Call repertoire of an endemic avian species, the Indian chat *Cercomela fusca*

Vinaya Kumar Sethi and Dinesh Bhatt*

Avian Diversity and Bioacoustics Lab, Department of Zoology and Environmental Sciences, Gurukula Kangri University, Haridwar 249 404, India

Almost all birds produce acoustic signals either in the form of calls or songs or both, while communicating. These signals play an important role in their social life. Songs play a somewhat restricted role in many species in territorial establishment and mate attraction, while calls are generally used for immediate requirements throughout the year and seem to be more important than the songs. The present study deals with the physical characteristics and significance of different types of calls used by the Indian chat, *Cercomela fusca*. A total of eight types of calls, namely territorial calls, begging call, feeding call, alarm call, threat call, contact call, distress call, and roosting and emergence calls were observed in the call repertoire of this species. Three of these are used by the young ones, while adults produce the remaining five types. The possible functions of these call-types have been deduced from the contexts under which they are produced.

Keywords: Call repertoire, endemic avian species, Indian chat, sociobiological significance.

A number of avian species communicate with a set of acoustic signals. Each of these signals is thought to be unique, having both its own physical structure and its own inherent 'messages' and associated 'meanings'[1,2]. Birds possess a unique repertoire of sounds, and studies have shown that they have the ability to use vocalizations to convey contextual information about motivation levels[3].

Sound signals in birds may be divided into songs and calls. Functionally songs that are generally produced by the male during the breeding period, play a role in territory establishment and maintenance and in mate attraction, while calls are used in all seasons by both sexes and play an important role in their social life, namely social contact, parent–offspring interactions, cohesiveness among flock/family members, threat and danger. These are more deeply involved than songs with immediate issues of life and death[4,5].

Almost all birds have a repertoire of calls, sometimes quite small and sometimes very large. In order to give a reliable estimate of call repertoire size, it is required to record the entire behaviour of a species during all seasons and circumstances. According to Marler[5], calls are a goldmine of insights into animal semantics, and many other aspects of vocal communication. India has a large number of songbirds, which are known for their elaborate, complex and varied songs and calls. Unfortunately, in India systematic studies on the structure and sociobiological significance of bird signals are scanty and have been carried out in only a few species[6–9]. Thus, a number of Indian species remain for the study of their detailed acoustic behaviour and the need therefore arises to fill this gap.

A review of the literature reveals the complete absence of scientific information on any aspect (viz. breeding, foraging, communication, etc.) available for a complex dawn singer, the Indian chat *Cercomela fusca*. In the light of the above background, we planned to study the call repertoire of an endemic avian species, the Indian chat. We recorded and analysed the different call-types used by this species under different behavioural contexts. The possible functions of these call-types have been deduced from these contexts.

Materials and methods

Cercomela fusca

C. fusca, endemic to the Indian subcontinent, is an insectivorous, plain brown bird with darker wings and a blackish tail (Figure 1 *a*), which breeds during February to August and lives in rocky hills, ravines, ruins, old buildings, walls, etc. in the towns and suburbs[10]. It is a territorial species and is frequently found in the same locality throughout the year[11]. During the breeding phase males of this species sing discrete, loud and complex songs during dawn and the calls are used by both sexes throughout the year (V. K. Sethi and D. Bhatt, unpublished).

Methodology

Observations on *C. fusca* were recorded at 14 different sites over a period of two years, from January 2004 to December 2005 in the urban areas (the natural habitat of this species) of Haridwar (29°55′N; 78°08′E) Uttarakhand, India. Calls were recorded using Sony digital audio tape-corder, TCD-D100 (frequency response: 20–22,000 kHz ± 1 dB) and Sennheiser ME 66 microphone (frequency response: 40–20,000 Hz ± 2.5 dB). After editing,

*For correspondence. (e-mail: dineshharidwar@gmail.com)

cuts of high quality recordings were analysed with the help of AviSoft SASLabPro (version 4.1) software. Observations were made mostly with naked eye and sometimes with the help of 7× binoculars, usually at a distance of 6–20 m and we did not use any blinds, as the birds seemed unaffected by our presence. Three nests were videotaped (Sony handycam DCR-DVD 803/E) to record and understand the provisioning to nestlings. In the present study minimum frequency, maximum frequency, duration of signal and gap between signals were measured to define the acoustic features of the calls. Number and type of elements and rate of production were also measured. Results were expressed as mean ± SD. Behavioural correlates were used to infer the possible meanings of the signals[12].

Results and discussion

The call repertoire of Indian chat was found to consist of eight distinct types of calls produced under different circumstances. Among these, adults gave five types of calls and the young ones three. The frequency and temporal characteristics are presented in Figure 2 and Table 1.

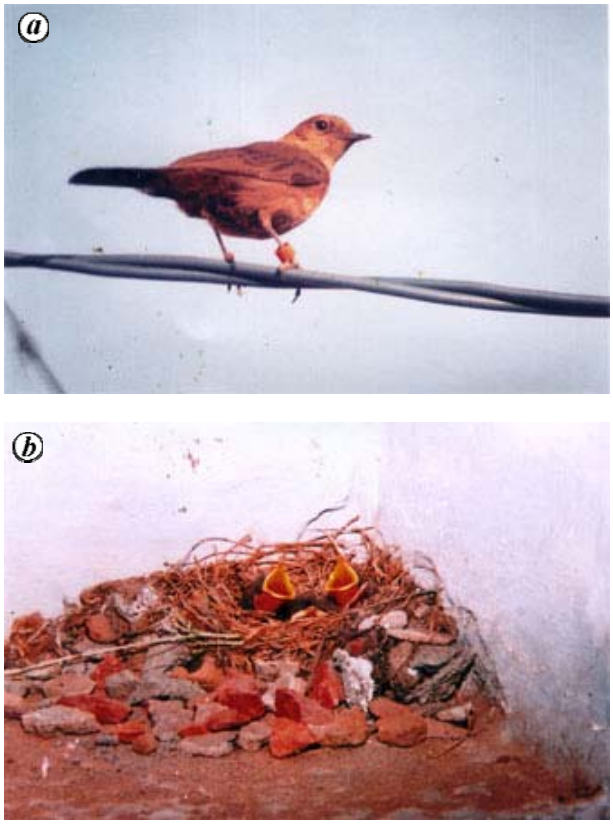

Figure 1. ***a***, The Indian chat, *Cercomela fusca*. ***b***, Nestlings producing begging call.

Territorial call

These whistles were the most commonly heard vocalization of the Indian chat. This call was generally produced from high perches by the bird, assuming an alert posture, year round but most frequently during the breeding period. The function of this call was to mainly defend the territory and both sexes produced it. Mean territory size of the Indian chat was 55,168.93 ± 10,356.0 sq. ft (n = 9). Territorial call was often directed towards conspecific adjacent territorial holders, to warn them not to encroach upon the territory. The bird generally uttered this call in a stereotyped sequence of notes (29 ± 3.67/min) in a continuous manner for a period of 3–5 min. However, during the onset of the breeding season, we observed (n = 4) more than 350 call notes delivered for a period of 12–15 min without any pause. These calls had a minimum and maximum frequency of 3.99 ± 0.51 and 4.98 ± 0.31 kHz respectively (Figure 2 *a*). A single call note was of 0.19 ± 0.02 s duration, followed by 2.41 ± 0.91 s interval (Table 1). In some cases birds used this call with alarm calls (n = 9), but the significance of the use of this call with other calls is not yet certain. It has been observed that these notes are uttered and responded to by both members of the pair when they are apart from each other in search of food for the offspring. Thus it seems that the territorial call could also be used to keep the pairs informed about each other's location.

In a few cases (n = 5) the bird was also observed producing territorial call with double note with a high level of excitement (as exhibited by high rate of bobbing), when it noticed any territorial fight between two individuals in a nearby area. This call was probably used to discourage the possible intruder from a distance, thus avoiding a fight. If this is the case, this species appears to be equipped with such natural signal system to reduce chances of physical injury, as actual fighting between two animals can be costly in terms of risk of physical injury as well as in terms of time and energy[3].

Like the Indian chat, the Oriental magpie robin, *Copsychus saularis* has also been observed to deliver territorial calls (besides songs) during the breeding period[7], while most songbirds use mainly songs to defend their breeding territories[13–18]. It is interesting to note that Indian chat maintains its feeding territory also during the non-breeding period (September–January) using these whistle calls. However, the level of excitement and vigilance decreased in this phase significantly compared to the breeding phase. The male Indian chat allowed its female and offspring also to forage in the feeding territory, but not for a longer period. Intermittently it showed low-level aggression to them and as soon as pre-breeding month (January) approached, the level of aggression with aerial chases increased and finally it excluded them completely from the territory. In some species winter territory is advertised/defended by 'chip' (territorial) calls[19–23]; in others species

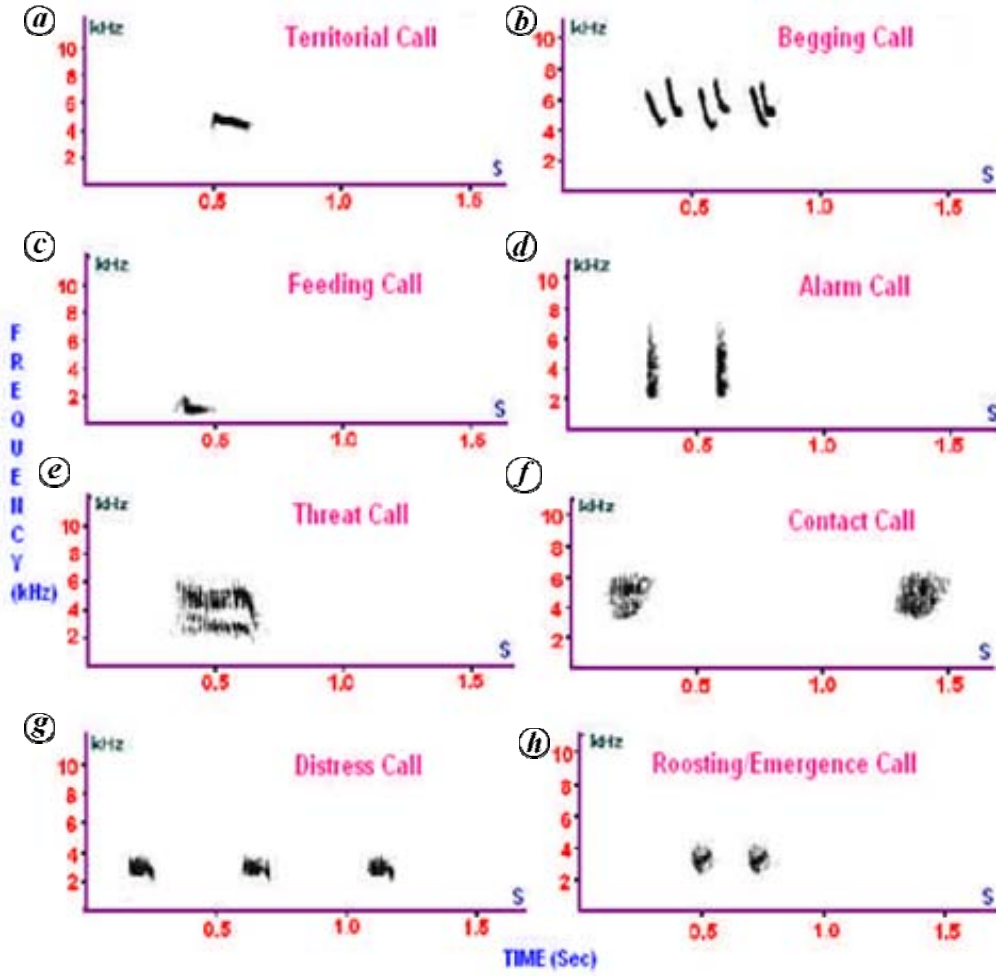

Figure 2. Spectrogram of different calls of *C. fusca*.

songs play an important role in defence of the winter territories[24,25], while the greenish leaf warbler, uses both songs and calls for this purpose[8].

Begging call

These soft calls were produced by the nestlings (at least 4–5-day-old) from the nests. The minimum and maximum frequencies were 4.22 ± 0.46 and 6.80 ± 0.52 kHz respectively, and duration of the call was 0.11 ± 0.02 s, with 0.09 ± 0.01 s internote interval (Figure 2 *b*). The nestlings produced these calls almost throughout the day from their nests, exhibiting begging display (Figure 1 *b*) and the calling rate increased in the presence of the parents. These calls were loud enough to attract the attention of the predators and observers. During our study we were able to locate the nests of this species ($n = 3$) by listening to these begging calls.

The loud and rapid begging calls of nestling birds have been reported to signal their hunger, as parents generally respond to these signals by directing feeding to the most intensively begging nestling in their brood[26–28]. However, broods that beg more intensely may suffer increased predation risk[29], and experimental playbacks from artificial nests have confirmed that increased calling can indeed attract more predators[30–32]. Parental alarm calls have been suggested to reduce the begging of great tit *Parus major* and stonechat *Saxicola torquata* nestlings[33,34]. In the present study, however, nestlings of Indian chat were unaffected by the alarm calls of the parents given to the predator or observers, as they continued to produce begging calls. Like the Indian chat, Scrubwren nestlings (*Sericornis frontalis*) also did not suppress their begging vocalization on hearing the alarm calls; in fact, nestlings responded with increased vocalizations to alarm calls[35].

Table 1. Physical characteristics of different types of calls in Indian chat, *Cercomela fusca*

Type of call	Phonetic representation	Minimum frequency (kHz)	Maximum frequency (kHz)	Duration (s)	Interval (s)
Territorial call	*Chee . . . chee . . .*	3.99 ± 0.51 (*N* = 10, *n* = 32)	4.98 ± 0.31 (*N* = 10, *n* = 32)	0.19 ± 0.02 (*N* = 10, *n* = 32)	2.41 ± 0.91 (*N* = 10, *n* = 32)
Begging call	*Che . . . che . . . che . . . che*	4.22 ± 0.46 (*N* = 6, *n* = 21)	6.80 ± 0.52 (*N* = 6, *n* = 21)	0.11 ± 0.02 (*N* = 6, *n* = 21)	0.09 ± 0.01 (*N* = 6, *n* = 21)
Feeding call	*Chuk . . . chuk . . . chuk . . .*	0.57 ± 0.01 (*N* = 4, *n* = 11)	1.96 ± 0.01 (*N* = 4, *N* = 11)	0.14 ± 0.02 (*N* = 4, *n* = 11)	0.11 ± 0.01 (*N* = 4, *n* = 11)
Alarm call	*Cheik . . . cheik . . . cheik . . .*	2.06 ± 0.09 (*N* = 11, *n* = 26)	6.10 ± 0.44 (*N* = 11, *n* = 26)	0.06 ± 0.01 (*N* = 11, *n* = 26)	0.26 ± 0.44 (*N* = 11, *n* = 26)
Threat call	*Cheurr . . . Cheurr . . .*	2.81 ± 0.10 (*N* = 9, *n* = 27)	6.09 ± 0.06 (*N* = 9, *n* = 27)	0.34 ± 0.02 (*N* = 9, *n* = 27)	2.13 ± 0.87 (*N* = 9, *n* = 27)
Contact call	*Cheu . . . cheu . . .*	3.13 ± 0.39 (*N* = 8, *n* = 16)	5.48 ± 0.26 (*N* = 8, *n* = 16)	0.19 ± 0.02 (*N* = 8, *n* = 16)	1.27 ± 0.81 (*N* = 8, *n* = 16)
Distress call	*Terr . . . terr . . . eerr . . .*	2.15 ± 0.11 (*N* = 9, *n* = 24)	3.42 ± 0.05 (*N* = 9, *n* = 24)	0.11 ± 0.01 (*N* = 9, *n* = 24)	0.33 ± 0.72 (*N* = 9, *n* = 24)
Roosting/emergence call	*Cheik . . . cheik . . . cheik . . .*	2.25 ± 0.07 (*N* = 6, *n* = 16)	4.73 ± 0.03 (*N* = 6, *n* = 16)	0.12 ± 0.02 (*N* = 6, *n* = 16)	1.02 ± 0.74 (*N* = 6, *n* = 16)

N, Numbers of individuals; *n*, Total number of calls analysed (2–4 calls were analysed per individual).

Feeding call

In the Indian chat, both parents feed the nestlings and give the feeding call when they arrive at the nest with food in their beak. The minimum and maximum frequencies of this call were 0.57 ± 0.01 and 1.96 ± 0.01 kHz respectively (Figure 2 *c*). The duration of the call note was 0.14 ± 0.02 s, with a call interval of 0.11 ± 0.01 s. The parents used this call for about a week from the date of hatching and during this early phase, the nestlings did not produce any begging call. After listening to the feeding calls of the parents, the young ones open their mouths and receive the food. The begging response of the nestlings (by elevating their head and opening their mouth without producing any call) was essential for provisioning, as sometimes the young ones did not respond to the parental feeding call and in such situations the parents did not give food to the nestlings and ate it themselves. It is worth mentioning here that the parents do not attempt to touch or shake the mouth of the non-responding nestlings (tactile communication) and that they visit the nest again sometime with new feeding bait. As soon as the nestlings started the production of the begging calls, the parents did not use the feeding calls. It seems that the feeding call is simply a kind of stimulatory call that parents use to initiate the begging call by the nestlings when they do not respond to the parental arrival cue. Biparental provisioning to altricial nestlings and fledglings, as noticed in the Indian chat, is a common phenomenon in a number of passerines and the parents have to invest considerable efforts for this task[36–39]. However, the use of feeding calls by the parents has been reported only in some species like barn swallow, *Hirundo rustica* and white-browed scrub-wren[40,41].

Alarm call

These calls are given by both members of the pair, especially during the breeding period. It is a simple type of call composed of a series of monosyllabic elements. The minimum and maximum frequencies of this call were 2.06 ± 0.09 and 6.10 ± 0.44 kHz respectively (Figure 2 *d*). The duration of the call was 0.06 ± 0.01 s and the interval between calls was 0.26 ± 0.44 s (Table 1). This vocalization consisted of a rapid series of 4–17 notes, with 4–10 being the most common. A series of this call was given by both sexes of the Indian chat whenever they noticed any potential danger, like a sparrow-hawk, shikra, tree pie, crow, owl or cat in their territory and particularly in the close proximity of the nest. At the time of the alarm call delivery, the bird also sometimes used a special wing expanded posture and we call it the threat posture. The rate of production of this call had a direct correlation with the distance between the predator and the nest or the young ones. The birds produced this call at a rate of 26 ± 3.15 calls/min (n = 29) when the distance was more than 25 m between the danger and the nest/fledgling, and probably the predator was not aware about the exact location of the nest/fledgling. The rate increased up to 51 ± 4.12 calls/min (n = 21) when the predators/observers were less than 10 m away from the nest/fledgling, indicating that the birds experienced high level of disturbance/excitement as the predators/observers were close to the nest. We did not notice any change in the physical characteristics of this call uttered under the above situations and also in the presence of different predators. However, some other avian and mammalian species have been reported to use more than one type of alarm call under different circumstances or for predators[42–45].

Threat call/family segregation call

The adults used this call only during the starting phase of breeding in early spring. This call was harsh with minimum and maximum frequencies of 2.81 ± 0.10 and 6.09 ± 0.06 kHz respectively (Figure 2 *e*). The call duration was 0.34 ± 0.02 s, with an interval of 2.13 ± 0.87 s between the calls. An interesting aspect of the breeding behaviour of this species is that the parents force their offspring to leave their natal territory (as the young ones were trying to retain themselves associated with the parents) during the onset of breeding. For this purpose and to deter intruder(s), this type of call was used by both sexes. During this phase, aerial fighting and chasing occurred more frequently between parents and offspring and/or territory holder and the intruder(s). This call was used mostly on wings and sometimes birds used few more elements with this call. There may be extrinsic (environmental), endogenous or some combination of the two factors influencing the timing and duration of the dispersal of the young ones[46–48]. In the Indian chat, parental aggression towards the young ones using threat calls is the cause of family break-up. Other studies have also shown that parental aggression is responsible for dispersal of young ones[49–51].

Contact call

So far as the feeding and protection of fledgling(s) are concerned, this call is of great significance. The young ones gave these signals when they had left the nest. After leaving the nest, the fledglings were in the open ground, prone to attacks by predators and hence they tended to hide themselves behind any large urban objects, stones, bushes or inside dense shrubs. Due to continuous movement of the fledglings with the help of small jumps and/or short flights in all directions of the territory, it would be difficult for the parents to locate them individually. But whenever fledglings noticed their parents carrying feeding bait in their beaks, they produced this contact call for their parents to contact them.

Contact call consisted of a single note averaging 0.19 ± 0.02 s in duration, with interval of 1.27 ± 0.81 s. The minimum and maximum frequencies of this call were 3.13 ± 0.39 and 5.48 ± 0.26 kHz respectively (Figure 2 *f*). Production of contact calls (begging calls) by dependent nestlings is a common feature in many bird species[52–54]. The biological significance of this call was a step ahead than the begging call. As this call not only signalled hunger (like begging call), but also informed the parents about the exact location of the fledglings without which provisioning could be difficult for the parents. Physical characteristics of this call also differed from the begging call (Table 1). Like the Indian chat, differences in the physical characteristics between begging and contact calls (in spite of similarity in the phonation) have also been observed in quail finch, *Ortygospiza atricollis* and Oriental magpie robin[7,55].

Distress call

The nestlings and fledglings of *C. fusca* gave these calls as they were being captured or held for ringing or other measurements. However, none of the six adults captured at night for ringing from their roosting sites (during the present study) uttered this call. The minimum and maximum frequencies of this call were 2.15 ± 0.11 and 3.42 ± 0.05 kHz respectively (Figure 2 *g*). The mean duration of the call was 0.11 ± 0.01 s, with internote interval averaging 0.33 ± 0.72 s.

The response of birds to capture by predators varies greatly both among and within species; for example, a captured bird may fight back, struggle to escape, give a distress call or remain motionless and silent, or it may also do some or all of these in sequence[56]. Distress calls, given when animals are in considerable danger or after they have been captured, are loud, easy to locate and common among birds[5]. In the present study also, distress calls were loud, harsh, easily located and had a penetrating quality. After listening to these calls the parents were observed to become excited and restless, and sometimes they attacked the predators (like *Corvus macrorynchus*, *Corvus splendens*, *Dendrocitta vagabunda*, etc.) and the researchers. Different hypotheses have been proposed to explain the possible significance of distress scream in birds, but the exact function of the distress call is still unclear[57].

Roosting/emergence call

The minimum and maximum frequencies of this call were 2.25 ± 0.07 and 4.73 ± 0.03 kHz respectively (Figure 2 *h*). The duration of the call was 0.12 ± 0.02 s and the interval between calls was 1.02 ± 0.74 s. These monosyllabic and harsh calls were audible only over relatively short distances and were used by both male and female birds at the time of roosting and emergence throughout the year. Sometimes during the breeding period, the birds first delivered songs and then emergence calls which were followed by a series of songs. The birds used these signals for a short period of 2–6 min only.

The phonation of these calls resembles that of the alarm calls of this species. However, analysis of the physical characteristics of the signals reveals that they both differ significantly from each other in their frequency and temporal characteristics. Our earlier findings on the roosting/emergence call and threat call of the Oriental magpie robin and also on the alarm and roosting signals of the red-vented bulbul, *Pycnonotus cafer* revealed similarity in their phonation, but their sonogram characteristics were quite dissimilar[6]. Biological significance of roosting calls in communal roosting avian species has been proposed to

play an important role in the group assembly process[58]. However, the function of this call in territorial and solitary-roosting avian species like the Indian chat is still not known.

1. Smith, W. J., Message, meaning and context in ethology. *Am. Nat*., 1965, **99**, 405–409.
2. Smith, W. J., Message-meaning analysis. In *Animal Communication* (ed. Sebeok, T. A.), Indiana University Press, Bloomington, 1968, pp. 44–60.
3. Gottfried, B. M., Andrews, K. and Haug, M., Breeding robins and nest predators: Effect of predator type and defense strategy on initial vocalisation patterns. *Wilson Bull*., 1985, **97**, 183–190.
4. Geoff, S., Bird songs and calls of Britain and northern Europe. In *Bird Songs and Calls of Britain and Northern Europe*, Harper Collins, London, 1996.
5. Marler, P., Bird calls: A cornucopia for communication. In *Nature's Music: The Science of Birdsong* (eds Marler, P. and Slabbekorn, H.), Elsevier, California, 2004, pp. 132–176.
6. Kumar, A. and Bhatt, D., Vocal signals in a tropical avian species, the redvented bulbul *Pycnonotus cafer*: Their characteristics and importance. *J. Biosci*., 2000, **25**, 387–396.
7. Kumar, A. and Bhatt, D., Characteristics and significance of calls in Oriental magpie robin. *Curr. Sci*., 2001, **80**, 77–82.
8. Katti, M., Vocal communication and territoriality during the nonbreeding season in a migrant warbler. *Curr. Sci*., 2001, **80**, 419–423.
9. Ishtiaq, F. and Rahmani, A. R., The forest owlet, *Heteroglaux blewitti*: Vocalisation, breeding biology and conservation. *Ibis*, 2005, **147**, 197–205.
10. Ali, S. and Ripley, S. D., *Handbook of the Birds of India and Pakistan*, Oxford University Press, New Delhi, 1998.
11. Grimmett, R., Inskipp, C. and Inskipp, T., *Birds of the Indian Subcontinent*, Oxford University Press, New Delhi, 1998.
12. Byers, B. E., Message encoded in the songs of chestnut-sided warbler. *Anim. Behav.*, 1996, **52**, 691–705.
13. Catchpole, C. K., Variation in the song of the great reed warblers, *Acrocephalus arundinaceus* in relation to mate attraction and territory defense. *Anim. Behav.*, 1983, **31**, 1217–1225.
14. Kroodsma, D. E., Bereson, R. E., Byers, B. E. and Minear, E., Use of song types by the chestnut-sided warbler: Evidence for both intra- and inter-sexual functions. *Can. J. Zool*., 1989, **67**, 447–456.
15. Spector, D. A., Wood warbler song systems: A review of paruline singing behaviors. *Curr. Ornithol.*, 1992, **9**, 199–238.
16. Weary, D. M., Lemon, R. E. and Perreault, S., Different responses to different song types in American redstarts. *Auk*, 1994, **111**, 730–734.
17. Catchpole, C. and Leisler, B., Female aquatic warblers (*Acrocephalus paludicola*) are attracted by playback of longer and more complicated songs. *Behaviour*, 1996, **133**, 1153–1164.
18. Forstmeir, W. and Balsby, T. J. S., Why mated dusky warblers sing so much: Territory guarding and male quality announcement. *Behaviour*, 2002, **139**, 89–111.
19. Holmes, R. T., Sherry, T. W. and Reitsma, L., Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *Condor*, 1989, **91**, 545–561.
20. Mabey, S. E. and Morton, E. S., Demography and territorial behaviour of wintering kentucky warblers in Panama. In *Ecology and Conservation of Neotropical Migrant Land Birds* (eds Hagan, III J. M. and Johnston, D. W.), Smithsonian Institute Press, Washington DC, 1992.
21. Rappole, J. H. and Warner, D. W., In *Migrant Birds in the Neotropics: Ecology, Behaviour, Distribution and Conservation*, Smithsonian Institute Press, Washington DC, 1980, pp. 353–393.
22. Stutchburg, B. J., Competition for winter territories in a Neotropical migrant, the role of age, sex and color. *Auk*, 1994, **111**, 63–69.
23. Neudorf, D. L. and Tarof, S. A., The role of chip call in winter territoriality of Yellow warblers (*Dendroica petechia*). *J. Field Ornithol*., 1998, **69**, 30–36.
24. Searcy, W. A. and Anderson, M., Sexual selection and the evolution of song. *Annu. Rev. Ecol. Syst*., 1986, **17**, 507–533.
25. Falls, J. B., Does song deter territorial intrusion in white-throated sparrows (*Zonotrichia albicollis*)? *Can. J. Zool*., 1988, **66**, 206–211.
26. Kilner, R. M., When do canary parents respond to nestling signals of need? *Proc. R. Soc. London, Ser. B*, 1995, **259**, 259–263.
27. Price, K., Harvey, H. and Ydenberg, R., Begging tactics of nestling-headed blackbirds, *Xanthocephalus xanthocephalus* in relation to need. *Anim. Behav.*, 1996, **51**, 421–435.
28. Kolliker, M., Richner, H., Werner, I. and Hebb, P., Begging signals and biparental care: Nestling choice between parental feeding locations. *Anim. Behav*., 1998, **55**, 215–222.
29. Redondo, T. and Castro, F., The increased risk of predation with begging. *Ibis*, 1992, **134**, 180–187.
30. Haskell, D., Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proc. R. Soc. London, Ser. B*, 1994, **257**, 161–164.
31. Leech, S. M. and Leonard, M. L., Begging and the risk of predation in nestling birds. *Behav. Ecol*., 1997, **8**, 644–646.
32. Dearborn, D. C., Brown-headed cowbird nestling vocalisation and risk of nest predation. *Auk*, 1999, **116**, 448–457.
33. Ryden, O., Differential responsiveness of great tit nestlings, *Parus major* to natural auditory stimuli–response–strength as related to stimulus significance and previous individual exposure. *Z. Tierpsychol.*, 1978, **47**, 236–253.
34. Greig-Smith, P. W., Parental investment in nest defense by stonechats (*Saxicola torquata*). *Anim. Behav.*, 1980, **28**, 604–619.
35. Maurer, G., Magrath, R. D., Leonard, M. L., Horn, A. G. and Donnelly, C., Begging to differ: Scrubwren nestlings beg to alarm calls and vocalize when parents are absent. *Anim. Behav*., 2003, **65**, 1045–1055.
36. Skutch, A. F., *Parent Birds and their Young*, University of Texas Press, Austin, Texas, 1976.
37. Breitwisch, R., Mortality patterns, sex ratios, and parental investment in monogamous birds. *Curr. Ornithol.*, 1989, **6**, 1–50.
38. Zaias, J. and Breitwisch, R., Intra-pair cooperation, fledgling care, and renesting by Northern mockingbirds (*Mimus polyglottos*). *Ethology*, 1989, **80**, 94–110.
39. Clutton-Brock, T. H., *The Evolution of Parental Care*, Princeton University Press, Princeton, New Jersey, 1991.
40. Sacchi, R., Saino, N. and Galeotti, P., Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. *Behav. Ecol.*, 2002, **13**, 268–273.
41. Higgins, P. J. and Peter, J. M., *Handbook of Australian, New Zealand & Antarctic Birds*, Oxford University Press, Melbourne, 2002.
42. Sayfarth, R. M., Cheney, D. L. and Marler, P., Vervet monkey alarm calls: Semantic communication in a free ranging primate. *Anim. Behav.*, 1980, **28**, 1070–1094.
43. Owings, D. and Leger, D., Chatter vocalisation of California ground squirrels: Predator and social-role specificity. *Z. Tierpsychol.*, 1980, **54**, 163–184.
44. Gyger, M., Marler, P. and Pickert, R., Semantics of an avian alarm call system: The male domestic fowl, *Gallus domesticus*. *Behaviour*, 1987, **102**, 15–40.
45. Ficken, M. S. and Popp, J., A comparative analysis of passerine mobbing calls. *Auk*, 1996, **113**, 370–380.
46. Howard, W. E., Innate and environmental dispersal of individual vertebrates. *Am. Midl. Nat.*, 1960, **63**, 152–161.

47. Ritchinson, A. J., Belthoff, J. R. and Sparks, E. J., Dispersal restlessness: Evidence for innate dispersal by juvenile Eastern screech owls? *Anim. Behav.*, 1992, **43**, 57–65.
48. Belthoff, J. R. and Duffy, A. M., Locomotor activity levels and the dispersal of Western screech-owl, *Otus kennicottii*. *Anim. Behav.*, 1995, **50**, 558–561.
49. Alonso, J. C., Gonzalez, L. M., Heredia, B. and Gonzalez, L., Parental care and the transition to independence of Spanish imperial eagle *Aquila heliaca* in Donama National Park, South-west Spain. *Ibis*, 1987, **129**, 212–224.
50. Hiraldo, F., Delibes, M. and Estrella, R. R., Observations of a zone-tailed hawk family during the post-fledgling period. *J. Raptor Res.*, 1989, **23**, 103–106.
51. Wiggett, D. R. and Boag, D. A., The proximate cause of male-biased natal emigration in Columbian ground squirrels. *Can. J. Zool.*, 1993, **71**, 201–218.
52. Godfray, H. C. J., Evolutionary theory of parent–offspring conflict. *Nature*, 1995, **376**, 133–138.
53. Harper, A. B., The evolution of begging: Sibling competition and parent–offspring conflict. *Am. Nat.*, 1986, **128**, 99–114.
54. Stamp, J., Begging in birds. *Etologia*, 1993, **3**, 69–77.
55. Payne, R. B. and Payne, L. L., Song mimicry and species associations of West African indigobirds Vidua with quail-finch *Ortygospiza atricollis*, goldbreast *Amandava subflava* and brown twinspot *Clytospiza monteiri*. *Ibis*, 1994, **136**, 291–304.
56. Perrone, M., Factors affecting the incidence of distress call in passerines. *Wilson Bull.*, 1980, **92**, 404–408.
57. Koenig, W. D., Stanback, M. T. and Hooge, P. N., Distress calls in the acorn woodpecker. *Condor*, 1991, **93**, 637–643.
58. Hill, B. G. and Lein, M. R., The non-song vocal repertoire of the white-crowned sparrow. *Condor*, 1985, **87**, 327–335.

ACKNOWLEDGEMENTS. We thank the Head, Department of Zoology and Environmental Science, Gurukul Kangri University, Haridwar and Coordinator, UGC–SAP for providing infrastructural facilities to carry out this work. We also thank Dr Maria Luisa da Silva, Department of Biology, Federal University of Parß, Belum for useful comments on the first draft of the manuscript. DST fellowship to V.K.S. during the course of this study is acknowledged.

Received 7 July 2006; revised accepted 28 February 2008