# Bats Limit Arthropods and Herbivory in a Tropical Forest

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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*).

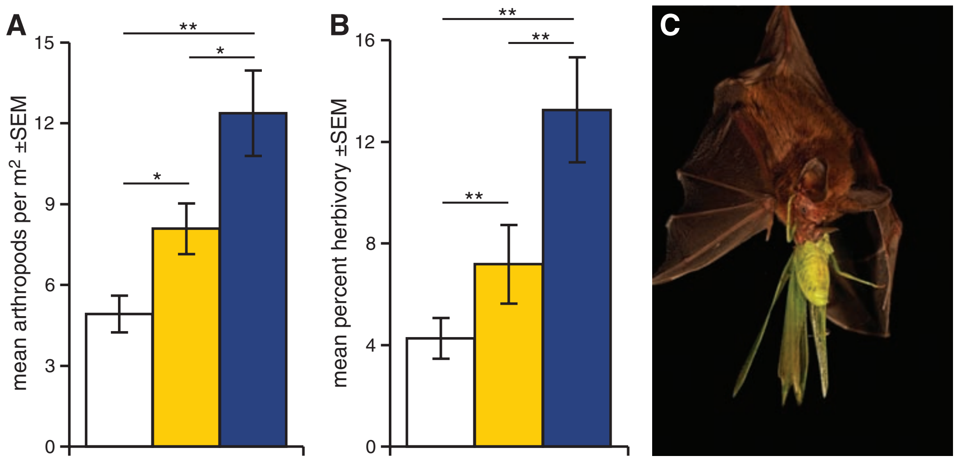


**Fig. 1.** (**A**) Mean number of arthropods per m$^2$ per census. (**B**) Mean herbivory as percent of total leaf area. White bars represent controls (birds and bats present); yellow bars, diurnal exclosures (birds absent and bats present); and blue bars, nocturnal exclosures (bats absent and birds 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]

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*).

**References and Notes**

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7. Materials and methods are available on *Science* Online.
8. M.B.K. was supported by STRI and Bat Conservation International, A.R.S. by SENACYT Panama, and E.K.V.K. by Deutsche Forschungemeinschaft Germany and STRI. S. A. van Bael and S. A. Mangan assisted with experimental design and data analysis, respectively.

**Supporting Online Material**
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Materials and Methods
Table S1
References

26 November 2007; accepted 12 February 2008
10.1126/science.1153352

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www.sciencemag.org/cgi/content/full/320/5872/71/DC1

# Supporting Online Material for

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Published 4 April 2008, *Science* **320**, 71 (2008)
DOI: 10.1126/science.1153352

**This PDF file includes:**

**Supplementary Online Material:**

The study was conducted from April 1 to June 15, 2006, during the onset of the rainy season, on Barro Colorado Island (BCI), Panama (9°09'N, 79°51'W), a moist semi-deciduous tropical lowland forest. The bat and bird faunas of BCI are described in (*S1*, *S2)*. We chose 35 trios and seven additional pairs of conspecific, neighboring plants found along a 4km forested trail loop as our experimental blocks. We used 50-150cm high individuals of five species of common understory plants (*Hybanthus prunifolius* n=52, *Psychotria horizontalis* n=26, *Acalypha diversifolia* n=18, *Croton billbergianus* n=17, *Miconia argentea* n=6) in our experiment. Within each block, we randomly assigned treatment (control, diurnal exclosure, or nocturnal exclosure; the pairs contained only nocturnal exclosures and controls).

Exclosures were made of two circular wire hoops connected by PVC columns covered on all sides except the bottom with agricultural netting (mesh size 2.2 x 2.2 cm). The mesh allowed arthropods and *Anolis* lizards to access the treatment plants, but excluded bats and birds. As owls sometimes glean large insects, our nocturnal exclosures also include the effect of excluding owl predation. We covered bird-exclosed plants from sunrise to sunset, and bat-exclosed plants from sunset to sunrise. Control plants were never covered. We censused arthropods during both the day and night (pooled for analysis) six times throughout the study by visually inspecting each side of each leaf included in the study, except for the final census which was a daytime collection of all study leaves and arthropods present on them. We did not include colonial arthropods, following (*S3*). The arthropods censused (Table S1) were not necessarily the ones responsible for measured herbivory, as most leaf damage did not have an associated arthropod. We collected and photographed all study leaves at the conclusion of the study and calculated leaf damage area from digital photographs. Only herbivory incurred during our study was included in the analysis. We assigned each plant a light level score of high (sunlight most of the day), medium (some direct sunlight), or low (shade all day).

To test the effect of treatment on arthropod density, we used a repeated-measures general linear model (GLM) in SPSS 10.0 with the six census measurements (square-root transformed to correct for positive skew) entered as within-subject factors, and both block and treatment as between-subject factors with the following results: block $F_{41,75}=3.27$, treatment $F_{2,75}=17.11$, census period $F_{5,375}=9.92$; all $P<0.001$ (there was no significant interaction between census period and treatment). To examine the effect of treatment on herbivory, treatment was entered as a fixed effect and block as a random effect in a univariate GLM, and percent leaf damage (log transformed to correct for positive skew) was the dependent variable with the following results: block $F_{42,75}=6.54$, treatment $F_{2,75}=41.89$; both $P<0.001$. In both analyses we found no significant interactions between treatment and plant species, light level, leaf area, or number of new leaves emerged during the study. We thus dropped these terms from the final models.

Gleaning insectivorous bats are common in temperate as well as in tropical lowland forests, thus it is likely that bat predation reduces herbivory in the temperate zone as well. However, whereas lowland tropical gleaners, in the Neotropics from the endemic family *Phyllostomidae*, tend to be gleaning specialists, temperate gleaning insectivorous bats are predominately from the family *Vespertilionidae*, and facultatively switch between gleaning insects from substrate and aerially hunting insects on the wing (*S4*). Because of this behavioral flexibility, as well as the inherent difficulty of estimating bat abundance from capture data (*S1*), it is currently impossible to assess the relative strength of bat and bird predation on herbivory in the temperate zone without future experimental studies that consistently separate between the two groups.

**References:**

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**Table S1.** All arthropods encountered in the censuses, listed by taxonomic identification. Below each exclosure treatment is listed the number (#) of arthropods found for each taxon, and the percent (%) of the total number of arthropods in the treatment group represented by that taxon in parentheses.

| **Arthropod Taxon** | **Control** | | **Diurnal exclosures** | | **Nocturnal exclosures** | | **Total** | |
|---|---|---|---|---|---|---|---|---|
| | **#** | **%** | **#** | **%** | **#** | **%** | **#** | **%** |
| Araneae | 25 | (12.4) | 36 | (16.8) | 46 | (12.6) | **107** | **(13.7)** |
| Isopoda | 0 | (0) | 1 | (0.5) | 0 | (0) | **1** | **(0.1)** |
| Blattaria | 8 | (4) | 8 | (3.7) | 6 | (1.6) | **22** | **(2.8)** |
| Mantodea | 1 | (0.5) | 0 | (0) | 0 | (0) | **1** | **(0.1)** |
| Orthoptera | 10 | (5.0) | 10 | (4.7) | 13 | (3.6) | **33** | **(4.2)** |
| Hemiptera: not Reduviidae | 90 | (44.6) | 80 | (37.4) | 152 | (41.6) | **322** | **(41.2)** |
| Hemiptera: Heteroptera: Reduviidae | 6 | (3) | 9 | (4.2) | 7 | (1.9) | **22** | **(2.8)** |
| Coleoptera: not Staphylinidae | 37 | (18.3) | 38 | (17.8) | 45 | (12.3) | **120** | **(15.4)** |
| Coleoptera: Staphylinidae | 3 | (1.5) | 7 | (3.3) | 11 | (3) | **21** | **(2.7)** |
| Diptera | 6 | (3) | 4 | (1.9) | 6 | (1.6) | **16** | **(2)** |
| Adult Lepidoptera | 8 | (4) | 9 | (4.2) | 15 | (4.1) | **32** | **(4.1)** |
| Juvenile Lepidoptera | 8 | (4) | 8 | (3.7) | 48 | (13.2) | **64** | **(8.2)** |
| Hymenoptera | 0 | (0) | 2 | (0.9) | 11 | (3) | **13** | **(1.7)** |
| Unidentified | 0 | (0) | 2 | (0.9) | 5 | (1.4) | **7** | **(0.9)** |
| **Total** | **202** | | **214** | | **365** | | **781** | |