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JIM MOORE*‡
RAUF ALI†

* *Anthropology Department,
Harvard University,
Cambridge, Massachusetts 02138, U.S.A.*

† *Mahidol University,
Faculty of Science,
Department of Biology,
Rama VI Road,
Bangkok 4, Thailand.*

‡ Present address: Box 4091, Berkeley, California
94704-0091, U.S.A.

References

- Altmann, S. A. & Altmann, J. 1970. *Baboon Ecology: African Field Research*. Chicago: University of Chicago Press.
- Bateson, P. 1983. Optimal outbreeding. In: *Mate Choice* (Ed. by P. Bateson) pp. 257-277. Cambridge: Cambridge University Press.
- Chapais, B. 1983. Matriline membership and male rhesus reaching high ranks in natal troops. In: *Primate Social Relationships* (Ed. by R. A. Hinde), pp. 171-175. Sunderland, Massachusetts: Sinauer.
- Fredrickson, W. T. & Sackett, G. P. 1984. Kin preferences in primates (*Macaca nemestrina*): relatedness or familiarity? *J. comp. Psychol.*, **98**, 29-34.
- Moore, J. 1984. Female transfer in primates. *Int. J. Primatol.*, **5**, 537-589.
- Moore, J. & Ali, R. 1984. Are dispersal and inbreeding avoidance related? *Anim. Behav.*, **32**, 94-112.
- Packer, C. 1979a. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.*, **27**, 1-36.
- Packer, C. 1979b. Male dominance and reproductive activity in *Papio anubis*. *Anim. Behav.*, **27**, 37-45.
- Packer, C. 1985. Dispersal and inbreeding avoidance. *Anim. Behav.*, **33**, 676-678.
- Smith, D. G. 1982. Inbreeding in three captive groups of rhesus monkeys. *Am. J. Phys. Anthropol.*, **58**, 447-451.
- Wu, H. M. H., Holmes, W. G., Medina, S. R. & Sackett, G. P. 1980. Kin preference in infant *Macaca nemestrina*. *Nature, Lond.*, **285**, 225-227.

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Acoustical Resource Partitioning by Two Species of Phyllostomid Bats (*Trachops cirrhosus* and *Tonatia sylvicola*)

Bats are the most numerous and diverse mammals in the neotropics. Such species diversity can only be achieved through utilization of different resources, especially food. However, few studies suggest the mechanisms by which similar species partition resources (Fenton 1982; Neuweiler 1983). The

purpose of this study is to investigate the sensory basis of resource partitioning between two species of carnivorous bats.

On Barro Colorado Island (BCI), Panama, 16 species of bats in the subfamily Phyllostominae coexist in an area of only 2400 ha. Two of these species, *Trachops cirrhosus* and *Tonatia sylvicola*, are closely related and remarkably similar in size (Bonaccorso 1979), morphology (Smith & Starrett 1979), habitat requirements (Handley 1976), activity patterns (Bonaccorso 1979) and geographic distribution (Jones & Carter 1976). Both species also have the most modified brains in the subfamily (McDaniel 1976). *T. cirrhosus* and *T. sylvicola* eat insects; however, *T. cirrhosus* also eats small vertebrates (Gardner 1977), especially frogs (Tuttle & Ryan 1981; Ryan et al. 1982).

We have shown that *T. cirrhosus* is able to locate frogs by orienting to the calls used by male frogs to attract females (Tuttle & Ryan 1981, 1982; Ryan et al. 1982), and that the hearing of these bats appears to be especially sensitive to the relatively low frequency sounds in frog calls (Ryan et al. 1983). Preliminary observations suggested that *T. sylvicola* might also locate prey by use of prey-emitted acoustic cues. In this study we demonstrate that *T. sylvicola* is attracted to calls produced by one of its prey items, an orthopteran insect, in the absence of other relevant cues. We then ask if a differential response to acoustic cues might be the basis for resource partitioning between these species.

We captured bats in mist-nets on BCI and used recorded frog calls and imitations of orthopteran insect calls to lure the bats into the nets.

The response of the bats to frog and orthopteran calls was tested in a flight cage on BCI. A detailed description of the flight cage and testing procedure can be found in Ryan et al. (1982). Briefly, the flight cage was square, 4.5 m on each side, 2.3 m high, and illuminated with a 25-W red bulb. The observers sat in one corner and the bat perched in the opposite corner. One speaker was located in each of the other two corners, about 4 m from the bat.

Calls were broadcast from tape recorders at 38 cm/s. A Stellavox tape recorder with a small extension speaker was used to broadcast the frog call. This call was a complex mating call produced by *Physalaemus pustulosus* which consisted of a whine plus two chucks (Fig. 1A; see Ryan 1980 and Rand & Ryan 1981 for a discussion of the complex mating call of this frog species). The insect call was broadcast from the speaker of a Nagra IV-D tape recorder. The internal speaker of the Nagra had greater fidelity to the higher frequencies of the insect call than the extension speakers. All speakers were camouflaged to control for visual differences, and were controlled remotely. The frog call (Fig.

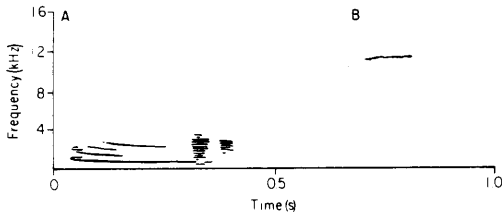


Figure 1. A sonagram of (A) the mating calls of the frog, *Physalaemus pustulosus* and (B) the insect (species unidentified) used in the playback experiments. Calls were recorded with a Nagra IV-D tape recorder and a Sennheiser MKH 104 microphone at 38 cm/s and were analysed on a Kay model 7029A sonograph.

1A) was broadcast at 75 dB SPL (re: 20 μ Pa) 1 m from the speaker, and the orthopteran call (Fig. 1B; Tettigoniidae, Phaneropterinae; unidentified species) was broadcast at 65–68 dB SPL.

A response was recorded if a bat flew within 30 cm of a speaker, or landed on a speaker during the 1 min of stimulus presentation. There were no rewards for a correct response, and speakers were switched between corners after each trial. Trials were repeated at 5–15-min intervals. Because the sample sizes for each individual were not identical, the null hypothesis of no preference was tested by comparing $-2\sum \ln P$ to a chi-squared distribution (Sokal & Rohlf 1969).

At various times from January 1980 to August 1983, we netted *T. cirrhosus* near streams on BCI and in neighbouring areas. Often we used recordings of frog calls to lure the bats into the nets. Even though we netted in areas where *T. sylvicola* occurs, this species was never captured while we broadcast frog calls. However, at the same location we were able to capture *T. sylvicola* by imitating orthopteran calls. We either mimicked the calls with an Audubon 'bird tweeter', or ran the teeth of a comb back and forth along a dry palm frond. In fact, we were able to lure both *T. cirrhosus* and *T. sylvicola* into a single net by alternately presenting frog calls and insect calls respectively. From December 1982 to December 1984 we captured *T. sylvicola* in nets that were 'baited' with live, singing male katydids. These bats were not captured in nets baited with non-singing female katydids.

We tested five *T. cirrhosus* and four *T. sylvicola* for preference between frog calls and insect calls that were presented simultaneously. All bats tested were attracted to one of the calls. *T. cirrhosus* was always preferentially attracted to the frog call (41 versus 0, $P < 0.005$), and *T. sylvicola* to the insect call (24 versus 0, $P < 0.005$). *T. cirrhosus* did respond to the insect call in the absence of the frog call, but *T. sylvicola* never responded to the frog call we used in these experiments, nor to the calls of

three other edible frog species we later tested in addition to *P. pustulosus*.

This study demonstrates that the sensory basis for resource partitioning between *T. cirrhosus* and *T. sylvicola* is a preferential response to prey-emitted acoustic cues. A number of other bats also seem to have the potential to utilize prey-emitted acoustic cues, at least in part, for prey localization (e.g. Fiedler 1979; Bell 1982; Poussin & Simmons 1982). We suggest that an investigation of the sensory cues used by other bats to locate prey combined with detailed analyses of diets may provide further insight into how resources are partitioned.

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MERLIN D. TUTTLE*
MICHAEL J. RYAN†§
JACQUELINE J. BELWOOD‡

* Vertebrate Division,
Milwaukee Public Museum,
Milwaukee, WI 53233, U.S.A.

† Department of Zoology,
University of Texas,
Austin, TX 78712, U.S.A.

‡ Department of Entomology and Nematology,
University of Florida,
Gainesville, FL 32611, U.S.A.

§ To whom all correspondence should be addressed.

References

- Bell, G.P. 1982. Behavioral and ecological aspects of gleaning by a desert insectivorous bat, *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.*, **10**, 217–223.
- Bonaccorso, F.J. 1979. Foraging and reproductive ecology in a Panamanian bat community. *Bull. Flor. Mus. Biol. Sci.*, **25**, 1–100.
- Fenton, M. B. 1982. Echolocation, insect hearing and feeding ecology of insectivorous bats. In: *Ecology of Bats* (Ed. by T. H. Kunz), pp. 261–285. New York: Plenum Press.
- Fiedler, J. 1979. Prey catching with and without echolocation in the Indian false vampire bat (*Megaderma lyra*). *Behav. Ecol. Sociobiol.*, **6**, 155–160.
- Gardner, A.L. 1977. Feeding habits. In: *Biology of Bats of the New World Family Phyllostomatidae, Part II* (Ed. by R. J. Baker, J. K. Jones, Jr & D. C. Carter), pp. 293–350. Lubbock: Texas Tech University.
- Handley, C. O., Jr. 1976. Mammals of the Smithsonian Venezuelan Project. *Sci. Bull., Biol. Ser.*, **20**, 1–89.
- Jones, J. K., Jr & Carter, D. C. 1976. Annotated checklist.

- with keys to subfamilies and genera. In: *Biology of Bats of the New World Family Phyllostomatidae, Part I* (Ed. by R. J. Baker, J. Knox Jones, Jr & D. C. Carter), pp. 7–38. Lubbock: Texas Tech University.
- McDaniel, V. R. 1976. Brain anatomy. In: *Biology of Bats of the New World Family Phyllostomatidae, Part I* (Ed. by R. J. Baker, J. K. Jones, Jr & D. C. Carter), pp. 147–200. Lubbock: Texas Tech University.
- Neuweiler, G. 1983. Echolocation and adaptivity to ecological constraints. In: *Neuroethology and Behavioral Physiology* (Ed. by F. Huber & H. Markl), pp. 280–302. Berlin: Springer Verlag.
- Poussin, C. & Simmons, J. 1982. Low frequency hearing sensitivity in the echolocating bat, *Eptesicus fuscus*. *J. Acoust. Soc.*, **72**, 340–342.
- Rand, A. S. & Ryan, M. J. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z. Tierpsychol.*, **57**, 209–214.
- Ryan, M. J. 1980. Female mate choice in a neotropical frog. *Science, N. Y.*, **209**, 523–525.
- Ryan, M. J., Tuttle, M. D. & Barclay, R. M. R. 1983. Behavioral responses of the frog-eating bat, *Trachops cirrhosus*, to sonic frequencies. *J. comp. Physiol.*, **150**, 413–418.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Bat predation and sexual advertisement in a neotropical anuran. *Am. Nat.*, **119**, 136–139.
- Smith, J. D. & Starrett, A. 1979. Morphometric analysis of chiropteran wings. In: *Biology of Bats of the New World Family Phyllostomatidae, Part III* (Ed. by R. J. Baker, J. K. Jones & D. C. Carter), pp. 229–316. Lubbock: Texas Tech University.
- Sokal, R. R. & Rohlf, F. K. 1969. *Biometry*. San Francisco: W. H. Freeman.
- Tuttle, M. D. & Ryan, M. J. 1981. Bat predation and the evolution of frog vocalizations in the neotropics. *Science, N. Y.*, **214**, 677–678.
- Tuttle, M. D. & Ryan, M. J. 1982. The role of synchronized calling, ambient light and ambient noise in anti-bat-predator behavior of a treefrog. *Behav. Ecol. Sociobiol.*, **11**, 125–131.

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The Evolution of the Teddy Bear

The factors moulding the development of human social behaviour in the individual can be grouped into three interdependent categories: those deriving from his social and cultural environment, from his physical situation, and from his biological nature. These act both directly by affecting behaviour, and by affecting preferences through which one style of behaviour is selected over another. Whilst the ubiquitous nature of cultural factors often masks the importance of the others, full understanding requires appreciation of all three. Similar principles apply to human artefacts, and here biological

determinants are sometimes more apparent: clothes and chairs are made to fit human bodies. Usually, of course, factors of all three types interact. For instance, the shape of cars is determined by cultural heritage from the horse carriage and by continuously changing fashions, by the pressure of the physical environment (streamlining, etc.) and by the need to accommodate people.

Greater interest attaches to cases in which the biological factors involve not physical characteristics of the human body but human behavioural propensities. Lorenz (1950) called attention to such influences on the shapes of dolls and cartoon characters. He suggested that nurturance and affection are elicited by certain key features: a short face in relation to a large forehead, protruding cheeks, maladjusted limb movements, etc. Dolls have come to emphasize or exaggerate these features, cartoon characters do likewise, and those animals most often selected as pets tend also to have them. Lorenz's suggestion has received some experimental support (Gardner & Wallach 1965; Fullard & Reiling 1976; Sternglanz et al. 1977).

Further evidence in favour of the operation of selection through these human proclivities is provided by changes in artefacts over time. Gould (1980) has documented the manner in which, as the early mischievous and somewhat cruel Mickey Mouse evolved into the more lovable character of recent years, his head proportions changed in a manner conforming with Lorenz's suggestions.

Such a correlation cannot by itself provide convincing evidence for a role of human propensities to respond nurturantly to particular stimulus characteristics. However parallel evolution in an unrelated species renders such an interpretation more plausible. A recent exhibition of teddy bears in the Cambridge Folk Museum provided some further relevant data. The teddy bear originated at the beginning of the century from a picture associating the U.S. President, Theodore Roosevelt, after a hunt in the Rocky Mountains, with a brown bear in the background. The earliest teddy bear in the collection, dated 1903, had a low forehead and a long snout, and was muzzled. A survey of the other bears in the collection showed a trend over time towards a larger forehead and a shorter snout relative to the dimensions of the head as a whole.

Figure 1A shows how the ratio of vertical distance between the eyes and the highest point of the crown, to the vertical distance between the eyes and the base of the head, has changed over time. On the assumption that the museum specimens were drawn from the population at each time at random with respect to this character, there is evidence for a clear trend over time towards a larger forehead (Spearman rank order correlation, $r_s = 0.52$,