://birdtree.org (Jetz et al. 2012), which was sufficient to control for the phylogenetic uncertainty for my analyses. I used 1000 trees from the dataset for the analyses described in the following section.

Phylogenetic comparative analyses

Ancestral state reconstruction

To determine the evolutionary history of diet (termite-eating and invertebrate-eating) and white dots in male and female Estrildid finches, I performed ancestral state reconstructions. I used the maximum-likelihood method using the R package "phytools" (Revell 2012), wherein 1000 phylogenetic trees were used repeatedly for ancestral state

reconstruction. The outcomes were averaged to calculate the likelihood of common

ancestral states. When averaging each likelihood, I weighted the parameter estimates

based on the AIC of the respective model corresponding to an individual tree

(Garamszegi and Mundry 2014).

Regression models

To elucidate the phylogenetic relationship between white dots and termite-eating, I built

regression models in two ways. First, to test whether termite-eating affects dots, I

conducted phylogenetic logistic regression analysis using the function phyloglm in the

R package "phylolm" (Ho et al. 2018). In the phylogenetic logistic regression models,

termite-eating or invertebrate-eating were used as explanatory variables, while the

presence/absence of white dots in each sex was used as a response variable, using the

male and female datasets. I used the same set of 1000 phylogenetic trees as those used

for the ancestral reconstructions, from which I obtained the model-averaged mean

coefficients, standard errors (SEs), and 95% confidence intervals (CIs). When averaging

the models, I weighted the parameter estimates based on the AIC of the respective

model corresponding to an individual tree (Garamszegi and Mundry 2014). Second, I

tested whether dot conspicuousness affects termite-eating using the male and female

datasets. I fitted Phylogenetic Generalized Least Squares (PGLS) regressions, in which

white dots size was used as an explanatory variable and the termite-eating/invertebrate-

eating was used as a response variable using the R packages "ape" (Paradis and Schliep

2018) and "caper" (Orme et al. 2018). I repeatedly fitted the same model using each of

the 1000 phylogenetic trees and obtained the mean and CI for the estimated parameters

by model averaging the 1000 outcomes. To average 1000 outcomes, I used parameters

weighted by AIC for each model corresponding to an individual tree (Garamszegi and

Mundry 2014). All analyses were carried out in R 3.5.1 (R Core Team 2018).

Evolutionary transition analyses

To estimate the evolutionary transitions between the presence/absence of white dots in association with the presence/absence of termite-eating, I used discrete modules of the maximum likelihood function of BayesTraits V 3.0.1 (Meade and Pagel 2017). Firstly, I compared a dependent model, wherein white dots and termite-eating evolved dependently, with an independent model, wherein these traits evolved independently. Secondly, I investigated the direction of the significant evolutionary transition by sequentially restricting all eight possible changes in the character state of the dependent model to zero and comparing these to the original model. Statistical significance of model comparisons was determined using likelihood ratio tests (LR tests), with α set at 0.05 ($P < 0.05$). Likelihoods were estimated using 1000 optimisation attempts per run. I reported the model-averaged estimates from 1000 alternative trees based on the log-likelihood of the model. In addition, to investigate whether eating invertebrates affects the presence of white dots regardless of their shape or colour, I also ran the same analyses for the transitions between invertebrate-eating and white dots. These analyses were repeatedly performed using species or male/female datasets for dots.

Results

Among the 134 Estrildid finches, 30 species had white dots in both sexes, while a few species showed male-biased or female-biased sexual dichromatism in the presence of dots. Specifically, the females of 34 species and the males of 31 species in total had white dots. Sixty-one species of Estrildids (46%) are termite-eaters. More than 65% of the termite-eaters had white dot patterns on their plumages (females: 23 out of 34 species, males: 21 out of 31 species), whereas less than 40% of the non-termite eating species had white dots (females: 38 out of 98 species, males: 40 out of 101 species).

18

Ancestral state reconstruction

The ancestral states for termite-eating were unclear, since the reconstruction showed that the likelihood of having each trait was almost equal to that of lacking it (proportional likelihood of termite-eating = 0.517; Fig. 1-1b). On the other hand, common ancestor was found to have a high likelihood of invertebrate-eating (proportional likelihood of invertebrate-eater = 0.989). The estimated ancestral state for white dots revealed that common ancestor did not have white dot plumage patterns (proportional likelihood of white dots on both sexes = 0.051; Fig. 1-1a, proportional likelihood of white dots on males = 0.039, proportional likelihood of white dots on females = 0.042).

Correlations between white dots and diets

Using the male and female datasets, I performed two sets of regression models, testing the effects of diet on the presence of white dots, and the effects of dot size on diet. I did not find a significant effect of termite-eating on the presence of white dot patterns on their plumages (Table 1-1). Likewise, I did not find a significant effect of invertebrate-eating on the presence of white dots (Table 1-1). Conversely, I found that the diameter of white dot had a significant positive effect on the presence of termite-eating in Estrildids (Table 1-2a, Fig. 1-2), while invertebrate-eating was not affected by the diameter of white dot (Table 1-2b).

Evolutionary transitions

The evolutionary transition analyses supported the idea that white dots and termite-eating evolved significantly dependently at the species level (species datasets: average LR = 11.176, df = 4, P = 0.025; Fig. 1-3). When I conducted the same analyses in males and females separately, I found that these two traits evolved dependently in the female dataset, but not in the male dataset (female dataset: average LR = 10.265, df = 4, P =

0.036, male dataset: average LR = 8.769, df = 4, P = 0.067). There was no statistically

significant difference between the evolutionary models that white dots and invertebrate-

eating evolved independently, and those models that evolved dependently (species

datasets: average LR = 6.766, df = 4, P = 0.149). Further evolutionary transition

analyses on the species dataset revealed that white dot patterns caused the evolution of

termite-eating, but not vice versa (Fig. 1-3). When Estrildids were termite-eaters, the

evolutionary transitions between the presence and absence of white dots were not

statistically significant (gaining white dots: average LR = 0.176, df = 1, P = 0.675,

losing white dots: average LR = 1.294, df = 1, P = 0.740; Fig 1-3). Similarly, when

Estrildids were non-termite eaters, the evolutionary transitions between the presence

and absence of white dots were not statistically significant (gaining white dots: average

LR = 1.252, df = 1, P = 0.263, losing white dots: average LR = 1.294, df = 1, P = 0.255;

Fig. 1-3). However, Estrildids with white dot plumages were more likely to become

termite-eaters than non-termite eaters (Fig. 1-3). Estrildids without white dot patterns

were more likely to become non-termite eaters than termite-eaters (Fig. 1-3).

Discussion

The results obtained from this phylogenetic comparative study partially support the idea

of the sensory bias hypothesis that white dot patterns in Estrildids have evolved due to

the sensory bias that facilitates termite-eating. Estrildid finches with conspicuous white

dots (i.e., larger dots) were found to tend to be termite-eaters (Table 1-2). Moreover, the

evolutionary transition analyses revealed that species with dot patterns were likely to

become termite-eaters, while those without dots were likely to lose the behaviour of

termite-eating (Fig. 1-3). The evolutionary process revealed from the present study is in

contrast with the prediction made using the sensory bias hypothesis that diet promotes

the evolution of visual signals. These results are rather unexpected, but do not deny the

possible role of sensory bias on diet and plumage patterns. Sensory systems that help visual detection or individual identification of conspecifics with dot patterns are likely to be useful for foraging on small gregarious invertebrates appearing as repeated dots, and beneficial for protein-rich nutrients (Goodwin 1982; Payne 2010). In addition, I cannot deny the possibility that detected evolutionary transitions might be affected by the limit of information regarding termite-eating.

Although I found a relationship between white dots and termite-eating, it is not probable that white dots directly reflect the dietary nutrition obtained from termites or other invertebrates. White feathers are structurally colourless and made of unpigmented feather keratins, and are therefore assumed to require fewer resources for their production, compared to the feathers of carotenoid- or melanin based plumages (Jawor and Breitwisch 2003; Prum 2006). However, it is also unlikely that white plumage ornamentations do not require any maintenance. White feathers are known to be more susceptible to parasites and abrasion than feathers with melanin (Swaddle and Witter 1995; Kose and Møller 1999; Griggio et al. 2011), which is the reason why white plumage serves as an ornamentation that is a good indicator of the individual's condition. For example, the whiteness of the tail patches in male dark-eyed juncos *Junco hyemalis* are affected by the quality of their diet (McGlothlin et al. 2007), with whiter males also having larger body sizes and have greater mating success (McGlothlin et al. 2005). In Estrildid finches, Diamond firetail *S. guttata* females have more white dots along their flanks than males on average (Zanollo et al. 2014; Fig. I-1a). The number of dots is representative of the physical condition (Zanollo et al. 2012) and predicts feeding dominance in females (Crowhurst et al. 2012). Although the expression of white dots is likely to be low cost, it may incur a maintenance cost, such that white dots can be considered as a good indicator, as reported in diamond firetails *S. guttata* (Crowhurst et al. 2012; Zanollo et al. 2012, 2014). I also assume that it is unlikely that the white dots of Estrildids evolved for the purpose of camouflage. In Estrildids, dots

appear mainly on the ventral side, and in some species dots are tiny and small in number (Fig. I-1b and I-1d), which would be ineffective for camouflage.

Within the literature on the sensory bias hypothesis (Ryan 1990, 1998; Endler and Basolo 1998), few studies have investigated the possibility of female traits evolving in parallel with male traits (e.g., Funk and Tallamy 2000). It is often the case that females are considered to be exploited by males (e.g., Endler and Basolo 1998). However, considering that males and females are likely to share the same sensory systems for foraging and surviving, both sexes may be attracted by similar stimuli. For example, in some Goodeinae species, in which males have terminal yellow bands (TYB) on their tails, used to attract the females by exploiting their prey-detection system (Garcia and Ramirez 2005), both males and females have been found to bite tails with conspicuous TYB (Garcia and Ramirez 2005). This indicates that mutual deception may lead to the evolution of prey-like patterns in both sexes. Otherwise, sensory systems shared between sexes also explain the evolution of mutual ornamentations that do not involve any deception scenario, especially when such ornamentations are used for individual recognition and social signalling. This idea is supported by the fact that white dotted patterns are found in both sexes in many Estrildid species, where only a few species have sexually biased white dots (i.e., where only the males or females have white dots). Furthermore, females often have more dots than males in an Estrildid species (Zanollo et al. 2012; Fig. I-1a). As such, the white dot ornamentations found on the plumage of Estrildids may play an important role in recognizing conspecifics in addition to their function as sexual signals.

Figures and Tables

Figure 1-1. Ancestral reconstructions of (a) white dot plumage patterns and (b) termite-eating by maximum likelihood reconstruction.
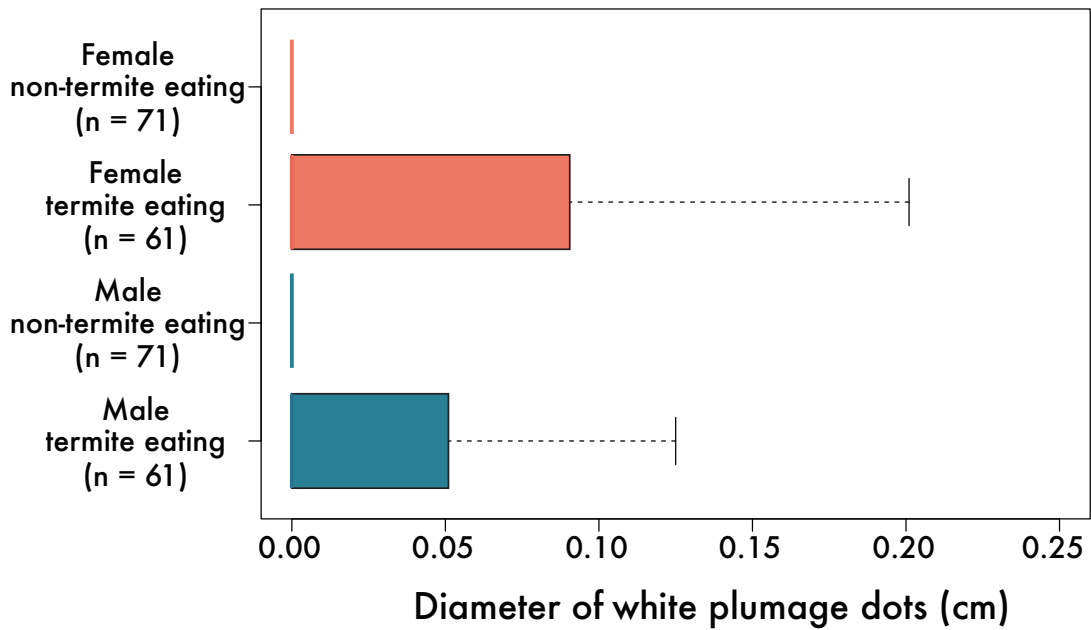
Figure 1-2. Comparison of male and female white dots sizes between termite-eater and non-termite eater species. Although termite-eating (vertical axis) is included, the diameter of the white dots in 11 species of females is unknown due to a lack of measurable specimens. The same is true for 10 species of males. Species without dots are shown the graph as "0.00 cm". All box plots denote quartiles.

Figure 1-3. Evolutionary transitions for the presence/absence of white dots in termite-eaters and non-termite eaters. There are four possible trait states with eight potential transitions among them (gains and losses for each): black-filled arrows illustrate the significant evolutionary transitions of these traits, while grey-dashed arrows show non-significant evolutionary transitions.

CHAPTER 1 The evolutionary relationships between termite-eating and white dot plumage patterns

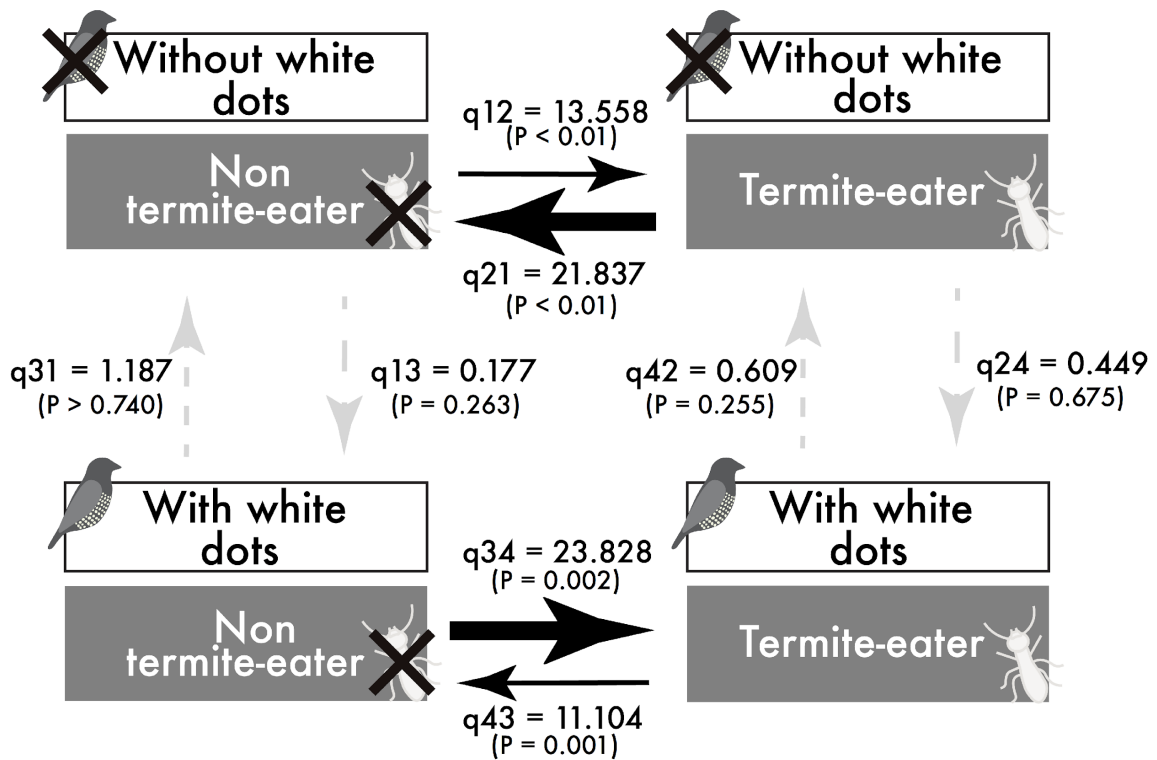**Table 1-1.** The effect of diet (either termite or invertebrate eating) on the presence of dots in (a) males and (b) females estimated using phylogenetic logistic regression analysis.

Response variable	Explanatory variable	Coefficient	SE	95%CI
(a) Male white dots	Intercept (Termite-eater)	−1.043	0.727	(−2.497, 0.411)
	Termite-eater	0.296	0.305	(−0.314, 0.906)
	Intercept (Invertebrate-eater)	−1.035	0.775	(−2.586, 0.516)
	Invertebrate-eater	0.011	0.245	(−0.578, 0.500)
(b) Female white dots	Intercept (Termite-eater)	−0.865	0.673	(−2.210, 0.481)
	Termite-eater	0.167	0.258	(−0.348, 0.683)
	Intercept (Invertebrate-eater)	−1.036	0.695	(−2.426, 0.354)
	Invertebrate-eater	0.017	0.247	(−0.478, 0.511)

Table 1-2. The effects of the white dot size (either males or females) on (a) termite-eating and (b) invertebrate-eating estimated using phylogenetic generalised least-square models. Significant effects of white dot size on (a) termite-eating, not (b) invertebrate-eating. Bold typeface is used when 95% confidence interval (CI) does not contain zero; therefore, it can be shown as a significant effect.

Response variable	Explanatory variable	Coefficient	SE	95%CI
(a) Termite eating	Intercept (Male dot size)	0.424	0.102	(0.223, 0.625)
	Male white dot size (cm)	**2.197**	**0.901**	**(0.430, 3.963)**
	Intercept (Female dot size)	0.421	0.101	(0.223, 0.619)
	Female white dot size (cm)	**2.456**	**0.835**	**(0.820, 4.092)**
(b)Invertebrate eating	Intercept (Male dot size)	0.803	0.092	(0.984, 0.622)
	Male white dot size (cm)	0.936	0.767	(− 0.567, 2.439)
	Intercept (Female dot size)	0.095	0.610	(0.610, 0.984)
	Female white dot size (cm)	1.034	0.727	(− 0.391, 2.459)

27

CHAPTER 2 Visual preference for white dot patterns in Star finches *Neochmia ruficauda*

Introduction

The results of chapter 1 indicated the role of foraging-related visual preference in the evolution of plumage patterns shared between the sexes of Estrildid finches. Males and females of many species of Estrildid finches are characterised by conspicuous white dot patterns with signalling functions (Crowhurst et al. 2012; Zanollo et al. 2012; Soma and Garamszegi 2018), which evolved in association with a diet with spotty appearance (Fig. 1-3, Table 1-2a; Mizuno and Soma 2020). Specifically, the species that regularly consume whitish small round gregarious prey, such as termites and ant larvae or eggs (Goodwin 1982; Payne 2010), tend to have white dot patterns (Fig. 1-3; Mizuno and Soma 2020). In addition, their white dot patterns often cover the flanks but not the whole body (Morris 1958; Somveille et al. 2016; Soma and Garamszegi 2018), meaning that dots can attract attention in close distance communication, especially when Estrildid finches perform bilateral courtship display perching side by side (Goodwin 1982; Payne 2010). In such species, males are known to fluff up and fully display their dotted plumage during courtship display (Goodwin 1982; e.g., Fig. 2-1). Having a visual preference for white dots would be crucial for both signalling communication and foraging in Estrildid species with dotted patterns. This could be applied to both sexes, explaining the evolution of mutual ornamentation associated with diet sensory preference (Chapter 1; Mizuno and Soma 2020). Consistent with this idea, in a species of Estrildid fiches, diamond firetails *Stagonopleura guttata*, the number of dots is associated with the physical condition (Zanollo et al. 2012), and social dominance in females (Crowhurst et al. 2012).

In this chapter, I expected that the Estrildid species with white dot patterns would show strong visual attention to white dots. To test this, I presented abstract dot patterns to the star finch *Neochmia ruficauda* (Fig. 2-2a), an endemic Australian Estrildid finch (Goodwin 1982; Payne 2010). Both sexes have conspicuous plumage dot patterns, and the species derives its name from a striking pattern of white dots (stars) on the red face and olive-green flanks. Visual attention to white dots can affect individual fitness in two ways. First, plumage dots in the species are highly likely to function as sexual and social signals (Crowhurst et al. 2012; Soulsbury et al. 2016; Soma and Garamszegi 2018), considering the sexual and among-individual variations in dot patterns. Second, images of dot patterns can indicate the presence of food sources, such as tiny seeds and termites (Goodwin 1982; Payne 2010).

Therefore, I expect both hunger-related and hunger-neutral visual preferences for dot patterns in the star finch *N. ruficauda*. In other words, hungry individuals would pay attention to dots, looking for foods, while non-starving individuals would also pay attention to dots because of their potential roles in social/sexual signalling. Considering the moderate sexual difference in the size of facial dot pattern areas (Goodwin 1982; see also Fig. 2-2a), I predict that males and females differ slightly in their responses to dot patterns. I prepared monochrome printed images of white dots and stripes as a matching stimulus and presented them simultaneously first under food-deprived conditions and then under food-supplied conditions to test their visual preference towards dots. If dot preference exists, the subject birds would show stronger responses towards dot stimuli than stripes. If such preference is related to diet, the subject birds would show more visual attention towards dots in the food-deprived condition than in the following food-supplied condition. They would also show less or no foraging-like behaviours towards dots in the food-supplied condition after they had learned that dot stimuli are not food-rewarding in the preceding food-deprived condition. Alternatively, if dot preference is not solely for foraging, they may show visual attention towards dots even under food-

supplied conditions, suggesting sensory bias towards dot patterns. These also mean that the idea of sensory bias should be rejected in unlikely case that dot preference exists only in the food-supplied condition.

Materials and methods

Subjects

I used 15 male and 11 female adult star finches *N. ruficauda* obtained from several local breeders. Each bird was identified with a unique combination of two-coloured leg rings. All birds were kept in unisex cages on a 12:12 h light: dark schedule (lights on 08:00–20:00) at approximately 25–26 °C and 50–60% humidity. They were provided with a finch seed mixture, cuttlebone, water, and fresh green vegetables every day, unless tested under food-deprived conditions. Each bird was tested in the experiments that were conducted between May and June 2019 or June and September 2020.

Presented stimuli

I used monochrome dot— (φ 2.0 mm) or stripe— (W 2.0 mm) printed paper (Fig. 2-2b) as the experimental/control stimulus. I chose stripes as a control because they are widely seen on the plumage of other Estrildid species (Goodwin 1982; Payne 2010), and also because they are characterised by simple motif shapes comparable to dots. As the distances between motifs were set to 2.0 mm for both dot and stripe patterns, black areas were not exactly the same between the two stimuli (dot: 873.8 mm^2; stripe: 668.8 mm^2). The dot size was adjusted to match the largest white dots of Estrildid finches' plumage patterns (Soma and Garamszegi 2018) to derive high responses from the birds. Stimuli were created using Adobe Illustrator CC 2018 (Adobe Systems, San Jose, CA), printed on white paper using an inkjet printer (DocuPrint C2110, FUJI XEROX, Tokyo, Japan), and set on the inner bottom of food cups (35.0 mm maximum diameter, 40.0

mm height) using double-sided tape. I used food cups to avoid neophobia and to prevent the stimuli from coming into the sight of birds easily without approaching.

Experimental procedure

Each bird was individually introduced into an experimental cage (8.0 × 15.0 × 14.0 cm), which was equipped with food and water cups, and two other empty cups with white paper lining at the bottom, which was used for stimuli presentation during the tests (Fig. 2-2c). They were allowed to habituate there 1 day before the tests (Day 0) and tested for pattern preference under the food-deprived condition on Day 1 and the food-supplied condition on Day 2. On Day 1, food cups were removed 3 h before presenting the stimuli and restored immediately after the experiment, whereas on Day 2, food was available all the time. Under each condition, I presented stimuli at the start of 1 h of behavioural recording using a video camera (GC-PX1, Victor, Tokyo, Japan) and removed them immediately after the end of the tests. The stimulus position was reversed from Day 1 to control for side preferences. The order of conditions was not randomised across birds.

Behavioural quantification

To assess visual preference for each pattern, I measured the frequency of gazing and pecking behaviours towards each stimulus during each condition, assuming that gazing reflects visual preference (Dawkins 2002; Endler and Mappes 2017), and pecking is associated with foraging (Martin 2007). In this study, gazing refers to a bird looking down at the stimuli, which was defined based on the perched position (i.e., on the perch or the floor close to the stimulus, or the edge of the stimulus cup), body/head orientation towards the stimulus (i.e., anterior half of the body/head facing the stimulus), and the bill angle (i.e., pointing below horizontal). Pecking was defined based on the up-down head movements towards the stimulus shown by the bird standing on the stimulus cup.

Frequently, the birds repeated pecking behaviours in a row, where I counted the total number of up-down movements. As pecking always accompanied gazing, I counted one gazing per series of peckings.

Statical analysis

To investigate whether the proportion of subjects' responses to each stimulus (dots vs. stripes) deviated from those expected by chance (0.5), I ran intercept-only generalised linear mixed effect models (GLMM) with a binomial error distribution using the glmer function from the lme4 package (Bates et al. 2015). In these models, gazing/pecking frequency towards the two stimuli (dots vs. stripes) was entered as a bound response variable. I also tested the effect of experimental conditions (food-supplied vs. food-deprived) on dot preference using a GLMM with Poisson error distribution, with conditions specified as an independent variable. Possible sexual differences in response were also analysed using a separate GLMM in which sex was entered as an independent variable. The identity of the subject was incorporated in all three models as a random effect to address the possibility that individuals differed in their performance. All analyses were performed using R version 3.5.1 (R Core Team 2018).

Results

Star finches *N. ruficauda* gazed at the white dot pattern more frequently than the stripe pattern under both food-deprived and -supplied conditions (deprived condition: $N = 26$, $Z = 3.959$, $P < 0.001$, supplied condition: $N = 26$, $Z = 2.258$, $P = 0.024$; Fig. 2-3a). Gazing preference towards dots was more pronounced under the food-deprived condition ($N = 26$, $Z = 20.300$, $P < 0.001$; Fig. 2-3a). The pecking frequency (Fig. 2-3b) showed similar results with those for the gazing frequency (Fig. 2-3a), but with pronounced difference between the two (food-derived and -supplied) conditions. Star

finches *N. ruficauda* pecked white dot patterns more frequently than stripes under the food-deprived condition ($N = 26$, $Z = 4.293$, $P < 0.001$; Fig. 2-3b), but not under food-supplied conditions ($N = 26$, $Z = 0.531$, $P = 0.596$; Fig. 2-3b). The subject birds showed almost no pecking when food was supplied (Fig. 2-3b); therefore, the condition effect was statistically significant ($N = 26$, $Z = 27.508$, $P < 0.001$, Fig. 2-3b). There were no sex differences in either gazing or pecking behaviour (gazing, food-deprived, $N = 26$, $Z = -0.958$, $P = 0.338$, food-supplied, $N = 26$, $Z = 0.254$, $P = 0.800$; pecking, food-deprived, $N = 26$, $Z = 0.282$, $P = 0.778$, food-supplied, $N = 26$, $Z = 0.527$, $P = 0.598$).

Discussion

Star finches *N. ruficauda* showed both hunger-related and hunger-neutral preference for dots by their frequent gazing and pecking at dot patterns compared with stripes, regardless of whether food was supplied (Fig. 2-3). This result is in accordance with my prediction but may seem rather surprising, given how strongly the subjects were attracted by completely abstract patterns without organic texture. Considering the visual acuity and depth perception of birds (Bischof 1988; Martin 2017; Caves et al. 2018), it is unlikely that they failed to perceive the clear image of dot patterns at a close distance, which suggests that they have an intrinsic visual preference for abstract dot patterns. If I could have controlled for prior visual experience of the subject birds (e.g., exposure to cage fences, round seed diet, or conspecifics plumage), that could give more support to the idea that star finches *N. ruficauda* have the sensory bias for white dots.

Star finches' visual preference for abstract dots can be partially explained in association with foraging. Hunger experience solicited foraging-like behaviour (i.e., pecking) towards dots (Fig. 2-3b), which was likely promoted by the method of stimuli presentation using food cups. However, their frequent gazing towards dots was likely not merely because of hunger, as they looked at dot patterns very frequently even under

the food-supplied condition, after having experienced that the exact dot pattern was not food-rewarding the day before. These results suggest that dot stimuli for the star finch *N. ruficauda* are worth paying attention to both in foraging and non-foraging contexts.

Evidence from previous research indirectly supports the idea that dots can play a role in within-species communication, i.e., sexual/social signalling (Alatalo et al. 1992; Roulin 1999; Summers et al. 1999; Siddiqi et al. 2004; Reynolds and Fitzpatrick 2007; Maan and Cummings 2008, 2009; Crothers et al. 2011; Crowhurst et al. 2012; Zanollo et al. 2012; Soma and Garamszegi 2018; Soulsbury et al. 2016). Like many Estrildid or other species that are characterised by dotted plumage patterns functioning for within-species signalling (Roulin 1999; Crowhurst et al. 2012; Zanollo et al. 2012; Soulsbury et al. 2016; Soma and Garamszegi 2018), star finches *N. ruficauda* also bear conspicuous white dots covering from face to flank, wherein their visual attention to white dots would facilitate identification of conspecifics or potential mates. They would also tend to show visual preference towards abstract dot patterns when no cost exists in paying attention to white dot patterns. Although I did not find any sex difference in dot preference, this could be associated with the fact that both sexes have dot patterns. It is also possible that the sample size of this study was not sufficient to detect it. At least what is clear from the present results is that male star finches *N. ruficauda* pay attention to dots like females do. This could be either because dot plumage pattern plays a role in social dominance in each sex (e.g., Crowhurst et al. 2012), or because dots function in mutual mate choice, given that most Estrildid finches are characterised by behavioural and morphological sexual signals shared between the sexes and functioning for mutual courtship (Gahr and Güttingery 1986; Geberzahn and Gahr 2011; Ota et al. 2015; Soma and Garamszegi 2015; Soma and Iwama 2017; Soma 2018; Soma and Garamszegi 2018). It should be also noted that plumage patterns in Estrildid finches can be used in social and sexual contexts (Swaddle and Cuthill 1994; Crowhurst et al 2012; Zanollo et

al 2012; Marques et al. 2016; Soma 2018; Soma and Garamszegi 2018), making it hard to disentangle them.

The findings have an important implication for how signalling traits originate and evolve in animals. According to the sensory bias hypothesis, sensory systems tuned for particular stimuli precedes the evolution of mating signals (Ryan et al. 1990; Ryan and Keddy-Hector 1992; Basolo 1995; Endler and Basolo 1998; Ryan 1998; but see also Ron 2008). This idea is supported by some research findings that females of closely related species with or without a mating signal show similar preferences, meaning that their common ancestor likely already had such a sensory preference, possibly because of diet (Proctor 1992; Garcia and Ramirez 2005). However, it should be noted that Chapter 1, Mizuno and Soma (2020), and this chapter did not directly examine whether plumage dots evolved as a result of sensory bias driven by foraging preferences. Theoretically, intrinsic dot preference could have originated from either plumage signalling or diet. I cannot completely deny the possibility that dietary choices arose as a result of an underlying preference for plumage dot patterns, but I think it is unlikely. It is because Estrildid's common ancestor is assumed to lack white dot plumage patterns (Fig. 1-1a; Mizuno and Soma 2020), while all living Estrildid species are granivorous (Goodwin 1982; Payne 2010).

Figures

Figure 2-1. Example of Estrildids' courtship display (male star finch *N. ruficauda*). Some Estrildid species with white dot plumage patterns fluff up their flank plumages where dot patterns are present.
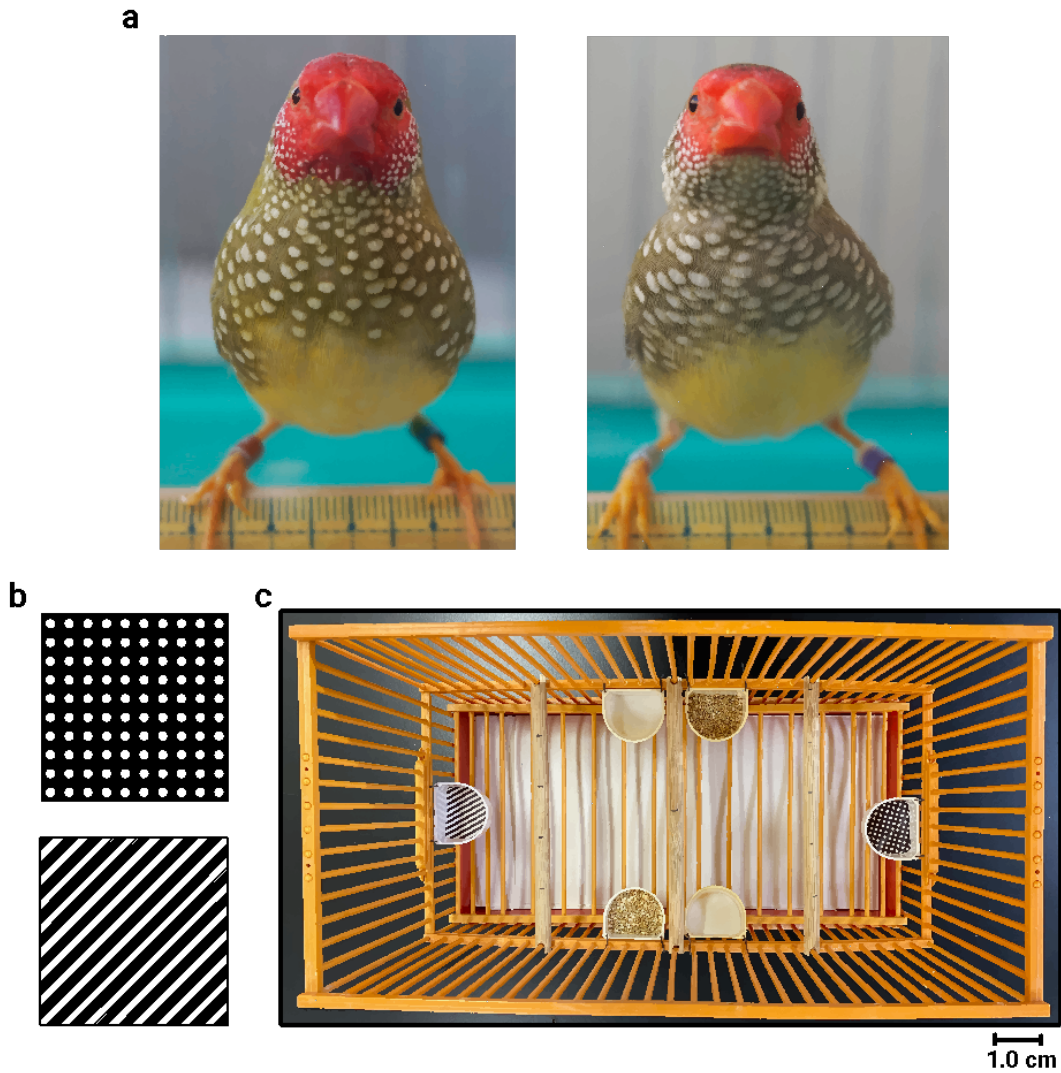
Figure 2-2. (a) Adult male (left) and female (right) star finch *N. ruficauda*. (b) Dot and stripe stimuli. (c) Top view of the experimental cage, showing the food-supplied condition. The four cups in the middle contain water and seed mix, whereas the two on both sides contain stimulus-printed paper, which was replaced with plain white paper outside the tests.

(a) Gazing   (b) Pecking

Figure 2-3. (a) Total frequency of gazes toward dot and stripe stimuli under the food-deprived and food-supplied conditions. (b) Total frequency of pecks toward dots and stripes under the food-deprived and food-supplied conditions.

CHAPTER 3 Testing pre-existing visual preference for white dot patterns in Estrildidae through interspecific comparative behavioural experiments

Introduction

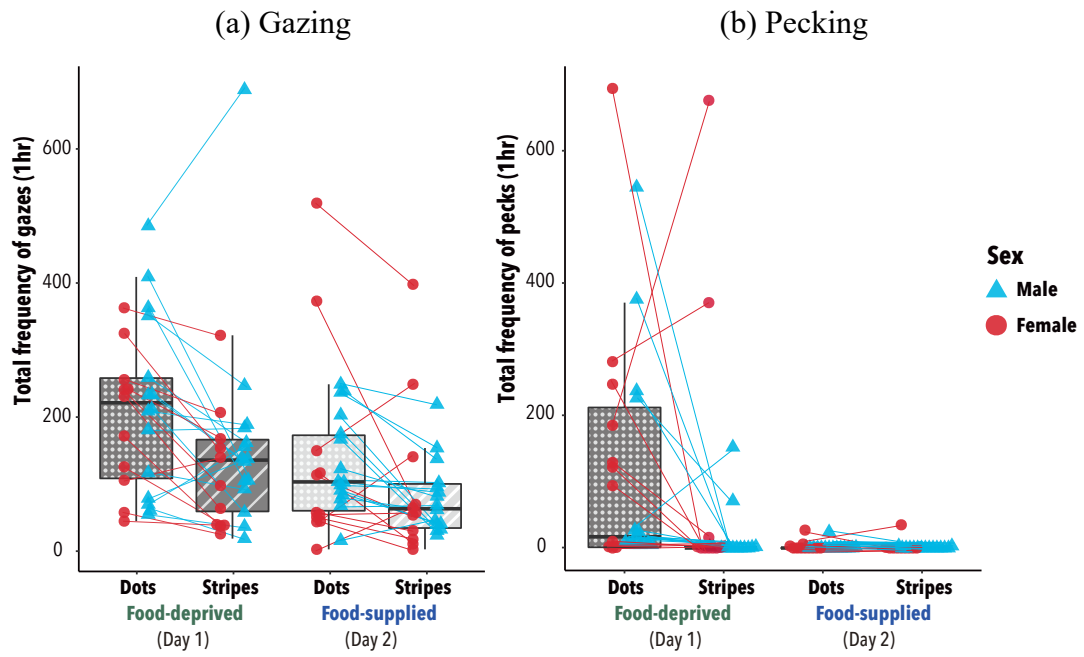The sensory bias hypothesis explains the evolutionary origin of signal design (Reviewed in Ryan et al. 1990; Endler and Basolo 1998; Arnqvist 2006). This hypothesis assumes the presence of pre-existing sensory bias for a particular stimulus in females that facilitates the evolution of an ornamental trait in males. Particularly, fish are rich in examples of female visual preferences contributing to the evolution of sexual ornaments (e.g., Rodd et al. 2002; Garcia and Ramirez 2005; MacLaren and Rowland 2006). Some Goodeinae species males have terminal yellow bands (TYB) on their tails to attract females with a visual sensitivity for foraging yellow worms (Garcia and Ramirez 2005). Similarly, male guppies *Poecilia reticulata* also utilise a red dot pattern on their body surfaces to attract the attention of females that have a foraging preference for red-colour fruits (Rodd et al. 2002).

The crucial premise of the sensory bias hypothesis, the presence of pre-existing sensory bias, can be tested by investigating if a particular sensory preference is shared among species of a focal taxonomic group regardless of whether they possess the signalling trait (Endler and Basolo 1998). If we could directly assess whether the common ancestor of the focal taxa already had the sensory bias, it would be ideal, but behavioural experiments using fossil species are not feasible. Therefore, we can only infer the cognitive states of ancestral species based on the outcomes from behavioural experiments using extant species. In túngara frogs *Engystomops pustulosus* and related species within the genus Engystomops, females commonly share a preference for complex calls, irrespective of whether conspecific males produce such calls, which is

seen as one of notable examples of pre-existing bias playing a role in signal evolution (Ryan et al. 1990; Gridi-Papp et al. 2006). Similar findings have been reported for fiddler crabs *Uca beebei* (Christy 1995), guppies (Rodd et al. 2002), and water mites *Neumania papillator* (Proctor 1991, 1992). All these studies seem to indicate the presence of pre-existing bias (e.g., Madden and Tanner 2005), but many of them tend to lack the consideration of phylogenetic relationships among focal species, without which the estimation of the ancestral state could be affected by sampling of species (Shaw 1995; Ryan and Cummings 2013).

In addition, the previous empirical studies tended to overlook the possibility that the sensory bias hypothesis does not necessarily require sexual contexts. That is, the hypothesis can help to understand female mate choice and male ornamentation, but its prediction can also be applied to the sensory bias shared between the sexes and its role in the evolution of social signals, such as status signalling outside the reproductive context. Although a few previous studies have indicated that males and females share biases (Ryan and Rand 1998; Basolo 2002; Rodd et al. 2002) or that species have mutual ornamental traits (Jones and Hunter 1993; Kraaijeveld et al. 2007), it has remained unclear whether species with shared ornamental traits between males and females have a similar sensory bias.

In this chapter, it is intended to test pre-existing visual bias towards white dot patterns in Estrildid species (family Estrildidae), by looking into whether they share and show similar visual behaviours towards patterned stimuli relying on the experimental protocols used for star finches *Neochmia ruficauda* (Chapter 2; Mizuno and Soma 2022). We assume that visual bias can be assessed by measuring visual preference, specifically gazing (Berlyne 1958; Fantz 1963; Winters et al. 2015). Around 25 % of 134 Estrildid species are characterised by white dot plumage patterns, likely with signalling functions (Crowhurst et al. 2012; Zanollo et al. 2012; Soma and Garamszegi 2018). Both sexes often have similar white dot patterns on their plumages (e.g., Fig. I-

1). Given that Estrildid species are mainly granivores (Goodwin 1982; Payne 2010), and that some species consume whitish gregarious round invertebrates (e.g., termites) in the breeding season to obtain protein (Goodwin 1982), the visual preference for white dot patterns is thought to also be important in foraging (Chapter 1; Mizuno and Soma 2020). The results from Fig. 1-1a and Mizuno and Soma (2020) indicated that white dot plumage patterns were highly likely absent in the Estrildid common ancestor, but it is yet to be elucidated as to whether sensory bias (visual preference) for dots existed in the ancestor of Estrildids. If the pre-existing sensory bias for white dots existed in the ancestor, extant species of Estrildids would likely share a visual preference for white dots regardless of whether the species have white dot plumage patterns. In addition, if the original function of the preference was for foraging, they may show a stronger visual preference for dots when they are hungry, and males and females may share similar preferences. Alternatively, when dot preference does not pre-exist, and evolves in particular extant species, among-species variations in diet (e.g., termite-eating, see Chapter 1; Mizuno and Soma 2020) or plumage (i.e., presence of plumage dots) would probably have associations with the preference.

Materials and methods

Subjects

Adult individuals of 12 Estrildid species ($N = 95$; Fig. 3-1, Table 3-9) were used: African silverbills *Lonchura cantans* (male: $n = 3$, female: $n = 3$), chestnut-breasted mannikins *Lonchura castaneothorax* (male: $n = 1$, female: $n = 3$), chestnut munias *Lonchura atricapilla* (male: $n = 0$, female: $n = 2$), double-barred finches *Taeniopygia bichenovii* (male: $n = 3$, female: $n = 1$), gouldian finches *Erythrura gouldiae* (male: $n = 3$, female: $n = 4$), Java sparrows *Lonchura oryzivora* (male: $n = 7$, female: $n = 10$), painted firetail *Emblema pictum* (male: $n = 0$, female: $n = 1$), plum-headed finches

Neochmia modesta (male: $n = 1$, female: $n = 5$), red-cheeked cordon-bleus *Uraeginthus bengalus* (male: $n = 7$, female: $n = 5$), star finches *N. ruficauda* (male: $n = 15$, female: $n = 11$), white-headed munias *Lonchura maja* (male: $n = 2$, female: $n = 0$), and zebra finches *Taeniopygia guttata* (male: $n = 4$, female: $n = 4$), obtained from several local breeders or kept in Wada or Soma laboratory in Hokkaido University. Each bird was identified with a unique combination of coloured leg rings. Birds were kept in unisex cages on a 12:12 h light:dark schedule (lights on 08:00–20:00) at approximately 25–26 °C and 50–60% humidity. They were given a finch seed mixture, cuttlebone, water, and fresh green vegetables every day, unless tested under food-deprived conditions. Each bird was tested in the experiments that were conducted between May and June 2019, January and June 2020, or November 2021 and March 2022.

Experimental procedure

The behavioural experiments were run using the same methods described in Chapter 2 and in Mizuno and Soma (2022). Briefly, each experimental bird was placed in an experimental cage and presented with pairs of paper printed with white dotted ($\varphi 2.0$ mm) and white striped (W2.0 mm) stimuli for 1 hour. During the experimental period, all their behaviours were recorded on a video camera (GC-PX1, Victor, Tokyo, Japan). The experiment was carried out over two days after 24 h habituation. On Day 1, the experiment was conducted under the food-deprived condition to examine the foraging-derived preference. On Day 2, the experiment was conducted under the food-supplied condition to test the hunger-neutral preference. To control for side preferences, the stimulus positions were reversed between Days 1 and 2. From video recordings, I focused on gazing behaviour as an index of visual preference (Dawkins 2002; Endler and Mappes 2017), but also measured pecking behaviour as a foraging-like behaviour (Martin 2007) towards each stimulus during each condition for every subject bird. The data of gazing and pecking frequency on Days 1 and 2 were analysed separately under

42

the assumption that they reflect hunger-related and hunger-neutral responses, respectively.

Statistical analysis

Within-species analyses

To investigate whether the proportion of subjects' responses to each stimulus (dots vs. stripes) deviated from those expected by chance (0.5) in each subject species, intercept-only generalised linear mixed effect models (GLMM) were used with a binomial error distribution using the glmer function from the "lme4" package (Bates et al. 2015). In these models, gazing/pecking frequency towards the two stimuli was entered as a bound response variable. The subject's identity was included in all models as a random effect to address the dependence of the data from the same individuals. For the painted firetail *E. pictum*, for only one subject bird could be acquired, the binomial test was used instead of GLMM.

Phylogenetic comparative analysis

To take into account the limited sample size (number of individuals) and lack of balanced sex data for some species, for the below-mentioned analyses I used both full-species data including all subject species (*n* = 12 species) and subset data excluding species without behavioural data on one sex (*n* = 9 species) except otherwise stated (Fig. 3-1). To test taxon-wide dot preference in Estrildid finches, the intercept-only model was applied to full and subset data of gazing/pecking frequency towards dot vs. stripe stimuli using a Bayesian linear mixed model by the R package "MCMCglmm" (Hadfield 2010) with binomial distribution with consideration of their phylogenetic relationships. Phylogenetic information was entered as a random effect to control for possible phylogenetic non-independence. Phylogenetic tree was obtained from Olsson and Alström (2020) and modified using the force.ultrametric function of the R package

"phytools" to include only focal species (Revell 2012). To examine whether the proportion of subjects' responses to each stimulus (dots vs. stripes) deviated from those expected by chance (0.5), gazing/pecking frequency towards the two stimuli (dots vs. stripes) was entered as a bound response variable. In the models, the priors were set as [G=list(G1=list(V=1, nu=1, alpha.mu=0, alpha.V=100))], and a chain was run for 500,000 iterations, sampling every 500 iterations after a 1,000 burn-in. After running, convergence was checked by visually inspecting plots and Heidelberg and Welch diagnostic tests (Hadfield 2010). I also tested the effect of experimental conditions (food-supplied vs. food-deprived) on dot preference using MCMCglmm with Poisson error distribution, with conditions specified as an independent variable.

The factors that can have an influence on the difference in gazing/pecking responses between white dot and stripe pattern stimuli were also examined. Specifically, the effects of sex, diet (termite-eating: whether subject species consume whitish round tiny invertebrates, such as termites or ant eggs), and the presence/absence of white dot plumage patterns on gazing/pecking frequency towards the two stimuli were tested by adding explanatory variables to the above-mentioned intercept-only MCMCglmm. As the correlation between white dot plumage patterns and termite-eating has already been shown by Fig. 1-3, Table 1-2a, and Mizuno and Soma (2020) and the MCMC did not converge, two sets of MCMCglmm, one with sex and termite-eating as explanatory variables and the other with sex and the presence of white dots, were prepared, instead of full models including all three explanatory variables. The data on the presence/absence of white dots and termite-eating were based on Chapter 1, Soma and Garamszegi (2018), and Mizuno and Soma (2020). All analyses were carried out in R 3.5.1 (R Core Team 2018).

Results

Gazing

Visual preference of each Estrildid species

Under the food-deprived condition, six out of 12 Estrildid species (chestnut-breasted mannikins *L. castaneothorax*, Java sparrows *L. oryzivora*, painted firetail *E. pictum*, red-cheeked cordon-bleus *U. bengalus*, star finches *N. ruficauda*, zebra finches *T. guttata*) gazed at white dots significantly more than stripes, while the others (African silverbills *L. cantans*, chestnut munias *L. atricapilla*, double-barred finches *T. bichenovii*, gouldian finches *E. gouldiae*, plum-headed finches *N. modesta*, white-headed munias *L. maja*) did not (Fig. 3-1, Table 3-8). Under the food-supplied condition, only star finches *N. ruficauda* showed significantly higher gazing responses to dots than stripes (Fig. 3-1, Table 3-8).

Taxon-wide dot visual preference

The result from intercept-only MCMCglmm using full-species ($n = 12$) data revealed a statistically significant visual preference towards dots over stripes under food-deprived condition, but not under the food-supplied condition (Table 3-1a). Gazing preference towards dots was more pronounced under the food-deprived condition than the food-supplied condition. (Table 3-3a). I also found marginally significant sex differences in gazing responses between white dots and stripes under the food-deprived condition, suggesting that females tended to gaze at dots more frequently than stripes more than males did (Table 3-4a). Termite-eating and the presence of white dot plumage patterns had no significant effects on gazing behaviour under either the food-deprived or food-supplied conditions (Table 3-4a, 5a). These results are consistent with those from the subset ($n = 9$) data (Table 3-2a, 3b, 6a, 7a).

Pecking

Across the analyses of the pecking data of each species, full-species ($n = 12$), and subset ($n = 9$), I found a similar tendency as gazing. Specifically, seven species pecked at white dots more frequently than stripes under the food-deprived condition, while three species did so under the food-supplied condition (Fig.3-2, Table 3-8). The results from MCMCglmm models were similar to those of gazing in both full-species (Table 3-1b, 3a, 4b, 5b) and subset data (Table 3-2b, 3b, 6b, 7b).

Discussion

By testing visual preference in a total of 95 subjects of 12 species, it is revealed that both sexes of Estrildid finches generally prefer to look at white dots over stripes (Table 3-1a) regardless of whether the species have white dot plumage patterns or termite diet (Table 3-4a). The obtained results are based on a relatively small number of species, but can be seen as reflecting taxon-wide visual preference because the subject species cover major genera of the family Estrildidae. Some species are from the same genus, but my analyses considered them by using phylogenetic comparative methods. The visual behaviours of extant species focused on in this study suggest that a pre-existing sensory bias for dot patterns is the ancestral trait of Estrildids. Preference for dots was significant only when the birds were hungry (Table 3-1a, 3a), meaning that the visual preference is associated with foraging, in accordance with the previous studies that indicated the role of foraging-related visual preference in the evolution of male ornamental traits (e.g., Proctor 1991, 1992; Rodd et al. 2002; Garcia and Ramirez 2005). Considering that Estrildid finches are all granivores and often take tiny grain seeds from the ground (Goodwin 1985; Payne 2010), their visual preference for white dot patterns would be associated with searching for grain seeds.

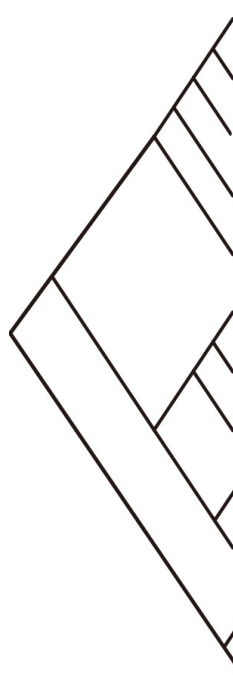In accordance with the prediction that males and females may share similar

preferences, there was little sex difference in gazing responses between white dots and stripes (Fig. 3-4a), so it is unlikely that the visual preference for white dots promoted only the evolution of male ornamental traits. The present finding shows that pre-existing sensory bias would be shared in species where the signal trait is shared between males and females. Although several empirical research has indicated that both sexes share sensory biases (e.g., Rodd 2002; Garcia and Ramirez 2005), it has not been tested whether the evolution of ornamental traits shared between sexes was promoted by pre-existing sensory bias. Plumage dot patterns in Estrildids are considered to function as sexual and social signals (Crowhurst et al. 2012; Soma and Garamszegi 2018), suggesting that their visual preference for white dot patterns played a role in the evolution of not only sexual but also social signalling traits. Sensory bias for particular stimuli can be a factor in the evolution of signalling traits shared between the sexes.

Although the results suggest a trend that Estrildid finches have a diet-related visual preference for white dot pattern stimulus (Table 3-1a), some Estrildid species did not show the preference in experiments (Fig. 3-1, Table 3-8). One possibility is that the sample size of some subject species was insufficient for detecting the visual preference towards white dot patterns. Alternatively, it may be due to the weakening or loss of visual preferences for white dot patterns during evolution to the extant Estrildid species. Yet, given that pre-existing visual preferences of Estrildid finches are clearly linked with foraging (Table 3-1a), it is unlikely that this evolutionary process occurred. Further behavioural experiments using more subject birds are needed to examine the species differences and improve the validity of the results. If no differences in gazing responses to stimuli are observed even after increasing the sample size, having visual preferences for dot patterns may have no benefit for some Estrildid species. For instance, dot patterns may no longer act as foraging cues, or losing dot preferences may be the result of anti-predator adaptation. However, it is unclear whether their predators have dot patterns on their body surfaces.

Figures and Tables

Figure 3-1. Summary of GLMM in visual preference for dots in each Estrildid species.
Subset data species are included in pale yellow boxes. Statistically significant
differences ($p < 0.05$) in responses to dots vs. stripes are indicated with red, and grey
colour means non-statistically significant differences. The value indicates the z-value.
Termite eating means whether subject species consume whitish gregarious round
invertebrates (e.g., termites and ant eggs or larvae). For the painted firetail *E. pictum*,
for which only one subject bird could be tested, the binomial test was used instead of
GLMM. Therefore, I could not obtain the z-value.
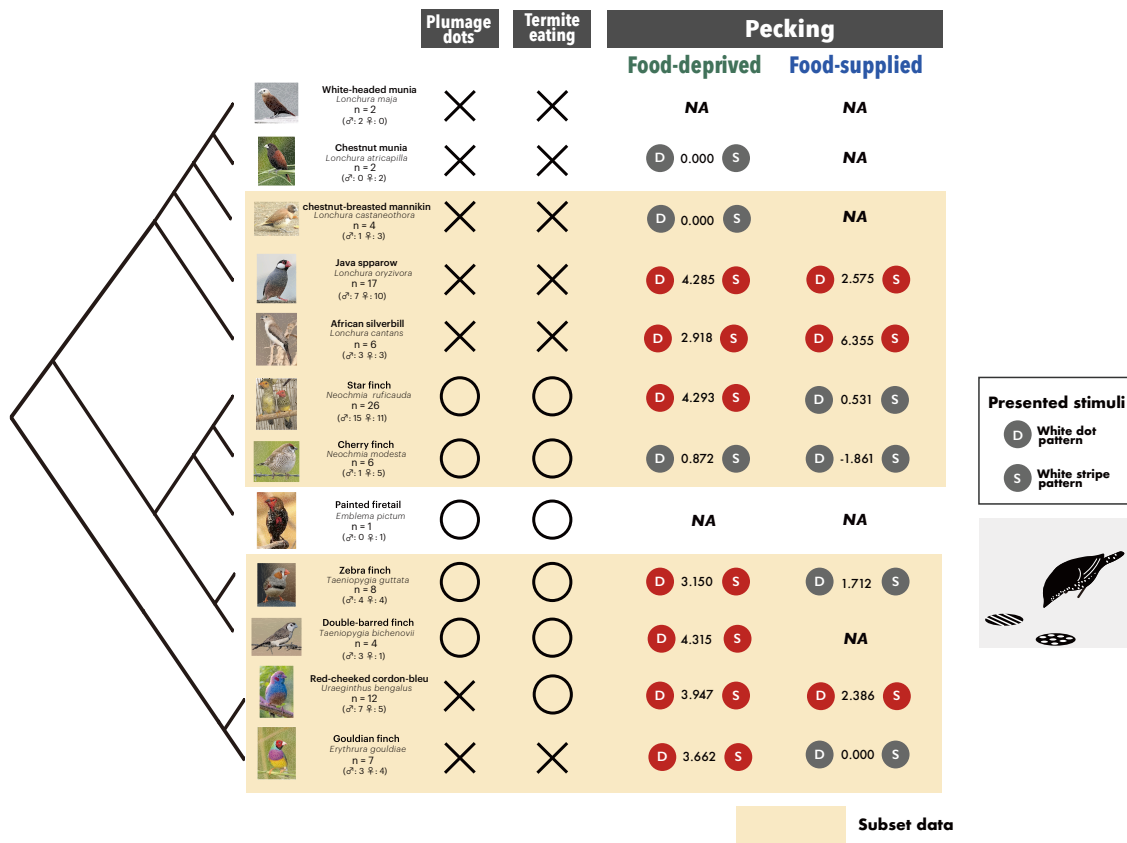
Figure 3-2. Summary of GLMM in pecking behaviour for dots in each Estrildid species. Subset data species are included in pale yellow boxes. Statistically significant differences (p < 0.05) in responses to dots vs. stripes are indicated with red, and grey colour means non-statistically significant differences. NA represents that the subjects did not respond to dots or stripes at all, and the value indicates the z-value. Termite eating means whether subject species consume whitish gregarious round invertebrates (e.g., termites and ant eggs or larvae).

Figure 3-3. (a) Total frequency of gazes toward dot and stripe stimuli under the food-deprived and food-supplied conditions.

(b) Total frequency of pecks toward dots and stripes under the food-deprived and food-supplied conditions. Each plot represents the average of each subject species gazing/pecking frequency per 1 hour.
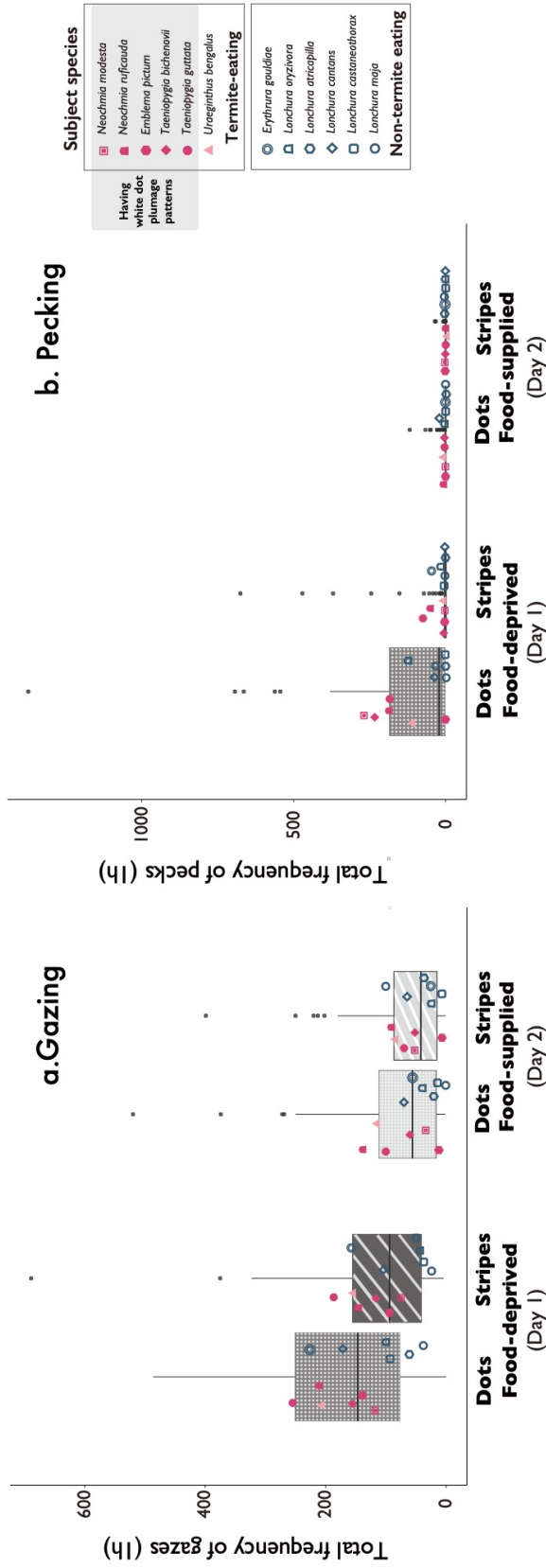
Table 3-1. Summary of MCMCglmm in (a) gazing behaviour and (b) pecking behaviour using the full-species data. Bold typeface is used when 95% confidence interval (CI) does not contain zero; thus, it can be interpreted as an existing significant difference between gazing/pecking frequency towards the two stimuli.

Observed behaviour	Condition	Mean of posterior distribution	95%CI	pMCMC
(a) Gazing				
	Food-deprived	**0.485**	**(0.233, 0.722)**	**0.004**
	Food-supplied	0.174	(-0.546, 0.802)	0.457
(b) Pecking				
	Food-deprived	**3.912**	**(2.087, 5.726)**	**0.001**
	Food-supplied	4.217	(-0.192, 9.849)	0.046

Table 3-2. Summary of MCMCglmm in (a) gazing behaviour and (b) pecking behaviour using the subset data. Bold typeface is used when 95% confidence interval (CI) does not contain zero; thus, it can be interpreted as an existing significant difference between gazing/pecking frequency towards the two stimuli.

Observed behaviour	Condition	Mean of posterior distribution	95%CI	pMCMC
(a) Gazing				
	Food-deprived	**0.518**	**(0.253, 0.791)**	**0.004**
	Food-supplied	0.361	(-0.024, 0.710)	0.056
(b) Pecking				
	Food-deprived	**3.879**	**(2.098, 5.737)**	**0.003**
	Food-supplied	4.170	(-0.352, 9.500)	0.049

Table 3-3. Summary of MCMCglmm in difference in gazing and pecking behaviours between food-deprived and food-supplied conditions towards white dot pattern stimulus using (a) full-species and (b) subset data. Bold typeface is used when 95% confidence interval (CI) does not contain zero; thus, it can be interpreted as an existing significant difference in gazing/pecking frequency towards dot stimulus between the two experimental conditions.

Used data	Response	Explanatory variable	Mean of posterior distribution	95%CI	pMCMC
(a) Full-species	Gazing	Intercept	4.763	(3.929, 5.657)	< 0.001
		Food-supplied	**-1.068**	**(-1.342, -0.802)**	**< 0.001**
	Pecking	Intercept	2.667	(0.1422, 5.279)	0.048
		Food-supplied	**-4.861**	**(-5.919, -3.815)**	**< 0.001**
(b) Subset	Gazing	Intercept	4.825	(4.075, 5.568)	< 0.001
		Food-supplied	**-1.017**	**(-1.300, -0.766)**	**< 0.001**
	Pecking	Intercept	2.964	(1.633, 4.411)	0.002
		Food-supplied	**-4.837**	**(-5.930, -3.785)**	**< 0.001**

Table 3-4. Summary of MCMCglmm in the food-deprived condition using the full-species data.

Observed behaviour	Model	Explanatory variable	Mean of posterior distribution	95%CI	pMCMC
(a) Gazing					
	Sex + termite-eating	Intercept	0.683	(0.290, 1.092)	0.009
		Sex (male)	-0.340	(-0.689, 0.010)	0.058
		Termite-eating	-0.066	(-0.580, 0.414)	0.717
	Sex + plumage white dots	Intercept	0.663	(0.324, 1.003)	0.002
		Sex (male)	-0.342	(-0.690, 0.052)	0.052
		Plumage white dots	-0.042	(-0.522, 0.427)	0.850
(b) Pecking					
	Sex + termite-eating	Intercept	5.216	(2.564, 7.853)	0.004
		Sex (male)	-1.364	(-3.250, 0.456)	0.143
		Termite-eating	-1.011	(-3.935, 2.348)	0.428
	Sex + plumage white dots	Intercept	4.848	(2.577, 7.158)	0.002
		Sex (male)	-1.332	(-3.165, 0.542)	0.150
		Plumage white dots	-0.785	(-3.921, 2.242)	0.559

53

Table 3-5. Summary of MCMCglmm in the food-supplied condition using the full-species data.

Observed behaviour	Model	Explanatory variable	Mean of posterior distribution	95%CI	pMCMC
(a) Gazing					
	Sex + termite-eating	Intercept	-0.123	(-1.355, 0.862)	0.843
		Sex (male)	0.099	(-0.428, 0.628)	0.716
		Termite-eating	0.430	(-0.959, 2.006)	0.450
	Sex + plumage white dots	Intercept	0.095	(-0.774, 0.949)	0.721
		Sex (male)	0.124	(-0.438, 0.667)	0.666
		Plumage white dots	-0.079	(-1.279, 0.924)	0.932
(b) Pecking					
	Sex + termite-eating	Intercept	6.363	(-2.513, 16.994)	0.104
		Sex (male)	2.264	(-4.009, 9.351)	0.446
		Termite-eating	-3.591	(-16.069, 7.327)	0.429
	Sex + plumage white dots	Intercept	5.984	(0.061, 13.440)	0.029
		Sex (male)	2.391	(-3.557, 9.081)	0.397
		Plumage white dots	-6.128	(-16.040, 2.191)	0.098

Table 3-6. Summary of MCMCglmm in the food-deprived condition using the subset data.

Observed behaviour	Model	Explanatory variable	Mean of posterior distribution	95%CI	pMCMC
(a) Gazing					
	Sex + termite-eating	Intercept	0.764	(0.345, 1.175)	0.005
		Sex (male)	-0.321	(-0.693, 0.019)	0.076
		Termite-eating	-0.150	(-0.616, 0.375)	0.494
	Sex + plumage white dots	Intercept	0.713	(0.346, 1.060)	0.002
		Sex (male)	-0.326	(-0.677, 0.037)	0.077
		Plumage white dots	-0.093	(-0.588, 0.392)	0.674
(b) Pecking					
	Sex + termite-eating	Intercept	5.103	(2.325, 7.851)	0.006
		Sex (male)	-1.357	(-3.232, 0.458)	0.146
		Termite-eating	-0.908	(-4.034, 2.467)	0.500
	Sex + plumage white dots	Intercept	4.786	(2.363, 7.191)	0.002
		Sex (male)	-1.300	(-3.069, 0.598)	0.166
		Plumage white dots	-0.784	(-3.885, 2.210)	0.573

Table 3-7. Summary of MCMCglmm in the food-supplied condition using the subset data.

Observed behaviour	Model	Explanatory variable	Mean of posterior distribution	95%CI	pMCMC
(a) Gazing					
	Sex + termite-eating	Intercept	0.253	(-0.406, 0.887)	0.385
		Sex (male)	0.250	(-0.245, 0.752)	0.317
		Termite-eating	-0.030	(-0.808, 0.754)	0.922
	Sex + plumage white dots	Intercept	0.309	(-0.239, 0.793)	0.210
		Sex (male)	0.275	(-0.231, 0.776)	0.283
		Plumage white dots	-0.237	(-0.965, 0.454)	0.497
(b) Pecking					
	Sex + termite-eating	Intercept	6.375	(-2.416, 17.145)	0.108
		Sex (male)	2.324	(-4.213, 9.357)	0.442
		Termite-eating	-3.621	(-15.411, 7.624)	0.411
	Sex + plumage white dots	Intercept	5.976	(-0.272, 13.180)	0.029
		Sex (male)	2.439	(-3.497, 8.934)	0.373
		Plumage white dots	-6.133	(-16.136, 2.013)	0.097

Table 3-8. Results of within-species analysis. NA indicates that the subject did not respond to dots or stripes at all. *E. pictum* had only one experimental individual, so the binomial test was used.

Species	behaviour	Condition	Estimate	SE	Z	P
N. modesta	(a) Gazing	Deprived	0.586	0.483	1.216	0.224
		Supplied	-0.475	0.437	-1.087	0.277
	(b) Pecking	Deprived	1.484	1.701	0.872	0.383
		Supplied	-3.689	1.983	-1.861	0.063
N. ruficauda	(a) Gazing	Deprived	0.487	0.123	3.959	<0.001
		Supplied	0.480	0.212	2.258	0.024
	(b) Pecking	Deprived	4.075	0.949	4.293	<0.001
		Supplied	1.146	2.160	0.531	0.596
U. bengalus	(a) Gazing	Deprived	0.316	0.138	2.283	0.022
		Supplied	0.412	0.258	1.600	0.110
	(b) Pecking	Deprived	2.903	0.736	3.947	<0.001
		Supplied	3.217	1.348	2.386	0.017
E. pictum	(a) Gazing	Deprived	0.597	-	-	0.004
		Supplied	0.667	-	-	0.239
	(b) Pecking	Deprived	NA	NA	NA	NA
		Supplied	NA	NA	NA	NA
L. maja	(a) Gazing	Deprived	-2.522	3.625	-0.696	0.487
		Supplied	-0.403	0.582	-7.229	<0.001
	(b) Pecking	Deprived	NA	NA	NA	NA
		Supplied	NA	NA	NA	NA
T. guttata	(a) Gazing	Deprived	0.339	0.173	11.957	0.0050
		Supplied	0.687	0.377	1.822	0.068
	(b) Pecking	Deprived	1.941	0.616	3.150	0.002
		Supplied	9.132	5.334	1.712	0.087

Species	behaviour	Condition	Estimate	SE	Z	P
L. cantans	(a) Gazing	Deprived	0.469	0.491	0.955	0.3339
		Supplied	0.575	0.564	1.018	0.309
	(b) Pecking	Deprived	3.708	1.271	2.918	0.004
		Supplied	3.714	0.584	6.355	<0.001
L. castaneothorax	(a) Gazing	Deprived	0.946	0.204	4.627	<0.001
		Supplied	0.095	0.563	0.168	0.867
	(b) Pecking	Deprived	39.22	2.122e+07	0	1
		Supplied	NA	NA	NA	NA
L. atricapilla	(a) Gazing	Deprived	0.209	0.135	1.544	0.123
		Supplied	-1.470	1.933	-0.761	0.447
	(b) Pecking	Deprived	22.57	4.820e+4	0	1
		Supplied	NA	NA	NA	NA
T. bichenovii	(a) Gazing	Deprived	0.244	0.243	1.004	0.315
		Supplied	0.172	0.095	1.801	0.072
	(b) Pecking	Deprived	4.243	0.983	4.315	<0.001
		Supplied	NA	NA	NA	NA
E. gouldiae	(a) Gazing	Deprived	0.503	0.329	1.528	0.127
		Supplied	0.186	0.669	0.278	0.781
	(b) Pecking	Deprived	2.988	0.816	3.662	<0.001
		Supplied	39.79	3.001e+07	0	1
L. oryzivora	(a) Gazing	Deprived	0.802	0.289	2.772	0.006
		Supplied	0.467	0.293	1.597	0.11
	(b) Pecking	Deprived	13.560	3.165	4.285	<0.001
		Supplied	16.089	6.248	2.575	0.010

57

Table. 3-9. Total frequency of all subject birds' pecking and gazing during each experimental condition.

Pattern type	termite eating	Species name	Bird ID	Sex	Food-deprived condition (1h)				Food-supplied condition (1h)			
					Total freq. of gazes		Total freq. of pecks		Total freq. of gazes		Total freq. of pecks	
					Dot	Stripe	Dot	Stripe	Dot	Stripe	Dot	Stripe
	Yes	Uraeginthus bengalus	CBR0005	M	67	71	13	3	42	43	0	0
		Uraeginthus bengalus	CBR0007	M	165	106	52	54	114	164	11	1
		Uraeginthus bengalus	CBR0009	M	126	66	6	1	165	15	10	0
		Uraeginthus bengalus	CBR0014	M	75	72	2	2	76	48	0	0
		Uraeginthus bengalus	CBR0031	M	142	85	0	0	86	85	1	0
		Uraeginthus bengalus	CBR0032	M	126	297	288	1	242	213	49	5
		Uraeginthus bengalus	CBR0044	M	295	135	163	15	99	83	28	0
		Uraeginthus bengalus	CBR0010	F	317	314	269	3	240	102	2	0
		Uraeginthus bengalus	CBR0011	F	256	154	13	0	143	17	0	0
		Uraeginthus bengalus	CBR0020	F	260	91	0	0	76	65	1	0
		Uraeginthus bengalus	CBR0024	F	335	199	351	3	12	17	0	0
		Uraeginthus bengalus	CBR0025	F	310	260	176	3	87	157	2	5
		Erythrura gouldiae	GF001	M	183	111	151	10	6	23	0	0
		Erythrura gouldiae	GF003	M	175	375	196	9	269	34	0	0
		Erythrura gouldiae	GF005	M	456	45	401	1	24	55	0	0
		Erythrura gouldiae	GF006	F	90	61	1	0	8	15	0	0
		Erythrura gouldiae	GF008	F	225	250	534	149	44	1	5	0
		Erythrura gouldiae	GF009	F	261	157	470	4	4	19	0	0
		Erythrura gouldiae	GF010	F	210	105	126	142	43	36	0	0
Unpatterned	No	Lonchura atricapilla	CM0001	F	71	51	1	0	1	57	0	0
		Lonchura atricapilla	CM0002	F	51	48	0	0	40	13	0	0
		Lonchura maja	WHM0001	M	0	15	0	0	2	180	0	0
		Lonchura maja	WHM0002	M	75	31	0	0	1	21	0	0
		Lonchura oryzivora	JS194	M	20	28	51	17	11	3	0	0
		Lonchura oryzivora	JS248	M	147	15	315	0	10	13	0	0
		Lonchura oryzivora	JS275	M	6	39	0	0	34	24	0	0
		Lonchura oryzivora	JS279	M	118	12	136	0	25	41	0	0
		Lonchura oryzivora	JS282	M	142	23	87	0	32	21	0	0
		Lonchura oryzivora	JS301	M	127	56	343	1	11	5	0	0
		Lonchura oryzivora	JS302	M	33	147	0	245	33	6	0	0
		Lonchura oryzivora	JS256	F	78	14	195	0	21	5	0	0
		Lonchura oryzivora	JS268	F	274	45	1373	0	67	68	6	0
		Lonchura oryzivora	JS284	F	105	43	251	0	15	6	0	0
		Lonchura oryzivora	JS292	F	30	25	0	0	12	1	0	0
		Lonchura oryzivora	JS298	F	168	65	167	0	13	54	0	1
		Lonchura oryzivora	JS315	F	14	12	0	0	22	15	0	0
		Lonchura oryzivora	JS319	F	147	116	91	12	272	14	118	0
		Lonchura oryzivora	JS322	F	81	50	24	0	22	69	0	0
		Lonchura oryzivora	JS400	F	79	8	76	0	4	14	0	0
		Lonchura oryzivora	JS401	F	131	41	70	0	75	52	0	0

Category		Species	ID	Sex								
White dots	Yes	Neochmia ruficauda	SF0001	M	410	107	22	0	104	89	0	0
		Neochmia ruficauda	SF0002	M	118	94	0	1	100	97	0	0
		Neochmia ruficauda	SF0003	M	80	139	2	1	176	32	1	0
		Neochmia ruficauda	SF0006	M	210	190	0	0	105	103	0	0
		Neochmia ruficauda	SF0009	M	260	157	544	0	240	139	0	3
		Neochmia ruficauda	SF0011	M	62	163	4	0	69	83	0	0
		Neochmia ruficauda	SF0014	M	486	689	20	152	204	47	0	0
		Neochmia ruficauda	SF0015	M	56	38	0	0	85	42	0	0
		Neochmia ruficauda	SF0016	M	71	20	1	0	124	34	1	0
		Neochmia ruficauda	SF0018	M	364	106	232	1	79	70	0	0
		Neochmia ruficauda	SF0020	M	182	185	5	2	168	25	1	0
		Neochmia ruficauda	SF0025	M	234	135	221	71	17	63	0	3
		Neochmia ruficauda	SF0026	M	213	59	370	2	92	41	24	0
		Neochmia ruficauda	SF0029	M	235	140	1	0	238	155	0	0
		Neochmia ruficauda	SF0032	M	352	248	14	0	250	220	0	0
		Neochmia ruficauda	SF0004	F	242	99	247	2	46	4	0	0
		Neochmia ruficauda	SF0010	F	46	40	0	0	4	66	0	0
		Neochmia ruficauda	SF0012	F	173	39	693	0	118	12	0	0
		Neochmia ruficauda	SF0013	F	232	65	10	3	52	19	0	0
		Neochmia ruficauda	SF0019	F	326	155	185	0	45	142	0	2
		Neochmia ruficauda	SF0021	F	257	208	281	370	151	250	3	35
		Neochmia ruficauda	SF0022	F	107	141	129	675	59	32	27	0
		Neochmia ruficauda	SF0023	F	364	323	2	0	520	399	0	1
		Neochmia ruficauda	SF0024	F	127	41	1	0	374	71	6	0
		Neochmia ruficauda	SF0027	F	243	169	122	16	56	59	0	0
		Neochmia ruficauda	SF0030	F	59	27	94	1	115	55	0	0
		Neochmia ruficauda	PFT0001	F	139	94	0	0	12	6	0	0
Stripes	No	Lonchura castaneothorax	CBM0004	M	271	104	3	0	48	13	0	0
		Lonchura castaneothorax	CBM0001	F	45	30	3	0	1	4	0	0
		Lonchura castaneothorax	CBM0002	F	12	4	0	0	2	4	0	0
		Lonchura castaneothorax	CBM0003	F	44	9	4	0	7	7	0	0
White dots and stripes	Yes	Neochmia modesta	CF0020	M	135	89	185	7	39	19	0	0
		Neochmia modesta	CF0010	F	42	5	0	0	52	43	0	0
		Neochmia modesta	CF0011	F	84	32	0	0	6	90	0	32
		Neochmia modesta	CF0012	F	362	66	1	6	24	51	0	0
		Neochmia modesta	CF0013	F	52	212	1	0	9	10	1	0
		Neochmia modesta	CF0014	F	30	36	0	0	74	97	1	3
		Taeniopygia bichenovii	OF0001	M	124	192	0	0	19	9	0	0
		Taeniopygia bichenovii	OF0002	M	27	26	0	0	18	30	0	0
		Taeniopygia bichenovii	OF0003	M	210	107	562	2	110	89	0	0
		Taeniopygia bichenovii	OF0004	M	261	136	380	20	94	75	17	0
		Taeniopygia guttata	ZF525B	M	166	213	40	14	64	89	1	0
		Taeniopygia guttata	ZF525	M	301	87	664	42	60	4	20	0
		Taeniopygia guttata	ZF533	M	285	288	0	0	116	114	0	0
		Taeniopygia guttata	ZF667	M	156	94	48	5	90	99	1	8
		Taeniopygia guttata	ZF280	F	209	281	249	471	42	16	0	0
		Taeniopygia guttata	ZF429	F	455	209	222	1	233	105	2	0
		Taeniopygia guttata	ZF483	F	221	139	54	14	129	15	0	0
		Taeniopygia guttata	ZF574	F	245	182	193	32	68	104	3	0
Complex	No	Lonchura cantans	ASB0002	M	64	193	6	2	75	17	2	0
		Lonchura cantans	ASB0003	M	94	125	13	4	14	2	0	0
		Lonchura cantans	ASB0004	M	82	89	7	0	8	2	0	0
		Lonchura cantans	ASB0001	F	232	26	27	0	155	202	66	1
		Lonchura cantans	ASB0005	F	414	58	149	0	16	108	4	1
		Lonchura cantans	ASB0006	F	144	125	22	2	151	51	51	1

59

GENERAL DISCUSSION

White dot plumage patterns evolved in a considerable proportion of Estrildid finches. To understand their evolution, this thesis focused on the sensory bias hypothesis, which predicts that pre-existing sensory bias promoted the evolution of signal traits. Specifically, I looked into the possibility that diet-related visual preference towards white dot patterns may play a role in the evolution of plumage patterns possessed by both sexes of Estrildid finches (Fig. D-1). My findings are in accordance with the predictions from the hypothesis. By conducting behavioural experiments based on the preferential-looking paradigm on multiple Estrildid species (Chapters 2 and 3; Mizuno and Soma 2022), I revealed foraging-related visual preference for dot patterns, which is inferred to be inherited from their common ancestor (pre-existing sensory bias). I also found that the visual preference towards white dot patterns was shared between the sexes (Fig. 2-3, Table 3-3). By phylogenetic comparative analyses on all Estrildids' diet and plumage patterns, I found that the species with dot plumage patterns were more likely to become termite-eaters (species that consume whitish, round, and gregarious invertebrates), whereas those without dots were more likely to become non-termite eater. This suggests that the diet of extant species co-evolved with plumage dot patterns in Estrildid finches (Fig. 1-3). This trend was consistent for both sexes. Although this thesis revealed the possible evolutionary relationships between the visual preference and plumage dot patterns in Estrildids, it did not directly demonstrate the causal relationship. This stems from the limitation of evolutionary analyses that can only infer the past based on the information of extant species. In other words, the proposed scenario of plumage pattern evolution (Fig. 1-1) is subject to the information available now. It may possibly be updated when more knowledge on the diet and behaviour of each species is gained.

60

The sensory bias hypothesis is also called the sensory exploitation hypothesis (e.g., Endler and Basolo 1998; Fuller et al. 2005), as the two hypotheses are similar in their prediction that female mating preference is a byproduct of their sensory system, where males evolved traits that match those sensory system characteristics (e.g., Endler and Basolo 1998; Fuller et al. 2005). However, the two differ in terms of the potential cost that females have to pay for having sensory preferences. Specifically, sensory exploitation means that females are deceived by males and suffer the cost for being attracted to males that do not necessarily offer fitness benefits. In contrast, the sensory bias hypothesis predicts that females are attracted to signal traits possessed by males that stimulate sensory traits obtained from natural selection, and assumes that females suffer no costs from being attracted to male sexual signals. Therefore, male sexual traits can evolve towards two different directions. Whether a particular signalling trait is deceiving a female, or just stimulating the female sensory system can affect its evolution. When males deceive females and the females pay the cost for being deceived, antagonistic coevolution may ensue. The antagonistic coevolution can result from female deception by males and the subsequent cost incurred. Females may enhance their sensory system to distinguish between male signals and important natural stimuli. Meanwhile, males may evolve increasingly elaborate traits to compete with the sensory ability of females (e.g., Garcia & Ramirez 2005). Males can evolve sexual traits that only stimulate the female sensory systems when they do not exploit females. Such traits need not be identical to the natural stimuli to which females originally respond.

Given the above, what was observed in Estrildid finches can be explained in light of the sensory bias hypothesis, but not exploitation. First, their plumage dot patterns could have evolved mainly to play roles in conspecific and individual recognition rather than sexual signals. Plumage patterns function as signals within- and between- sexes (e.g., Crowhurst et al. 2012; Zanollo et al. 2014; Marques et al. 2016;

GENERAL DISCUSSION

Soma and Garamszegi 2018), so it is unlikely that either one of the sexes suffers costs. Both sexes often have similar white dot patterns on their plumages in Estrildids (Chapter 1; Mizuno and Soma 2020), and there are no sex differences in their conspicuousness (Soma and Garamszegi 2018). The evolution of dot plumage patterns is also similar in males and females (Soma and Garamszegi 2018). Second, Estrildids would not mistake the dot patterns for diet, as birds have very good visual acuity (Martin 2007). Estrildids need to stimulate conspecific's visual preference that is associated with foraging, and do not need to mimic plumage patterns on their diet. Simple visual stimuli can trigger animal responses with limited information, as seen in many taxa like fishes (Tinbergen 1948), birds (Tinbergen and Perdeck 1951), and lizards (Scali et al. 2019). Those responses would have evolved, because it is advantageous to respond quickly to the trigger when they encounter it. The same might be true for Estrildid finches. Third, birds rarely face forced copulations (Gowaty and Buschhaus 1998), so female Estrildids would be unlikely to suffer costs for it.

The experimental protocols in chapters 2 and 3 provided new insights into the visual preferences of Estrildids and can improve our knowledge of how birds see the world. Using other stimuli will enable us to understand more about visual preference in Estrildids or any other captive birds. The use of stimuli with different motif sizes, colours, densities, and shapes can demonstrate which elements are crucial for attracting visual preference for birds.

Birds are well known to have good colour vision (Osorio and Vorobyev 2008), and a wide variety of plumage colours and patterns exist in living avian species. Therefore, many researchers have concentrated on understanding the functions and evolution of plumage colours in birds, but little attention has been paid to patterns. Even the eyespot patterns on peacock upper tail-coverts are still debated over their functions and evolution (e.g., Petrie et al. 1991; Petrie and Halliday 1994; Takahashi 2008).

Besides plumage colours and patterns, birds possess various signalling traits, such as sounds, movements, and smells (e.g., Searcy and Andersson 1986; Gill and Gahr 2002; Nowicki and Searcy 2004; Dalziell et al. 2015; Soma and Garamszegi 2015; Ota et al. 2015; Grieves et al. 2022), whose functions have also been studied. However, what factors were associated with the evolutionary origins of such traits remain unknown. The sensory bias hypothesis can provide one possible explanation for the origin of signalling trait evolution in birds.
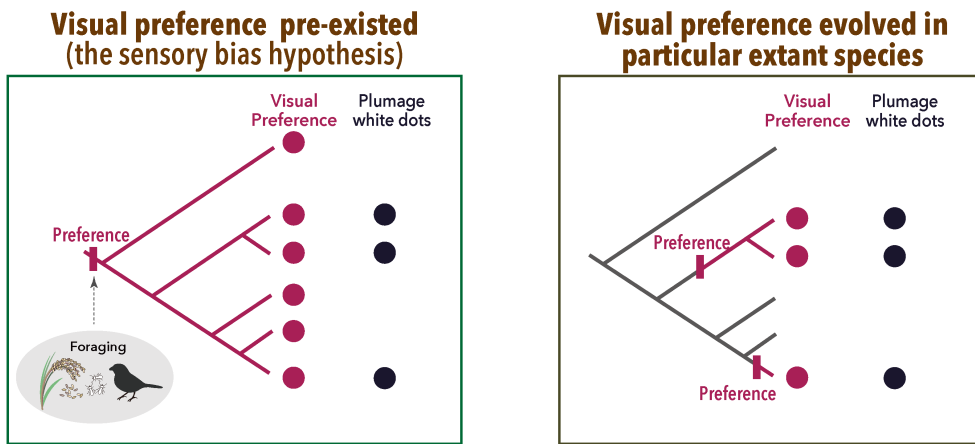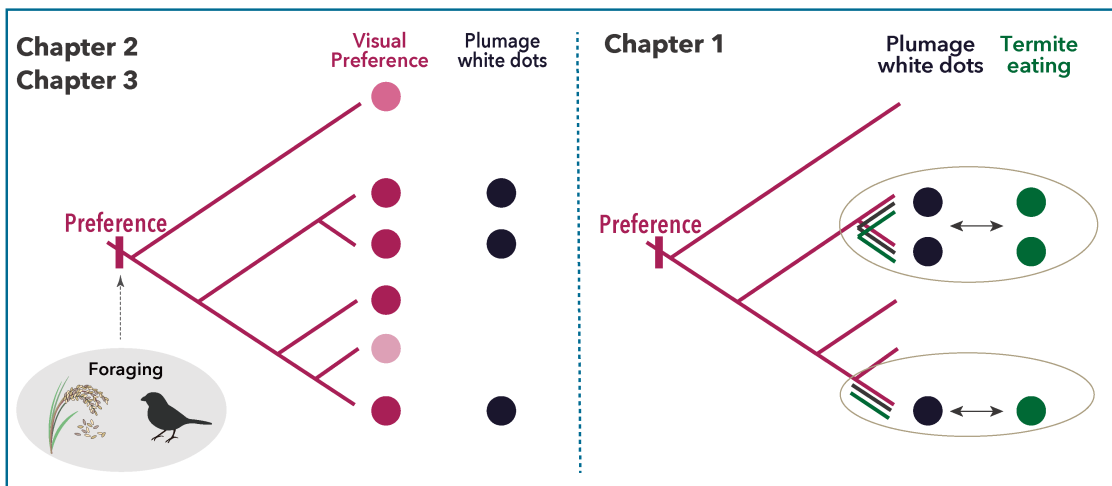
Figure D-1. Summary of this thesis. The findings suggest that Estrildid's common ancestor would have a diet-related visual preference for white dot patterns, and such preference may promote the evolution of white dot plumage patterns and termite-eating (whether species consume whitish gregarious round invertebrates). The colour gradient of pink lines indicates possible species variation of dot visual preference (dark pink means a strong visual preference, whereas light pink illustrates a weak visual preference). Blue and green lines represent that the evolution of plumage dot patterns and termite-eating influenced one another in extant species.

ACKNOWLEDGEMENTS

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RESEARCH ACHIEVEMENTS

Publications

1. **Ayumi Mizuno** & Masayo Soma (2020)

"Potential role of sensory bias in plumage pattern evolution: termite-eating and polka-dots in estrildid finches."

Ethology Ecology & Evolution 33:49–61.

https://doi.org/10.1080/03949370.2020.1803414

2. **Ayumi Mizuno** & Masayo Soma (2022)

"Star finches *Neochmia ruficauda* have a visual preference for white dot patterns: a possible case of trypophilia."

Animal Cognition 25:1271–1279.

https://doi.org/10.1007/s10071-022-01609-5

Other publications

1. 水野歩, 丸山温, 相馬 雅代 (2019)

「ハシブトガラスの貯食行動における貯食場所の選好性」

日本鳥学会誌 68:67–71.

Presentations

International conference

1. **Ayumi Mizuno** & Masayo Soma

"Sensory exploitation may promote the evolution of plumage patterns in Estrildidae."

The 56th Annual Conference of the Animal Behavior Society

Chicago USA. 2019 July (Poster)

2. **<u>Ayumi Mizuno</u>** & Masayo Soma

"Testing the sensory bias hypothesis in birds: relationship between diet seed size and

plumage dots."

The 57th Annual Conference of the Animal Behavior Society

Online. 2020 July (Oral)

3. **<u>Ayumi Mizuno</u>** & Masayo Soma

"Food-mimicking ornamental traits in Estrildid finches."

The 18th International Society for Behavioral Ecology Congress

Stockholm Sweden. 2022 July (Poster)

Japanese conference

1．水野歩，相馬 雅代

「カエデチョウ科鳥類の羽装の模様の進化のなぞ」

日本動物学会北海道支部第 63 回大会，札幌．2019 年 3 月（口頭）

2．水野歩，相馬 雅代

「系統種間比較による羽装の模様進化の検討：粒々への感覚バイアスと水玉模様」

日本鳥学会 2019 年度大会，東京．2019 年 9 月（ポスター）

3．水野歩，相馬 雅代

「鳥類における感覚バイアス仮説の検証：水玉模様を持つ種は水玉が好き？」

第 38 回日本動物行動学会大会，大阪．2019 年 11 月〔ポスター〕

4．水野歩，相馬 雅代

「鳥類の羽装模様と採餌由来の視覚選好の進化的関連」

第 39 回日本動物行動学会大会，オンライン．2020 年 11 月〔口頭〕

5．水野歩，相馬 雅代

「カエデチョウ科鳥類は水玉模様が好き：食性由来の視覚選好か」

第 40 回日本動物行動学会大会，オンライン．2021 年 9 月〔ポスター〕