DECREASE IN VEGETATION DECREASE IN ALBEDO DECREASE IN WATER VAPOR DECREASE IN WATER VAPOR DECREASE IN EVAPORATION

VEGETATION AND RAINFALL

Figure 4. Schematic diagram for the interaction between vegetation and climate.

Neelin¹⁰. They assume, however, that the vertical stability of the atmosphere is invariant. The present model indicates, however, that the vertical stability of the atmosphere depends strongly upon the integrated water vapour and hence will not remain constant during deforestation.

We have demonstrated that it is possible to construct a simple thermodynamic model of the monsoon based on energy and moisture balance. This model is able to simulate accurately the seasonal variation of rainfall in large tropical continents. The model indicates that three important parameters control the seasonal variation of monsoon rainfall. They are the net radiation at the top of the atmosphere, evaporation and the vertically integrated water vapour in the atmosphere. The intriguing feature of this model is that it does not explicitly contain any parameter related to land-sea contrast in temperature. Hence it provides a new perspective on the factors that cause large seasonal variation in rainfall in the tropics. This model will be useful to understand why some GCMs are poor in simulating the seasonal variation of monsoon rainfall. The manner in which radiative and cloud processes are modelled in a GCM will determine the accuracy in the estimate of Q_{net} . The manner in which surface processes are parameterized will determine the accuracy in the estimate of surface evaporation. The manner in which the vertical transport of moisture is parameterized will determine the accuracy in the estimate of integrated water vapour $(p_{\rm w})$. Moreover, the inaccuracy in estimate of one quantity (e.g. evaporation) may influence the accuracy of the other quantities (e.g. water vapour). The simple diagnostic model proposed here will be useful to identify which aspect of a GCM needs further refining.

- 1. Gates, W. L., Bull. Am. Meteorol. Soc., 1992, 73, 1962-1970.
- 2. Gadgil, S. and Sajani, S., Climate Dyn., 1998, 14, 659-689.

- 3. Neelin, J. D. and Held, I. M., Mon. Weather Rev., 1987, 115, 3-12
- 4. Fortelius, C. and Holopainen, E., J. Climate, 1990, 3, 646-660.
- 5. Kalnay, E. et al., Bull. Am. Meteorol. Soc., 1996, 113, 2158-2172.
- Barkstrom, B. R., Harrison, E., Smith, G., Green, R., Kibler, J., Cess, R. and ERBE Science Team, Bull. Am. Meteorol. Soc., 1989, 70, 1254–1262.
- Xie, P. and Arkin, P. A., Bull. Am. Meteorol. Soc., 1997, 78, 2539–2558.
- 8. Li, C. and Yanai, M., J. Climate, 1996, 9, 358-374.
- 9. Charney, J. G., Q. J. R. Meteorol. Soc., 1975, 101, 193–202.
- 10. Zeng, N. and Neelin, J. D., J. Climate, 1999, 12, 857-872.

ACKNOWLEDGEMENTS. I thank Ms Lavanya and Ms Anagha for their assistance in the analysis of the data. This work was supported by the Indian Space Research Organization.

Received 7 November 2000; revised accepted 5 December 2000

Characteristics and significance of calls in oriental magpie robin

Anil Kumar* and Dinesh Bhatt

Department of Zoology and Environmental Science, Gurukul Kangri University, Haridwar 249 404, India

*Present address: Desert Regional Station, Zoological Survey of India, Jodhpur 342 009, India

Birds use a variety of vocal signals while communicating with their conspecifics. These signals play an important role in their social life. A number of avian species often deliver either calls or songs or both in a variety of contexts. Information in a call usually relates to the immediate circumstances of the caller. This study characterizes different types of calls on the basis of their physical characteristics and sociobiological functions, in a tropical avian species *Copsychus saularis*. This species has been found to use mainly six types of calls, namely territorial calls, emergence and roosting calls, threat calls, submissive calls, begging calls and distress calls in their communication. In addition, members of this species have been observed to use escape call, anger call, etc. occasionally.

VOCAL signals in birds can be classified into songs and calls. A number of avian species often deliver either calls or songs or both in a variety of contexts. In general, songs are longer than calls. The former represent complex vocalizations produced by males in the breeding season. The latter are short, simple and less spontaneous. The calls are contextual and often produced with reference to a particular function¹. However, there are many examples of overlaps between simple songs and calls².

[†]For correspondence. (e-mail: anil_rathi@yahoo.com)

The study of communication not only enriches our knowledge about behaviour associated with signals, but also allows us to work out the evolutionary history of any species or relationships between closely related species.

The oriental magpie robin is known for its highly varied and complex songs used for territory establishment and mate acquisition^{3,4}. In the present study different types of calls have been characterized on the basis of their physical characteristics and the context, in the species *Copsychus saularis*.

Acoustic signals of C. saularis in a local population (18 colour-banded males and 8 females) of Haridwar, Uttar Pradesh, (29°55'N, 78°8'E) were recorded across three seasons periodically from January 1996 to December 1999, using a JVC zoom MZ-500 unidirectional microphone and SONY CFS 1030S tape recorder. Most signals were recorded at 2 to 10 m distances. After editing, cuts of high quality recordings (few seconds to some minutes duration) were used for physical analysis (characteristics based on frequency and time duration). The analysis was made with the help of Scientific 25 MHz Digital Storage Oscilloscope HM205-3 with Interface HO 79-4, IEEE Controller card HO 80 (this card makes the PC an IEEE controller for receiving and controlling the instrument) and a signal analyser software (SP 91) installed in a Pentium DX2 100 MHz 16 MB RAM. The samples were analysed at the maximum sampling rate 20 kHz/s, memory size $2 \text{ K} \times 8$ bit per channel. The horizontal resolution was 200 points/cm and vertical resolution was 28 points/cm. Spectrograms were generated by the DSP SonagraphTM 5500 machine using SIGNALTM, a software package for sound generation and analysis.

Vocalizations uttered in a single articulation for the purpose of an immediate requirement, viz. food, social contact, threat, alarm, begging, etc. are known as calls. A call may be composed of a single element/note (in a spectrogram an element is simply a continuous sound, preceded and followed by a silent gap). If the call has a single element, it is known as a simple call and if the call has several elements, it is categorized as a complex call. A complex call is generally made up of a number of distinct sections called phrases. Each phrase consists of a series of similar or dissimilar structured elements^{1,2,4}.

In the present study minimum frequency, maximum frequency, range of frequency, duration (mean \pm SE) and number of elements per phrase, type of phrases, etc. were used to define the physical characteristics of signals. The circumstances in which signalling occurred were used to infer the meaning of the signals and in some cases (when applicable), the playback experiments were used to confirm the information made available by the signals. For this purpose, few minutes recording of a respective call was used for playback and the behaviour of target birds was observed and the acoustic signals, if any replied, were recorded.

Table 1. Physical characteristics of different types of calls in oriental magpie robin

Type of call	Phonetic representation	Nature of call	Number of elements per call	Type of elements per call	Min. freq. (kHz)	Max. freq. (kHz)	Range of freq. (kHz)	Duration (s)	Interval (s)	Rate (calls/min)
Territorial call	Swee swee	Simple	1	1	4.18 ± 0.51 ($N = 8$,	6.04 ± 0.38 ($N = 8$,	1.93 ± 0.16 (N = 8,	0.63 ± 0.02 $(N = 10,$	2.07 ± 0.17 $(N = 10,$	17.91 ± 2.39 $(N = 10,$
Juvenile call	Sweerr sweerr	Simple	1	1	n = 16) 2.36 ± 0.02 (N = 14,	n = 16) 6.68 ± 0.02 (N = 14,	n = 16) 4.33 ± 0.01 (N = 14,	n = 20) 0.35 ± 0.02 (N = 14,	n = 20) 2.87 ± 0.27 ($N = 14$,	n = 20) 18.80 ± 1.11 (N = 14,
Emergence and roosting call	Charr charr	Simple	1	1	n = 28) 2.56 ± 0.01 (N = 12,	n = 28) 7.82 ± 0.01 (N = 12,	n = 28) 5.24 ± 0.01 ($N = 12$,	n = 28) 0.61 ± 0.01 (N = 16,	n = 28) 2.10 ± 0.31 (N = 16,	n = 28) 20.18 ± 0.85 (N = 16,
Threat call	Charr charr	Simple	1	1	n = 24) 1.95 ± 0.03 ($N = 9$,	n = 24) 6.52 ± 0.02 (N = 9,	n = 24) 4.58 ± 0.02 (N = 9,	n = 29) 0.82 ± 0.03 (N = 9,	n = 29) 1.58 ± 0.27 (N = 9,	n = 29) 23.6 ± 2.46 (N = 9,
Submissive call	Cheo che che	Complex	4–8	2	n = 18) 1.52 ± 0.02 (N = 6,	n = 18) 5.88 ± 0.28 (N = 6,	n = 18) 3.67 ± 0.06 ($N = 6$,	n = 18) 0.76 ± 0.04 (N = 6,	n = 18) 1.73 ± 0.35 (N = 6,	n = 18) 21 ± 1.12 (N = 6,
Begging call (Type-I)	Che che	Simple	1	1	n = 18) 4.05 ± 0.08 (N = 12,	n = 18) 7.47 ± 0.08 ($N = 12$,	n = 18) 3.46 ± 0.12 ($N = 12$,	n = 18) 0.16 ± 0.02 (N = 12,	n = 18) 0.75 ± 0.08 (N = 12,	n = 18) 37.73 ± 1.29 ($N = 12$,
Begging call (Type-II)	Chee chee	Simple	1	1	n = 24) 6.27 ± 0.06 (N = 10,	n = 24) 8.78 ± 0.03 (N = 10,	n = 24) 2.48 ± 0.09 (N = 10,	n = 24) 0.17 ± 0.01 (N = 10,	n = 24) 1.05 ± 0.12 (N = 10,	n = 24) 35.2 ± 0.91 ($N = 10$,
Begging call (Type-III)	Cheer cheer	Simple	1	1	n = 20) 0.36 ± 0.01 (N = 13,	n = 20) 6.36 ± 0.01 (N = 13,	n = 20) 6.01 ± 0.02 (N = 13,	n = 20) 0.35 ± 0.01 (N = 13,	n = 20) 2.07 ± 0.12 ($N = 13$,	n = 20) 20.55 ± 1.48 (N = 13,
Distress call	Teee cerr cheer	Simple	1	1	n = 26) 0.04 ± 0.02 (N = 5, n = 10)	n = 26) 7.55 ± 0.02 (N = 5, n = 10)	n = 26) 7.56 ± 0.01 (N = 5, n = 10)	n = 26) 0.53 ± 0.01 (N = 5, n = 10)	n = 26) 0.32 ± 0.03 (N = 5, n = 10)	n = 26) 38.22 ± 1.38 (N = 5, n = 10)

N, number of individuals; n, total number of calls analysed (2 to 3 calls were analysed per individual).

The following types of vocal signals were observed during the course of study in *C. saularis*. Summary of the calls has been given in Table 1.

Territorial calls are whistle-like calls, phonetically rendered as swee . . . swee During non-breeding season (and sometimes in the breeding season also) male C. saularis utters this call in a stereotyped sequence of notes (17.91 ± 2.39) calls in a continuous manner at a time). However, several times we observed more than one hundred call notes delivered continuously. These calls had a minimum and maximum frequency of $4.15 \pm 0.51 \, \text{kHz}$ and $6.04 \pm 0.38 \, \text{kHz}$ respectively. The frequency range was found to be $1.93 \pm 0.16 \, \text{kHz}$ (Figure 1). The call notes were of 0.63 ± 0.02 s duration, followed by 2.07 ± 0.17 s interval (Table 1). Male birds uttered these calls (Figure 2) specially to defend food resources (mainly insect larvae) in their winter territories⁴. Observations revealed that though female magpie robins also uttered these signals, they did not defend any territories during winter. Females remained in the area as floaters among male territory owners. It was interesting to note

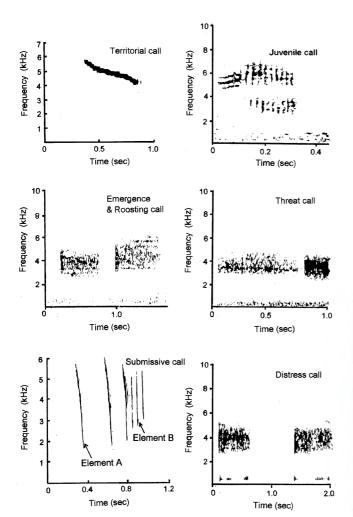


Figure 1. Spectrogram of different types of calls in oriental magpie robin.

that this species has a tendency to steal food from each other's territory. When a female or male was found foraging (insects) in the neighbour's territory the intruder never produced any call, while in its own territory this species generally uttered calls during feeding time.

Unlike most resident species of the tropical region, the magpie robin forms and defends winter territory⁵. However, many of the passerine species that breed in the temperate zone and migrate to tropical or sub-tropical habitats for the winter have been reported to defend exclusive winter feeding territories⁶⁻¹⁰. In some species song plays an important role in defence of winter territories^{11,12}, while in others, viz. American redstart *Setophaga ruticilla*, black-throated blue warbler *Dendroica caerulescens*, Kentucky warbler *Oporornis formosus*, hooded warbler *Wilsonia citrina*, yellow warblers *Dendroica petechia*, etc. winter territory is advertised/defended by 'chip' calls (territorial calls)^{6,7,9,10,13}.

Juvenile calls are calls used by juveniles. Phonetically these calls are rendered as sweetr... sweetr.... The minimum, maximum and range of frequencies were 2.36 ± 0.02 , 6.68 ± 0.02 and 4.33 ± 0.01 kHz respectively (Table 1, Figure 1). The duration of call notes was 0.35 ± 0.02 s, followed by 2.87 ± 0.27 s interval. The rate of production was found to be 18.80 ± 1.11 calls/min. Since juveniles are generally not much involved in territory defence, then for what purpose is this call uttered? Probably this type of call is uttered by juveniles in the process of learning territorial or threat calls and so components of both types of calls (territorial and threat calls) are mixed in juvenile calls. However, further investigations are needed to know about the biological function of this type of call.

Emergence and roosting calls are the shrill (harsh), monosyllabic, wide band calls used by both male and female individuals at the time of roosting and emergence (when birds leave the roosting place in the morning) throughout the year. However, sometimes during the breeding season



Figure 2. Magpie robin (male) delivering territorial calls from a prominent position.

males were observed to use emergence song instead of emergence calls. The minimum, maximum and range of frequencies were $2.56\pm0.01,\ 7.82\pm0.01$ and 5.24 ± 0.01 kHz respectively (Table 1, Figure 1). The bird generally produced 16 to 21 calls at a time. The duration of call notes was 0.61 ± 0.01 s and these call notes were separated by 2.10 ± 0.31 s gap. The rate of call production was 20.18 ± 0.85 calls/min. Phonetically these calls are rendered as charr . . . charr . . ., same as threat calls. However analysis of data revealed that the calls given during emergence and roosting are different from threat calls in their physical characteristics and frequency spectrum.

Threat calls are harsh, shrill, broad band, low amplitude signal, phonetically described as charr . . . charr This signal is used by both male and female, specially during the breeding season, when predators are noticed in the close vicinity of the nesting site or are approaching the nest (Figure 3). While chasing the predator with threat calls, the bird exhibited special posture also⁵. Other members of this species were not observed to respond to threat calls, since all males were engaged in defending their territories. It is a simple type of call composed of a series of monosyllabic elements. The minimum, maximum and range of frequencies of the calls were 1.95 ± 0.03 , 6.52 ± 0.02 and 4.58 ± 0.02 kHz respectively. The duration of the calls was 0.82 ± 0.03 s and the interval between calls was 1.58 ± 0.27 s (Table 1, Figure 1). The rate of call delivery varied according to the situation. The bird produced calls more rapidly when the predator arrived close to the nest or juveniles. The average rate of call production was 23.60 ± 2.46 calls/min. The threat call of magpie robin has a wide frequency range and abrupt onset and termination. These characteristics of the magpie robin's threat call resemble mobbing calls (when birds mob a predator) of a number of species, viz. wood warb-



Figure 3. Magpie robin (male) using threat calls, when the nest is approached by a predator.

lers willow flycatcher, dusky-capped flycatcher, tree swallow, barn swallow, steller's jay, white-breasted nuthatch, brown creeper, wood thrush, American robin, common crow, etc. ^{14–17}.

Marler¹⁸ demonstrated the antithetical acoustic structure of two types of vocalizations elicited by predators. Calls given when a hawk is flying overhead are often high pitched, cover a narrow frequency range and lack abrupt onsets or terminations, while those given during mobbing cover a wide range of frequencies and show abrupt onsets. Calls in the first category may have features making them difficult to localize, while mobbing calls have features enhancing locatability¹⁸⁻²⁰, and may facilitate the recruitment of other individuals in harassing the predator. Marler18 also suggested that the 'seeep', an alarm call, produced in almost identical form by a variety of European passerines, had converged on that form in different species because it was ideal to avoid localization. Producing a call in the presence of a predator such as a hawk is a risky business, and selection might be expected to minimize the risk. The 'seeep' is an almost pure tone at around 8 kHz. This frequency is too high for the unambiguous use of phase differences and too low for intensity differences between the ears to be marked²¹. However, Marler's suggestion on convergent evolution of acoustic structure of mobbing call could get only weak support from later workers¹⁷. Ficken and Popp¹⁷ suggested that convergence may result from selection for interspecific communication rather than for calls that are easily locatable. It is worth mentioning that magpie robin does participate in mobbing with other species uttering the same threat call. In wood warbler also, the same calls seem to occur in mild alarm and therefore, are not specific to mobbing¹⁷. This trend may be true for other species.

Submissive calls are produced generally by the rival, when chased by a territory owner. During non-breeding season if a female arrives in a territory of a male for feeding, the male territory owner chases and fights with the female; then the female gives this submissive call, phonetically rendered as cheo . . . chee . . . chee . . . chee . . . This call is made up of two types of elements with their own time-varying frequency and duration (Figure 1). Sometimes the bird repeats the first element (element A) more than once and the number of second element (element B) may vary 2 to 6 times. The duration of element A was 0.16 ± 0.01 s (n = 12), while the duration of element B was very low $(0.066 \pm 0.003 \text{ s}, n = 12)$ compared to element A. It appears that submissive calls are not common in avian species. Survey of the literature reveals that there is no report available on such types of calls. However, submissive postures are reported in some birds and $mammals^{20,22}$.

Begging calls were observed in nestlings and fledgelings (Figure 4). The nestlings (3 to 4 days old) uttered a soft che... che... call. These are the simple calls made up of monosyllabic elements. The minimum, maximum and range of frequencies were 4.05 ± 0.08 , 7.47 ± 0.08 and 3.46 ± 0.12 kHz respectively. The duration of the calls was $0.16 \pm 0.02 \; s$ and the interval between calls was 0.75 ± 0.08 s. The rate of call production was 37.73 ± 1.29 calls/min (Table 1, Figure 5). The rate of these calls was increased in the presence of parents. The well-developed nestlings (7 to 10 days old) used begging calls with a higher frequency range and higher amplitude compared to 4-day-old nestlings. The minimum, maximum and range of frequencies were 6.27 ± 0.06 , 8.78 ± 0.03 and 2.48 ± 0.09 kHz. The duration of calls was 0.17 ± 0.01 s, followed by 1.05 ± 0.12 s interval. The rate of call production was 20.55 ± 1.48 calls/min (Table 1, Figure 5). In the last phase (after 14 days) when the nestlings fledged or were ready to fledge, they used another type of begging call/contact call with a higher frequency range and higher amplitude than 7-day-old nestlings. Fledglings gave calls with two bands of frequencies. The minimum, maximum and range of these signals were 0.36 ± 0.01 , 6.36 ± 0.01 and 6.01 ± 0.02 kHz respectively. The duration of these signals was 0.35 \pm 0.01 s, followed by 2.07 \pm 0.12 s interval. The rate of

call production was 20.55 ± 1.48 calls/min (Table 1, Figure 5). The physical characteristics and structure of begging calls are given in Table 1 and Figure 5, respectively.

Field observations revealed that the nestlings used begging calls to get food from parents, while in the fledgling stage these begging calls changed their characteristics and also acted as 'contact calls'. In the absence of parents or presence of predators, the fledglings hide themselves inside dense shrubs or trees. On the arrival of parents the fledglings contact them with the help of these calls, listening to which the parents approach them. In many species of birds parent-offspring interactions are characterized by calls of nestlings (begging calls/contact calls) and calls of parents (provisioning calls)^{23–27}. However, magpie robin does not use any provisioning call when it approaches the nest, probably because the magpie robin breeds inside a hole having lesser depth (10 to 30 cm) compared to other deep hole-nesting birds (which use more than a meter deep nests)⁵. However, the ecophysiological advantage of the absence of provisioning calls in magpie robin is not clear and needs further investigations. As observed in



Figure 4. Magpie robin delivering begging calls. a, Four-day-old nestlings using slow che... che... calls after receiving the indication of the presence of parents; b, Newly fledged young one uttering begging/contact calls.

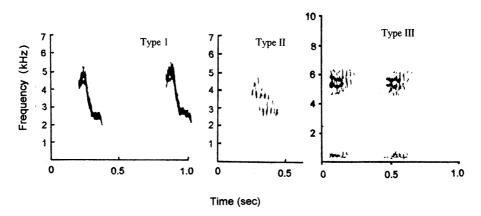


Figure 5. Spectrogram of the types of begging calls in oriental magpie robin.

magpie robin, some other species also exhibit changes in physical characteristics of begging calls of nestlings/fledglings as they grow up. For example, in the early phase the nestlings of quail-finch use a series of louder calls (sisisi) that rise in pitch and older nestlings use low-pitched begging calls (klik klik . . . klee . . . sisi . . .) which are shifted into higher-pitched elements as the parents approach the young and feed them²⁸.

Distress calls were produced generally by nestlings and fledglings when captured by a predator. These signals phonetically rendered as tseerr tseerr, are composed of a wide range of frequencies. The signal had double band frequencies (i) frequency range 0.01 to 0.75 kHz and (ii) 2.2 to 7.00 kHz and the range of frequencies was $7.56 \pm 0.01 \, \text{kHz}$. The duration of the signal was 0.53 ± 0.01 s and the call interval was 0.32 ± 0.03 s. The rate of these calls was 38.22 ± 1.38 calls/min (Table 1, Figure 1). One evening an adult magpie robin (male) entered our room and was captured by us. It produced distress calls as given by fledglings. Obviously, these signals were used to get the help of conspecifics/ allospecifics during the stress period, as observed in many other avian species $also^{29,30}$. Like threat calls, distress calls also have a wide frequency range, abrupt onset or termination probably to enhance the chance of locatability so that other birds could easily locate the individual in distress.

Other than the calls described above, the magpie robin was observed to use certain other call-types occasionally. For example, when any predator or large-sized bird visits the territory of magpie robin suddenly, the bird utters a sound out of fear and hides itself inside a nearby bush or tree. This vocal signal is phonetically rendered as 'che' and may be categorized as 'escape call'. The escape call is monosyllabic in nature (call duration 0.15 ± 0.02 s; n = 4). During incubation when the female magpie robin gets disturbed by the presence of tree ants in the nest, it gives a very slow 'chick-chick' call. After listening to this call the nest-guarding male immediately visits the nest-site and starts killing ants with its beak with a feeble 'chick-chick' sound. This sound may be categorized as 'anger call'.

- 1. Thielcke, G. A., in *Bird Sounds*, The University of Michigan Press, Ann Arbor, USA, 1976.
- Fisher, J. B., in Wildlife Sound Recording, The University of Michigan Press, Ann Arbor, USA, 1977.
- 3. Ali, S., in *The Book of Indian Birds*, Oxford University Press, Mumbai, 1996.

- Bhatt, D., Kumar, A., Singh, Y. and Payne, R. B., Curr. Sci., 2000, 78, 722–728.
- Kumar, A., Ph D thesis, Gurukul Kangri University, Haridwar, 1999
- Holmes, R. T., Bonney, R. E. and Pacala, S. W., Ecology, 1979, 60, 512–520.
- Mabey, S. E. and Morton, E. S., in *Ecology and Conservation of Neotropical Migrant Landbirds*, Smithsonian Institution Press, Washington, DC, 1992, pp. 329–336.
- Marra, P. A., Sherry, T. W. and Holmes, R. T., Auk, 1993, 110, 565-572.
- Rappole, J. H. and Warner, D. W., in Migrant Birds in the Neotropics: Ecology, Behaviour, Distribution and Conservation, Smithsonian Institution Press, Washington, DC, 1980, pp. 353– 393.
- 10. Stutchbury, B. J., Auk, 1994, 3, 63-69.
- 11. Falls, J. B., Can. J. Zool., 1988, 66, 206-211.
- Searcy, W. A. and Andersson, M., Annu. Rev. Ecol. Syst., 1986, 17, 507-533.
- Neudorf, D. L. and Tarof, S. A., J. Field Ornithol., 1998, 69, 30–36.
- 14. Curio, E., Z. Tierpsychol., 1978, 48, 175-183.
- Klump, G. M. and Shalter, M. D., Z. Tierpsychol., 1994, 66, 189– 226.
- 16. Brown, E. D., Z. Tierpsychol., 1985, 67, 17-33.
- 17. Ficken, M. S. and Popp, J., Auk, 1996, 113, 370-380.
- 18. Marler, P., Nature, 1955, 176, 6-8.
- Marler, P., in *Darwin's Biological Work* (ed. Bell, P.), Cambridge University Press, New York, 1959.
- Marler, P. and Hamilton, J., in Mechanisms of Animal Behaviour, John Wiley and Sons, New York, 1966.
- Catchpole, C. K. and Slater, P. J. B., in *Bird Song: Biological Themes and Variations*, Cambridge University Press, 1995.
- 22. Hinde, R. A., Ibis, 1955, 97, 706-745.
- 23. Armstrong, E. A., in *A Study of Bird Song*, Dover Publications, New York, 1973.
- 24. Bengtsson, H. and Ryden, O., Z. Tierpsychol., 1981, 56, 255-272.
- 25. Clemmons, J. R., Behaviour, 1995, 132, 1-20.
- 26. Clemmons, J. R., Auk, 1995, 112, 603-612.
- Lessells, C. M., Rowe, C. L. and McGregor, P. K., Anim. Behav., 1995, 49, 244–247.
- 28. Payne, R. B. and Payne, L. L., Ibis, 1994, 136, 291-304.
- Bright, M., in *Animal Language*, British Broadcasting Corporation, London W1M 4AA, 1984.
- Welty, J. C. and Baptista L., in *The Life of Birds*, Saunders College Publishing, USA, 1988.

ACKNOWLEDGEMENTS. We thank Prof. B. D. Joshi, Coordinator, Environmental Science and Dr A. K. Chopra, Head Department of Zoology and Environmental Science for providing laboratory facilities. We are grateful to Prof. Robert Payne, University of Michigan, Ann Arbor, Michigan, USA for the preparation of spectrograms. We also thank Prof. Asha Saklani and Dr A. K. Pati for their suggestions during this study. Financial support from the DST, Govt of India is gratefully acknowledged.

Received 28 June 2000; revised accepted 6 November 2000