Bats Limit Arthropods and Herbivory in a Tropical Forest

Margareta B. Kalka,[1]* Adam R. Smith,[1] Elisabeth K. V. Kalko[1,2]

Bats are diverse and abundant insectivores that consume many herbivorous insects (*1*, *2*). Insect herbivory, in turn, constrains plant reproduction and influences plant diversity and distribution (*3*). However, the impact of bat insectivory on plants has never been studied. Previous studies measuring top-down reduction of insect herbivory focused on birds (*4*–*6*) but actually measured the combined impact of birds and bats because predator exclosures were left in place day and night. Partitioning the effects of each predator group is essential for both basic ecological questions, such as the top-down maintenance of tropical diversity (*3*), and applied studies, such as the biological control of agricultural pests (*2*, *6*). We experimentally separated the ecological effects of insectivorous birds from those of insectivorous bats in a tropical lowland forest in Panama.

We covered plants with mesh exclosures that permitted access to arthropods but prevented birds or bats from gleaning them off of the plants. However, we left our exclosures in place only during the day or night, allowing us to compare arthropod abundance and herbivory on plants inaccessible to bats (nocturnal exclosures, $N = 42$), plants inaccessible to birds (diurnal exclosures, $N = 35$), and uncovered controls ($N = 43$) in a randomized block design using five common understory plant species. We visually censused arthropods throughout the 10-week study to test the direct effect of treatment (i.e., absence of bats or birds) on insect and other arthropod abundance and measured leaf damage incurred during the study to test the indirect effect of treatment on herbivory (*7*).

Nocturnal (bat) and diurnal (bird) exclosures each directly increased arthropod abundance on plants, and nocturnal exclosures had a significantly stronger effect than diurnal exclosures (table S1 and Fig. 1A) [repeated measures generalized linear model (GLM) treatment $F_{2,75} = 17.11$, $P < 0.001$; all Tukey's honestly significantly different (HSD) posthoc pairwise comparisons between treatments, $P < 0.05$]. Control plants averaged 4.9 ± 0.7 (SEM) arthropods per m^2 of leaf area per census; bird-exclosed plants, 8.1 ± 1.0; and bat-exclosed plants, 12.4 ± 1.6. Nocturnal and diurnal exclosures also each indirectly increased herbivory, and nocturnal exclosures again had a significantly stronger effect than diurnal exclosures (Fig. 1B; univariate GLM treatment $F_{2,75} = 41.89$, $P < 0.001$, all Tukey's HSD posthoc pairwise comparisons between treatments $P < 0.005$). Control plants averaged 4.3 ± 0.8% leaf area lost to herbivory; bird-exclosed plants; 7.2 ± 1.6%; and bat-exclosed plants, 13.3 ± 2.1% (*7*).

Treatment effects on both arthropod abundance and herbivory were consistent across plant species, and potential confounding variables such as light intensity, number of new leaves emerged during the study, and total leaf area neither differed between treatments nor interacted with treatment in either GLM (*7*).

Our data suggest that bat predation both directly reduces arthropod abundance on plants and indirectly reduces herbivory. We also show that the ecological effects of insectivorous gleaning bats can be considerably stronger than those of birds. Our estimates of the direct and indirect impacts of both groups are likely conservative because (i) predation away from exclosures also reduces herbivory (*2*), (ii) very large arthropods may have been excluded along with bats and birds, (iii) predatory arthropods in the exclosures may have mitigated the effect of bird or bat exclusion (table S1), and (iv) top-down reduction of herbivory may be greater in the more-productive forest canopy (*5*). Gleaning insectivorous bats are common in tropical and temperate lowland forests; thus, it is likely that bat predation of herbivorous insects reduces herbivory in the temperate zone as well (*7*). Given their ecological importance, bats should be included in future conservation plans aimed at preserving the integrity of tropical forests and also considered in agricultural management strategies based on natural pest control (*2*, *6*).

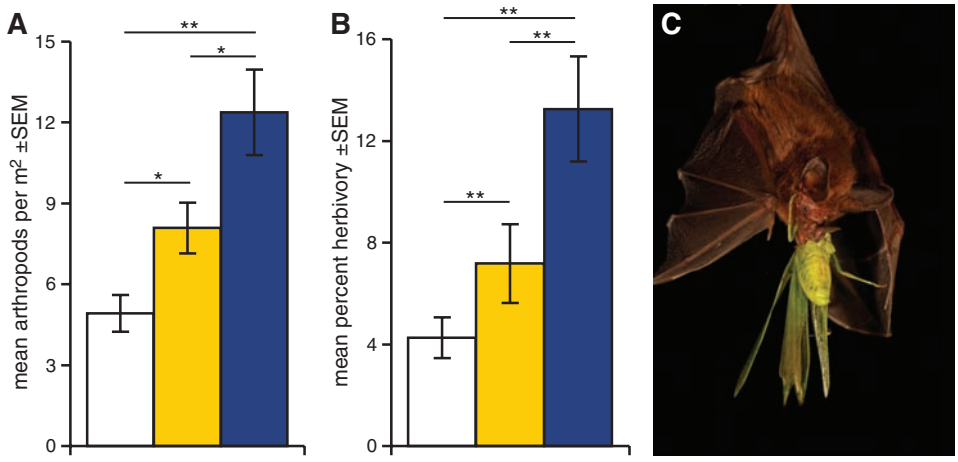

Fig. 1. (**A**) Mean number of arthropods per m^2 per census. (**B**) Mean herbivory as percent of total leaf area. White bars represent controls (birds and bats present); yellow bars, diurnal exclosures (birds absent and bats present); and blue bars, nocturnal exclosures (bats absent and birds present); $*P < 0.05$ and $**P < 0.005$ according to Tukey's HSD. (**C**) A bat (*Micronycteris microtis*) consuming a katydid, Barro Colorado Island, Panama. [Photo: C. Ziegler]

References and Notes

1. M. Kalka, E. K. V. Kalko, *J. Trop. Ecol.* **22**, 1 (2006).
2. C. J. Cleveland *et al.*, *Front. Ecol. Environ.* **4**, 238 (2006).
3. P. V. A. Fine, I. Mesones, P. D. Coley, *Science* **305**, 663 (2004).
4. R. T. Holmes, J. C. Schultz, P. Nothnagle, *Science* **206**, 462 (1979).
5. S. A. Van Bael, J. D. Brawn, S. K. Robinson, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 8304 (2003).
6. R. Greenberg *et al.*, *Ecology* **81**, 1750 (2000).
7. Materials and methods are available on *Science* Online.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/320/5872/71/DC1
Materials and Methods
Table S1
References

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[1]Smithsonian Tropical Research Institute, Apdo. 0843-03092, Balboa, Ancon, Panama. [2]Institute of Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany.

*To whom correspondence should be addressed. E-mail: mbkalka@gmail.com