Sexual selection in Estrildid finches, with further review of the evolution of nesting material holding display in relation to cooperative parental nesting

MASAYO SOMA¹⁾

Abstract Estrildid finches (family: Estrildidae) are characterised by great intraspecific and intersexual variations in sexual traits, which include courtship song, dance and ornamental colourations of plumage. These features are expected to help us answer some questions about the evolution of sexual signals: (1) why multiple ornaments evolve in socially monogamous species; and (2) why, in certain species, males and females share identical sexual traits. To discuss these, first, I briefly review the past phylogenetic comparative studies of Estrildids and show that the three sexual traits evolved independently. Secondly, I focus on one behavioural component of the courtship dance, nesting material holding display, and test the idea that the display evolved as a signal of nest building ability using phylogenetic comparative approaches. The results showed that males exhibited nesting material holding displays in species where males tend to work harder to prepare nests, which indicates that parental cooperation plays a role in the evolution of sexual signals.

Key words : courtship display, Estrildid finches, nest-building, sexual selection, songbird

1. Introduction: The multiple sexual traits of Estrildid finches

Estrildid finches (family: Estrildidae) are gaining considerable popularity in ethology, comparative cognitive science, neurobehavioral biology, and their related disciplines in recent decades, mostly due to the intensive birdsong studies on the two ‘star’ species in the taxonomic group: the zebra finch (*Taeniopygia guttata*), and the Bengalese finch (*Lonchura striata* var. *domestica*). Previous studies have contributed to our understanding of both the proximate and ultimate factors that explain

the evolution of birdsong, i.e. mechanisms of vocal (song) learning, and sexual selection on birdsong (Zann, 1996; Brainard & Doupe, 2002; Riebel, 2009; Okanoya, 2004a; Okanoya, 2004b). In contrast with male song, however, other intriguing features of Estrildid finches tend to be neglected.

Estrildid finches represent a taxonomic group of songbirds that consists of over 130 species, characterised by multiple sexual traits and their interspecific and intersexual variations. They have at least three major sexual signals that play roles in mate choice: courtship songs, visual displays (referred to as courtship dance hereafter), and ornamental colourations of plumage. For example, when male zebra finches sing courtship songs towards potential mates nearby, they simultaneously perform a courtship dance, containing waltz-like pivoting motions to approach females (Morris, 1954; Kunkel, 1959; Williams, 2001; Ullrich, Norton, & Scharff, 2016). In

1) Behavioral Neurobiology Group, Department of Biology, Faculty of Science, Hokkaido University
Hokkaido University, Kita 10 Nishi 8, Kita-ku Sapporo, Hokkaido 060-0810, Japan
Corresponding author: MASAYO SOMA
E-mail: masayo.soma@sci.hokudai.ac.jp

addition, males, but not females, of the zebra finch have orange cheeks, chest stripes and flank spots, some of which are known to be both related with individual quality or conditions, and subject to female preference (Swaddle & Cuthill, 1994; Zann, 1996; Birkhead, Fletcher, & Pellatt, 1999; Bolund, Martin, Kempenaers, & Forstmeier, 2010). Just like the zebra finch, all males of the Estrildid species are assumed to possess courtship-related song and dance, although some lack sexual dichromatism in plumage colouration (Goodwin, 1982). Generally, intense sexual selection promotes the evolution of exaggerated sexual traits or multiple ornamentations (Møller & Pomiankowski, 1993; Candolin, 2003), yet the question remains as to why multiple sexual signals evolved in a socially monogamous species like Estrildid finches. Furthermore, what evolutionary factors explain the among-species variations they present?

The above-mentioned three aspects of sexual signalling (song, dance, and plumage characteristics) can be shared between the sexes in some Estrildid species (cf. Soma & Garamszegi, 2015), which provides a potential key in solving the mystery of the evolution of female ornamentation (Amundsen, 2000; Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007; Clutton-Brock, 2009). As shown in Table 1, Estrildid finches show great interspecific variations regarding the presence and ab-

sence of female sexual signalling, implying that each trait evolved independently (for more details, see Soma & Garamszegi, 2015).

2. The evolution of courtship dance in relation to other sexual traits

Following the progression of comprehensive understanding of sexual signals in Estrildid finches, phylogenetic comparative approaches have started to be adopted (Gomes, Sorenson, & Cardoso, 2016; Gomes et al., 2017; Soma & Garamszegi, 2015, 2018). Previous studies aimed to explore what selective forces promoted the evolution of each sexual trait (song, dance, and plumage characteristics) in each sex, and to further investigate whether these traits show correlated evolution. This was conducted by comparing trait expressions among species, whilst controlling for phylogenetic relationships. The degree of elaboration in one trait is expected to be associated with those of the others, if the traits are not independent; for example, when they have the same signalling functions, and/or are under the control of the same pleiotropic mechanisms, such as hormones, genes or neurotransmitters. It is also possible that there is a trade-off between two traits, when it is too costly to maintain them both (Badyaev, Hill, & Weckworth, 2002; Shutler, 2011). Alternatively, each sexual signal may evolve independently of the others under the influence of different

Table 1. Examples of sexual differences in three sexual traits (song, dance, and plumage characteristics).

	Species	Female song	Female dance	Sexual dichromatism in plumage	References
Zebra finch	<i>Taeniopygia guttata</i>	no	no	yes	1
Bengalese finch	<i>Lonchura striata</i> var. <i>domestica</i>	no	no	no	2-4
White-rumped munica	<i>Lonchura striata</i>				
Java sparrow	<i>Lonchura oryzivora</i>	no	yes	no	4-7
Blue-capped cordon-bleu	<i>Uraeginthus cyanocephalus</i>	yes	yes	yes	8-12
Red-cheeked cordon-bleu	<i>Uraeginthus bengalus</i>				

1: Zann, 1996; 2: Okanoya, 2004a; 3: Okanoya, 2004b; 4: Restall, 1996; 5: Kagawa & Soma, 2013; 6: Ota & Soma, 2014; 7: Soma & Iwama, 2017; 8: Gahr & Güttinger, 1986; 9: Geberzahn & Gahr, 2011; 10: Geberzahn & Gahr, 2013; 11: Ota, Gahr, & Soma, 2015; 12: Ota, Gahr, & Soma, 2017

aspects of reproductive ecology or life history.

Considering the behavioural features of Estrildid courtship, it is plausible that courtship dance may well be associated with both song and plumage (Figure 1). As courtship song and dance are performed at the same time, in a well-coordinated manner, at least in some species (e.g. Ota, Gahr, & Soma, 2015, 2017; Ullrich, Norton, & Scharff, 2016), they are assumed to function for the same purpose. As courtship dance and plumage colouration are both visual signals, motions are likely to affect the animal's perception of the visual signals (Zahavi, 1978; Hasson, 1991). However, against these predictions, the outcomes from the previous phylogenetic comparative studies showed little evidence for joint evolution of the three sexual signals (song, dance, and plumage characteristics), except for a positive correlation between dance and the conspicuousness of plumage patterns (Soma & Garamszegi, 2018; Figure 1). When we measure the degree

of elaboration of dance based on the repertoire of motions that constitutes dance displays (see the next section for details), males of the species with more elaborate dances do not necessarily have more ornamented plumage colourations (Soma & Garamszegi, 2015) or complex songs (Gomes et al., 2017; Figure 1). In addition, there were no clear associations between song and plumage (Soma & Garamszegi, 2015; Gomes et al. 2017; Figure 1).

Overall, the available evidence so far suggests that the multiple sexual signals of Estrildid species evolved independently, in response to different selection pressures (Gomes, Sorenson, & Cardoso, 2016; Gomes et al., 2017; Soma & Garamszegi, 2015, 2018). In fact, Gomes, Sorenson, and Cardoso (2016) found that gregariousness and higher investment in reproduction are related to ornamental colourations, whereas larger bodied species tended to have more complex dances (Soma & Garamszegi, 2015). Furthermore, the presence of intra-specific brood parasitism was shown to be related to the evolution of visual signals (i.e. dance and plumage patterns) (Soma & Garamszegi, 2015, 2018). In short, we are yet to see the whole picture of the evolution of sexual signals in this taxonomic group, however socio-ecological factors, especially those concerned with breeding, most likely hold a key to understanding it.

What is already clear for Estrildid finches is that the elaborations of both plumage and dance are positively correlated between males and females within the species (Soma & Garamszegi, 2015, 2018). Unfortunately, intersexual song correlations remain unknown because acoustic features of female song are not documented except for a couple of species, where males and females sing quite similar songs (Gahr & Güttinger, 1986; Geberzahn & Gahr, 2011, 2013). I can infer two functional reasons why Estrildids show intersexual correlation for plumage and dance. Firstly, mutual mate choice may have promoted the evolution of sexual signals in both sexes, though it is also possible that

Figure 1. Schematic view of the evolutionary relationships between courtship dance and the other two sexual signals (plumage and song), revealed by the previous phylogenetic comparative studies of Estrildid finches (1: Soma & Garamszegi, 2015; 2: Gomes, Funghi, Soma, et al. 2017; 3: Soma & Garamszegi, 2018). The results were mixed when multiple measures were taken for song or plumage elaboration (2: Gomes, Funghi, Soma, et al. 2017), but generally indicated a lack of consistent and strong correlation.

the same signalling trait is used for intrasexual competition in each sex (review in Tobias, Montgomerie, & Lyon, 2012; see also Crowhurst et al., 2012; Zanollo et al., 2014). Secondly, as shown in the Java sparrow (*Lonchura oryzivora*), in which duet dancing is a key predictor of mating success (Soma & Iwama, 2017), behavioural displays that allow interactive communication between males and females can contribute to pair-formation, and possibly pair-bonding as well (cf. Hall, 2004; Hall & Magrath, 2007; Ręk & Magrath, 2016; Takeda & Kutsukake, 2018).

3. The ethological meaning of courtship dance

Song and plumage have been well-studied as targets of sexual selection in birds (Hill & McGraw, 2006; Catchpole & Slater, 2008), however, in comparison, dance (or visual display) has had less attention and therefore leaves room for further investigations. Estrildid finches perform quite simple courtship dances. They are usually composed of several basic components of body motions, which our previous study (Soma & Garamszegi, 2015) organised into 9 categories: (1) bobbing, i.e., up and down movement of head; (2) horizontal body movement, such as turning, changing body angle or pivoting; (3) wing movement; (4) tail movement, such as angling or spreading the tail, or tail quivering; (5) erection of body feathers; (6) hopping or stepping; (7) holding nesting material in the bill; (8) bill wiping, i.e., rubbing the bill on the perch; and (9) opening the mouth or showing the tongue. Interspecific and intersexual variations of Estrildid dance are characterised by the presence/absence of these components. Evolutionary loss or gain of each dance component might be caused by the differences in selective force: repertoire size of dance components might increase/decrease depending on species ecology, just like song repertoire size increased under intense sexual selection pressure (MacDougall-Shackleton, 1997). Alternatively, it is also possible that each dance component codes different information respectively.

Past ethological literature has provided detailed descriptions of each dance component and tried to infer their meanings and evolutionary origins (Kunkel, 1967; Morris, 1954, 1957, 1958; Goodwin, 1982; Baptista et al., 1999). For example, showing an open-mouth apparently resembles with the begging behaviour of chicks (Goodwin, 1982; Baptista et al., 1999), which makes sense in the view of the sensory trap hypothesis that juvenile-like behaviour in males can facilitate female response (Hasegawa et al., 2013). It would be natural to think that holding nesting material in the bill is related with nest preparatory behaviours (Goodwin, 1982) (see also the next section). In addition, bill-wiping, which is shown during courtship in non-Estrildid species as well, has been recently proposed to function as an olfactory display (Whittaker et al., 2015). However, the other components of Estrildid dance are hard to interpret semantically. Perhaps some components are just for demonstrating one's physical condition, especially when they include acrobatic motions (e.g. tap-dancing in cordon-bleus: Ota, Gahr, & Soma, 2015), or for grabbing the receiver's attention.

4. Interspecific relationships between nest building and nesting material holding display

In an effort to integrate the ethological and evolutionary views of courtship dance in Estrildid finches, here, I would like to shed light on one specific dance component: nesting material holding (Figure 2a). This behaviour is so characteristic of this taxonomic group's mating rituals, courtship itself is sometimes referred to as 'straw display' or 'stem display'. According to the recent research (De Silva et al., 2017), Estrildid finches are closely related, phylogenetically, to weaverbirds (family: Ploceidae), a family known for intricately woven nests that are typically made by males and subject to female mate choice (Collias & Collias, 1984; see also Quader, 2005). In general, Estrildid finches do not seem to be as good at weaving as weaverbirds, but, presumably,

Figure 2. Nesting material holding display of Estrildid finches (a). Ancestral reconstruction of nesting material holding display in males (b), in relation to parental cooperation of nesting material collecting and nest building (c).

holding nesting materials in the bill during courtship can function as an advertisement of an individual's ability to collect and carry nesting materials.

Unlike the weaverbird's many polygynous species, Estrildid finches are socially monogamous, and males and females cooperate to prepare nests. Typically, males collect nesting

materials, such as straws or grass, for females to sit in and build nests, however there is wide interspecific variation in the way they cooperate. If nesting material holding display functions as an indicator of nesting ability, the presence/absence of the display would be evolutionarily correlated with two things; firstly, the pattern of

division of labour of nesting between the sexes, and secondly, the amount of materials the nest requires. Specifically, I predicted as follows:

- (1) Male nesting material holding display will be present in species where males take on a considerable proportion of nest making, whereas both sexes might display if they need to cooperate to prepare nests.
- (2) Nesting material holding display may disappear in species that use other species nests or cavities/holes to avoid labourious collection of nesting materials.

To test these ideas, I ran small phylogenetic comparative analyses, based on the phylogenetic data and presence/absence of nesting material holding displays in each species that had been previously studied (for details see Soma & Garamszegi, 2015). Note that the definition of the presence of ‘nesting material holding display’ is that birds hold nesting materials during courtship, regardless

of whether they keep on holding them whilst singing. In addition, I checked how much males and females participate in nest preparations (i.e. collection of nesting materials and nest building) and scored them as follows: 2: males do, 1: both sexes do, or 0: females do, based on the relevant literature (Goodwin, 1982; Payne, 2010). As some species were reported to use multiple types of nests (Goodwin, 1982; Payne, 2010), the nest types of each species were scored based on whether grass nests were used or not, and whether cavities or other species nests were used or not, relying on the literary descriptions. Using phylogenetic generalized least-square (PGLS) regressions (see detailed methods in Soma & Garamszegi, 2015), I tested the effects of division of nesting-based labour between the sexes, and nest types on the presence of nesting material holding displays in males and females.

I found that males present nesting material holding displays in species where

Table 2. Phylogenetic multiple regression models relating division of labour of nesting and nest type with the presence of nesting material holding display in males (a) and females (b). To consider intersexual correlation, the presence of female/male straw-holding display was also entered as an explanatory variable in male/female models respectively. * indicates statistical significance ($P < 0.05$).

(a) Male nesting material holding display

			Coefficient	SE	<i>t</i>	<i>P</i>
(Intercept)			-0.096	0.784	-0.12	0.904
Presence of female nesting material holding display			0.001	0.007	0.12	0.909
Division of labour						
Collecting nesting materials	(2: male, 1: both, 0: female)		0.445	0.157	2.84	0.009 *
Building nest	(2: male, 1: both, 0: female)		0.480	0.132	3.64	0.001 *
Nest type						
Grass nest	(0: absent, 1: present)		-0.391	0.639	-0.61	0.546
Use of cavity or other species nest	(0: absent, 1: present)		-0.010	0.064	-0.16	0.878

(b) Female nesting material holding display

			Coefficient	SE	<i>t</i>	<i>P</i>
(Intercept)			0.367	0.742	0.49	0.625
Presence of male nesting material holding display			0.416	0.193	2.16	0.042 *
Division of labour						
Collecting nesting materials	(2: male, 1: both, 0: female)		-0.330	0.219	-1.50	0.146
Building nest	(2: male, 1: both, 0: female)		-0.113	0.151	-0.75	0.461
Nest type						
Grass nest	(0: absent, 1: present)		0.335	0.524	0.64	0.529
Use of cavity or other species nest	(0: absent, 1: present)		-0.011	0.186	-0.06	0.955

males tend to work more for preparing nests, but that nest type had no influence on it (Table 2, Figure 2). In contrast, there were no statistically significant effects of nesting division of labour and nest type on female display, but females tended to display when males displayed also (Table 2b).

These findings suggest that how much males work for preparing nests is an illustrative factor in the evolution of nesting material holding display, which is compatible with the idea that the display may function as an indicator of nesting ability. In contrast, in females, intersexual correlation alone accounts for the evolution of the display. This is presumably because females exhibit courtship dancing with the aim of mutual communication with their partners (e.g. duet dancing; Soma & Iwama, 2017) rather than demonstrating nesting ability. As available information for analyses was limited (Figure 2c), these findings should be seen as preliminary. Moreover, the direct association between the display and the ability of nesting material carrying should be tested to support this view.

5. Progressing understanding of courtship as male-female communication

Sexual selection and parental investment are interlinked. For instance, one recent avian-wide phylogenetic comparative study has revealed negative associations between them; males, under intense sexual selection pressure, exert increasing amounts of effort to attract females. This results in decreased investment in rearing of the offspring, overall lowering parental cooperation. (Remeš et al., 2015). Similarly, when comparing cuckoo species with and without parental care (i.e. brood parasites or not), parasitic species were shown to be more ornamented (Hasegawa & Arai, 2018). However, another phylogenetic comparative study on passerine species proposed that nest-building activity itself could serve as a sexually selected display (Soler, Møller, & Soler, 1998). These previous findings might look contradictory, but were probably influenced by the heterogeneity in

the breeding ecologies of the targeted species. Contrasting biparental-care species with those that totally lack paternal care (e.g. brood parasites, lek breeding) can highlight the negative associations between paternal investment and ornamentation. However, insight can be gained from the positive correlation between sexual signalling and parental investment (i.e. nest preparation), shown in the previous section; interspecific comparisons focusing on all monogamous and pair-bonding species may reveal the possibility that female mate choice is based on ‘good father’ traits.

To conclude, understanding male-female communication is key in understanding the evolution of sexual signals, especially in socially monogamous species like Estrildid finches. Multiple sexual signals (i.e. song, dance, and plumage characteristics) that can be shared between both sexes of Estrildids have only just begun to be understood evolutionarily, or ecologically. However, based on the available evidence, I am sure that at least some components of said signals play roles in mutual communication in pairing partners. To further understanding of sexual signals such as these, I expect future empirical studies to reveal their breeding ecology, such as the pair-bonding periods and its effect on reproductive success, or the occurrence of extra-pair mating. In addition, more information on female song would be sure to advance this area of research.

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