iour of Red-winged Blackbird incubating several egg sizes. Behaviour 36: 74–83.
LIVNE, A. 1972. A Goldfinch story. Sal'it 1(4): 168. (In Hebrew.)
PAZ, U. 1987. The birds of Israel. New York, Penguin Books.
POWERS, L. R. 1978. Record of prolonged incubation by a Killdeer. Auk 95: 428.
RAHN, H., & A. AR. 1974. The avian egg: incubation time and water loss. Condor 76: 147–152.
TICKELL, W. L. N. 1962. The Dove Prion *Pachyptila desolata* Gmelin. Falkland Island Depend. Surv., Sci. Rep. 33: 1–55.
WHITTOW, G. C. 1986. Regulation of body temperature. Pp. 221–252 *in* Avian physiology (P. D. Sturkie, Ed.). New York, Springer-Verlag.

Received 20 January 1989, accepted 7 April 1989.

Himalayan Birds Face Uphill While Singing

MALCOLM L. HUNTER JR.
Department of Wildlife, University of Maine, Orono, Maine 04469 USA

Animal vocalizations are not omnidirectional. A few species such as bats are able to beam their transmissions (Schnitzler and Grinnell 1977); in many species there is an acoustic shadow behind and beside the animal (Archibald 1974, Gerhardt 1975, Witkin 1977), probably produced by sound wave interference patterns (Hunter et al. 1986). Laboratory experiments in which various sounds were broadcast from the mouth of a European Starling's (*Sturnus vulgaris*) body and rerecorded in three planes determined that the acoustic shadow effect was strongest behind and below the bird, i.e. in the direction of the tail (Hunter et al. 1986). I observed the orientations of birds singing on steep slopes which imply that their choice of direction may be affected by the directionality of their vocalizations.

In March and April 1980, four colleagues and I observed 40 different birds that sang on steep slopes in the Kulu and Ravi valleys of the Western Himalayas, India (see Gaston et al. 1983 for a description of the study area). We recorded the orientation to slope (upslope, downslope, or parallel), beak level with respect to a horizontal plane (the bisector of the angle formed by the mandibles was within 15° of level, or up, or down), bird species, time, tree height, perch height, and tree height relative to forest canopy. In March 1988, I made eight similar observations in the Langtang area of central Nepal. The observations were made on 21 species of passerine (sample sizes >1 are indicated in parentheses): *Dicrurus leucophaeus, Hypsipetes madagascariensis, Pomatorhinus erythrogenys, Garrulax lineatus, Culicicapa ceylonensis, Seicercus xanthoschistos, Erithacus cyanurus, Phoenicurus frontalis* (3), *Saxicola ferrea* (4), *Monticola cinclorhynchus, Turdus boulboul, T. viscivorus, Parus monticolus* (4), *P. melanolophus* (8), *P. rubidiventris* (2), *P. dichrous, Sitta leucopsis* (3), *Anthus hodgsoni, Coccothraustes icterioides* (8), *C. affinis* (3), and *Pyrrhula erythrocephala.* (Taxonomy follows Ali and Ripley 1983.) Only initial observations were recorded, not subsequent changes, and thus each observation represented a different individual.

Of the 48 observations, 37 were upslope, 9 parallel to the slope, and 2 were downslope. If birds were oriented without respect to slope, the distribution would presumably be 25% upslope, 50% parallel, and 25% downslope. The observed distribution differs significantly from the expected ($\chi^2 = 69.79$, $P \ll 0.005$). Even with a very conservative interpretation in which 50% of the observations were expected to be upslope and 50% parallel or downslope, the observed and expected still differ ($\chi^2 = 13.04$, $P \ll 0.005$). Steepness of slope (range 35–70%), tree height (2–38 m), and perch height (2–38 m) had no detectable relationship with orientation. However, most of the perch heights recorded were quite high ($\bar{x}$ = 92% of tree height); we probably undersampled birds that sang from low, inconspicuous perches, and these birds may have had a different orientation.

The directionality of sounds emitted by birds will differ depending on whether they face upslope or downslope (Fig. 1). Sounds produced by birds that face upslope will carry relatively far in that direction because sound emission in front of a bird and above horizontal is relatively strong. For the same reason, the sounds produced by birds that face downslope will carry best up into the air and not be readily heard near the ground. Unless there is a need to communicate with birds flying overhead, this may explain our observation that birds almost never sing facing downhill. It is probably not possible for birds to correct for this effect by changing the orientation of their beak because the beak has virtually no effect on directionality (Hunter et al. 1986). Other anatomical constraints may inhibit birds from leaning forward or lowering their beaks to sing. We recorded 28 cases in which the beak was held above the horizontal, 9 in which it was level, and none in which it was pointed down.

There are some alternative explanations for the ob-

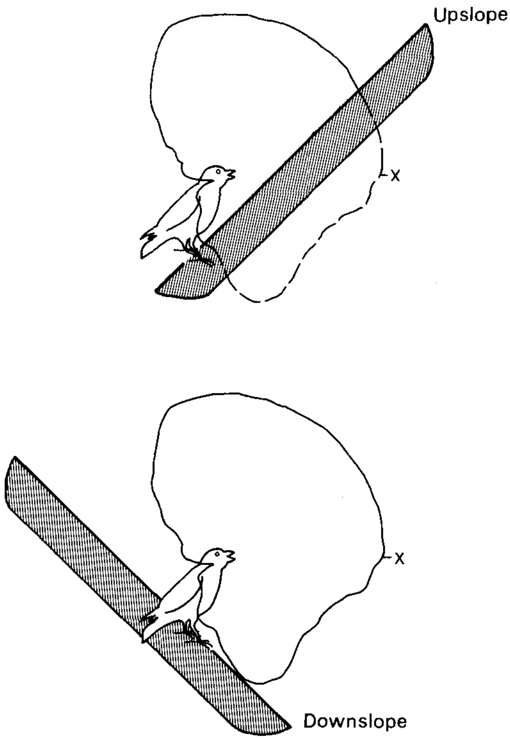

Fig. 1. The directionality of vocalizations produced by a bird facing upslope or downslope. The envelope of sound around the bird represents the distance from the bird a sound could be heard at any given sound pressure level. The distance to X represents a normalized reference value; all other values are expressed as linear proportions. This particular envelope was generated by broadcasting an 8-kHz pure tone from the back of a starling's mouth and rerecording it in an anechoic chamber (Hunter et al. 1986). For lower frequencies the pattern is less pronounced. For example, in the acoustic shadow, 2- and 4-kHz sounds are reduced to ca. 67% and 50%, respectively, of their normalized value. Sound directionality in a dorsolateral plane is indicated. Directionality patterns of emission in the horizontal and transverse planes also are strongest in front of the bird and above horizontal. The dashed line on the upper figure represents sound absorbed by the ground. (Redrawn from Hunter et al. 1986.)

served behavior. Perhaps the birds faced uphill because a raptor attack was more likely to come from this direction, or they were looking or listening for conspecifics. It is also possible that atmospheric structure (e.g. wind direction or temperature profiles) could favor singing upslope.

Birds that sing on slopes merit further research along three lines. First, the alternative explanations outlined above should be explored. Second, the consequences of singing upslope on other activities should be studied. For example, the effect on location and use of song perches within a territory, or the distribution of intrusions and boundary disputes, are essentially unexplored. (For an example of the consequences of song directionality, see Breitwisch and Whitesides 1987). Finally, it would be useful to document the generality of singing uphill. In the Himalayas almost all the land is steep and a majority of any bird population would experience this constraint, but in regions where most members of a population live on level ground, individuals living on isolated hillsides may not show a predilection for singing upslope.

I thank Peter Garson, Tony Gaston, Girish Kumar, and Vivek Matthai for field assistance, Shirley Moulton and Eric Stefanovich for help in preparing the manuscript. Alex Kacelnik and Brian Sullivan reviewed a draft. The many conservation agencies listed in Gaston et al. (1983) provided financial support. Maine Agricultural Experiment Station Publ. No. 1360.

Literature Cited

Ali, S., & S. D. Ripley. 1983. A pictorial guide to the birds of the Indian subcontinent. Delhi, India, Oxford Univ. Press.

Archibald, H. L. 1974. Directional differences in the sound intensity of the Ruffed Grouse. Auk 91: 517–521.

Breitwisch, R., & G. H. Whitesides. 1987. Directionality of singing and non-singing behaviour of mated and unmated Northern Mockingbirds, *Mimus polyglottos*. Anim. Behav. 35: 331–339.

Gaston, A. J., P. J. Garson, & M. L. Hunter Jr. 1983. The status and conservation of forest wildlife in Himachal Pradesh, Western Himalayas. Biol. Conserv. 27: 291–314.

Gerhardt, H. C. 1975. Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. J. Comp. Physiol. 102: 1–12.

Hunter, M. L., Jr., A. Kacelnik, J. Roberts, & M. Vuillermoz. 1986. Directionality of avian vocalizations: a laboratory study. Condor 88: 371–375.

Schnitzler, H. U., & A. D. Grinnell. 1977. Directional sensitivity of echolocation in the Horseshoe Bat (*Rhinolophus ferrumequinum*): I. Directionality of sound emission. J. Comp. Physiol. 116: 51–61.

Witkin, S. R. 1977. The importance of directional sound radiation in avian vocalization. Condor 79: 490–493.

Received 5 December 1988, accepted 9 April 1989.