THE EFFECT OF A SINGLE SPECIES OF AVIAN PREDATOR ON THE ARTHROPODS OF AERIAL LEAF LITTER[1]

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Recent studies have shown that insectivorous birds can have an effect on their arthropod prey populations. Holmes et al. (1979) found that exclosures in the understory of a temperate deciduous forest had a pronounced effect on Lepidoptera larvae. Solomon et al. (1976) showed that codling moth larvae had higher survivorship inside cages in an apple orchard in England. Dahlston and Copper (1979) found that birds reduced the population of overwintering tussock moth pupal egg masses, and Askenmo et al. (1977) reported the impact of birds on spider populations in a spruce forest. In all of these studies, many sympatric bird species may have been responsible for the observed increased mortality of arthropods.

Here we report on an exclosure experiment conducted in moist tropical forest understory in Panama. The results indicate that predation by one species of insectivorous bird, *Myrmotherula fulviventris* (Checker-throated Antwren, Formicariidae), had a pronounced effect upon the arthropod prey populations in a single, easily sampled microhabitat.

On our study area *Myrmotherula fulviventris* spends 98% of its foraging time searching aerial leaf litter for arthropods. Aerial leaf litter consists of dead leaves that fall from canopy trees and get caught in vegetation and vine tangles. As the leaves dry and curl they are colonized by many types of arthropods. These arthropods are abundant and many species appear to be unique to aerial leaf litter (J. A. Gradwohl, *personal observation*).

While two or more species of aerial leaf litter foragers often occur in lowland Neotropical forests (Ridgely 1976, Munn and Terborgh 1979, Wiley 1980), on our study site there is only one, *M. fulviventris*. We have observed two species of antbird that usually forage by gleaning live foliage, checking dead leaves on our study site (*Myrmotherula axillaris* and *Thamnophilus punctatus*, Greenberg and Gradwohl 1980), but this behavior is very rare (<5% of total foraging repertoire).

Myrmotherula fulviventris lives in pairs or small family groups on small (≈1.5–3 ha) territories which are co-defended with *Microrhopias quixensis* (Formicariidae). These areas are traversed several times daily, and areas of high use correspond with the presence of dense vine tangles (Gradwohl and Greenberg 1980). The density of aerial leaf litter is greater in vine tangles because tangles catch more falling leaves than vegetation in the open understory. In this study we exclosed vine tangles for 6 wk and found that aerial leaf litter arthropods were nearly twice as common inside the exclosures as outside. Because they experience heavy use by antwrens and contain high densities of dead leaves, we made vine tangles the focus of our exclosure experiment.

Methods

We worked on Orchid Island, a 16-ha island located 150 m north of Barro Colorado Island in Lake Gatun, Panama. We chose to work on Orchid Island because it is not a strict reserve like Barro Colorado Island, so that we could cut the vegetation to set up the exclosures. Further, Orchid Island is a windblown ridge which has many vine tangles, prime *M. fulviventris* habitat.

We chose vine tangles and dense vegetation that were low to the ground and large enough to hold abutting $1.8 \times 1.8 \times 1.8$ m exclosures and control areas. We divided each of five sites in half and covered half with plastic Gro-netting (Ross Daniels, Incorporated, 4×3 cm mesh) covering the top and suspended on string around the vegetation. In two sites it was necessary to cut the tops of some small palms in the exclosures and we made corresponding cuts in the control areas. The mesh size allowed easy passage of even the largest arthropods but was too small for the antwrens to pass through. The strands of the plastic netting were 1 mm thick and unlikely to have changed the microclimate inside the exclosure.

We sampled both exclosures and control areas before the experiment started and found no difference between them in numbers of arthropods (t test, multiple-paired comparisons, $t = 1.4$, df = 3, NS). In order to minimize disturbance, these samples were made by peering into 50 randomly chosen leaves. The exclosures were left in place for 6 wk, from 1 August to 11 September 1980, a period of high but stable abundance of dead-leaf arthropods (Gradwohl and Greenberg, *in press*). At the end of the experiment we opened the exclosures and carefully collected as many dead leaves as possible into large plastic bags. The dead leaf arthropods do not flush readily and this is the most accurate way to sample aerial leaf litter. Samples consisting of an equal number of leaves from each exclosure and control were frozen and each leaf was individually checked for arthropods (Table 1). Unless otherwise stated, all tests are one-tailed and significant at $P < .05$.
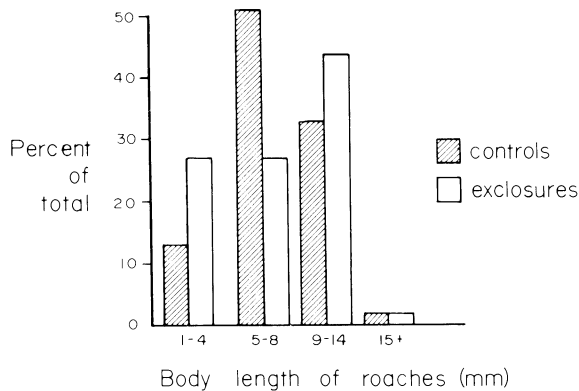
FIG. 1. Percentage of roaches (Blattidae) in four size classes in controls and exclosures ($n = 131$).

Results

We found 187 arthropods in the control areas and 293 (61% of the total) in the exclosures. Only a portion of these were potential prey items. We consider potential prey items to be any soft-bodied arthropod 4 mm or more in body length, a value based upon both field observation and preference experiments with caged birds (J. A. Gradwohl, *personal observation*). Almost all (93%) of the potential prey items in both controls and exclosures were roaches (Blattidae) (110, 44%), spiders (Arachnida) (75, 30%), or crickets (Gryllidae) and katydids (Tettigoniidae) (49, 19%). Of the potential prey items, 85 were in controls and 152 were in exclosures. This difference is highly significant (t test multiple paired comparisons, $t = 4.25$, df $= 3$, $P < .0025$; Snedecor and Cochran 1967:91). There was no significant difference between hard-bodied, non-prey arthropods within or outside exclosures (63 total in controls, 71 in exclosures, $t = 0.54$, df $= 3$, NS).

Of the three major groups of prey arthropods, only

roaches showed a nearly significant difference between exclosures and controls ($t = 1.88$, df $= 3$, $P < .10$). Crickets and katydids (67% in exclosures, total $= 49$) and spiders (53%, $n = 75$) also had more individuals in exclosures but the sample sizes were considerably smaller.

Roaches experienced differential mortality of size classes in the control areas (Fig. 1). There was a significant difference in the size classes with medium-sized roaches (body length 5–8 mm) most common in controls and large and small roaches more common in the exclosures (Kolmogorov-Smirnov test, maximum difference $= 0.15$, df $= 2$, $P < .01$). The largest roaches (≥ 10 mm) are potentially reproductive and some of the smallest roaches (1–2 mm) may be their progeny produced during the experiment. None of the other groups of arthropods showed similar trends in the distribution of size classes.

Discussion

Many studies of avian communities have concentrated on partitioning of the foraging microhabitat (Mac Arthur 1958, Root 1967). It is generally assumed that different microhabitats support different populations of prey arthropods, and that each species of bird is capable of depleting the prey population found in a particular microhabitat. It is very difficult to test these assumptions, and it is particularly so for foliage-gleaning birds. Many bird species may forage in more than one microhabitat, and it is difficult to isolate given microhabitats sufficiently for the effect of predators on prey populations to be studied. This is most effectively done with exclosures; however, exclosures usually do not allow fine-tuned study of single microhabitats and single bird species.

Aerial leaf litter is not only a discrete microhabitat which can be exclosed, but as far as we have observed there is little or no mixing with arthropod species in any other microhabitat in the forest during the day.

TABLE 1. Results at end of exclosure experiment.

Site	Number of leaves sampled	Total items	Total soft bodied	Total crickets, spiders, katydids, roaches	Total crickets, katydids, spiders, roaches ≥ 4 mm
Control 1	40	16	9	7	5
Exclosure 1	40	33	30	29	22
Control 2	90	41	23	22	12
Exclosure 2	90	55	43	39	28
Control 3	150	55	37	36	29
Exclosure 3	150	70	51	49	30
Control 4	100	44	33	33	25
Exclosure 4	100	92	64	62	50
Control 5	100	31	20	18	14
Exclosure 5	100	43	34	32	22

Furthermore, the two major predators on arthropods in aerial leaf litter on Orchid Island are *Myrmotherula fulviventris* and spiders that live in the leaves. Because the spiders were not excluded from the exclosures, any differential mortality between exclosures and controls is most readily attributed to the birds; the presence of spiders may have confounded the effect of bird predation because spider mortality was probably lower in the leaves inside exclosures. Increased spider predation in the exclosure would counteract the effects of antwren predation outside the exclosures. The effect of *M. fulviventris* on the arthropods was marked despite this confounding factor.

In 6 wk a single bird species reduced its preferred prey items by almost 50%. In addition, the largest adult roaches and smallest nymph size classes were particularly underrepresented outside the exclosures, suggesting that the antwrens drastically reduced prey productivity as well as standing crop. Antwrens are clearly capable of causing marked deterioration in the quality of the dead leaf foraging site which could discourage its use by less specialized birds.

Literature Cited

Askenmo, C., A. von Bromssen, J. Ekman, and C. Jansson. 1977. Impact of some wintering birds on spider abundance in spruce. Oikos **28**:90–94.

Dahlsten, D. L., and W. A. Copper. 1979. The use of nesting boxes to study the biology of the Mountain Chickadee (*Parus gambeli*) and its impact on selected forest insects. Pages 217–260 *in* J. G. Dickson, R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, New York, New York, USA.

Gradwohl, J. A., and R. S. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. Auk **97**:385–395.

Gradwohl, J. A., and R. S. Greenberg. *In press.* The breeding season of antwrens on Barro Colorado Island. *In* E. G. Leigh, editor. Seasonal rhythms in a tropical forest. Smithsonian Institution Press, Washington, D.C., USA.

Greenberg, R. S., and J. A. Gradwohl. 1980. Leaf surface specializations of birds and arthropods in a Panamanian forest. Oecologia **46**:115–124.

Holmes, R. T., J. C. Shultz, and P. Nothnagle. 1979. Bird predation on forest insects: an exclosure experiment. Science **206**:462–463.

Mac Arthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology **39**:599–619.

Munn, C. A., and J. W. Terborgh. 1979. Multispecies territoriality in neotropical foraging flocks. Condor **81**:338–347.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton University Press, Princeton, New Jersey, USA.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecological Monographs **37**:317–350.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Sixth edition. Iowa State University Press, Ames, Iowa, USA.

Solomon, M. E., D. M. Glen, D. A. Kendall, and N. F. Milsom. 1976. Predation of overwintering larvae of Codling Moth (*Cydia pomonella* (L.)) by birds. Journal of Applied Ecology **13**:341–352.

Wiley, R. H. 1980. Multispecies antbird societies in lowland forests of Surinam and Ecuador: stable membership and foraging differences. Journal of Zoology (London) **191**:127–145.

MALE PERSISTENCE AND MATING SUCCESS IN WOODHOUSE'S TOAD (BUFO WOODHOUSEI)[1]

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The operational sex ratio is commonly biased towards males in anurans and a small subset of the males successfully mate. Numerous investigations have established that mating is nonrandom, typically biased towards large males (Whitney and Krebs 1975, Licht 1976, Davies and Halliday 1977, 1979, Wells 1977a, b, 1979, Howard 1978a, b, 1980, Wilbur et al. 1978, Fellers 1979, Ryan 1980, Fairchild 1981). Several mechanisms have been proposed to cause this pattern. Here I report an additional simple mechanism which affects male mating success in *Bufo woodhousei*.

In 1978 a *B. woodhousei* breeding aggregation was monitored on 41 of 49 nights from 31 March until 19 May in Albuquerque, Bernalillo County, New Mexico,