



Male nestling-like courtship calls attract female barn swallows, *Hirundo rustica gutturalis*



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ARTICLE INFO

Article history:

Received 12 May 2013

Initial acceptance 3 June 2013

Final acceptance 6 August 2013

Available online 26 September 2013

MS. number: 13-00392

Keywords:

barn swallow

courtship display

Hirundo rustica gutturalis

intraspecific mimicry

sensory exploitation

sexual selection

Courtship behaviours of males often resemble the food-begging behaviour of their young, at least from a human perspective. Although it is argued that this represents a sensory trap, it is still unclear whether such behaviour in males is objectively similar to nestling behaviour and can elicit female parental care (e.g. attraction to nestlings) in courtship, as predicted by the sensory trap hypothesis. In this study, we demonstrated that the enticement calls of male barn swallows structurally resemble the food-begging calls of nestlings, compared with the other three male vocalizations (i.e. songs, alarm calls and contact calls). In addition, we used experimental playback of the vocalizations to compare the response of females towards male enticement calls and nestling food-begging calls during the courtship period. We found that females were attracted to the playback of nestlings' food-begging calls during the courtship period, despite nestlings being absent at this time. The response of females to food-begging calls was similar and positively correlated with their response to male enticement calls. These observations support the sensory trap hypothesis, i.e. that male signals mimic stimuli to which females respond for parental care.

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Males often possess similar morphological traits to their eggs or young (e.g. human morphology: Crook 1972; eggspots of cichlids: Tobler 2006; nuptial gifts of spiders: Stålhandske 2002). The sensory trap hypothesis proposes that this similarity is a consequence of signal evolution, whereby male signals mimic stimuli to which females respond in other contexts (i.e. parental care, in this case), eliciting female behaviours that increase male mating success (Christy 1995). For example, Stålhandske (2002) showed that the nuptial gifts of male spiders, which resemble egg sacs, function as sensory traps, as they elicit female parental care (i.e. attraction to the egg sac) even during the courtship period, benefiting courting males.

Similarly, courtship behaviours of males often resemble the behaviours of their young. In some species of birds, males (and sometimes females) often flutter their wings and utter a sound that is similar to the food-begging calls of the nestlings (e.g. the copulation invitation display of the tree sparrow, *Passer montanus*: Summers-Smith 1995). These behaviours appear to be sensory traps whereby male signals mimic stimuli to which females respond during parental care, eliciting female behaviours that increase male mating success (Krebs & Dawkins 1984; Christy 1995;

Bradbury & Vehrencamp 1998). However, these perceived similarities are based on a human perspective, and so it is still unclear whether the two behaviours are objectively similar and actually elicit female attraction to nestling food begging, both of which are required to demonstrate the presence of a sensory trap. In theory, this can be tested by analysing the two behaviours quantitatively and comparing the signal receivers' responses to the two behaviours during courtship (Christy 1995; Stålhandske 2002).

The barn swallow is a monogamous, migratory species with biparental care, during which both parents feed nestlings, which give typical food-begging calls, for approximately 3 weeks (e.g. Sacchi et al. 2002; reviewed in Turner 2006). Before the start of breeding (i.e. laying clutches, incubating clutches, feeding nestlings), males court females for pair formation when females arrive at breeding sites (Møller 1994; Turner 2006). The courtship display involves males leading females to an old nest or a potential nest site and uttering characteristic enticement calls: a series of 'wi-wi-wi' notes (Møller 1994; Turner 2006; Hasegawa 2011). Once females arrive at the nest, males cease uttering the calls and start singing complex songs, suggesting that the function of the enticement calls is to attract females to the nest site, which is necessary for males to pair (Hasegawa 2011; note that this courtship display is not used in the context of extrapair mating; Møller 1994; Turner 2006). Males often use the enticement call when they cannot be seen by females and females often respond to begging calls of nestlings before they

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are in sight of their nest. This makes it possible to test realistically the responses of females to enticement calls and begging calls without the potentially confounding effects of visual stimuli from males or nestlings, respectively.

In this study, we quantified the similarity between the enticement call of male barn swallows and the food-begging call of nestlings. In addition, we used experimental playback of the vocalizations to compare the response of females towards male enticement calls and nestling food-begging calls during the courtship period in which nestlings are absent (i.e. soon after migration). If the enticement call is a sensory trap to exploit female parental care for nestlings, we would predict that (1) enticement calls of males and food-begging calls of nestlings structurally resemble each other; and (2) females respond to nestling begging calls during their courtship period, and this response is comparable to their response towards male enticement calls.

METHODS

Study Site and Observations

This study was conducted in a residential area of Joetsu City, Niigata Prefecture, Japan (37°07'N, 138°15'E; 10 m above sea level) from 2007 to 2009. In this area, barn swallows nest under the eaves of a covered sidewalk along the street and breed in a loose colony (cf. Tajima & Nakamura 2003). Each day, we recorded the time of arrival and pair formation for each marked bird (Arai et al. 2009).

Sound Recordings

Sound recordings were made from within 5 m of birds, using an Edirol R-09 digital recorder (Roland Corporation US, Los Angeles, CA, U.S.A.) or video camera recorders (SONY CCD-TRV92). Although the camera could not pick up frequencies above 7.5 kHz, this might not be a problem: this is much higher than the maximum sensitivity of birds (1–5 kHz: Dooling 1982) and is almost outside the song frequency spectrum of barn swallows (ca. 0–8 kHz: Cramp 1988), which is believed to match closely the hearing range of birds (Okanoya & Dooling 1988). We recorded each vocalization (i.e. enticement calls, songs, contact calls and alarm calls: Turner 2006) from six different nests. Enticement calls and songs were recorded from males when they courted females; contact calls and alarm calls were recorded between pair formation and the nestling period, although in some cases we were unable to distinguish between the calls of males and females. Food-begging calls were recorded when nestlings were 12 days old. By about this age, nestlings start to beg before the parents arrive and attract their parents' attention with loud begging calls (Turner 2006).

We analysed recordings using the computer program Audacity 1.2.4 (<http://audacity.sourceforge.net>) and measured three variables: peak amplitude frequency (the frequency of the harmonic over which most energy was distributed), syllable rate (the number of syllables per 5 s), and syllable repertoire size (the number of different syllables). Unfortunately, echo effects and other noise disturbances at our study site prevented any further analyses from being carried out.

Capture and Mate Removal

Sweep nets were used to capture adult males and females while they were roosting at night. Birds were marked with a numbered aluminium ring and an individual combination of two or three coloured rings (Arai et al. 2009). The sex of each individual was determined from morphological measurements (e.g. males have longer tails: Turner 2006).

We removed 17 paired males ($N = 14$ in 2008 and $N = 3$ in 2009) from their territories during the night soon after they had paired. Birds were transported to the laboratory by car. During transport, birds were individually held in small, dark cardboard boxes to reduce stress. They were then put into small metal cages (80 × 40 cm and 50 cm high) and kept overnight in the indoor laboratory of Joetsu University of Education, which is at least 2 km from the study site in the residential area of Joetsu city. Since the laboratory has large windows that provide sunlight to the room, birds were kept at the local/outdoor photoperiod. In addition, since the laboratory has a ventilation fan that provides outdoor air to the room, birds were kept at the local/outdoor temperature (the fan was always running during the study period). The cage had a single perch on which the birds rested and a single food tray filled with wing-clipped flies, *Lucilia* sp. Birds were fed ad libitum with these flies (barn swallows can feed on the ground, Turner 2006). No water was provided, as swallows fed with live flies do not need to drink. This period in captivity had no apparent adverse effects on the males. They stayed calm in the cage and did not sing, shiver or call loudly (i.e. they showed no stress responses). Since we did not observe whether the birds paired again after the experiment, it is unclear whether all birds remained with their partner or not. However, since barn swallows sometimes switch their mates before egg laying (Møller 1994), the experimental protocol did not create an unnatural situation.

Females that naturally lose a mate respond again immediately to courtship and some females change mates before they lay eggs (Møller 1994). This allowed us to test realistically the responses of females the morning after the night we removed their mates. These males were released immediately after their mates had been tested in the morning. Since we captured swallows at midnight (2300–0300 hours), males were kept in cages less than 9 h (at a time when they would be roosting). Capturing, ringing, measurements and mate removals were conducted with permission from Niigata prefecture (no. 386) and the Ministry of Environment of Japan (no. 090305003).

Playback Experiments

We conducted playback experiments between 0530 and 0800 hours from March to April in 2008 and 2009 under sunny or cloudy weather conditions. We carried out three 10 min trials in each of the 17 territories from which the male mate had been removed. In each trial, we used a Sony SRS-M30-S speaker to broadcast sequentially recordings of the food-begging calls of nestlings, contact calls and enticement calls with short intervals (i.e. <3 min) between trials. The order of playback was always the same, which may potentially confound the effect of each treatment with the order of presentation (e.g. because of habituation). However, females responded clearly and very differently to the treatments and in a manner consistent with a functional interpretation of their behaviour suggesting that sequence effects per se are unlikely.

We used three food-begging calls, three contact calls and two enticement calls for the playback experiments. Each call was obtained from a different nest; in each trial, one of each type of call was randomly selected and broadcast. We used two enticement calls because we were unable to obtain a third good recording of an enticement call. In this experiment, we only used contact calls that were known to have originated from males. We broadcast each recording approximately 3 m from a territory boundary. During the 10 min of playback, we recorded the number of female responses (i.e. the number of times females came within 1 m of the speaker). In 13 of the territories, we also recorded the number of female responses to the speaker for an additional 10 min at the end of the

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