

daughters. However, our finding that α -males sired their daughters' offspring less frequently than non-daughters' offspring remains highly significant when the analysis is restricted to the 34 offspring known to have been born to non-first time mothers (Fisher's exact $p = 0.0003$).

A third alternative explanation for our findings is that father-daughter matings are not avoided, but when they occur they result in early fetal loss. This phenomenon would result in longer interbirth intervals for the daughters of resident α -males, compared with other females. However, known interbirth intervals of these two classes of females were indistinguishable: for non-daughters ($n = 11$) they were 23 months and for daughters ($n = 7$) 22.5 months (Mann-Whitney $U = 32.0$, $p = 0.55$).

Thus, the most parsimonious explanation of our results is that father-daughter pairs of white-faced capuchin monkeys actively avoid mating. Female primates are generally more averse to inbreeding than males [6]. However, because courtship and copulations involving fertile females are rarely observed in this species [7], it cannot yet be determined whether it is the male, the female, or both, that avoid inbreeding. Individuals may avoid inbreeding by recognizing kin through long-term co-membership in the same group. The Westermarck effect, in which individuals develop sexual aversion to close childhood companions, is well supported in nonhuman primates [6,8]. In our data set, eight offspring that were produced by seven different females (including the single case of father-daughter inbreeding) were nonetheless sired by males who had been co-resident with the female during her infancy. However, white-faced capuchin infants generally spend substantially more time in proximity to the α -male than to subordinate males, so we cannot rule out a role for social familiarity in producing inbreeding avoidance. Several recent studies also support a role for phenotype

matching in mediating recognition of paternal kin in primates [9–11], suggesting that closely related male–female pairs would be predicted to avoid mating even in the absence of close familiarity early in life.

Supplemental data

Supplemental data including Experimental Procedures and Acknowledgements are available at <http://www.current-biology.com/cgi/content/full/16/5/R156/DC1/>

References

1. Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28, 1140–1162.
2. Silk, J.B. (2002). Kin selection in primate groups. *Int. J. Primatol.* 23, 849–875.
3. Altmann, S.A. (1962). A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Ann. N Y Acad. Sci.* 102, 338–435.
4. Charpentier, M., Peignot, P., Hossaert-McKey, M., Gimenez, O., Setchell, J.M., and Wickings, E.J. (2005). Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behav. Ecol.* 16, 614–623.
5. Cowlshaw, G., and Dunbar, R.I.M. (1991). Dominance rank and mating success in male primates. *Anim. Behav.* 41, 1045–1056.
6. Paul, A., and Kuester, J. (2004). The impact of kinship on mating and reproduction. In *Kinship and Behavior in Primates*, Chapais, B., Berman, C.M., Eds. (Oxford University Press, Oxford), pp271–291.
7. Manson, J.H., Perry, S., and Parish, A.R. (1997). Nonconceptive sexual behavior in bonobos and capuchins. *Int. J. Primatol.* 18, 767–786.
8. Westermarck, E., *The History of Human Marriage*. (Macmillan, London, 1891).
9. Alberts, S.C. (1999). Paternal kin discrimination in wild baboons. *Proc. R. Soc. Lond. B. Biol. Sci.* 266, 1501–1506.
10. Widdig, A., Nürnberg, P., Krawczak, M., Streich, W.J., and Bercovitch, F.B. (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proc. Natl. Acad. Sci. USA* 98, 13769–13773.
11. Smith, K., Alberts, S., and Altmann, J. (2003). Wild female baboons bias their social behaviour towards paternal half-sisters. *Proc. R. Soc. Lond. B. Biol. Sci.* 270, 503–510.

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Prey conspicuousness can explain apparent prey selectivity

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To study prey selection, ecologists compare the abundance of food resources with the actual prey spectrum [1,2]; selectivity is inferred when some prey are markedly overrepresented in an animal's diet [3]. However, the capabilities of an animal's sensory systems and the cues provided by potential prey both constrain its foraging behavior and access to food [4–9]. Here we report evidence from a study of the greater mouse-eared bat (*Myotis myotis*) which supports the hypothesis that selectivity patterns can be explained in part by the specific conspicuousness of the prey to the foragers' sensory systems ('passive prey selection'). Active prey selection might come into play as a second step within the food spectrum accessible to the bats' sensory systems. We conclude that considering sensory ecology is vital for understanding mechanisms of food selection in animals.

Greater mouse-eared bats are an ideal model system for investigating the role of sensory ecology in prey selection, because their foraging behavior and their sensory basis of prey detection are both well known. These bats, which each weigh about 30 g, occur in central and southern Europe and forage for ground-dwelling, surface-running (epigaeic) arthropods [1,10–12], which they glean from open, accessible ground [12–15]. As the echoes of an arthropod sitting on a textured substrate are masked by echoes from substrate, mouse-eared bats do not use echolocation to find prey, but rely on listening for rustling noises produced by

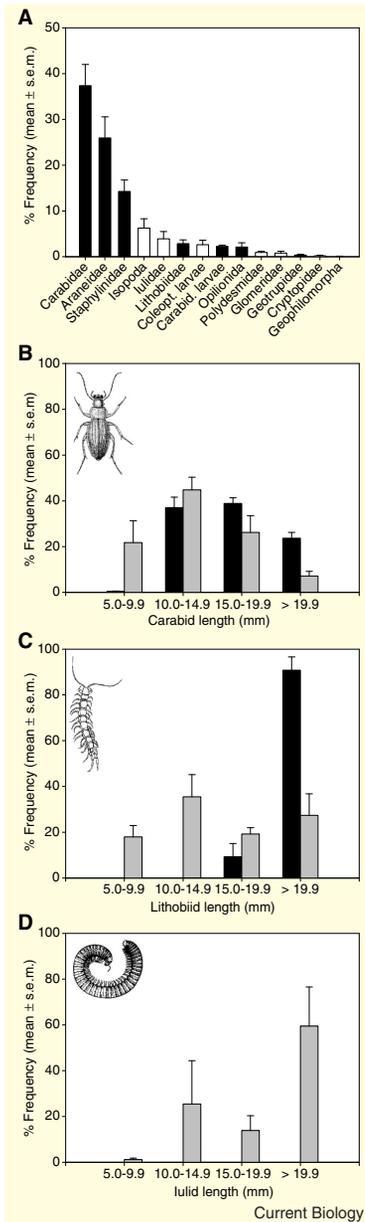


Figure 1. Abundance of epigaeic arthropods and prey use by mouse-eared bats.

(A) Relative abundance of different arthropod taxa in mouse-eared bat foraging habitats (16151 arthropods from eight field sites). Black bars indicate taxa present in the bats' diet, white bars indicate taxa not eaten by the bats (740 faecal pellets from three years). Panels (B) carabid beetles, (C) lithobiids and (D) iulids contrast relative frequencies of four arthropod size classes in the bats' diet (black bars) and in their foraging habitats (gray bars); only sites were included that yielded >1% of the total number collected for the respective taxon. Bars indicate means and standard error of the mean (s.e.m.) averaged for all years (diet) or sites (field data); for statistics see text.

arthropods when moving or walking [16,17].

We used pitfall traps to sample the abundance of epigaeic arthropods in the foraging habitats of mouse-eared bats in Switzerland [15] and faecal analysis to determine their incidence in the bats' diet. In accordance with other studies [1,10–12,18], we found that carabid beetles (Carabidae, Coleoptera) are a very important component of the bats' diet (77% of 740 faecal pellets analyzed contained carabid remains). The bats showed an apparent taxon selectivity; i.e., they did not take arthropod taxa in proportions of their abundance (Figure 1A; Pearson Chi Square test, $X^2 = 968.44$, $df = 3$, $P < 0.0001$). Within the arthropod taxa taken, there was an obvious overrepresentation of large individuals or species in the diet (Figure 1B,C; carabids: Mann-Whitney U test: $U = 576427$, $P < 0.0001$, diet: $n = 543$ individuals, body length 17.2 ± 4.3 mm mean \pm sd, field: $n = 4904$, 12.8 ± 5.1 mm; lithobiids: $U = 2007$, $P < 0.0001$; diet: $n = 27$, 20.6 ± 2.3 mm, field: $n = 416$, 14.7 ± 4.9 mm). Some taxa, especially iulid millipedes (Iulidae, Myriapoda) and woodlice (Isopoda), were never found in the faeces, although they were relatively commonly caught in the traps (Figure 1A and 1D, iulids: $n = 584$). A feeding experiment showed that remains of iulids, woodlice, and small beetles can be retrieved from bat droppings if they are eaten, so they were not simply missing because they had been completely digested (see Supplemental Data available online).

To assess the conspicuousness of arthropods to the bats, we recorded rustling sounds produced by different taxa and sizes. Generally, the amplitudes of rustling sounds from prey arthropods were higher than those from non-prey (Figure 2A). Within all three taxa that we studied, the amplitude of walking sounds increased with individual size (Figure 2B), but the relationship differed markedly between taxa (Figure 2B; Table S1). While iulid amplitudes were

very low and increased slowly with size, those of lithobiid centipedes (Lithobiidae, Myriapoda), and especially those of carabids, were louder and increased more quickly with size, likely reflecting allometric weight increase. The amplitude corresponding to the smallest carabid ever found in the bats' diet was about the same as of the smallest lithobiid eaten. Carabids, lithobiids and other arthropods above this 'threshold' all belonged to size classes present in the bats' diet at or above their relative abundances (Figures 2B and 1B,C). Size classes or taxa not taken were below it (Figure 2B). There was a clear substrate effect on amplitude, but taxon and size effects were consistent across substrates and for all three acoustic parameters analyzed (Table S1).

Our data show a close match between the acoustic conspicuousness of epigaeic arthropods and the apparent prey selectivity with respect to taxon and size by mouse-eared bats. A simple explanation is that the bats prey opportunistically on every rustling arthropod they are able to detect. Motor constraints associated with subduing and handling prey and prey defensive behavior (conjecturable for large carabids), or distastefulness (possible in iulids, if a bat ever found one) could further affect 'specific prey availability'. From a theoretical perspective, it is evident that sensory limitation is the first step in a prey selection process, while active optimal foraging decisions [19,20], which are well conceivable for mouse-eared bats, can only be the second step (see supplement for further data and discussion). The evolutionary adaptation of sensory systems to a food niche can render species specialists for certain prey from an ecological viewpoint, although the individuals may largely feed opportunistically on every prey item they detect. This view could resolve the apparent paradox of a specialized predator acting as an opportunistic forager.

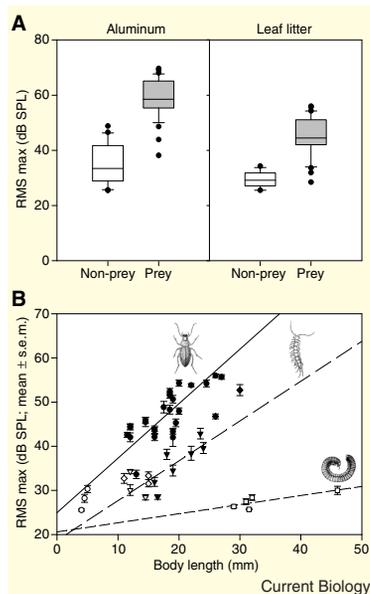


Figure 2. Arthropod acoustic conspicuousness and prey use by mouse-eared bats.

(A) Prey arthropods had higher rustling sound amplitudes, so they were acoustically more conspicuous than non-prey arthropods on the walking substrates aluminum foil (Mann-Whitney U test: $U = 12$, $n(\text{prey}) = 34$, $n(\text{non-prey}) = 22$, $P < 0.0001$; see Supplemental Experimental Procedures for numbers per taxon and for definition of prey versus non-prey; Table S2 gives a list of the specimens) and leaf litter ($U = 11$, $n(\text{prey}) = 33$, $n(\text{non-prey}) = 14$, $P < 0.0001$). The boxes include the 25th to 75th percentile (median indicated by horizontal line), the whiskers give 10th and 90th percentile respectively, and dots depict data points outside these. (B) Rustling sound amplitude on leaf litter increased with arthropod size for carabids (circles), lithobiids (triangles) and iulids (squares). Diamonds depict other prey taxa (two *Ocypus* beetles, Staphylinidae) and non-prey taxa (two woodlice; one glomerid). The lines show linear regressions for the three taxa carabids (solid line, $R^2 = 0.81$, $y = 24.9 + 1.2x$), lithobiids (medium dash, $R^2 = 0.63$, $y = 18.6 + 0.9x$) and iulids (short dash, $R^2 = 0.69$, $y = 20.6 + 0.2x$); increase of amplitude with size differed among taxa (for analysis of covariance see Table S1). Filled symbols indicate prey arthropods and open symbols non-prey, as determined from diet analysis (for details, see Supplemental Data).

Acknowledgments

We thank Holger Görlitz for writing the sound analysis script and discussion, Werner Rose, Thomas Wesener and Marion Schmid for help with determining arthropods and Jörg Kindermann, Steffi Schubert and Gerhard Seifried for technical assistance. Bernhard Nievergelt,

Hans-Ulrich Schnitzler, Christian Dietz, Sue Swift, Holger Görlitz, Ewald Müller, Klemen Koselj, Heinz-Ulrich Reyer and three anonymous referees provided constructive criticism and valuable comments. We acknowledge the German Research Foundation (Deutsche Forschungsgemeinschaft, Si 816/2-1) and the Swiss Federal Office for the Environment, Forests and the Countryside (BUWAL) for research grants to B.M.S. and R.G., respectively.

Supplemental data

Supplemental data, including Tables S1 and S2, Supplemental Experimental Procedures, and Supplemental Discussion are available at <http://www.current-biology.com/cgi/content/full/16/5/R157/DC1/>

References

- Arlettaz, R., and Perrin, N. (1995). The trophic niches of sympatric sibling *M. myotis* and *M. blythii*: do mouse-eared bats select prey? *Symp. Zool. Soc. Lond.* 67, 361–376.
- Whitaker, J.O., Jr. (1994). Food availability and opportunistic versus selective feeding in insectivorous bats. *Bat. Res. News* 35, 75–77.
- Bagchi, S., Goyal, S.P., and Sankar, K. (2003). Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *J. Zool.* 260, 285–290.
- Endler, J.A. (1991). Interactions between predators and prey. In *Behavioural ecology: an evolutionary approach*, Third edition, J.R. Krebs, N.B. Davies, eds. (Oxford: Blackwell Scientific Publications), pp. 169–196.
- Faure, P.A., and Barclay, R.M.R. (1992). The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. *Anim. Behav.* 44, 31–39.
- Siemers, B.M., and Schnitzler, H.-U. (2004). Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* 429, 657–661.
- Houston, R.D., Boonman, A.M., and Jones, G. (2004). Do echolocation signal parameters restrict bats' choice of prey? In *Echolocation in bats and dolphins*, J. Thomas, C.F. Moss, M. Vater, eds., (Chicago: University of Chicago Press), pp. 339–345.
- Siemers, B.M., and Swift, S.M. (2006). Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.* 59, 373–380.
- Getty, T., and Pulliam, H.R. (1993). Search and prey detection by foraging sparrows. *Ecology* 74, 734–742.
- Bauerova, Z. (1978). Contribution to the trophic ecology of *Myotis myotis*. *Folia Zool. (Brno)* 27, 305–316.
- Pereira, M.J.R., Rebelo, H., Rainho, A., and Palmeirim, J.M. (2002). Prey selection by *Myotis myotis*

- (Vespertilionidae) in a Mediterranean region. *Acta Chiropterol.* 4, 183–193.
 - Arlettaz, R. (1996). Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. *Anim. Behav.* 51, 1–11.
 - Arlettaz, R. (1999). Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol.* 68, 460–471.
 - Audet, D. (1990). Foraging behavior and habitat use by a gleaner bat, *Myotis myotis* (Chiroptera: Vespertilionidae). *J. Mamm.* 71, 420–427.
 - Güttinger, R. (1997). Jagdhabitats des Grossen Mausohrs (*Myotis myotis*) in der modernen Kulturlandschaft, (BUWAL-Reihe Umwelt: Bundesamt für Umwelt, Wald und Landschaft).
 - Kolb, A. (1961). Sinnesleistungen einheimischer Fledermäuse bei der Nahrungssuche und Nahrungsauswahl auf dem Boden und in der Luft. *Z. vergl. Physiol.* 44, 550–564.
 - Arlettaz, R., Jones, G., and Racey, P.A. (2001). Effect of acoustic clutter on prey detection by bats. *Nature* 414, 742–745.
 - Güttinger, R., Zahn, A., Krapp, F., and Schober, W. (2001). *Myotis myotis* (Borkhausen, 1797) - Großes Mausohr, Großmausohr. In *Handbuch der Säugetiere Europas*, J. Niethammer, F. Krapp, eds. (Wiebelsheim: Aula), pp. 123–207.
 - Stephens, D.W., and Krebs, J.R. (1986). *Foraging theory*. (Princeton, New Jersey: Princeton University Press).
 - Jones, G. (1990). Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *J. Anim. Ecol.* 59, 587–602.
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