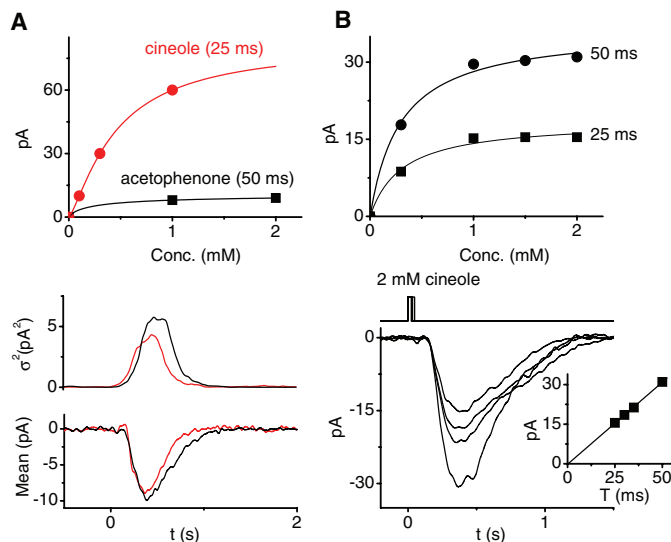


Fig. 4. (A) Unitary responses for two odors with different potencies on the same cell are very similar. (Top) Relation between response amplitude and odorant concentration for acetophenone and cineole odors. Each point represents the average of four to eight stimulus trials. Although the duration of acetophenone stimulation was twice as long as that for cineole, the response with all receptors bound by acetophenone was a factor of 7 less than the response to cineole. (Bottom) Variance/mean analysis of the unitary response to the two odors. The quantal responses to the two odors were similar (0.48 pA for cineole and 0.56 pA for acetophenone). Thirty trials each of 100 μ M cineole at 25-ms duration and 2 mM acetophenone at 50-ms duration. The two stimuli were chosen to produce responses of comparable amplitudes. The slight difference in response kinetics for the two odors was due to a change in cell condition during the experiment; this was not observed in other experiments. We chose this cell because of the large difference in efficacy between the two odors. (B) Estimation of cineole dwell-time on the receptor. (Top) Relation between response amplitude and cineole concentration at two durations. Even when all receptors were bound (≥ 1 mM cineole), the response amplitude increased linearly with the odorant pulse duration. Each point represents the average of 3 to 20 stimulus trials. (Bottom) Complete data from the same experiment at a saturating cineole concentration of 2 mM and applied for four different durations. (Inset) Linear increase of the response with odorant duration. The time intercept of the linear-regression fit is near zero.



the stimulus duration-response relation in Fig. 4B would not have remained linear). Thus, phosphorylation and arrestin binding are unlikely to constitute the standard termination of olfactory responses. Possibly, phosphorylation is important for desensitization in situations of prolonged and intense stimulation. A short-lived receptor-odorant complex does not preclude an overall high olfactory sensitivity. Repeated bindings of odorant molecules to the same receptor allow signal integration, especially if receptor phosphorylation does not occur (unlike in vision, where a photon acts only once and a photobleached pigment molecule is nonfunctional). The total rate of odorant-binding events is also amplified by orders of magnitude by the total number of receptor molecules on an ORN. The supralinear interactions occurring when unitary transduction domains overlap can further enhance sensitivity at intermediate odorant concentrations and durations. Finally, a high convergence of sensory input at the glomerulus (23) may boost sensitivity. The glomerulus is the synaptic plexus in the olfactory bulb that integrates signals from all ORNs expressing the same odorant receptor species. In principle, this convergence can increase indefinitely by simply expanding the surface area of the olfactory epithelium and therefore the number of ORNs expressing a given odorant receptor. This increase in convergence may explain why the olfactory sensitivity in many

animals is much higher than it is in humans. Unlike the retinotopic map in vision, which imposes a functional limit on the degree of convergence from photoreceptors, no corresponding limitation exists in olfaction.

References and Notes

1. L. B. Buck, *Cell* **100**, 611 (2000).
2. D. Schild, D. Restrepo, *Physiol. Rev.* **78**, 429 (1998).

3. H. R. Matthews, J. Reisert, *Curr. Opin. Neurobiol.* **13**, 469 (2003).
4. A. Menini, C. Picco, S. Firestein, *Nature* **373**, 435 (1995).
5. G. Lowe, G. H. Gold, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 7864 (1995).
6. G. H. Gold, G. Lowe, *Nature* **376**, 27 (1995).
7. S. Firestein, C. Picco, A. Menini, *J. Physiol.* **468**, 1 (1993).
8. D. A. Baylor, T. D. Lamb, K.-W. Yau, *J. Physiol.* **288**, 613 (1979).
9. T. D. Lamb, P. A. McNaughton, K.-W. Yau, *J. Physiol.* **319**, 463 (1981).
10. G. Lowe, G. H. Gold, *J. Physiol.* **442**, 147 (1991).
11. J. Reisert, H. R. Matthews, *J. Gen. Physiol.* **112**, 529 (1998).
12. Materials and methods as well as additional notes are available as supporting material on Science Online.
13. S. J. Kleene, *Neuroscience* **66**, 1001 (1995).
14. J. del Castillo, B. Katz, *J. Physiol.* **124**, 560 (1954).
15. S. Serizawa et al., *Science* **302**, 2088 (2003).
16. J. W. Lewcock, R. R. Reed, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 1069 (2004).
17. J. J. Tesmer, R. K. Sunahara, A. G. Gilman, S. R. Sprang, *Science* **278**, 1907 (1997).
18. Leskov et al., *Neuron* **27**, 525 (2000).
19. K.-W. Yau, *Invest. Ophthalmol. Vis. Sci.* **35**, 9 (1994).
20. T. M. Dawson et al., *Science* **259**, 825 (1993).
21. S. Schleicher, I. Boekhoff, J. Arriza, R. J. Lefkowitz, H. Breer, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 1420 (1993).
22. K. Peppel et al., *J. Biol. Chem.* **272**, 25425 (1997).
23. P. Mombaerts et al., *Cell* **87**, 675 (1996).
24. K. Nakatani, K.-W. Yau, *Nature* **334**, 69 (1988).
25. K. Nakatani, K.-W. Yau, *J. Physiol.* **395**, 695 (1988).
26. We thank D. A. Baylor, P. A. Fuchs, J. S. Kauer, T. D. Lamb, J. Nathans, R. R. Reed, F. Rieke, D. T. Yue, and members of the Yau laboratory, especially J. Bradley and C.-Y. Su, for critique and discussions, V. Kefalov for help in initial experiments, and D. Chaudhuri for help in computations using MatLab. V.B. also thanks D. McClellan for instruction in scientific writing. This work was supported by Howard Hughes Medical Institute and grants from NIH (DC06904) and the Human Frontier Science Program.

Supporting Online Material

www.sciencemag.org/cgi/content/full/308/5730/1931/DC1
 Materials and Methods
 Figs. S1 to S4
 References and Notes

18 January 2005; accepted 3 May 2005
 10.1126/science.1109886

Allometry of Alarm Calls: Black-Capped Chickadees Encode Information About Predator Size

Christopher N. Templeton,^{1*}† Erick Greene,¹ Kate Davis²

Many animals produce alarm signals when they detect a potential predator, but we still know little about the information contained in these signals. Using presentations of 15 species of live predators, we show that acoustic features of the mobbing calls of black-capped chickadees (*Poecile atricapilla*) vary with the size of the predator. Companion playback experiments revealed that chickadees detect this information and that the intensity of mobbing behavior is related to the size and threat of the potential predator. This study demonstrates an unsuspected level of complexity and sophistication in avian alarm calls.

Predation is a major cause of mortality for most species of animals, and many produce alarm signals when they perceive a potential predator (1). Alarm calls often differ in acoustic structure, depending on the situation

in which they are produced (2–5). If a species is preyed upon by different predators that use different hunting strategies or vary in the degree of danger they present, selection can favor variation in alarm signals

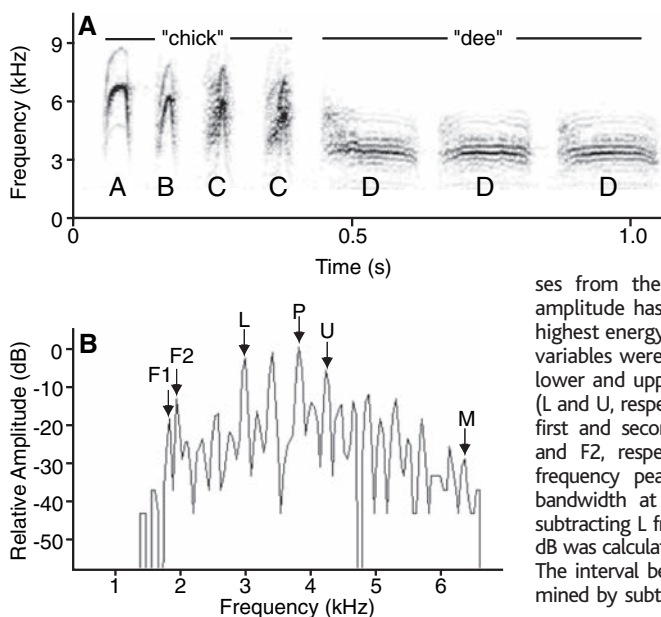


Fig. 1. Features of the “chick-a-dee” mobbing vocalization. (A) The call usually contains both “chick” sections (A, B, and C syllable types) and “dee” sections (D syllable types) (11). (B) Acoustic variables measured from power spectrum analyses from the center of a D note. The amplitude has been scaled relative to the highest energy overtone (dB = 0). Acoustic variables were the peak frequency (P), the lower and upper frequencies above -10 dB (L and U, respectively), the frequency of the first and second peaks above -30 dB (F1 and F2, respectively), and the maximum frequency peak above -30 dB (M). The bandwidth at -10 dB was calculated by subtracting L from U; the bandwidth at -30 dB was calculated by subtracting F1 from M. The interval between overtones was determined by subtracting F1 from F2.

that encode this information (6). Such variation in alarm signals can be used to transfer information about the type of predator [referential alarm call systems (7)], the degree of threat that a predator represents [risk-based systems (8)], or both (9, 10).

In addition to discriminating among broad types of predators (e.g., raptor versus snake), discriminating among morphologically similar predators within a single type (e.g., different species of raptors) could also be adaptive if the predators vary in the degree of threat they pose. One species that is faced with numerous, morphologically similar predators is the black-capped chickadee (*Poecile atricapilla*). Chickadees are small, common songbirds that are widespread throughout North America. In the non-breeding season, chickadees form flocks of six to eight birds (11). They use an elaborate system of vocalizations to mediate social interactions in these flocks (12, 13) and to warn conspecifics about predators (14, 15).

Chickadees produce two very different alarm signals in response to predators: When flying raptors are detected, chickadees produce a high-frequency, low-amplitude “seet” alarm call; in response to a perched or stationary predator, they produce a loud, broadband “chick-a-dee” alarm call that is composed of several types of syllables (16) (Fig. 1A). Whereas the “seet” alarm call functions to warn of flying predators, the “chick-a-dee” mobbing alarm call recruits other chickadees

[and often many other species (17)] that harass, or mob, a perched predator. This “chick-a-dee” call is a complex vocalization that is also produced in many other situations and encodes information about food and identity (both individual and flock) in addition to information about predators (11).

We examined variation in the mobbing vocalizations and behavior of black-capped chickadees by conducting predator presentations and playback experiments with chickadees living under semi-natural conditions in large, outdoor experimental aviaries (18). We presented flocks of color-marked chickadees with 13 species of live, perched raptors and two species of live mammalian predators. The predators varied considerably in body size (e.g., factor of 20 difference in body mass between northern pygmy-owl and great horned owl), activity patterns, hunting strategies, and diet (Table 1). The raptors ranged from small, maneuverable predators whose diets include many small birds, to large, less maneuverable predators that eat few small birds. We also used two types of controls: a procedural control with a live bobwhite quail (*Colinus virginianus*); and no presentation, with observers present as they would be during predator presentations. During each predator presentation, two observers recorded chickadee vocalizations, noting the color band combination of each calling individual. By conducting controlled presentations of live predators to birds living under semi-natural conditions, we could isolate vocal responses to specific species of predators from other features such as the location, behavior, or movement pattern of the predator.

Spectrographic analyses of the more than 5000 “chick-a-dee” mobbing alarm calls we

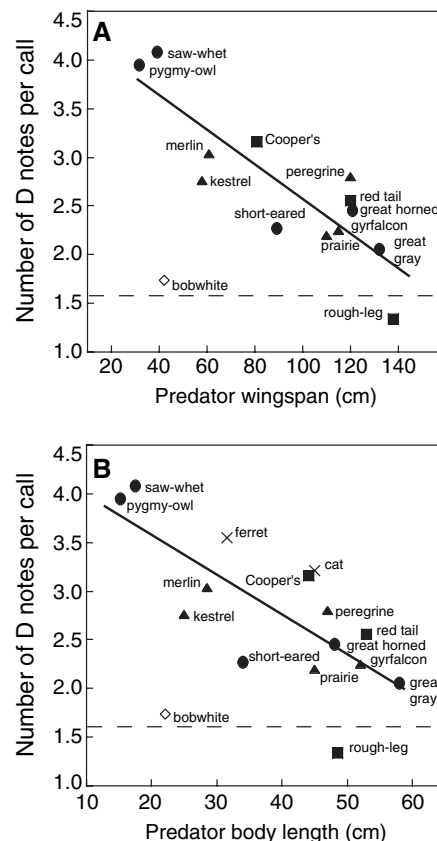


Fig. 2. Chickadees vary their mobbing calls in response to variation in predator body size. (A) Mean number of D syllables per call as a function of wingspan for raptors ($y = 4.4 - 0.02x$; $r^2 = 0.512$, $P < 0.0001$). (B) Mean number of D syllables per call as a function of body length for raptors and mammals ($y = 4.4 - 0.4x$; $r^2 = 0.361$, $P < 0.0001$). Each taxonomic group of raptors is represented by a different symbol (●, owl; ▲, falcon; ■, hawk; ×, mammal). A bobwhite quail (◇) was used as the procedural control. The dashed line displays the mean number of D notes per control trial without any stimulus.

recorded (Fig. 1) revealed previously unsuspected levels of acoustic variation. The number of mobbing calls produced in response to each predator was highly variable [analysis of variance (ANOVA): $F_{16,34} = 5.17$, $P < 0.0001$], with the smaller, higher risk, predators eliciting significantly more calls than the larger predators or controls (Tukey’s post hoc tests: $P < 0.05$). The total number of syllables per alarm call differed among predator treatments ($F = 3.05$, $P < 0.0001$). In particular, the average number of D syllables, or notes, per call differed significantly across predator treatments ($F = 7.771$, $P < 0.0001$). There was a strong inverse relationship between the number of D notes per alarm call and the wingspan of the raptors, with the smallest predators eliciting calls with the most D notes (Fig. 2A; $r^2 = 0.512$, $P < 0.0001$). There was also a strong inverse relationship between the number of D notes and predator body length when both the mammals and raptors were

¹Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA. ²Raptors of the Rockies, Post Office Box 250, Florence, MT 59833, USA.

*Present address: Department of Biology, Box 351800, University of Washington, Seattle, WA 98195, USA.

†To whom correspondence should be addressed. E-mail: ctemple2@u.washington.edu

REPORTS

included in the analysis (Fig. 2B; $r^2 = 0.361$, $P < 0.0001$).

Many other acoustic features of these mobbing calls (Fig. 1) also varied in relation to the predator treatment. For example, in comparisons of mobbing calls given in response to a northern pygmy-owl and a great horned owl (small and large predators, respectively), the duration of the “dee” section (all D notes) was significantly longer (ANOVA: $F_{1,14} = 9.984$, $P = 0.003$), the interval between the “chick” and “dee” sections was significantly shorter ($F = 11.364$, $P = 0.001$), the first D note of each call was shorter ($F = 9.984$, $P = 0.003$), and the interval between the first and second D notes was also shorter in small predator alarm call variants ($F = 9.043$, $P = 0.004$). Calls that chickadees produced during the large predator presentations tended to have D notes that contained more high-energy peaks above -10 dB ($F = 2.855$, $P = 0.097$) spanning a wider bandwidth ($F = 2.719$, $P = 0.105$) than those produced during encounters with small predators. D notes elicited by large predators also tended to have more widely spaced overtones

($F = 3.385$, $P = 0.071$). No differences were observed in any of the other measured features ($P > 0.2$ for all).

Do these acoustic differences in mobbing calls transmit information about the potential predator to other chickadees? We conducted playback experiments (18) to test how chickadees reacted to the mobbing calls that they produced in response to different predators by broadcasting variations of the “chick-a-dee” alarm vocalization associated with different predators. We played mobbing calls that flock mates produced in response to a great horned owl (large predator), a northern pygmy-owl (small predator), and control calls of a pine siskin (*Carduelis pinus*). Chickadees exhibited longer and more intense mobbing behavior when they heard alarm calls recorded in response to a pygmy-owl than when they heard alarm calls recorded in response to a great horned owl or control vocalizations (Fig. 3). They produced significantly more “chick-a-dee” calls in response to playback of mobbing alarm calls elicited by a small predator than they did when presented with playbacks of mobbing calls elicited by a

large predator or control vocalizations (Fig. 3A; Kruskal-Wallis $K = 11.50$, $P = 0.003$). Chickadees approached the hidden speaker more closely in response to the small predator mobbing call treatment than in response to the large predator mobbing call or control treatments ($K = 14.69$, $P = 0.001$); more individuals approached within 3 m (Fig. 3B; $K = 14.40$, $P = 0.001$) and within 1 m ($K = 11.34$, $P = 0.003$) of the speaker in response to the small predator alarm calls than in response to the large predator alarm calls or control vocalizations. After playback of small predator alarm calls, chickadees also mobbed for longer periods than they did after playback of large predator alarm calls and control sounds ($K = 12.69$, $P = 0.002$).

Previous studies have shown that animals produce different antipredator vocalizations for aerial and terrestrial predators. Most of these studies, however, have presented these two types of predators in different ways (19–21), potentially confounding the interpretation that prey distinguish between types of predators and not their location or

Table 1. Species presented to chickadee flocks. Length and wingspan were measured from animals used in experiments; mass (26) and diet information (27–29) were summarized from published accounts. The sex of each raptor used in the experiments is indicated in brackets.

Predator species	Mass (g)	Length (cm)	Wingspan (cm)	Time active	Primary diet
<i>Hawks</i>					
Cooper's hawk (<i>Accipiter cooperii</i>) [F]	450	44	81	Day	Small birds
Red-tailed hawk (<i>Buteo jamaicensis</i>) [F]	1,080	53	120	Day	Small mammals, few birds
Rough-legged hawk (<i>B. lagopus</i>) [M]	990	49	138	Day	Small mammals
<i>Falcons</i>					
American kestrel (<i>Falco sparverius</i>) [M]	117	25	58	Day	Inverts, small mammals, small birds
Merlin (<i>F. columbarius</i>) [F]	190	28	61	Day	Small birds
Peregrine falcon (<i>F. mexicanus</i>) [F]	720	47	120	Day	Medium-sized birds
Prairie falcon (<i>F. peregrinus</i>) [F]	720	45	100	Day	Small mammals, some birds
Gyrfalcon (<i>F. rusticolus</i>) [M]	1,400	52	115	Day	Medium-sized mammals and birds
<i>Owls</i>					
Northern pygmy-owl (<i>Glaucidium gnoma</i>) [M]	70	15	31	Day	Small birds, small mammals
Saw-whet owl (<i>Aegolius acadicus</i>) [M]	80	17	39	Night	Small mammals, some small birds
Short-eared owl (<i>Asio flammeus</i>) [M]	350	34	89	Both	Small mammals
Great horned owl (<i>Bubo virginianus</i>) [M]	1,400	48	121	Night	Small to medium-sized mammals
Great gray owl (<i>Strix nebulosa</i>) [M]	1,080	58	132	Both	Small mammals
<i>Mammals</i>					
Domestic cat (<i>Felis domesticus</i>)	15,000	45	—	Both	Birds, small mammals, insects
Ferret (<i>Mustela putorius</i>)	1,000	32	—	Day	Small mammals, eggs, some small birds
<i>Control</i>					
Bobwhite quail (<i>Colinus virginianus</i>)	170	22	42	Day	Seeds, insects

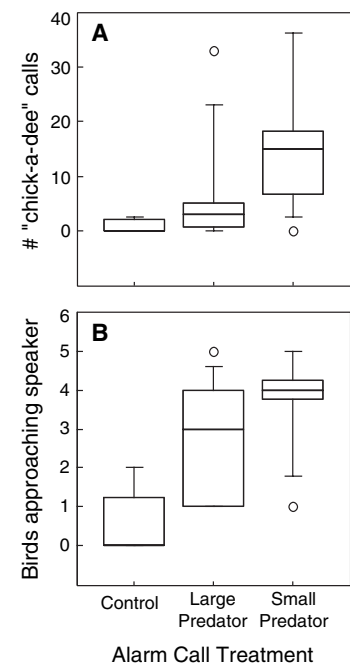


Fig. 3. Chickadees respond to predator-specific acoustic variations in their mobbing alarm calls. Two behavioral variables were used to quantify chickadees' responses to the three playback stimuli: control sounds (pine siskin calls), “chick-a-dee” calls produced in response to a large predator (great horned owl), and “chick-a-dee” calls produced in response to a small predator (northern pygmy-owl). (A) Boxplots (showing median, interquartile range (IQR), range, and outliers) of the number of “chick-a-dee” calls produced during the first 90 s after the start of each playback treatment. (B) Boxplots of the number of birds approaching within 3 m of the speaker after each treatment. All pairwise comparisons were significantly different (Mann-Whitney U , $P < 0.05$).

behavior. Our results show that chickadees do not vocally discriminate between raptors and mammals when they are presented in similar ways, and thus the “chick-a-dee” call does not refer specifically to the type of predator.

Instead, these vocal signals likely contain information about the degree of threat that a predator represents. Maneuverability (e.g., as measured by turning radius, or radial acceleration) is extremely important in determining the outcome of predator-prey interactions and is inversely related to wing-span and body size in birds (22, 23). Body size may be a good predictor of risk for chickadees: Small raptors tend to be much more maneuverable than larger raptors and likely pose a greater threat to chickadees.

In addition to being one of the most subtle and sophisticated signaling systems yet discovered, this system is unusual in that it combines aspects of both referential and risk-based antipredator vocalization systems (10, 24, 25). To denote the presence of a rapidly moving predator (e.g., raptor in flight), chickadees produce a “seet” alarm call. When they encounter a stationary predator (e.g., perched raptor), they use the “chick-a-dee” mobbing call. These two vocalizations appear to be functionally referential to the type of predator encounter (i.e., each denotes a specific type of encounter). In addition, we have shown that subtle variation in the “chick-a-dee” mobbing call reflects the size of a specific predator, a characteristic of a risk-

based system. Thus, chickadees convey information about predators at two different levels: A coarse level of encoding (“seet” or “chick-a-dee”) signifies the type of predator encounter, and a fine level of encoding (variants of “chick-a-dee”) signifies the degree of danger presented by that specific predator encounter.

The “chick-a-dee” vocalization is remarkably versatile; it is used in many different contexts and apparently conveys many different types of information. The fact that so much information can be transmitted by subtle variations in one type of vocalization raises some fascinating questions about how finely chickadees can discriminate between similar stimuli, and how they categorize different aspects of their environment.

References and Notes

1. J. W. Bradbury, S. L. Vehrencamp, *Principles of Animal Communication* (Sinauer Associates, Sunderland, MA, 1998).
2. P. Marler, *Nature* **176**, 6 (1955).
3. P. W. Sherman, *Science* **197**, 1246 (1977).
4. R. M. Seyfarth, D. L. Cheney, P. Marler, *Anim. Behav.* **28**, 1070 (1980).
5. C. S. Evans, L. Evans, P. Marler, *Anim. Behav.* **46**, 23 (1993).
6. M. D. Hauser, *The Evolution of Communication* (MIT Press, Cambridge, MA, 1996).
7. D. L. Cheney, R. M. Seyfarth, *How Monkeys See the World* (Univ. of Chicago Press, Chicago, 1990).
8. J. M. Macedonia, C. S. Evans, *Ethology* **93**, 177 (1993).
9. M. B. Manser, R. M. Seyfarth, D. L. Cheney, *Trends Cognit. Sci.* **6**, 55 (2002).
10. R. M. Seyfarth, D. L. Cheney, *Annu. Rev. Psychol.* **54**, 145 (2003).
11. S. M. Smith, *The Black-Capped Chickadee: Behavioral*

Ecology and Natural History (Cornell Univ. Press, Ithaca, NY, 1991).

12. S. Nowicki, *Behav. Ecol. Sociobiol.* **12**, 317 (1983).
13. D. J. Mennill, L. Ratcliffe, P. T. Boag, *Science* **296**, 873 (2002).
14. M. S. Ficken, S. R. Witkin, *Auk* **94**, 156 (1977).
15. M. C. Baker, A. M. Becker, *Wilson Bull.* **114**, 510 (2002).
16. M. S. Ficken, R. W. Ficken, S. R. Witkin, *Auk* **95**, 34 (1978).
17. C. R. Hurd, *Behav. Ecol. Sociobiol.* **38**, 287 (1996).
18. See supporting data on Science Online.
19. E. Greene, T. Meagher, *Anim. Behav.* **55**, 511 (1998).
20. D. T. Blumstein, *Behaviour* **136**, 731 (1999).
21. A. Le Roux, T. P. Jackson, M. L. Cherry, *Behaviour* **138**, 757 (2001).
22. H. C. Howland, *J. Theor. Biol.* **47**, 333 (1974).
23. K. P. Dial, *Auk* **120**, 941 (2003).
24. C. S. Evans, *Perspect. Ethol.* **12**, 99 (1997).
25. D. T. Blumstein, *Evol. Commun.* **3**, 135 (1999).
26. D. A. Sibley, *The Sibley Guide to Birds* (Knopf, New York, 2000).
27. P. A. Johnsgard, *Hawks, Eagles, and Falcons of North America* (Smithsonian Institution Press, Washington, DC, 1990).
28. P. A. Johnsgard, *North American Owls: Biology and Natural History* (Smithsonian Institution Press, Washington, DC, ed. 2, 2002).
29. K. R. Foresman, *The Wild Mammals of Montana* (Allen, Lawrence, KS, 2001).
30. We thank K. Dial for discussions about scaling; J. Graham for statistical advice; C. Eldermire, N. Schwab, and C. Putnam for help with data collection; and D. Emlen, B. Walker, and M. Parker for helpful comments on the manuscript. Supported by donations from Marchie's Nursery, Caras Nursery, Swift Instruments, and the Birdwatcher's Country Store.

Supporting Online Material

www.sciencemag.org/cgi/content/full/308/5730/1934/DC1
Materials and Methods

17 December 2004; accepted 4 May 2005
10.1126/science.1108841

Turn
a new
page
to...

www.sciencemag.org/books

Science
Books et al.
HOME PAGE

- ▶ the latest book reviews
- ▶ extensive review archive
- ▶ topical books received lists
- ▶ buy books online