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## Beauty alone is insufficient: female mate choice in the barn swallow

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**Abstract** The barn swallow, *Hirundo rustica*, is a model species for studying sexual selection, particularly female mate choice. Although there have already been several reviews of female mate choice and its geographic variation in this species, all of them have focused on secondary sexual characteristics. Here, for better understanding of the general pattern of female mate choice and their influence on male phenotype, I review all of the female mate choice criteria ever reported in the barn swallow, emphasizing the importance of relatively inconspicuous male traits. These include resources defended or provided by males, such as territory and paternal investment. In addition, females prefer a nestling-like vocalization, enticement call, which is particularly noteworthy because females prefer immature calls. This pattern contrasts with female choice based on secondary sexual characteristics, in which more mature, elaborate male traits are almost always favored. Nestling-like male traits are widespread, and thus female avoidance of, rather than preference for, mature forms might be common. In addition to selection on the target trait itself, these resources and nestling-like male traits would also matter in understanding the evolution of the overall male phenotype and its geographic variation, due to the interrelationships among male target traits and those among female mate preferences. Female preferences for inconspicuous traits are highly dependent on ecological factors such as nest predation pressure, and thus overall male phenotype including secondary sexual characteristics might be more predictable than previ-

ously thought. Future studies should focus on not only conspicuous secondary sexual characteristics but inconspicuous male traits.

**Keywords** Female mate preference · *Hirundo rustica* · Nestling-like traits · Secondary sexual characteristics · Territory quality

### Introduction

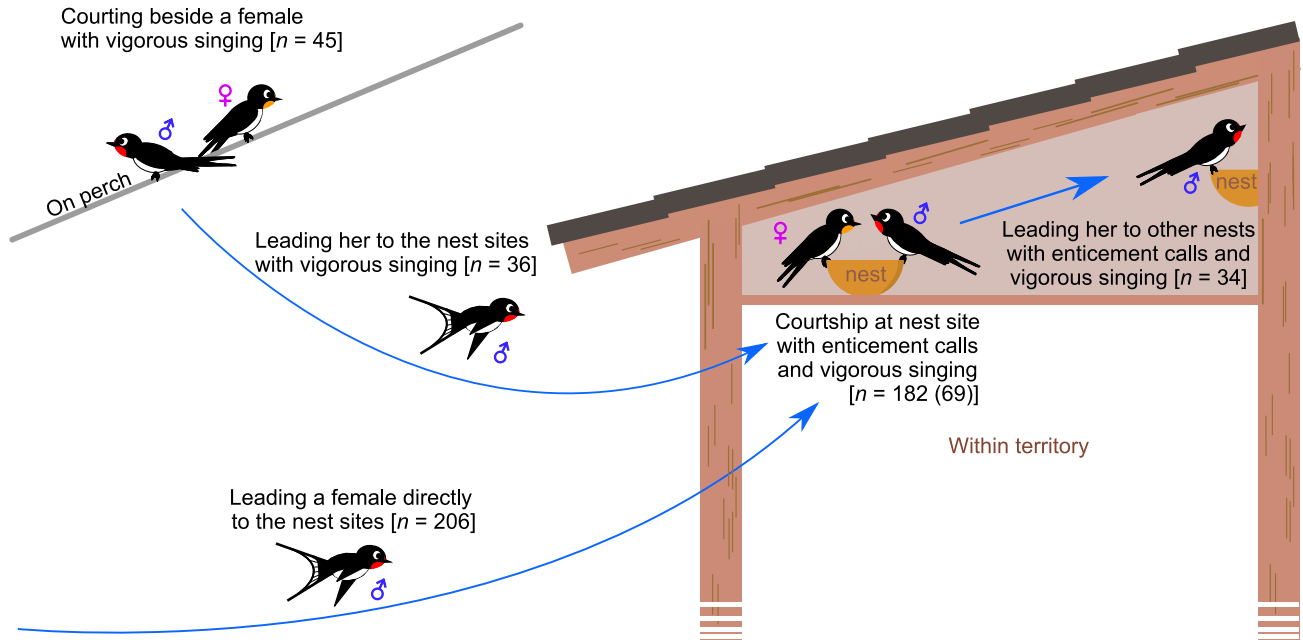
Female mate choice is a key issue in evolutionary ecology: it affects the evolution of elaborate male traits and their geographic variation, as well as population growth, extinction, and speciation, at least in theory (Andersson 1994; Coyne and Orr 2004; Brooks and Griffith 2010). In empirical studies, however, its understanding is still insufficient, because most studies have focused solely on secondary sexual characteristics (i.e., traits that are fully developed at maturation but are not a direct part of the reproductive organs; e.g., see Tazzyman et al. 2014 for a recent review), perhaps in part due to the intuitive importance of sexual selection (Andersson 1994) or simply due to its eye-catching nature (Tazzyman et al. 2014). This circumstance potentially biases our understanding of female mate choice and its evolutionary impact on male phenotype. To properly evaluate the general pattern of female mate choice and its evolutionary causes and consequences, not only secondary sexual characteristics but also other, relatively inconspicuous male sexual or courtship traits should be concerns.

One approach for studying general pattern (and variation) of female mate choice is to focus on a particular species and review all of the female mate choice criteria ever reported. Such an approach is particularly useful for a model system that has been studied by many researchers with different interests. The barn swallow, *Hirundo rustica* (see frontispiece picture; see Fig. S1), is such a model system of female mate choice. After Møller (1988) experimentally demonstrated fe-

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**Fig. 1** Courtship sequence of male barn swallows at pair formation, shown with blue arrows. Detailed behaviors are listed for each courtship element. The numbers of observations are denoted

in brackets; values in parentheses indicate the numbers of instances in which males successfully attracted females to their nests. Redrawn from Hasegawa (2011). Color figure online

male mate preference for elongated male tails in this monogamous bird (also see Bañbura 1986 for a correlational study), many other studies tested and demonstrated female mate preference for long tail feathers and other male characteristics (see below). Also, because this is a cosmopolitan species distributed across all continents except Antarctica, and exhibits different phenotypes (e.g., some subspecies have relatively short tails with dark rufous-chestnut underparts; Turner 2006), the barn swallow is a suitable system for studying geographic variation as well as speciation (sensu Scordato and Safran 2014). Until now, several reviews have been published concerning female mate choice and its geographic variation in this species (e.g., Møller 1994a; Turner 2006; Scordato and Safran 2014; Romano et al. 2017a). However, all of them are focused solely on secondary sexual characteristics (and mostly on plumage ornaments), simply because other kinds of sexually selected traits are less studied than secondary sexual characteristics.

Here, I reviewed female mate choice not only on secondary sexual characteristics (i.e., “beauty” traits) but also on other sexual or courtship traits. I gathered studies of female choice at pair formation, at (extra-pair) copulation, and differential allocation (i.e., increased maternal investment when paired with attractive males; Burley 1986, 1988; Møller and Thornhill 1998), which can be regarded as a form of mate choice (Sheldon 2000; Brooks and Griffith 2010). I start this review by describing courtship behavior of male barn swallows, which provides insights into the function of each male trait. As in previous studies (see review papers above), I

focused on breeding grounds, because males and females usually arrive at the breeding ground separately (though courtship behaviors can be observed even at wintering grounds; Turner 2006). Second, I listed all the known criteria of female mate choice with particular attention to the difference between secondary sexual characteristics and relatively inconspicuous male traits. Finally, I discuss how female preference for inconspicuous male traits affects overall male phenotype.

### Male courtship displays

Most male barn swallows commence pairing courtship in the air while some start courting beside perching females (Fig. 1). Males sing vigorously while courting. Then, they lead females to an old nest or to a potential nest site, emitting enticement calls. When the males have successfully led females to the nest site, they are often observed to sequentially show females other nests in their territories. Thus, males can attract females to nest sites by their plumage characteristics, songs, and enticement calls, and thereafter show off nest sites in their territories. These traits would be potentially important targets of sexual selection via female mate choice (i.e., mate choice criteria), compared to male traits that can be assessed only afterwards (e.g., paternal care behaviors), because sexual selection intensity (or strictly, effect size in each selection episode) decreases with the progress of the breeding season (Romano et al. 2017a).

**Table 1** Summary of female mate choice criteria reported for the barn swallow

Variables	Direction <sup>a</sup>	Context <sup>b</sup>	Representative studies <sup>c</sup>
Secondary sexual characteristics			
Plumage ornaments <sup>d</sup>			
Tail length/asymmetry	+	Both	Møller (1988), <sup>E</sup> (1990), <sup>E</sup> (1992a, b), <sup>E</sup> (1993b), <sup>E</sup> (1994a, b); <sup>E</sup> Møller et al. (2006); <sup>E</sup> Saino et al. (1997b); <sup>E</sup> Smith and Montgomerie (1991); <sup>A</sup> Vortman et al. (2011, 2013) <sup>M</sup>
White tail spots size/shape	+	Both	Kose and Møller (1999); <sup>E</sup> Kose et al. (1999); <sup>E</sup> Møller (2017); <sup>E</sup> Hasegawa (unpub. data) <sup>J</sup> (mentioned in Hasegawa et al. 2012b) <sup>J</sup>
Throat patch coloration/size	+	Both	Ninni (2003); <sup>E</sup> Safran et al. (2005); <sup>A</sup> Hasegawa et al. (2010a); <sup>J</sup> Hasegawa and Arai (2013a, b) <sup>J</sup>
Ventral coloration	+	Both	Safran and McGraw (2004); <sup>A</sup> Safran et al. (2005); <sup>E</sup> Vortman et al. (2011, 2013) <sup>M</sup>
Dorsal coloration	+	Social mate choice	Garamszegi et al. (2006) <sup>E</sup>
Song attributes			
Song rate	+	Sire choice	Møller et al. (1998b) <sup>E</sup>
Song duration	+	Social mate choice	Garamszegi et al. (2005) <sup>E</sup>
Bout rate	+	Social mate choice	Garamszegi et al. (2006) <sup>E</sup>
Song length	+	Social mate choice	Garamszegi et al. (2006) <sup>E</sup>
Repertoire size	+	Social mate choice	Garamszegi et al. (2006) <sup>E</sup>
Versatility	+	Social mate choice	Garamszegi et al. (2006) <sup>E</sup>
Peak amplitude frequency	+	Social mate choice	Garamszegi et al. (2006) <sup>E</sup>
Rattle impulse tempo	+	Social mate choice	Garamszegi et al. (2006) <sup>E</sup>
Song complexity	+	Sire choice	Wilkins et al. (2015) <sup>A</sup>
Song tempo	+	Sire choice	Wilkins et al. (2015) <sup>A</sup>
Resources defended or provided by males			
Territory quality	+	Social mate choice	Hasegawa et al. (2012a) <sup>J</sup>
Nest building behavior	+	Social mate choice	Soler et al. (1998) <sup>E</sup> ; Møller (2006) <sup>E</sup>
Mate guarding	+	Sire choice	Møller (1987) <sup>E</sup>
(Inter-territory distance) <sup>e</sup>	+	Sire choice	Hasegawa et al. (2010b) <sup>J</sup> ; Møller and Ninni (1998) <sup>E</sup> ; but see Saino et al. (1999) <sup>E</sup>
Nestling-like traits			
Enticement call	-	Social mate choice	Hasegawa et al. (2013) <sup>J</sup> ; Hasegawa and Arai (2016) <sup>J</sup>

<sup>a</sup>Direction indicates positive (exaggeration) or negative (reduced form). The direction of female mate preference is often difficult to judge, and thus I considered the direction as positive or negative when females preferred more or less adult male-like characteristics, respectively. Full song is emitted solely by adult males (Turner 2006), and so I considered the direction positive for the characteristics of full song

<sup>b</sup>Female mate preference can be divided into social mate choice (e.g., pair formation, pre-mating period, breeding date, brood numbers) and choosing sires (i.e., paternity allocation)

<sup>c</sup>For reference, I included study region information (*E* Europe, *A* North America, *M* Middle east, *J* Japan; see Romano et al. 2017a for the formal analysis of geographic variation in the intensity of sexual selection on plumage ornaments)

<sup>d</sup>See Romano et al. (2017a) for effect size and its population divergence

<sup>e</sup>See text for explanation

## Female mate choice criteria

In barn swallows, many studies have focused on female mate choice. I categorized female mate choice criteria into three groups: secondary sexual characteristics, resources, and nestling-like traits (Table 1). In this review, I did not include male arrival date (e.g., Møller et al. 2003), age (e.g., Lifjeld et al. 2011), kinship (Kleven et al. 2005), or body or physiological condition (e.g., Møller et al. 2003; Kojima et al. 2009; Romano et al. 2014). This is not because these traits are unimportant, but because females may use other phenotypic traits correlated with these traits for mate choice (Møller et al. 2003; Romano et al. 2014). In other words, these variables would be information (signal) contents rather than mate choice criteria itself. I also excluded female mate choice in unnatural environment (e.g., aberrant tail feathers in Chernobyl, which is virtually absent in other populations; Møller 1993a), although the same characteristics can be found in normal populations in smaller proportions.

## Secondary sexual characteristics

The most well-known target of female mate choice in the barn swallow, would be the long, sexually dimorphic tail (reviewed in Møller 1994a; Møller et al. 1998a). Although there are some notions that the aerodynamic advantages (i.e., maneuverability, here) of deep fork tails can explain the evolution of this trait (e.g., Thomas 1993; Norberg 1994; Evans 1998; also see e.g., Aparicio et al. 2012; Pap et al. 2015 for objection to this explanation: reviewed in Hasegawa et al. 2016b; Hasegawa and Arai 2017a), population mean tail length should be aerodynamically costly, indicating that female preference for long-tailed males should account for the evolution of long tails, at least in part (e.g., Buchanan and Evans 2000; Rowe et al. 2001). Because only high-quality (e.g., viable) males can bear the cost of long-tails, females obtain high-quality mates by preferring long-tailed males (reviewed in Møller 1994a; Turner 2006; also see Romano et al. 2017b). Likewise, two other tail characteristics have been reported to be important cri-

teria of female mate choice: fluctuating tail asymmetry (e.g., Møller 1992a, 1993b) and white tail spots (e.g., Kose and Møller 1999; Kose et al. 1999). These characteristics can evolve as byproducts of long tails (e.g., Johnstone 1994), as amplifiers (Fitzpatrick 1998; also see Møller 2017 for potential illusion effects of white tail spots), or as quality indicators, because these traits also indicate male quality (e.g., condition at molt; Møller 1994a, b; Saino et al. 2015).

In addition to these tail characteristics, plumage coloration would be important. A red throat patch (color: Ninni 2003; size: Møller 1994a; Hasegawa and Arai 2013a), and other ventral plumage feathers (e.g., breast and vent coloration; Safran and McGraw 2004; Safran et al. 2005) are related to several indices of female choice (e.g., mating success, paternity; reviewed in Romano et al. 2017a). Because all of these ornaments are sexually dimorphic, one may argue that female preference for these traits are as expected (Andersson 1994). However, this might not always be the case, as sexual dimorphism evolved in the past and might be maintained to achieve threshold levels of stimulation or for other reasons (Candolin 2003; van Doorn and Weissing 2004). For example, the blue-black coloration of dorsal feathers is highly sexually dimorphic in this species, but female preference for this coloration would be at best weak (Perrier et al. 2002; Galván and Møller 2009; also see Garamszegi et al. 2006; Table 1). Because ventral, but not dorsal, plumage is pheomelanin-based coloration, honest signaling via pleiotropy of pheomelanogenesis genes and resource tradeoff between pheomelanin production and somatic maintenance may facilitate female preference on the ventral coloration (reviewed in Ducrest et al. 2008; Roulin 2016). Consistent with this perspective, in the barn swallow, throat and ventral plumage coloration (and its pigmentation) is linked to several physiological traits (e.g., testosterone levels), age, body condition, and viability across the range of the species (e.g., Safran et al. 2008; Galván and Møller 2009, 2013; Hasegawa et al. 2014; Vitousek et al. 2016; but see Saino et al. 2013).

Song is another well-known secondary sexual characteristic in passerines including the barn swallow (reviewed in Turner 2006). There are several studies indicating that characteristics of song are related to male quality (e.g., parasite infection, hormone levels, immunity, and so on; Møller 1991a; Galeotti et al. 1997; Saino et al. 1997a; Garamszegi et al. 2005, 2006; Dreiss et al. 2008), which may facilitate female mate choice based on male traits. For example, Møller et al. (1998b) found that song rate is related to extra-pair paternity together with tail length, indicating female preference for a high song rate. Wilkins et al. (2015) found that song complexity together with feather length (including tail length) affects paternity success. A similar, but weaker, relationship has been found for song tempo (Table 1; also see Wilkins et al. 2015 for other non-significant song characteristics). Likewise, Garamszegi and his colleagues have reported relationships between the pre-

mating period, a measure of female preference, and song characteristics (e.g., song length; Garamszegi et al. 2005, 2006; Table 1; also see Garamszegi and Møller 2004 for unpublished non-significant data). Other characteristics of song (e.g., rattle duration) have not yet been demonstrated to be targets of female choice, although they might be used in male–male contests rather than for attracting females (Galeotti et al. 1997; Scordato and Safran 2014; Wilkins et al. 2015; also see Galeotti et al. 1997 for a strong positive correlation between testosterone level and rattle duration).

In summary, many secondary sexual characteristics would be used in female mate choice in this species (Table 1). The target, direction, and intensity of preference varies among populations at least for plumage ornaments (e.g., Safran et al. 2016; Wilkins et al. 2016; reviewed in Scordato and Safran 2014; Romano et al. 2017a), affecting the geographic variation in male trait expression, although most studies have found positive female preference (i.e., toward exaggerated traits; Romano et al. 2017a). Well-ornamented males provide less, rather than more, paternal care compared to less-ornamented males in barn swallows (e.g., de Lope and Møller 1993; Saino and Møller 1995; Maguire and Safran 2010; Hasegawa et al. 2014; Hasegawa and Arai 2015a), which may be costly for females even if well-ornamented males have fewer ectoparasites and thus lower risk of contagion (Møller 1994a). Females would rather obtain indirect benefits (i.e., genes for attractiveness and viability) by preferring well-ornamented males (Møller 1994a; also see Møller and Jennions 2001 for unpublished data on song in relation to direct benefits). Still, even in this model species of female mate choice, direct evidence of female mate choice is scarce (but see Møller 1988, 2001 for female extra-pair copulation behavior), and most of them rely on indirect evidence such as mating pattern or extra-pair paternity, both of which can be affected by male–male contests, male strategy, or ecological factors such as inter-nest distance, which cannot easily be teased apart by experimental manipulation (e.g., Hasegawa et al. 2010b; Lifjeld et al. 2011; reviewed in Westneat and Stewart 2003; also see Møller 1991b; Møller and Ninni 1998; Saino et al. 1999 for relationship between inter-nest distance and extra-pair copulation or paternity). Thus, these observations and even experiments should be interpreted carefully, though careful interpretation is required for other works as well (e.g., for those with small sample size; see below).

#### Resources defended or provided by males

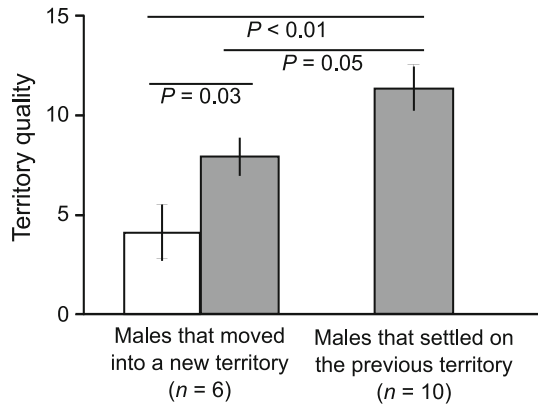
Together with male plumage and song characteristics, territory quality is one of the most well-known female mate choice criteria in passerine birds (e.g., Alatalo et al. 1986; Slagsvold 1986). Because barn swallows defend only a small territory ( $< 20 \text{ m}^2$ ) with few resources (i.e., nest and perch sites; Turner 2006), and because reproductive success does not depend on territory quality but

on male quality (Møller 1994a), territory is thought to be unimportant in this species (Møller 1990, p. 463). In the same colonial population, territory did not predict male settlement patterns, which was inconsistent with the hypothesis that territory quality is important in female mate choice (Møller 1990, 1994c). However, this might not be the universal pattern in the barn swallow. Although these studies focused on colonial breeders in livestock stalls where nest predation is virtually absent (Møller 1994a; Turner 2006), outdoor populations experience high nest predation rates (see Fig. 2 for nest predation attempt by the carrion crow). In Japan,

approximately 50% experience nest failure (Fujita 1993; Hasegawa et al. 2012a, 2017; also see Turner 2006 for the potential importance of crows as nest predators in this region; also see Liang et al. 2013; Su et al. 2017 for the potential importance of interspecific brood parasitism), though actual predation rates depend on population (e.g., see Møller 2010 for subtle differences between colony and outdoor populations in European subspecies). In Japan, territory quality, measured by the quality and quantity of old nests, predicts seasonal reproductive success (Hasegawa et al. 2012a), and males did settle in better territories than their previous terri-



**Fig. 2** A nest predation attempt by a carrion crow. Color figure online



**Fig. 3** Territory quality of males that moved into a new territory without their previous territories being occupied and males that settled in the same territories they held in the previous season in Joetsu population in Japan. White and black bars indicate the mean ( $\pm$  SE) quality of the previous and current territory, respectively. Statistics are based on *t* tests and paired *t* tests. Redrawn from Hasegawa (2011)

territories when they changed territories across years in outdoor breeding sites (Fig. 3). As expected, males with high-quality territories paired earlier, indicating female mate choice based on territory quality (Hasegawa et al. 2012a; though there may still be some population differences in the relationship between territory quality and reproductive parameters; see above). Although territory quality is often related to male morphological traits (e.g., throat coloration in this species; Hasegawa et al. 2014; Wilkins et al. 2015), multivariable analysis indicates that territory quality is an important mate choice criteria than male morphology (in fact, effect size,  $Z_r = 0.60$ , 95% CI = 0.14–1.06 for laying date and 0.62, 95% CI = 0.11–1.12 for pairing date, computed from  $R^2$  value, is quite high for female preference for territory quality, though sample sizes were small ( $n = 21, 18$ , respectively); note that mean overall effect size for plumage ornaments was 0.21; Romano et al. 2017a). As swallows choose high-quality (i.e., intact) nests within their territories (Hasegawa et al. 2012a) or choose colonies/breeding sites with many high-quality nests (Safran 2004, 2007; also see Ringhofer and Hasegawa 2014), it is not surprising that females choose territories with high-quality nests, though experimental validation remains to be carried out.

Because territory is not the sole resource provided by males in this biparental care species, it is natural to suppose that other types of resources may also be the targets of female preference. For example, Soler et al. (1998) argued that female swallows should invest more when breeding with males of high parental quality, and found that females provide larger amounts of reproductive investments, measured as total numbers of eggs laid during the breeding season, when paired with superior nest builders. Because male contribution to nest building reflects his willingness to invest in reproduction (i.e., feeding rate; Møller 1994a, 2006), female preference

for these males accompanies direct benefits (also see Soler et al. 2007 for additional indirect benefits). Although males provide several types of paternal cares (e.g., provisioning to nestlings and fledglings, and incubation in some subspecies; Turner 2006), whether females pay particular attention to specific paternal care behaviors is unknown. In addition to direct parental care, males may provide females with time and energy by mate guarding, which can improve female foraging efficiency (i.e., indirect parental care; sensu Fedy and Martin 2009). Møller (1987) showed that female extra-pair copulation decreased with increasing male mate guarding, which can be regarded as female preference for males who have high fertilization ability. Likewise, males that prevent other males from settling nearby suffer less paternity loss (e.g., Møller and Ninni 1998; Hasegawa et al. 2010b; but see Saino et al. 1999) and thus this might also be female preference for indirect parental care (Table 1).

In sum, resources defended or provided by males can directly affect reproductive success and thus facilitate female preference at least in some circumstances (Table 1). By preferring such males, females can obtain direct benefits, increasing the number and quality of offspring (note that indirect benefits should automatically arise whenever male target traits are heritable; Kokko et al. 2003). Apart from secondary sexual characteristics, some resources (e.g., territory) are not inherent characteristics of males, and thus promote male–male contest for resources. Therefore, female preference for resource holders results in indirect mate choice (sensu Wiley and Poston 1996) on the male traits used in male–male contests, confounding with direct mate choice for the male traits (note that direct mate choice for the male traits should also be enhanced if it increases female fitness; Wong and Candolin 2005). Unfortunately, unlike the plumage characteristics I noted in the previous subsection, resources defended or provided by males are difficult to experimentally manipulate and, thus, it is much more difficult to exclude confounding effects from unmeasured traits than when studying plumage characteristics (though not impossible as it has been done in the pied flycatcher: Alatalo et al. 1986). To understand how male traits (and female preference on the traits) evolved, researchers should take resources (e.g., territory) into account, possibly with experimental manipulation of resources.

#### Nestling-like traits

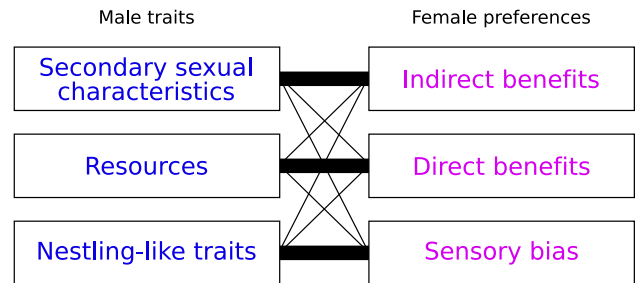
Although secondary sexual characteristics and territory quality are well-known criteria of female mate choice, there are several other criteria. In the barn swallow, enticement calls (Turner 2006, p. 64) are noticeable vocalizations emitted during pairing courtship (Fig. 1; also see supplementary sounds in Hasegawa and Arai 2016 for some examples). Given the resemblance to nestling food-begging calls, male enticement calls may

attract females by exploiting female parental care for nestlings (i.e., attraction to nestlings; sensu Christy 1995). As predicted, Hasegawa et al. (2013) showed that male enticement calls and nestling food-begging calls structurally resemble each other, as compared to other male vocalizations (Fig. 1 in Hasegawa et al. 2013) and unpaired females are similarly attracted to the playback of nestlings' food-begging calls and male enticement calls. Hasegawa and Arai (2016) further demonstrated that unpaired females were more attracted to heightened-pitch (i.e., more nestling-like) calls than to control enticement calls (though female swallows prefer lower, rather than higher, pitched songs; Garamszegi et al. 2005, 2006). Because male enticement calls pitched lower than typical nestling food-begging calls, the similarity to nestlings decreases with maturation at least in pitch height.

The most intriguing point of female preference for male enticement calls is that females are attracted to males with immature forms (Table 1), which contrasts with female mate choice based on secondary sexual characteristics that almost always favors more matured, elaborate traits (Table 1; also see Tazzyman et al. 2014 for other species). Although I focus here on nestling-like vocalizations, this may not be the sole nestling-like traits. Many adult birds including male barn swallows possess characteristics that resemble those of nestlings (or informally, “cute” traits; sensu Jones 1995), such as courtship begging, colorful gape, and so on (reviewed in Bradbury and Vehrencamp 1998), though it is premature to argue about their evolutionary relationship. Thus, the directionality of female mate preference, deduced from those for secondary sexual characteristics (i.e., toward exaggeration; reviewed in Tazzyman et al. 2014) might not be generalized into all courtship traits until female choice on these traits is tested. Unfortunately, except for enticement calls, experimental manipulation of nestling-like traits (e.g., courtship begging) is difficult to accomplish, which remains to be tested in the future with advanced statistical and manipulation techniques (e.g., use of robotic models: Patricelli et al. 2006). Female mate preference for mimetic male signal (nestling-like traits, here) is expected even if the preference is costly, given that female attraction to certain stimuli (nestlings, here) is adaptive (Christy 1995; Arnqvist 2006).

#### Differences among the three categories

It is interesting that three categories of female mate choice criteria listed here would have different sexual selection mechanisms (Fig. 4). Secondary sexual characteristics provide females with indirect benefits, while resources provide females with direct benefits (but note that males who provide resources can also provide indirect benefits; also see below). Nestling-like traits attract females via a sensory trap to exploit fe-



**Fig. 4** Schematic illustration of the three categories of female mate preference criteria in relation to the most likely causes of the preference in the barn swallow. Thick lines represent main linkages, while thin lines are also likely involved in the evolution of female preferences and corresponding male target traits (see text)

male parental care for nestlings, and thus exploit the sensory bias of females. These traits correspond to the three main mechanisms proposed to explain how mating preferences arise and select for male traits (Candolin 2003; also see Safran et al. 2013 for a variant). It should be noted that these three mechanisms are not mutually exclusive. For example, as noted above, indirect benefits should automatically arise whenever male target traits are heritable (Kokko et al. 2003), and direct benefits can affect female preference for secondary sexual characteristics to some extent (e.g., ectoparasites; Møller 1994a). Sensory bias may also exist in female preference for resources or secondary sexual characteristics (see above), which can promote subsequent coevolution between male traits and female preference (e.g., sexually antagonistic coevolution; Arnqvist 2006). Still, differences in the main mechanisms provide an excellent opportunity of simultaneous evaluation and prediction of the evolution of each focal trait and its correlates (see below).

#### Importance of inconspicuous male traits on overall phenotype

Given that females prefer relatively inconspicuous male traits as well as conspicuous secondary sexual characteristics, how can they influence overall male phenotype? Of course, female preference for each male trait would select for each target trait (Andersson 1994), as noted in the previous section. However, the evolution of one trait is rarely independent of other traits because of the interrelationships among male traits and among female preferences, as is often discussed in the context of multiple cues in mate choice (reviewed in Møller and Pomiankowski 1993; Candolin 2003; Bro-Jørgensen 2010). Here, I briefly discuss each topic, to facilitate understanding of the evolutionary consequences of female mate choice. Then, I present how consideration (or ignorance) of inconspicuous male traits affects our understanding of evolution of overall male phenotype with a simple hypothetical scenario.

## Interrelationships among male traits

Several studies have demonstrated positive intercorrelations among male secondary sexual characteristics in barn swallows (e.g., Møller et al. 1998a; Kose and Møller 1999; Kose et al. 1999; Saino et al. 2003; Hasegawa et al. 2010a; but see Vortman et al. 2011; Safran et al. 2016 for no detectable relationships). Still, it is often unclear whether these patterns reflect evolutionary covariation without a well-designed experiment (e.g., Wagner et al. 2012; van Noordwijk and de Jong 1986; Stearns 1992; Andersson et al. 2002; Saino et al. 2003), due to individual variation in resource availability (e.g., when the allocation between the traits varies less than the total investment, a positive correlation can be predicted even if there is a trade-off between two ornaments). For example, colorful ventral plumage and tail ornaments vary inversely across regions, subspecies, and even species within the genus *Hirundo* (Turner 2006; Hasegawa and Arai 2013b; Hasegawa et al. 2016b), indicating that within-population patterns do not always predict evolutionary relationships in swallows (also see Vortman et al. 2015 for heritable variation in the relative investment of the two ornaments). An exception is the case in which traits are developmentally and functionally (or genetically) integrated (Andersson et al. 2002), in which case the evolution of one trait accompanies those of others (e.g., long, symmetrical tails; Møller 1990, 1993b, Balmford and Thomas 1992). A positive correlation between territory quality and male plumage colorfulness might be one such case, because melanin pigmentation is often pleiotropically interrelated to several other traits such as aggressiveness (see above; Hasegawa et al. 2014; Wilkins et al. 2015; also see Møller 2002 for decreased aggressiveness in colonial populations where territory quality is negligible). Such an interrelationship might be reinforced by hormonal feedback perhaps via social interactions, because plumage coloration affects testosterone levels, which is linked to aggressive behavior (Safran et al. 2008). Other interrelationships (e.g., territory and song; Wilkins et al. 2015) might also be reinforced by hormonal feedback, which remains to be clarified. In addition, nestling-like traits should be related to male secondary sexual characteristics, although a negative relationship can be predicted in this case, because nestling-similarity decreases with maturation, which contrasts with secondary sexual characteristics that increase with maturation (see above; Table 1). Hasegawa and Arai (2016) found that males with less-colorful throat patches emitted more nestling-like calls. This can also be interpreted as less-ornamented males can still attract females with more nestling-like vocalizations (i.e., they are alternative female attractants; Candolin 2003), maintaining the variation in these traits or even predicting a negative evolutionary relationship between them. In another negatively correlated pair of female mate choice criteria, tail length and nest-building behavior, Møller (2006) found that a longitudinal decrease in nest size (and thus male

investment in nesting) could be accounted for by indirect selection on long tails, which have elongated over the past 25 years. Selection on one trait would affect the expression of correlated traits as well, and thus the evolution of one trait cannot be understood without considering the others.

## Interrelationship among female mate preferences

The evolution of female mate preference for a specific male trait would not be independent of the evolution of a preference for another trait, because the benefits and costs of one female preference depend on those of other preferences. As noted in Candolin (2003), theoretical models generally assume an increased cost of assessment when females use multiple cues in mate choice (which inhibits the evolution of multiple cues in mate choice; e.g., Schluter and Price 1993; van Doorn and Weissing 2004); however, in reality, costs as well as benefits of choice depend on focal traits (e.g., cost of assessment for adjacent traits should be low; Kose and Møller 1999; Arai et al. 2017). Thus, when females obtain higher net benefits by preferring specific combinations of male traits, preference for the combination is expected. Vortman et al.'s study may represent one such case: males with two experimentally enhanced ornaments (tail length and plumage coloration), but not males with either experimentally enhanced one ornament, had increased within-pair paternity, indicating female preference for the combination (Vortman et al. 2013). This preference would be adaptive for females to avoid interbreeding with other adjacent subspecies in this East-Mediterranean subspecies (where an adjacent subspecies has more colorful plumage with shorter tails and another has less colorful plumage with longer tails than the focal subspecies). Because the same treatment rather decreases paternity in the North American subspecies (Safran et al. 2016), female preference for each ornament (and combinations of ornaments) may be population-dependent (see Romano et al. 2017a for meta-analysis). Although these studies focused solely on plumage ornaments, interacting female preferences for plumage ornaments and song have also been reported. Møller et al. (1998b) found that female preference for song rate, measured by paternity allocation, increased with the sire's tail length, perhaps because females placed more weight on song (which indicates superior current condition) when males had longer tails (which indicate high long-term quality). These studies focused on paternity allocation, but some interrelationship among male ornaments at pair formation should also be expected, because females receive territory and paternal care in addition to sperm from social mates, which is further complicated by female–female competition for limited resources (e.g., territory). In a correlational study, the probability of pair formation was predicted by the negative interplay between tail length and plumage coloration (Hasegawa and Arai 2017b), though the relative



importance of female mate preference and male–male competition for resources remains to be clarified. Interrelationships between female preference for secondary sexual characteristics and other male traits have, unfortunately, not yet been reported but may also be interdependent. For example, it is unlikely that individual preference for male enticement calls has no influence on preference for male song (even if females, on average, prefer higher-pitched enticement calls and lower-pitched song; Hasegawa and Arai 2016; Garamszegi et al. 2005, 2006). In addition, it is likely that the benefits and costs of choosing well-ornamented males depend on whether they hold high-quality territories (i.e., whether they can avoid nest predation or parasitism), as explained in the next subsection. Ignoring some important female choice criteria may prevent to explain the evolution of the focal traits.

### Divergence between colonial and sparse populations

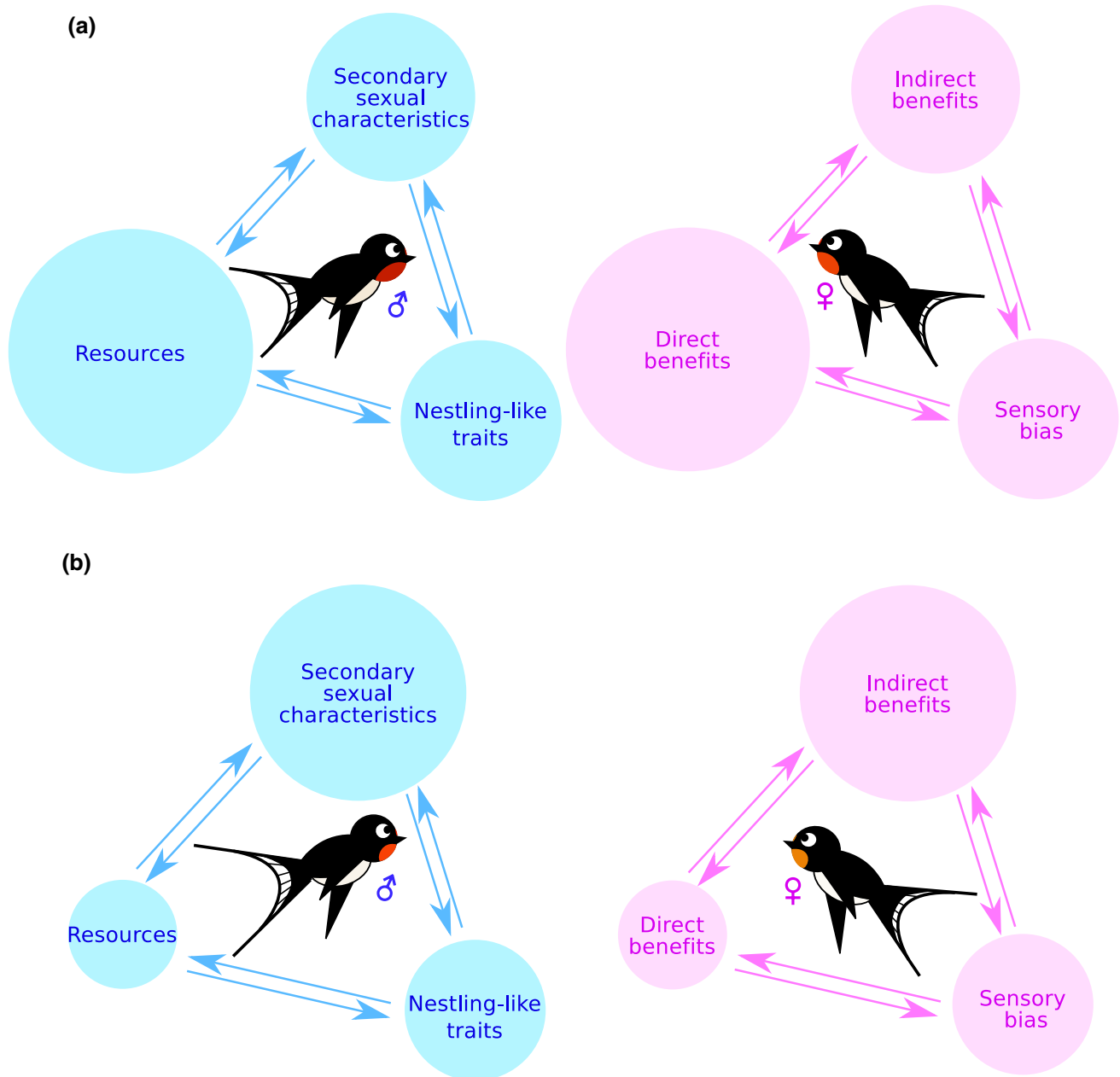
As discussed above, male traits and female mate choice are highly complicated, which makes it difficult to predict the causes and consequences of given female mate choice. Still, female preferences, particularly those for direct benefits, depend on environmental conditions (or, ecological factors; Safran et al. 2013), and thus a simple testable prediction can be made as follows.

Among others, breeding habitat should affect female choice in the barn swallow, particularly between colonial and sparse populations (Fig. 5). In sparse, outdoor populations where territory quality affects seasonal reproductive success, female preference for territory quality should be much more intense than in colonial populations in livestock stalls in which nest predation and interspecific brood parasitism are virtually absent (see above: note that conspecific brood parasitism can also be found in some populations which may select for intense nest guarding; Turner 2006). In the former populations, choosing attractive mates provides nothing when they have low-quality territories (in which offspring will be predated), reducing female preference for male attractiveness. By contrast, in colonial populations in which nest predation is virtually absent, choosing attractive mates produces high-quality offspring. Such benefits of choosing attractive males should increase with female preference for the trait through a runaway process, particularly in dense colonial populations due to the high frequency of extra-pair young (> 15% of nestlings; reviewed in Table 5.1 in Turner 2006; see Hasegawa et al. 2010a for sparse populations where extra-pair paternity is virtually absent: < 3%), which boosts sexual selection (e.g., eightfold compared to no extra-pair paternity; Kleven et al. 2006). At the same time, because courtship display at breeding sites is not necessary for extrapair paternity (e.g., Hasegawa et al. 2016a; also see Turner 2006), total female preference (and selection) for the traits displayed during courtship

(e.g., territory, enticement calls; see Fig. 1) should be relatively weak in colonies.

Such a population difference in breeding environment alone could explain the geographic variation in female preferences and male phenotypes, because territory quality, which is important in sparse populations but not in colonies, is positively linked to male plumage coloration, but not to tail ornaments (Hasegawa et al. 2014; Wilkins et al. 2015; note that nest predation pressure also depends on local fauna; see above). In support of this, Asian and North American subspecies, which are less colonial than European subspecies (e.g., only 1% breed in colonies in Japan; Ministry of Environment 1997; reviewed in Turner 2006, p. 101; though large colonies can also be found in the former subspecies; e.g., Brown and Brown 1999), have intense selection for colorful plumage rather than long tails (reviewed in Romano et al. 2017a). These subspecies have shorter tails and larger throat patches, which would be developmentally and functionally integrated to throat coloration, than European subspecies (where 47% breed in colonies with 7–22 pairs; Turner 2006; Hasegawa et al. 2010a; Hasegawa and Arai 2013a). Such a pattern is also found even within subspecies, because throat patch size decreases and tail ornaments increase with latitude (i.e., a correlate of coloniality; Hasegawa and Arai 2013b). Of course, colonial populations and outdoor populations differ in many other ecological factors (Table 2) and these additional factors may also contribute to the population differences in female preferences and thus male phenotype as well. For example, outdoor populations experience greater temperature cooling and fluctuation relative to those nesting in warm livestock stalls (Turner 2006; also see Löhrl and Gutscher 1973 for subtle differences in reproductive performance between warm and cold sites in European subspecies). Male contribution to incubation (and thus males that incubate more than others; e.g., short-tailed males: see Smith and Montgomerie 1992; Møller 1994a, p. 247) might be more important in outdoor populations than in colonial populations, even if male incubation is inefficient (Voss et al. 2008). In consistent with this perspective, male share of incubation is higher in less-colonial subspecies (Turner 2006) and outdoor populations than in colonial populations within subspecies (Kojima et al. 2009; Hasegawa et al. 2012b), though there is no direct evidence for now. Because coloniality varies widely even within each region and is genetically determined at least in part (e.g., see Møller 2002 for European subspecies), it might be relevant to study how female preference changes with population density (as Møller 2002 found decreased aggressiveness with increasing population density; see above).

This apparent match between the hypothetical scenario and actual geographic variation does not deny the importance of geographic variation in female preference for each secondary sexual characteristic (e.g., plumage coloration and tail length; Safran et al. 2016). Because each ornament has its own information content, some of



**Fig. 5** Hypothetical scenario of the relative importance of each category of male traits (blue) and the female preference (pink), denoted by the size of each node, in **a** sparse outdoor populations and **b** dense colonial populations of barn swallows. Arrows indicate (potential) mutual influences of nodes within each sex. High breeding density, which increases extra-pair paternity, and low nest predation favor female mate preference for traits

conferring indirect benefits in colonial populations, while low breeding density and high nest predation favor female preferences for traits conferring direct benefits (e.g., high-quality territory). Note that female mate preference for resources results in male–male contests favoring the exaggeration of some (but not all) secondary sexual characteristics. Color figure online

which seems to be population-dependent (e.g., Vitousek et al. 2016; also see above), female choice for each ornament should itself depend on population. Nevertheless, consideration of female preference for male traits other than secondary sexual characteristics would advance our understanding of geographic variation in female preference in a predictable manner (e.g., the exaggeration of plumage coloration might have evolved due to selection for males holding high-quality territory

in low-density sites; see above). Without considering it, researchers may fail to detect or misunderstand the link between ecological factors and sexual selection.

### Concluding remarks and future directions

Although recent studies have reported geographic variation in female preference for male secondary sexual

**Table 2** Notable differences in ecological factors between colonial populations in livestock stalls and sparse outdoor populations

	Colony	Sparse	Representative studies
Density	High	Low	Turner (2006); Hasegawa et al. (2010b)
Extra-pair paternity	High	Low	Turner (2006); Hasegawa et al. (2010b)
Nest predation	Negligible	Important	Fujita (1993); Hasegawa et al. (2012a)
Territory quality	Negligible	Important	Møller (1990); Hasegawa et al. (2012a)
Infanticide	Young	Young and Grown	Turner (2006); Hasegawa and Arai (2015b)
Air temperature	High	Low	Turner (2006)

characteristics, it remains unclear how such patterns arose (Scordato and Safran 2014). Because female mate preference covaries with ecological factors (e.g., nest predation), future studies should consider ecological factors causing such variation, rather than simply detecting female mate choice and its geographic variation. In this sense, female mate preference for inconspicuous male characteristics such as territory quality should be particularly important, because these characteristics are highly dependent on ecological factors (Safran et al. 2013) and may be interrelated with female mate preference for other traits such as secondary sexual characteristics. In other words, the local environment directly affects female preference for inconspicuous traits, which may then affect male phenotype, including secondary sexual characteristics, via intercorrelation of male traits or those of female preference. Rather than controlling habitat variability by using ideal study systems for efficient data collection (e.g., colonial breeders), researchers need to take into account ecological factors and its geographic variation to evaluate female mate choice (and male–male contests; Hunt et al. 2009) and its influence on overall male phenotype and other ecological events (e.g., speciation) in this model species of female mate choice and in other species as well.

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