Characteristics and Behavioral Correlates of Call Types in a Tropical Bird, the Pied Bush Chat Saxicola caprata

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Abstract.- Acoustic signals in birds may be classified in two categories: song and call. Songs are mostly used by males and play important role in territorial establishment and mate attraction during breeding season. In contrast, calls are generally used by both sexes to meet out immediate requirements throughout the year. The present study deals with the physical characteristics and sociobiological significance of different call types used by the Pied Bush Chat *Saxicola caprata*. Call types were recorded from January to December 2009 during morning and/or evening hours using Sennheiser ME 67 directional microphone attached to Marantz PMD 670 digital sound recorder. The bird used five types of calls, namely territorial call, begging call, alarm call, contact call and distress call in its call repertoire. Three of these are used by the young, while adults produce the remaining two types. The sociobiological significance of these call types has been deduced from the contexts under which birds used them.

Keywords: Call repertoires, Pied Bush Chat, Saxicola caprata, tropical bird.

INTRODUCTION

 \mathbf{C} ommunication is an integral part of animal behaviour that helps to maintain the social relationships between individuals (Catchpole and Slater, 2008; Rutovskaya, 2011). Animals such as primates and birds possess a unique repertoire of sounds that have the ability to convey contextual information about motivation levels (Gottfried et al., 1985; Fischer and Hammerschmidt, 2001; Fragaszy et al., 2004). Vocalization in birds is generally classified in two categories: song and call. Song is the characteristic of males that serves two important territorv establishment and functions: its maintenance through advertisement and mate acquisition (Catchpole and Slater, 2008). In addition to songs, birds use a variety of calls, more deeply involved than songs with immediate issues of life and death (Geoff, 1996; Marler, 2004). Almost all birds have a repertoire of calls, sometimes quite small, 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 in all seasons and circumstances. According to Marler (2004) calls are goldmines of insight into animal

* Corresponding author: dineshharidwar@gmail.com 0030-9923/2012/0005-1231 \$ 8.00/0 Copyright 2012 Zoological Society of Pakistan. semantics and many other aspects of vocal communication.

The Pied Bush Chat (Order Passeriformes, Family Muscicapidae) is a tropical songbird found in open habitats including scrub, grassland and cultivated areas. It is distributed discontinuously from Transcapsia and the Indian subcontinent to south-east Asia, the Philippines, Indonesia, New Guinea and New Britain (Bell and Swainson, 1985; Ali and Ripley, 2001). The male is mostly black with a white rump, wing patch and lower belly while the female is largely drab brown. Nest, an open cup of grasses and rootlets, is tucked into a hole, crevice or under a stone completely covered overhead by tussocks of grasses (Bell and Swainson, 1985). Pairs also select nest sites under dead vegetations in roadside ditches or at base of the clump of dead grasses to provide better concealment to the nest (Kumar, 2010). Clutch size varies from 2-4 eggs and only female incubates. Both parents feed the young (Bell and Swainson, 1985; Kumar, 2010).

Male Pied Bush Chat deliver complex song repertoires during dawn in the breeding season to mediate social relationships with neighbouring males to proclaim an established territory (Sethi *et al.*, 2011a,b). However, review of the literature reveals absence of detailed, scientific, and spectrogram based information on its call repertoire. It was therefore planned to study the structure and functions of different call types of the Pied Bush Chat used under different behavioural contexts.

MATERIALS AND METHODS

This study was carried out during January to December 2009 in the scrub lands, agricultural fields and suburban areas of district Haridwar (29° 55' N and 78° 08' E; Himalayan foothills of Uttarakhand state, India). Habitat in the study area was mainly bare stony grounds supporting small patches of tussock grass vegetation such as *Chrysopogon zizanioides*, *Cynodon dactylon* etc. Pied Bush Chat mainly nest in ground vegetation and these grasses help conceal the nest (Kumar, 2010).

Study area was visited once a week during the breeding season (March to July) of the Pied Bush Chat and at least once a month during rest of the year. Twenty eight individuals (11 males, 3 females and 14 fledglings) were captured in mist nets or from their roosting sites and ringed with unique combination of plastic colour rings. Call types were recorded (by VKS and AK) during morning (05:00-08:00 a.m.) and/or evening (04:00-07:00 p.m.) hours. Calls were recorded using Sennheiser ME 67 directional microphone attached to Marantz PMD 670 digital sound recorder. Most signals were recorded at 3-15 meter distance and were analyzed using Avisoft-SAS Lab Pro. 4.4. Minimum frequency, maximum frequency, duration of signal and interval between signals were measured to define the acoustic features of the calls. Number and type of notes and rate of production were also measured. Results were expressed as mean \pm SD. The respective behavior of the caller at the time calls were delivered, were used to infer the possible meanings of signals.

RESULTS AND DISCUSSION

The call repertoire of Pied Bush Chat was found to consist of five distinct types of calls produced under different circumstances. Of these, adults gave two types of calls and the young produced remaining three types of calls. The frequency and temporal characteristics of these call types are presented in Table I. Territorial call

This was the most common call delivered primarily by male Pied Bush Chat. Males produced this call year round, however, most frequently during breeding period. This call had a minimum and maximum frequency of 2.33 ± 0.04 and 3.71 ± 0.09 kHz respectively. A single call note was of 0.19 ± 0.02 seconds duration with an inter-note interval of 1.76 ± 0.59 seconds (Fig. 1A, Table I).

The bird generally uttered this call in a stereotyped sequence of notes (40.10±10.05 call notes/minute) in a continuous manner for a period of 3-10 minutes. However, during the onset of breeding season more than 220 call notes (n=11) were delivered for a period of 10-15 minutes without any pause. High call rate during the onset of breeding season was probably attributed to the establishment of the territory. The function of this call seemed to mainly defend the winter (nonbreeding) and breeding territories. A series of this call type was often directed towards conspecific adjacent territory holders probably to mediate social relationships with neighboring males to proclaim an established territory. For a number of times (n=59), when a male was delivering territorial call and as soon as we entered its territory (especially during nestling or fledgling stage), it started to produce alarm call intermittently within the continuous bout of the territorial call. Sporadic use of alarm calls within the bout of territorial calls (directed to conspecifics) seemed the result of bird's reaction to us (human intruders), probably considering us as predator.

Male Pied Bush Chat uses complex song repertoires also during dawn to defend the territory (Sethi *et al.*, 2011b, 2012). In contrast, territorial call was used equally during dawn and dusk. Use of this call by males on a daily basis seemed to defend territory from intruders from a distance and thus avoid fighting. 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 time and energy (Gottfried *et al.*, 1985).

Like Pied Bush Chat, other species such as Oriental Magpie Robin (*Copsychus saularis*) and Indian Chat (*Cercomela fusca*) also deliver

Type of call		Delivered by	Min. Freq. kHz	Max. Freq. kHz	Duration (s)	Interval between two call notes (s)
A.	Territorial call	Adults	2.33±0.04	3.71±0.09	0.19±0.02	1.76±0.59
B.	Begging call	Nestlings	(N=11, n=78) 4.79±0.29	(N=11, n=78) 6.44±0.56	(N=11, n=78) 0.08±0.01	(N=11, n=78) 0.23±0.02
C.	Alarm call	Adults	(N=8, n=42) 1.95±0.24	(N=8, n=42) 7.26±0.45	(N=8, n=42) 0.08±0.01	(N=8, n=42) 0.21±0.05
D.	Contact call	Fledglings	(N=8, n=36) 2.66±0.23	(N=8, n=36) 8.03±0.43	(N=8, n=36) 0.22±0.03	(N=8, n=36) 1.59±0.39
E.	Distress call	Nestlings and	(N=8, n=31) 3.24±0.49	(N=8, n=31) 9.84±0.21	(N=8, n=31) 0.18±0.04	(N=8, n=31) 0.21±0.05
		Fledglings	(N=9, n=44)	(N=9, n=44)	(N=9, n=44)	(N=9, n=44)

Table I.- Physical characteristics of call types of Pied Bush Chat Saxicola caprata.

N, number of individuals; n, number of calls analyzed; S, Seconds.



Fig. 1. Spectrograms of different call types used by Pied Bush Chat Saxicola caprata.

territorial calls (besides songs) during breeding period (Kumar and Bhatt, 2001; Sethi and Bhatt, 2008) while most of song birds use mainly songs to defend their territories (Kroodsma *et al.*, 1989; Spector, 1992; Weary *et al.*, 1994; Catchpole and Leisler, 1996; Forstmeier and Balsby, 2002). Pied Bush Chat used this call to defend its winter/feeding territory also during non breeding period. However, contrary to breeding season, bird used this call less frequently coupled with low level of excitement/ vigilance during non breeding period. Like Pied Bush Chat, many other avian species also defend winter territories (Marler, 2004). For example, in American redstart (Setophaga ruticilla), blackthroated blue warbler (Dendroica caerulescans), Kentucky warbler (Oporornis formosus), hooded (Wilsonia citrina), vellow warbler warbler (Dendroica petechia) etc. winter territory is advertised/defended by 'chip' (territorial) calls (Rappole and Warner, 1980; Holmes et al., 1989; Mabey and Morton, 1992; Stutchburg, 1994; Neudorf and Tarof, 1998). However, some other species use either song (see Searcy and Anderson, 1986; Falls, 1988) or song and calls both for this purpose (Katti, 2001).

Begging call

These soft calls were produced by the nestlings (at least 4 to 5 days old) when parents approached the nest with or without feeding bates. Young ones produced this call throughout the nestling period. The minimum and maximum frequencies were 4.79 ± 0.29 kHz and 6.44 ± 0.56 kHz, respectively and duration of the call was 0.08 ± 0.01 seconds with 0.23 ± 0.02 seconds internote interval (Fig. 1B, Table I).

In this study, the nestlings produced begging calls almost throughout the day exhibiting begging display. For a number of times, sightings of parents carrying feeding baits coupled with the production of begging calls of nestlings helped us to locate the well-hidden nests in the study area. The loud and rapid begging calls of nestling birds signal their hunger and stimulate parental provisioning (Kilner et al., 1999; Budden and Wright, 2001). Parents generally respond to begging calls by directing feeding to the most intensively begging nestling in their brood (Kilner, 1995; Price et al., 1996; Kolliker et al., 1998) or by increasing their provisioning rate to the brood as a whole (Hussell, 1988; Ottoson et al., 1997). However, these conspicuous calls of nestlings can also attract predators to the nest and consequently broods that beg more intensely may suffer increased predation risk (Redondo and Castro, 1992; Leech and Leonard, 1997: Dearborn, 1999).

If begging calls attract the predators towards the nest, it seems necessary to trade off the

nutritional benefits of begging calls against the cost of predation (Maurer et al., 2003). Parents could reduce this cost through warning noisy chicks of danger so that they do not vocalize when predators are near (Platzen and Magrath, 2004). There are evidences through playback studies conducted by Ryden (1978) and Greig-Smith (1980) that showed that great tit (Parus major) and stonechat (Saxicola nestlings, respectively, torquata) suppressed begging after hearing playbacks of alarm calls. Nestling American goldfinches (Carduelis tristis) also crouch into the nest upon hearing the alarm calls (Knight and Temple, 1986). Platzen and Magrath (2004), through a field playback experiment, have also suggested that parental alarm calls can warn the young from a distance about the presence of a predator and as a result nestling whitebrowed scrubwren (Sericornis frontalis) suppress begging vocalization that might otherwise be overheard. However, contrary to these studies, parental alarm calls in Pied Bush Chat did not cause the nestlings to become quiet and crouch in the nest. Moreover, they continued to beg even when the parents were giving alarm calls at a high rate and observer (one of us) was within 1-2 m from the nest. This suggests that parents either direct their alarm call to predators to lead them away from the nest or nestlings might not have the ability to respond to parental alarm calls. Maurer et al. (2003) have also suggested that nestlings of scrubwren (Sericornis frontalis) acquire the ability to respond appropriately to alarm calls late in the nestling period.

Alarm call

A series of this call-note was 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 notes. The minimum and maximum frequencies of this call were 1.95 ± 0.24 and 7.26 ± 0.45 kHz respectively. The duration of the call was 0.08 ± 0.01 seconds and the interval between calls was 0.21 ± 0.05 seconds (Fig. 1C, Table I).

A series of this call was given by both the sexes of the Pied Bush Chat whenever they noticed any potential danger or any observer in the nesting area. Potential threats to Pied Bush Chat observed in the study area included aerial (*Accipiter nisus*, *A*.

badius) as well as ground (Herpestes edwardsii, Sus domestica, and some unidentified snake species) predators. We assume that the bird considered humans (us) as a potential ground predators as suggested by other workers also (Ricklefs, 1977; Andersson et al., 1980; Greig-Smith, 1980). However, there seems a difference in the response of adult birds towards different threats. For example, noticing aerial predators the bird rarely produced alarm call and tended to be silent and hidden in nearby bushes. In contrast, ground predators were responded differently and more aggressively. Noticing ground predators (including human intruders), the birds produced a long series of alarm calls coupled with close and frequent dives of the bird over predators.

The calling rate of alarm call exhibited a relation with the distance between the ground predator and the nest or the young. The birds produced this call at a rate of 31±4.72 calls/minute (n=108) when the distance was more than 25 meters between the ground predator and the nest and during this time the predator was probably not aware of the exact location of the nest. This rate dramatically increased up to 74±6.15 calls/minutes (n=96) when the ground predators were less than 5 meters away from the nest indicating that the birds experienced high level of disturbance when predators/observers approached the nest. Like Pied Bush Chat, many other animal species such as vervet monkey (Chlorocebus aethiops), suricate (Suricata suricatta), ground squirrel (Spermophilus richardsonii) give alarm calls when encountering predators or facing dangerous situations (Seyfarth et al., 1980; Manser, 2001; Warkentin et al., 2001; Smirnova, 2011). Moreover, some species use more than one type of alarm calls encountering different circumstances/predators (Seyfarth et al., 1980; Owings and Leger, 1980; Gyger et al., 1987; Ficken and Popp, 1996; Gill and Sealy, 2003). However, we did not notice any difference in the physical characteristics of this call uttered under the above distance-based situations or in the presence of different predators.

Besides being directed to predators, alarm calls seemed also to alert mates about nest threats or probably to coordinate their defensive responses. For example, on a few occasions (n=12), when any

individual of the pair was away from the nesting area and the other one produced the alarm call, its mate quickly returned to the nesting area and started to give alarm calls. Use of alarm calls to alert mates about nest threats has been reported in other bird species also (Gill and Sealy, 2003). For example, Red-winged blackbirds (*Agelaius phoeniceus*) use alarm calls to alert conspecifics, including mates, about the approach of a predator (Burton and Yasukawa, 2001).

Contact call

So far as the feeding and the safety of the fledgling(s) is concerned, contact call is of great significance. Young ones used this call when they had left the nest and were in the open fields, very prone to the attacks of the predators. During this phase, due to continuous movement of fledglings with the help of short-flights in different directions of the territory, it could be difficult for parents to locate them individually. Moreover, fledglings also tended to hide themselves within the bushes. However, whenever fledglings noticed their parents carrying feeding bait in their beaks, they produced contact calls that directed parents towards them individually.

This call consisted of a single note averaging 0.22±0.03 seconds in duration with intervals of 1.59±0.39 seconds. The minimum and maximum frequencies of this call were 2.66±0.23 and 8.03±0.43 kHz respectively (Fig. 1D, Table I). Use of such calls by dependent nestlings is a common feature in many bird species (Harper, 1986; Stamp, 1993; Godfray, 1995; Kumar and Bhatt, 2000; Sethi and Bhatt, 2008). The biological significance of this call was the same as of the begging call of nestlings *i.e.* to signal their hunger and stimulate parental provisioning (Kilner et al., 1999). However, physical characteristics of this call were much altered from the begging call. Like Pied Bush Chat, variations in the physical characteristics between begging and contact calls have been observed in other avian species also (Payne and Payne, 1994; Kumar and Bhatt, 2001; Sethi and Bhatt, 2008).

Distress call

Nestlings and fledglings of the Pied Bush Chat gave this call when they were captured by a predator or captured in mist-net and handled for ringing. However, adults did not utter this call when they were captured for ringing. These calls were harsh and loud exhibiting harmonic. The minimum and maximum frequencies of this call were 3.24 ± 0.49 and 9.84 ± 0.21 kHz respectively. The mean duration of the call was 0.18 ± 0.04 seconds with the inter-note intervals averaging 0.21 ± 0.05 seconds (Fig. 1E, Table I).

The response of birds to capture by predators varies greatly both among and within species; for example a captured bird may fly back, struggle to escape, give distress call or remain motionless and silent or it may also do some or all of these, in sequence (Perrone, 1980). Distress calls, given when animals are in considerable danger or after they have been captured, are loud, easy to locate (Marler, 2004) and common among birds, but their function remains unclear (Koenig et al., 1991; Martin et al., 2011). Several hypotheses have been proposed to explain the function of distress calls, including startling attacking predators i.e. screams startle predators into inadvertently allowing captured individuals to escape (Wise et al., 1999; Neudorf and Sealy, 2002); attracting secondary predators that, in their attempt to pirate the prey, may either distract or fight the primary predator and allow the caller to escape inadvertently (Perrone, 1980; Koenig et al., 1991); warning conspecifics of the presence or location of the predator (Conover, 1994), or eliciting help from nearby conspecifics and heterospecifics (Rohwer et al., 1976; Greig-Smith. 1980).

In this study, distress calls of young Pied Bush Chat were loud, harsh, easily locatable, and had a penetrating quality. Listening to these calls of young ones, the parents got restless and even sometimes they dived and snarled the predators quite closely. During such interactions, for a number of times, other bird species such as Oriental magpie robin (*Copsychus saularis*), common myna (*Acridotheres tristis*), jungle babbler (*Turdoides striata*), Indian robin (*Saxicoloides fulicatus*) also gathered in a nearby tree and dived on the predator. Such observations indicate that distress call of young might serve to elicit help from conspecifics or heterospecifics.

In nut shell, it can be said that the Pied Bush

Chat uses a variety of calls each serving a different sociobiological function. For example, adult birds use territorial and alarm calls to defend territory and to defend nest/young ones respectively. Young ones (nestlings/fledglings) use begging and contact calls in order to signal their hunger and to stimulate parental provisioning. Moreover, contact call helps parents making the fledglings locatable for provisioning. Distress call, used by young ones, stimulates conspecifics and even heterospecifics to dive over predator to get the young one free out of predator's grip. We observed differences in the response of adult birds while responding to aerial and ground predators. Further studies on parental investment in nest defense using alarm calls seem necessary. Furthermore, the effect of brood size and age of young, if any, on parental nest defense strategy/mechanism using alarm calls would be interesting to study.

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REFERENCES

- ALI, S. AND RIPLEY, S.D., 2001. Handbook of the birds of India and Pakistan (Vol. 9). Oxford University Press, New Delhi.
- ANDERSSON, M., WIKLUND, C.G. AND RUNDGREN, H., 1980. Parental defence of offspring: a model and an example. *Anim. Behav.*, 28: 536-542.
- BELL, H.L. AND SWAINSON, G.W., 1985. The colonization, ecology and breeding of the Pied Stonechat Saxicola caprata at Port Moresby, Papua New Guinea. Ibis, 127: 74-83.
- BUDDEN, A.E. AND WRIGHT, J., 2001. Begging in nestling birds. In: *Current ornithology* (eds. V. Nolan Jr. and C.F. Thompson), Plenum Press, New York, pp. 83-118.

- BURTON, N. AND YASUKAWA, K., 2001. The "predator early warning system" of red-winged blackbirds. J. *Field Ornithol.*, **72**: 106-112.
- CATCHPOLE, C.K. AND LEISLER, B., 1996. Female aquatic warblers (*Acrocephalus paludicola*) are attracted by playback of longer and more complicated songs. *Behaviour*, **133**: 1153-1164.
- CATCHPOLE, C.K. AND SLATER, P.J.B., 2008. *Bird song— Biological themes and variations*. Cambridge University Press, Cambridge.
- CONOVER, M.R., 1994. Stimuli eliciting distress calls in adult passerines and response of predators and birds to their broadcast. *Behaviour*, **131**: 19-37.
- DEARBORN, D.C., 1999. Brown-headed cowbird nestling vocalization and risk of nest predation. *Auk*, **116**: 448-457.
- FALLS, J.B., 1988. Does song deter territorial intrusion in White-throated sparrows (*Zonotrichia albicollis*)? Can. J. Zool., 66: 206-211.
- FICKEN, M.S. AND POPP, J., 1996. A comparative analysis of passerine mobbing calls. *Auk*, **113**: 370-380.
- FISCHER, J. AND HAMMERSCHMIDT, K., 2001. Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Anim. Cogn.*, 4: 29-35.
- FORSTMEIER, W. AND BALSBY, T.J.S., 2002. Why mated dusky warblers sing so much: Territory guarding and male quality announcement. *Behaviour*, **139**: 89-111.
- FRAGASZY, D.M., VISALBERGHI, E. AND FEDIGAN, L.M., 2004. The complete capuchin: the biology of the genus Cebus. Cambridge University Press, Cambridge.
- GEOFF, S., 1996. Bird songs and calls of Britain and northern Europe. Harper Collians Publishers, London.
- GILL, S.A. AND SEALY, S.G., 2003. Tests of two functions of alarm calls given by yellow warblers during nest defence. *Can. J. Zool.*, 81: 1685-1690.
- GODFRAY, H.C.J., 1995. Evolutionary theory of parentoffspring conflict. *Nature*, **376**: 133-138.
- GOTTFRIED, B.M., ANDREWS, K. AND HAUG, M., 1985. Breeding robins and nest predators: effect of predator type and defense strategy on initial vocalization patterns. *Wilson Bull.*, **97**: 183-190.
- GREIG-SMITH, P.W., 1980. Parental investment in nest defense by Stonechats (*Saxicola torquata*). Anim. Behav., 28: 604-619.
- GYGER, M., MARLER, P. AND PICKERT, R., 1987. Semantics of an avian alarm call system: the male Domestic Fowl, *Gallus domesticus*. *Behaviour*, **102**: 15-40.
- HARPER, A.B., 1986. The evolution of begging: sibling competition and parent-offspring conflict. Am. Nat., 128: 99-114.
- HOLMES, R.T., SHERRY, T.W. AND REITSMA, L., 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica.

Condor, 91: 545-561.

- HUSSELL, D.J.T., 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. Am. Nat., 131: 175-202.
- KATTI, M., 2001. Vocal communication and territoriality during the non-breeding season in a migrant warbler. *Curr. Sci.*, 80: 419-423.
- KILNER, R.M., 1995. When do canary parents respond to nestling signals of need? Proc. R. Soc. Lond. B, 259: 259-263.
- KILNER, R.M., NOBLE, D.G. AND DAVIES, N.B., 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, **397**: 667-672.
- KNIGHT, R.L. AND TEMPLE, S.A., 1986. Why does intensity of avian nest defense increase during the nesting cycle? *Auk*, 103: 318-327.
- KOENIG, W.D., STANBACK, M.T., HOOGE, P.N. AND MUMME, R.L., 1991. Distress calls in the Acorn Woodpecker. *Condor*, **93**: 637-643.
- KOLLIKER, M., RICHNER, H., WERNER, I. AND HEBB, P., 1998. Begging signals and biparental care: nestling choice between parental feeding locations. *Anim. Behav.*, 55: 215-222.
- KROODSMA, D.E., BERESON, R.E., BYERS, B.E. AND MINEAR, E., 1989. Use of song types by the chestnutsided warbler: Evidence for both intra- and inter-sexual functions. *Can. J. Zool.*, 67: 447-456.
- KUMAR, A., 2010. Breeding biology of Pied Bush Chat Saxicola caprata with reference to the contextual analysis of its acoustic signals. Ph.D. Dissertation, Gurukula Kangri University, Haridwar, India.
- KUMAR, A. AND BHATT, D., 2000. Vocal signals in a tropical avian species, the Redvented bulbul *Pycnonotus cafer*: their characteristics and importance. *J. Biosci.*, 25: 387-396.
- KUMAR, A. AND BHATT, D., 2001. Characteristics and significance of calls in Oriental magpie robin. *Curr. Sci.*, 80: 77-82.
- LEECH, S.M. AND LEONARD, M.L., 1997. Begging and the risk of predation in nestling birds. *Behav. Ecol.*, 8: 644-646.
- MABEY, S.E. AND MORTON, E.S., 1992. Demography and territorial behaviour of wintering Kentucky warblers in Pannama. In: *Ecology and conservation of Neotropical migrant land birds* (eds. J.M. Hagan and D.W. Johnston), Smithsonian Institute Press, Washington DC.
- MANSER, M.B., 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proc. R. Soc. Lond. B*, **268**: 2315-2324.
- MARLER, P., 2004. Science and birdsongs: the good old days. In: *Nature's music: The science of birdsong* (eds. P. Marler and H. Slabbekoorn), Elsevier Academic Press,

California. pp. 1-38.

- MARTIN, J.P., DOUCET, S.M., KNOX, R.C. AND MENNILL, D.J., 2011. Body size correlates negatively with frequency of distress calls and songs in Neotropical birds. *J. Field Ornithol.*, **82**: 259-268.
- MAURER, G., MAGRATH, R.D., LEONARD, M.L., HORN, A.G. AND DONNELLY, C., 2003. Begging to differ: scrubwren nestlings beg to alarm calls and vocalize when parents are absent. *Anim. Behav.*, **65**: 1045-1055.
- NEUDORF, D.L. AND SEALY, S.G., 2002. Distress calls in birds of a Neotropical cloud forest. *Biotropica*, 34: 129-137.
- NEUDORF, D.L. AND TAROF, S.A., 1998. The role of chip call in winter territoriality of Yellow warblers (*Dendroica petechia*). J. Field Ornithol., **69**: 30-36.
- OTTOSON, U., BACKMANN, J. AND SMITH, H.G., 1997. Begging affects parental efforts in the Pied flycatchers *Ficedula hypoleuca. Behav. Ecol. Sociobiol.*, **41**: 381-384.
- OWINGS, D. AND LEGER, D., 1980. Chatter vocalization of California ground squirrels: Predator and social-role specificity. Z. Tierpsychol., 54: 163-184.
- PAYNE, R.B. AND PAYNE, L.L., 1994. Song mimicry and species associations of west African indigobirds Vidua with quail-finch Ortygospiza atricollis, goldbreast Amandava subflava and brown twinspot Clytospiza monteiri. Ibis, 136: 291-304.
- PERRONE, M., 1980. Factors affecting the incidence of distress call in passerines. *Wilson Bull.*, 92: 404-408.
- PLATZEN, D. AND MAGRATH, R.D., 2004. Parental alarm calls suppress nestling vocalization. *Proc. R. Soc. Lond. B*, **271**: 1271–1276.
- PRICE, K., HARVEY, H. AND YDENBERG, R., 1996. Begging tactics of nestling in blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim. Behav.*, 51: 421-435.
- RAPPOLE, J.H. AND WARNER, D.W., 1980. *Migrant birds in the Neotropics: Ecology, behaviour, distribution and conservation.* Smithsonian Institute Press, Washington DC.
- REDONDO, T. AND CASTRO, F., 1992. The increased risk of predation with begging. *Ibis*, **134**: 180-187.
- RICKLEFS, R.E., 1977. Reaction of some Panamanian birds to human intrusion at the nest. *Condor*, **79**: 376-379.
- ROHWER, S., FRETWELL, S.D. AND TUCKFIELD, R.C., 1976. Distress screams as a measure of kinship in birds. *Am. Midl. Nat.*, 96: 418-430.

- RUTOVSKAYA, M.V., 2011. Acoustic communication in the Mandarin vole (*Lasiopodomys mandarinus*, Rodentia). *Biol. Bull.*, **38**: 927-934.
- RYDEN, O., 1978. 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.*, **47**: 236-253.
- SEARCY, W.A. AND ANDERSON, M., 1986. Sexual selection and the evolution of song. Annu. Rev. Ecol. Syst., 17: 507-533.
- SETHI, V.K. AND BHATT, D., 2008. Call repertoire of an endemic avian species, the Indian Chat Cercomela fusca. Curr. Sci., 94: 1173-1179.
- SETHI, V.K., BHATT, D. AND KUMAR, A., 2011a. Song repertoire size of the Pied Bush Chat *Saxicola caprata*. *Curr. Sci.*, **100**: 302-304.
- SETHI, V.K., BHATT, D. AND KUMAR, A., 2011b. The effect of mate removal on dawn singing behaviour in male pied bush chats. *Curr. Zool.*, 57: 72-76.
- SETHI, V.K., BHATT, D. AND KUMAR, A., 2012. Structure and context of female song in a tropical bird, the Pied Bush Chat. *Curr. Sci.*, **103**: (in press).
- SEYFARTH, R.M., CHENEY, D.L. AND MARLER, P., 1980. Vervet Monkey alarm calls: semantic communication in a free ranging primate. *Anim. Behav.*, 28: 1070-1094.
- SMIRNOVA, A.A., 2011. On the capability of birds for symbolization. *Biol. Bull.*, 38: 878-884.
- SPECTOR, D.A., 1992. Wood warbler song systems: A review of paruline singing behaviors. *Curr. Ornithol.*, 9: 199-238.
- STAMP, J., 1993. Begging in birds. Etologia, 3: 69-77.
- STUTCHBURG, B.J., 1994. Competition for winter territories in a Neotropical migrant, the role of age, sex and color. *Auk*, **111**: 63-69.
- WARKENTIN, K.J., KEELEY, A.T.H. AND HARE, J.F., 2001. Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. *Can. J. Zool.*, **79**: 569–573.
- WEARY, D.M., LEMON, R.E. AND PERREAULT, S., 1994. Different responses to different song types in American redstarts. Auk, 111: 730-734.
- WISE, K.K., CONOVER, M.R. AND KNOWLTON, F.F., 1999. Response of coyotes to avian distress calls: testing the startle-predator and predator-attraction hypotheses. *Behaviour*, **136**: 935–949.

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