Male Barn Swallows Tolerate Nestling-Like Courtship Calls of Rival Males

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Animals often exhibit conspicuous, and sometimes curious, courtship traits, such as nestling-like courtship display in birds, though modern studies of nestling-like courtship display (and calls) are virtually lacking. An exception is previous experiments on the barn swallow *Hirundo rustica*, demonstrating that females are equally attracted to playback of two structurally similar calls, nestling-like male courtship calls and nestling food-begging calls. The experiments support the sensory trap hypothesis, i.e., that male signals mimic nestling stimuli to exploit female parental care for nestlings. However, female attraction might not be the sole function of nestling-like traits, and males might also have a sensory bias toward nestling-like traits, in which males would be less aggressive toward characteristics typical of immature individuals. Here, I conducted playback experiments to study the function of nestling-like male courtship calls in the context of male–male interactions. Playback of male courtship songs induced frequent approaches by neighbouring males, while nestling-like male courtship calls or nestling food-begging calls induced fewer approaches, though male responses to the latter two vocalisations increased when approaching the nestling period. The observed pattern indicates that, by mimicking immature individuals, males attract intended signal receivers (i.e., females) while avoiding interference from eavesdroppers (i.e., neighbouring males). This unique function can explain why species with parental care exhibit immature-like behaviour.

Keywords: courtship behaviour, *Hirundo rustica*, nestling-mimicry, signal design, dual function

INTRODUCTION

Animals often perform conspicuous, and sometimes curious, courtship behaviours, which attract the attention of evolutionary ecologists to study the origin and maintenance of these behaviours (Andersson, 1994). Nestling-like courtship displays in birds are one such behaviour: courting males (and females) often perform nestling-like behaviours, including wing fluttering and/or nestling-like vocalisation in many bird species (Bradbury and Vehrencamp, 1998). The resemblance to young may have evolved as a sensory trap to exploit the parental care of potential mates (Christy, 1995; Stålhandske, 2002), although there is only one series of experimental tests of the sensory trap hypothesis in birds (see below).

Hasegawa and colleagues experimentally demonstrated that, during the courtship period, female barn swallows *Hirundo rustica* were, similarly, attracted to playback of two structurally similar calls: male enticement calls (i.e., nestling-like courtship calls that are emitted from nest sites to attract females) and nestling food-begging calls, supporting the sensory trap hypothesis

[e.g., Hasegawa et al., 2013; Hasegawa and Arai, 2016; reviewed in Hasegawa (2018); also see Hasegawa and Arai, 2018 for close adult-young resemblance of appearance in parental, but not non-parental, birds]. This explains why male barn swallows emit enticement calls rather than courtship songs when attracting females to their nest sites (e.g., see **Supplementary Figure 1** for sonograms; see Hasegawa et al., 2016a for videos). In other words, as cuckoos exploit the parental care behaviour of the host species by mimicking the begging behaviour of their nestlings, males might exploit conspecific female parental care for nestlings (Hasegawa et al., 2013). Males utter the enticement calls only when attracting females to their nest sites, which seems necessary for males to pair (and use complex songs in other timings; Hasegawa et al., 2013).

Female attraction, however, might not be the sole function of courtship signals. It is now well-known that male courtship traits such as songs can be dual-function signals, by attracting females and stimulating rival males [e.g., see Berglund et al., 1996 for a general pattern; see Galeotti et al., 1997; Wilkins et al., 2015 for the song of the barn swallow; reviewed in Turner (2006)]. Even when courtship displays are solely directed at females, these displays can be exploited by eavesdroppers, including neighbouring males, which can affect the design of courtship signals (e.g., see Reichard and Anderson, 2015 for the use of low-amplitude song to avoid eavesdroppers). Because nestling-like courtship displays attract females as a sensory trap to exploit female parental care for nestlings (i.e., approaching to the vocalisation; see above), males might also have a sensory bias toward nestling-like behaviours, behaving less aggressively toward characteristics typical of immature birds (sensu Foster, 1987; see Turner, 2006 for tolerance of adult swallows toward food-begging young). In other words, male agonistic response to neighbouring males would be cancelled out by their tolerant response to immature birds. Nestling-like traits might therefore function to avoid interference from neighbouring males.

Here, I experimentally examined male responses to the playback of male enticement calls, male courtship songs, and nestling food-begging calls in the barn swallow. I predicted that, if nestling-like traits function to avoid interference from neighbouring males, there would be fewer male responses to male enticement calls and nestling food-begging calls than to male courtship songs. Although males would have limited intrinsic responsiveness to nestling calls compared with females due to the uncertain paternity [e.g., Møller, 1988; reviewed in Turner (2006)], I also predicted that male responses to male enticement calls and nestling food-begging calls would increase when approaching the nestling period, during which parents respond to nestling food-begging calls (e.g., Saino et al., 2000).

MATERIALS AND METHODS

Study Site and Observations

This study was conducted in a residential area in Tsurugi-machi (ca. 35 km^2), Ishikawa Prefecture, Japan (36°26N, 136°37E) from late-March to May 2019–2021. In this area, barn swallows nest under the eaves of a covered sidewalk along the street (Hasegawa

and Arai, 2016). This is in sharp contrast to the dense colonies often found in European subspecies [e.g., a similar outdoor population has 20.39 ± 20.02 m (mean $\pm$ SD, $N = 52$) distance between the nearest males, whereas European colonies have much dense populations (ca. 3–5 m between the nearest males); Hasegawa et al., 2010; reviewed in Turner (2006)]. Due to their low population density, extrapair paternity is virtually absent in Japanese outdoor populations, possibly including this population ($<3\%$; Hasegawa et al., 2010), and thus extrapair paternity would not confound the study design. Male enticement calls are, in fact, not used for extrapair mating (Møller, 1994; Turner, 2006). I inspected nests every third day to determine laying dates and clutch sizes (Hasegawa et al., 2016b). The permits for the current study including capturing were provided by Ishikawa Prefecture in Japan (#18148, #19109, and #20113) and Ishikawa Prefectural University (#31-14-1, #R2-14-1, and #R3-14-3), following the Wildlife Protection and Hunting Management Law.

Capture and Identification

After the start of incubation (i.e., after females completed their clutches), adult males were captured in sweep nets while roosting at night. The birds were fitted with a numbered aluminium ring and an individual combination of two coloured rings (Arai et al., 2009), and thus I could track the behaviour of the focal male. The sex of each individual was determined based on the presence or absence of a brood patch (Turner, 2006).

Playback Experiments

After capturing males, I conducted playback experiments between 0500 and 0800 h during the incubation period in 2019 and 2020 (1–13 days after the start of incubation, when all eggs remained unhatched) and during the pairing period in 2021, in which I used males with previously attached rings. I conducted three 10-min trials using 17 different males during the incubation period (14 males were tested in 2019 and the remaining 3 individuals were tested in 2020). Males were identified by their coloured rings to prevent confusion with other birds. In 2021, I conducted supplementary experiments using eight males that remained unpaired in the preceding day (i.e., eight different adult males were tested) to examine whether male responses observed in preceding years were unique to the incubation period or were applicable to the paring (and thus fertilization) period. Because three of them accompanied females at the start of the experiment, I also tested the effects of the treatment after excluding these seemingly "paired" males; see **Supplementary Table 1**. In each trial, I used a Sony SRS-M30-S speaker on a tripod to broadcast recordings of male enticement calls, male songs, and food-begging calls of nestlings with short intervals (1–10 min) between trials (i.e., after an interval of at least 1 min, although I had to wait a maximum of 10 min until the focal swallows returned after flying away).

I used three male enticement calls, three male songs, and three nestling food-begging calls for the playback experiments (see **Supplementary Figure 1** for some examples). Male enticement calls and songs were obtained from courting males. All of these vocalisations were obtained during previous years from the Joetsu or Yokosuka populations (see Hasegawa et al., 2010;

Hasegawa et al., 2016b for detailed information on these populations), and thus no males had ever heard these calls before. Each vocalisation (recorded as a .wav file) was obtained from a different nest; in the first ten trials, I randomly chose one of the two male enticement calls, one of the two male songs, and one of the two nestling food-begging calls; from the eleventh trial on, I started to use the third vocalisations (in addition to the other vocalisations) to minimise pseudoreplication (with no nests received the exact same call order with call ID). I broadcast each recording (again using a .wav file) approximately 3 m from a territory boundary (the sound level was about 70 dB(A) from a 1-m distance, which is audible from the focal males), as in the preceding study (Hasegawa and Arai, 2016; see Hasegawa et al., 2012 for detailed information of territory; note that *Hirundo rustica gutturalis* defend "visually isolated area" from the outsides and other territories, which corresponds to ca. 10–15 m^2 in our study populations; Fujita and Higuchi, 2007). The exact broadcasting point was not visible from breeding nests of focal swallows and was not defended by any swallows (note that I did not change the exact broadcasting point between trials). In these populations, males sometimes emit enticement calls to attract nearby females in such empty sites before establishing their territories, and thus the current study design would not be unnatural. In other words, the current study focussed on the behaviour of breeding males to (perceived) late-arriving males. During the 10 min of playback, I recorded the number of male responses (i.e., the number of times males came within 1 m of the speaker, which is an appropriate measure in this highly aerial species: see **Supplementary Videos 1a–c**; also see Hasegawa et al., 2013; Hasegawa and Arai, 2016 for female responses; note that I can follow only one bird during the experiment).
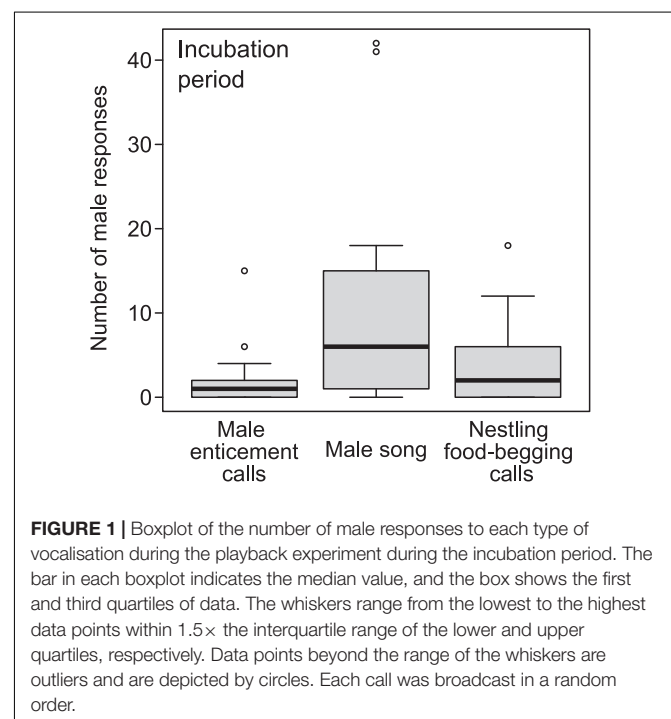
Statistical Analyses

A generalised linear mixed-effects model (GLMM) with a Poisson error distribution was used to test the effect of treatment (vocalisation type) on the number of male responses. Each playback trial (i.e., observation number) was included as a random factor, as was male identity, since the data were overdispersed (Bates et al., 2015). The order of presentation was first included as a fixed factor but was far from significant and hence removed from the model (pairing period; df = 2, χ^2 = 0.54, P = 0.76; incubation period: df = 2, χ^2 = 0.52, P = 0.77; also see Hasegawa and Arai, 2016 for the lack of a detectable effect of presentation order on the number of female responses to the playback of vocalisations). I also investigated the correlation among the numbers of male responses to each kind of call to study whether males that frequently responded to certain vocalizations (e.g., nestling food-begging calls), similarly responded to another (e.g., male enticement calls). The relationship between the number of male responses to each treatment and the progress of the incubation period (i.e., number of days after the start of incubation) was analysed using a GLM with a Poisson error distribution (using family = "quasipoisson"). For this analysis, I controlled for the potential confounding factors of observation date and male body condition, which would affect male responsiveness, to detect subtle patterns of male responses toward each vocalisation. I used body condition

as residual body mass against tarsus length as in previous studies (Hasegawa et al., 2017). All data analyses were performed using R version 3.5.0 (R Core Team, 2018).

RESULTS

During the incubation period, vocalisation type had a significant effect on the number of male responses (GLMM with a Poisson error distribution: n_{males} = 17, n_{total} = 51, χ^2 = 15.30, P < 0.001). The number of male responses to male enticement calls was significantly lower than that to male songs (**Figure 1** and **Table 1**; the number of male responses to nestling food-begging calls was also significantly lower than that to male songs: difference $\pm$SE = -1.01 ± 0.38, z = 2.69, P < 0.01). Similar pattern was found during the pairing period (**Supplementary Figure 2** and **Supplementary Table 1**), though sample size was limited (n_{males} = 8, n_{total} = 24).

No significant correlations were found between the numbers of male responses to each treatment (Spearman's rank correlation coefficient, $|r_s|$ < 0.44, n = 17, P > 0.07), although the sample size was small. When the male responses to each vocalisation were analysed separately, the number of male responses to the playback of each treatment increased with the progress of the incubation period, although this relationship was not significant in the analysis of male responses to male songs (**Figure 2** and **Table 2**). Rather, male responses to male songs marginally increased with body condition (**Table 2** and **Supplementary Figure 3**).

FIGURE 1 | Boxplot of the number of male responses to each type of vocalisation during the playback experiment during the incubation period. The bar in each boxplot indicates the median value, and the box shows the first and third quartiles of data. The whiskers range from the lowest to the highest data points within 1.5× the interquartile range of the lower and upper quartiles, respectively. Data points beyond the range of the whiskers are outliers and are depicted by circles. Each call was broadcast in a random order.

TABLE 1 | Multivariable generalised linear mixed-effects model (GLMM) with a Poisson error distribution predicting the number of male responses to the experimental playback of male enticement calls, male songs, and nestling food-begging calls during the incubation period (n_{male} = 17, $n_{observation}$ = 51).

Variable	Estimate ± SE	z	P
Intercept (Enticement calls)	−0.27 ± 0.45	−0.61	0.55
Song – Enticement calls	**1.78 ± 0.41**	**4.30**	**<0.0001**
Food-begging calls – Enticement calls	0.77 ± 0.43	1.77	**<0.0001**

I included observation number as an observation-level random effect to account for overdispersion (see section "Materials and Methods"; variance = 0.74, χ^2 = 42.98, P < 0.0001). I also included individual ID as a random effect (variance = 1.27, χ^2 = 8.84, P < 0.01; note that I obtained three data points per male). Bold indicates significant test results.
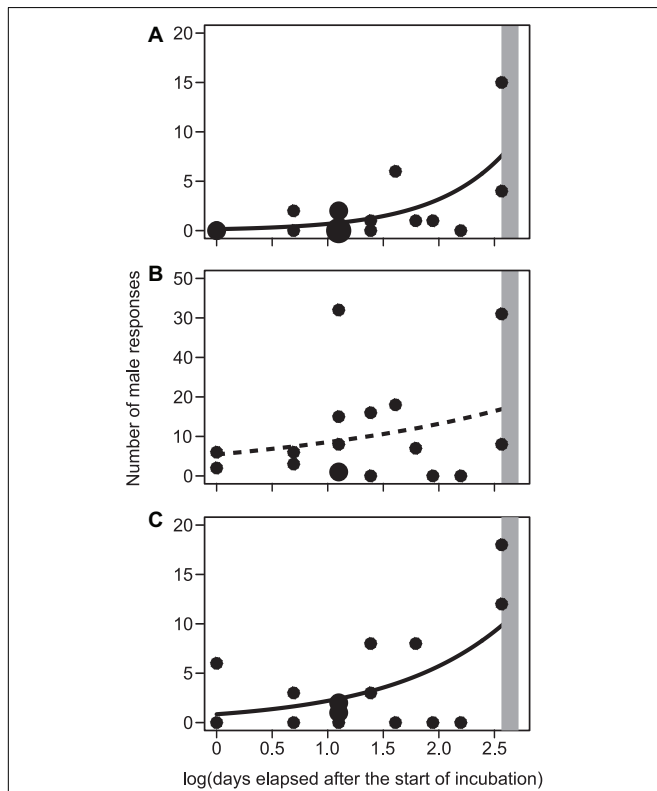
FIGURE 2 | Relationship between the number of male responses to the playback of male enticement calls **(A)**, male songs **(B)**, and nestling food-begging calls **(C)** in relation to the progress of incubation period, measured as log(days elapsed after the start of incubation). Lines indicate simple Poisson regressions [using the glm function with family = "quasipoisson"; y = slope (±SE)x + intercept (±SE); a: y = 1.54 (±0.47)x −1.92 (±0.99); b: y = 0.44 (±0.42)x + 1.69 (±0.71); c: y = 0.96 (±0.41)x −0.17 (±0.78)]. Circle size indicates the number of overlapping points. Dashed line indicates non-significant regression lines. Shaded bars indicate mean hatching dates (13–15 days; Turner, 2006). I confirmed that all eggs remained unhatched during our experiment.

DISCUSSION

The main finding of the current study is that, although both male enticement calls and songs function as courtship signals, male songs elicited frequent male responses, while male enticement

TABLE 2 | Separate multivariable GLM with a Poisson error distribution predicting the number of male responses to the experimental playback of male enticement calls (a), male songs (b) and nestling food-begging calls (c), respectively (n_{male} = 17 each).

Variable	Estimate ± SE	z	P
(a) Male enticement calls			
Days after the start of incubation	**1.27 ± 0.47**	**2.68**	**0.02**
Observation date (April 1 = 1)	2.05 ± 1.93	1.06	0.31
Body condition	0.31 ± 0.40	0.79	0.45
(b) Male songs			
Days after the start of incubation	0.28 ± 0.32	0.86	0.41
Observation date (April 1 = 1)	0.49 ± 1.50	0.32	0.75
Body condition	0.83 ± 0.39	2.14	0.052
(c) Nestling food-begging calls			
Days after the start of incubation	**0.80 ± 0.33**	**2.46**	**0.03**
Observation date (April 1 = 1)	2.91 ± 1.64	1.78	0.10
Body condition	0.42 ± 0.35	1.21	0.25

Days after the start of incubation and observation date were log-transformed before analysis (because it deviated from normal distribution before log-transformation: Shapiro–Wilk test, W = 0.82, P < 0.01; after: W = 0.95, P = 0.45; observation date: before: W = 0.97, P = 0.83; after: W = 0.99, P = 0.99).
Body condition was estimated as residual body mass against tarsus length (linear regression: coefficient ± SE = 1.17 ± 0.51, $F_{1,15}$ = 5.29, P = 0.036), as in previous studies (Hasegawa et al., 2017).
Overdispersion was accounted by using family = "quasipoisson" in the function glm in the R statistical package. Bold indicates significant test results.

calls (and nestling food-begging calls) elicited fewer responses. This indicates that males emitting enticement calls rather than songs would be selected for by avoiding interference from early-breeding, neighbouring males. Because males ignored male enticement calls near their territory boundaries (see section "Materials and Methods"), male enticement calls might allow for high density breeding in the barn swallow, which often breeds in nests that are close to (though visually hidden from) other nests (Fujita and Higuchi, 2007).

Previous studies on courtship signals have often focussed on the positive responses of potential signal receivers, in which signals that enhance the receiver's attention should be effective. An exception is the "soft song," a low-amplitude, short-range song, which confers a mating/reproductive advantage to males by not attracting the attention of conspecifics simply because it is inaudible from a distance (e.g., Vargas-Castro et al., 2017; reviewed in Reichard and Anderson (2015)]. Male enticement calls might have similar functions but, unlike the soft song, male enticement calls are loud, long-range vocalisations, with which males attract females from nest sites even when the females cannot see them (Hasegawa et al., 2013). By using vocalisations that are effective at drawing a response from potential mates, but not neighbouring males, males can attract females from a distance without the cost of reduced communication with the signal receivers.

Because the enticement call is emitted during the courtship sequence for pair formation (Hasegawa et al., 2013), the tolerance of male enticement calls increases the possibility that other males will breed nearby. Thus, as is the case for the male courtship song, neighbouring males should keep signallers away, even outside

of their own mating periods, from their territories to reduce nest competition for current and future clutches (Turner, 2006; also see Arai et al., 2009 for frequent re-clutches due to nest predation in Japanese barn swallows). An explanation for why neighbouring males rarely responded to male enticement calls is that males would be less aggressive toward characteristics typical of immature birds [sensu Foster, 1987; reviewed in Hawkins et al. (2012); see Turner, 2006 for tolerance of adult swallows toward food-begging young]. As females confuse male enticement calls with nestling food-begging calls (Hasegawa et al., 2013; Hasegawa and Arai, 2016), males might have similar sensory or perceptive bias toward nestling calls (i.e., non-hostile behaviour toward nestlings). Such male behaviour would be maladaptive but can have persisted through evolutionary time scale as was the case with other sensory trap systems even when mimics and models were temporally separated: for example, in some insects, male penis mimics egg ovulation to elicit females consuming the other males' sperm stored [reviewed in Christy (1995) and Arnqvist (2006)]. In consistent with this perspective, male responses toward enticement calls increased with progress of the incubation period, i.e., when approaching the nestling period (**Figure 2** and **Table 2**), supporting this sensory trap explanation, or more specifically, nestling-mimicry hypothesis. A previous study showed that less-competitive males with drab throat colouration mimic nestlings more than do colourful males (Hasegawa and Arai, 2016). This finding further supports the nestling-mimicry hypothesis, given that competitively inferior males should avoid, rather than compete with, dominant and colourful males that breed early in high-quality territories when they attempt pair formation among these competitive males (Hasegawa et al., 2014; Wilkins et al., 2015).

Clearly, this is not the sole explanation for the observed pattern, and males might tolerate nestling-like calls for other reasons. For example, males might ignore nestling-like calls and concentrate on songs to simplify their sensory pathways, which can effectively prevent most neighbours' breeding attempts nearby, because courting males often, but not always, use songs before/after emitting enticement calls (see section "Introduction"). However, this possibility alone cannot explain the reason why male responsiveness increased when approaching the nestling period. The actual mechanism remains to be shown in future studies.

In conclusion, I demonstrated here that the male enticement call, a nestling-like courtship behaviour of barn swallows, elicited few responses from neighbouring males. Together with a previous study showing female attraction to nestling-like calls,

the current study indicates that male enticement calls have a dual function. However, unlike male song, the nestling-like courtship call is unique in attracting females while being tolerated by neighbouring males. Males as well as females would have sensory bias (but have contrasting behaviour) toward signals with nestling characteristics, simultaneously selecting for nestling-like courtship signals. This could explain why species with parental care exhibit immature-like behaviour.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Ishikawa Prefectural University.

AUTHOR CONTRIBUTIONS

MH conducted all field work and wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.759438/full#supplementary-material

REFERENCES

Andersson, M. (1994). . *Sexual Selection*. Princeton, NJ: Princeton University Press.

Arai, E., Hasegawa, M., and Nakamura, M. (2009). Divorce and asynchronous arrival in Barn Swallows *Hirundo rustica*. *Bird Study* 56, 411–413. doi: 10.1080/00063650902968342

Arnqvist, G. (2006). Sensory exploitation and sexual conflict. *Phil. Trans. R. Soc. B* 361, 375–386. doi: 10.1098/rstb.2005.1790

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01

Berglund, A., Bisazza, A., and Pilastro, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* 58, 385–399. doi: 10.1006/bijl.1996.0043

Bradbury, J. W., and Vehrencamp, S. L. (1998). *The Principles of Animal Communication*. Sunderland, MA: Sinauer.

Christy, J. H. (1995). Mimicry, mate choice, and the sensory trap hypothesis. *Am. Nat.* 146, 171–181. doi: 10.1086/285793

Foster, M. S. (1987). Delayed maturation, neoteny, and social system differences in two manakins of the genus *Chiroxiphia*. *Evolution* 41, 547–558. doi: 10.1111/j.1558-5646.1987.tb05825.x

Fujita, G., and Higuchi, H. (2007). Barn swallows prefer to nest at sites hidden from neighboring nests within a loose colony. *J. Ethol.* 25, 117–123. doi: 10.1007/s10164-006-0005-0

Galeotti, P., Saino, N., Sacchi, R., and Møller, A. P. (1997). Song correlates with social context, testosterone and body condition in male barn swallows. *Anim. Behav.* 53, 687–700. doi: 10.1006/anbe.1996.0304

Hasegawa, M. (2018). Beauty alone is insufficient: female mate choice in the barn swallow. *Ecol. Res.* 33, 3–16. doi: 10.1007/s11284-017-1527-3

Hasegawa, M., and Arai, E. (2016). Female attraction to higher pitched male enticement calls in barn swallows. *Ethology* 122, 430–441. doi: 10.1111/eth.12492

Hasegawa, M., and Arai, E. (2018). Differential visual ornamentation between brood parasitic and parental cuckoos. *J. Evol. Biol.* 31, 446–456. doi: 10.1111/jeb.13240

Hasegawa, M., Watanabe, M., and Nakamura, M. (2016a). Promiscuous copulation attempts and discriminate pairing displays in male barn swallows as revealed by model presentation. *Ethol. Ecol. Evol.* 28, 163–174. doi: 10.1080/03949370.2015.1026404

Hasegawa, M., Arai, E., Ito, S., and Wakamatsu, K. (2016b). High brood patch temperature of less colourful, less pheomelanic female Barn Swallows. *IBIS* 158, 808–820. doi: 10.1111/ibi.12405

Hasegawa, M., Arai, E., Watanabe, M., and Nakamura, M. (2012). Female mate choice based on territory quality in barn swallows. *J. Ethol.* 30, 143–150. doi: 10.2326/osj.17.125

Hasegawa, M., Arai, E., Kojima, W., Kitamura, W., Fujita, G., Higuchi, H., et al. (2010). Low level of extra-pair paternity in a population of the Barn Swallow *Hirundo rustica gutturalis. Ornithol. Sci.* 9, 161–164. doi: 10.2326/osj.9.161

Hasegawa, M., Arai, E., Sato, M., and Sakai, H. (2017). Plasma testosterone levels increase with expression of male ornaments during mating, but not incubation, in Japanese barn swallows. *Zool. Sci.* 34, 261–266. doi: 10.2108/zs160187

Hasegawa, M., Arai, E., Watanabe, M., and Nakamura, M. (2013). Male nestling-like courtship calls attract female barn swallows *Hirundo rustica gutturalis. Anim. Behav.* 86, 949–953. doi: 10.1016/j.anbehav.2013.08.012

Hasegawa, M., Arai, E., Watanabe, M., and Nakamura, M. (2014). Colourful males hold high quality territories but exhibit reduced paternal care in barn swallows. *Behaviour* 151, 591–612. doi: 10.1163/1568539X-00003150

Hawkins, G. L., Hill, G. E., and Mercadante, A. (2012). Delayed plumage maturation and delayed reproductive investment in birds. *Biol. Rev.* 87, 257–274. doi: 10.1111/j.1469-185X.2011.00193.x

Møller, A. P. (1988). Paternity and paternal care in the swallow, *Hirundo rustica. Anim. Behav.* 36, 996–1005. doi: 10.1016/S0003-3472(88)80059-9

Møller, A. P. (1994). *Sexual Selection and the Barn Swallow.* Oxford: Oxford University Press.

R Core Team (2018). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Reichard, D. G., and Anderson, R. C. (2015). Why signal softly? The structure, function, and evolutionary significance of low-amplitude signals. *Anim. Behav.* 105, 253–265. doi: 10.1016/j.anbehav.2015.04.017

Saino, N., Ninni, P., Incagli, M., Calza, S., Sachi, R., and Møller, A. P. (2000). Begging and parental care in relation to offspring need and condition in the barn swallow (*Hirundo rustica*). *Am. Nat.* 156, 637–649. doi: 10.1086/316996

Stålhandske, P. (2002). Nuptial gifts of male spiders function as sensory trap. *Proc. R. Soc. Lond. B* 269, 905–908. doi: 10.1098/rspb.2001.1917

Turner, A. K. (2006). *The Barn Swallow.* London: T & AD Poyser.

Vargas-Castro, L. E., Sandoval, L., and Searcy, W. A. (2017). Eavesdropping avoidance and sound propagation: the acoustic structure of soft song. *Anim. Behav.* 134, 113–121. doi: 10.1016/j.anbehav2017.10.0008

Wilkins, M. R., Shizuka, D., Joseph, M. B., Hubbard, H. K., and Safran, R. J. (2015). Multimodal signalling in the North American barn swallow: a phenotype network approach. *Proc. R. Soc. Lond. B* 282, 20151574. doi: 10.1098/rspb.2015.1574