Bait Use in Tropical Litter and Canopy Ants—Evidence of Differences in Nutrient Limitation[1]

INCREASINGLY, RESOURCE (OR "BOTTOM-UP") LIMITATION is seen as key to understanding gradients of diversity, trophic structure, and population regulation (Oksanen *et al.* 1981, Powers 1992, Rosenzweig & Abramsky 1993). The essence of bottom-up control is that a taxon's density and diversity are tied to its ability to build and fuel tissue. Roughly, this corresponds to the taxon's ability to harvest both protein and carbohydrates (CHOs) from its environment. The quality of a food resource is thus linked to its carbon:nitrogen (C:N) ratio.

Plants yield C:N ratios of 40:1 or more while heterotroph organisms yield C:N ratios of *ca* 10:1 (Swift *et al.* 1979, Begon *et al.* 1996). A common assumption is that most terrestrial organisms are limited by the availability of N (White 1978). But the contribution of plants to the resource base of a food web varies widely among habitats (Polis *et al.* 1997). In mature tropical rain forests, the canopy harbors most of the forest's photosynthesizing tissue, whereas the understory contributes only a tiny fraction of the total photosynthate (S. Mulkey, pers. comm.). If true, consumers from the canopy would be more likely to be N-limited than consumers from the litter 20 m below.

Ants are diverse and conspicuous in the tropical canopy and litter (Stork & Blackburn 1993, Tobin 1994, Kaspari 1996, Davidson 1997, Yanoviak & Kaspari in press). While an ant assemblage may include many trophic specialists, most ant species are omnivores, harvesting exudates, scavenging insects, and capturing live prey as encountered. (Hölldobler & Wilson 1990, Tobin 1994). Tobin (1994) was the first to hypothesize that the CHO-rich and N-poor plant exudates sustain high ant biomass in the tropical forest canopy. Davidson (1997) and Patrell-Kim (1996) developed these ideas further, showing that canopy ants tend to have (1) less N in their exoskeletons and (2) modified proventriculi—both possible adaptations to N-poor environments.

We know of no direct measures of protein and CHO preferences in the tropical forest canopy and litter. Toward this goal, we ran bait choice trials (*i.e.,* "cafeteria experiments") in the crowns and litter of four common tree species in a Panamanian rain forest. We presented three baits to ants: disks of baked turkey, cotton balls soaked in a saturated solution of sucrose in distilled water, and, as a control for ant activity, cotton balls soaked in distilled water alone (hereafter, "meat baits," "sugar baits," and "water baits"). We used turkey for meat baits because it was readily available in bulk, could be standardized across all experiments, and presented N in biologically realistic matrix. We assumed: (1) protein and CHOs are non-substitutable resources (*sensu* Tilman 1982), and (2) workers from a colony will prefer resources that are in shortest supply (*i.e.,* most limiting to colony growth and reproduction). We predicted that canopy ant assemblages, with more access to CHOs, would spend more time recruiting to and harvesting meat baits compared to litter ant assemblages.

Studies were conducted from November to December 1997 in the forest canopy and understory litter on Barro Colorado Island, Panama (BCI)—a lowland, seasonal moist forest (Leigh *et al.* 1996). Trees differ greatly in chemistry (Coley & Barone 1996), phenology (Croat 1978), bark type (Whitmore 1962), and litter palatability (Dudgeon *et al.* 1990). We thus placed baits in the crown and litter of four common tree species (five individuals each): *Pseudobombax septenatum, Ceiba pentandra* (Bombacaceae), *Dipteryx panamensis* (Fabaceae), and *Anacardium excelsum* (Anacardiaceae). Tree crowns were accessed using the single-rope climbing technique (Perry 1978). Litter trials followed canopy trials, with baits placed on intact leaves beneath each tree.

All baits in a given trial were carefully size-matched to present the same volume (4 ml) and circumference (7–10 cm). Baits were placed 0.2–1.0 m apart on branches near the main fork of each tree crown, 17–35 m above the ground. The number of individuals of each ant species at a bait was recorded at 1, 2, 4, 8, 16, and 32 min. Trials were stopped at 32 min because: (1) 30 min is a common standard in an active ant community (Andersen 1992), and (2) pilot runs in July yielded no measurable changes in ant numbers or species composition between 30 and 60 min (SY, pers. obs). Ants were assigned to morphospecies in the field and representatives were collected for species determinations. Vouchers were deposited at the University of Oklahoma and the Museum of Comparative Zoology, Harvard University. A species list from this study is found in Yanoviak and Kaspari (in press).

Three times more ants visited baits in the canopy than in the litter (4621 vs. 1287) over the 32-min trials. Thirty two species (13 genera) used the 40 baits in the canopy, while 16 species (8 genera) used the 40 baits in the litter. *Azteca, Crematogaster,* and *Solenopsis* were the most common ants at baits in the canopy; *Ectatomma, Pheidole,* and *Wasmannia* were most common in the litter (Yanoviak & Kaspari in press). No species were found in both the canopy and the litter. In both habitats, and recruitment to sugar and meat baits was a positive decelerating function of time (Fig. 1).

We analyzed the effects of tree species and habitat (canopy or litter) on ant abundance ($\log_{10}$ transformed) at each bait type using two-way ANOVAs (Bonferroni adjusted $\alpha = 0.017$). The canopy and litter assemblages differed in their use of bait types. At 32 min, nine times as many ants used meat baits in the canopy as in the litter (Fig. 2; $F_{1,32} = 30.8$, $P = 0.0001$). In contrast, sugar baits attracted the same number of ants in the canopy and the litter (Fig. 2; $F_{1,32} = 1.47$, $P = 0.23$). The mean (± 1 SD) number of ants using water baits was negligible and did not differ between habitats (canopy = 0.6 $\pm$ 1.0, litter = 0.75 $\pm$ 1.5; $F_{1,32} = 0.07$, $P = 0.79$). For all bait types, tree effects and tree*habitat interactions were not significant ($F_{3,32} < 2.4$, $P > 0.09$ in all tests). In sum, the patterns of (1) higher recruitment to meat baits in the canopy and (2) no difference in recruitment to sugar baits between canopy and litter were consistent across tree species.

In the canopy, there was an average surplus [(ant abundance at sugar baits) − (ant abundance at meat baits)] of 78.2 (SD = 60.4) ants at meat baits. This yielded a ratio of 5.7 ants at meat for every
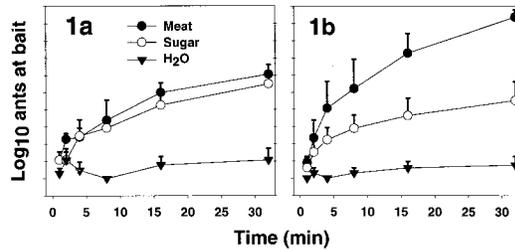
FIGURE 1.   Results of choice experiments in the canopy and litter of the tropical tree *Anacardium excelsum.* Ant workers in the litter (**1a**) and canopy (**1b**) accumulated at different rates on three bait types. Roughly equal numbers of workers used sugar and meat baits in the litter; more workers used meat baits in the canopy. Vertical bars = 1 SE, $N = 5$ for each mean.

1 at sugar baits in the canopy, a significant deviation from the null hypothesis of no preference ($t = 5.8$, $P < 0.0001$). In contrast, there was an average surplus of 4.55 (SD = 15.3) ants at sugar baits. This surplus did not differ significantly from the 1:1 ratio of no preference ($t = 1.33$, $P > 0.19$). Mean relative bait use differed between canopy and litter ($F_{1,32} = 36.6$, $P = 0.0001$) but tree species effects and tree*habitat interactions were not significant ($F_{3,32} < 1.35$, $P > 0.27$ in both cases). The ant assemblage showed preferences for meat in the canopy and no preference among sugar and meat in the litter; these results were consistent across tree species.

Could the increased use of meat baits in the canopy arise from a subset of canopy species monopolizing sugar baits (Pimm *et al.* 1985, Savolainen & Vepsäläinen 1988)? Our observations suggested that aggression, when it occurred, was not bait-specific; however, we quantitatively addressed this possibility by dividing observations into two intervals: (1, 2, and 4 min) and (8, 16, and 32 min). Three of 6 species (50%) in the litter and 8 of 13 (62%) species in the canopy showed trends of increased sugar bait use from the early to late interval, none significantly (Kruskal-Wallis test). This suggests that the accrual of a subset of behaviorally dominant species on sugar or meat baits was not skewing our measures of bait choice.

To further evaluate the generality of preferences for meat baits in the canopy, we studied trends (1) among genera and (2) within one genus found in both canopy and litter. In both cases, we gauged the preference of a species for a bait type by the mean fraction of its workers using the bait (*i.e.,* meat preference·ranged from 0.0 to 1.0). Five of 13 canopy genera showed stronger preferences for meat baits
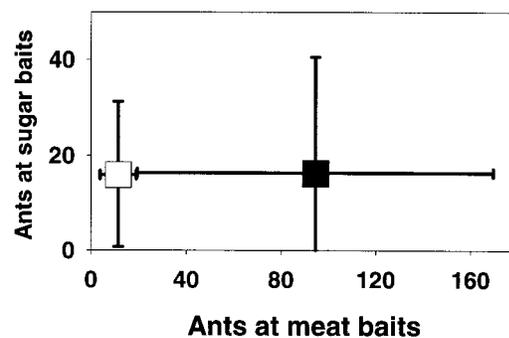
FIGURE 2.   Average number of workers (SD) recruiting to meat and sugar baits in the canopy (dark square) and the litter (light square) after 32 min. Sugar baits attracted the same average number of ants in each habitat, while meat baits attracted more ants in the canopy.

than any litter genus. In total, the 13 canopy ant genera were more likely to show a stronger preference for meat ($\bar{x} = 0.66$, SD = 0.30) than the 8 litter genera ($\bar{x} = 0.42$, SD = 0.32, $F_{1,20} = 3.69$, $P < 0.0398$).

Pheidole was the only genus that offered multiple species in both the canopy and the litter. *Pheidole* species in the canopy recruited 60 percent (SD = 14) of workers to meat baits. *Pheidole* species in the litter recruited an average of 18 percent of workers to meat baits (SD = 24). Canopy species showed stronger preferences for meat than litter species (Kruskal-Wallis $\chi^2_{2,5} = 3.15$, $P < 0.0380$).

Two caveats need to be addressed. First, we inferred protein versus CHO preferences from the balance of turkey and sugar water baits used. Turkey baits, however, contained protein, fats, and salts not found in the sugar baits. Thus we cannot rule out that ants showed similar preferences for protein in both habitats but much stronger preference for fat and/or salts in the canopy. One solution, subdividing baits into their constituent parts (*e.g.,* salt solution vs. protein powder), may gain precision at the cost of realism, because animal matter, alive or dead, is presented in complex packages.

A second caveat addresses turnover at baits. If ants are more adept at harvesting sugar than meat, the turnover at sugar baits would be higher and measured preference thus would be lower. This could be an important bias if taxa in the canopy (*e.g.,* Formicines and Dolichoderines) are able to load up on sugar water faster (*e.g.,* through modified proventriculi; Davidson 1997) than they can cut a strip of meat. To eliminate our result, however, canopy ants (but not the litter ants) would have had to harvest over five loads of sugar in the time it took to harvest one load of meat. While this hypothesis deserves further attention, two lines of evidence suggest that turnover differences did not confound our results. First, common canopy ants (*e.g.* the megacephalic *Azteca*) were adept at shredding a turkey bait. Second, *Pheidole,* a genus without obvious adaptations for liquid harvest and storage, mirrored the community pattern.

In conclusion, we showed that tropical canopy ant assemblages had a greater preference for meat than those in the litter. This shift was consistent across four tree species and existed at three levels of organization: all ants pooled, among genera, and among species in the genus *Pheidole.* If colonies send more ants to the resources that limit colony growth, then our results support the hypothesis that a surplus of CHOs in the canopy release canopy ants from CHO-limitation relative to the litter ant assemblage below. Increased protein limitation is tentatively added to the growing list of features associated with canopy life (Davidson 1997).

ANDERSEN, A. 1992. Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. Am. Nat. 140: 401–420.

BEGON, M., J. HARPER, AND C. TOWNSEND. 1996. Ecology: individuals, populations, and communities. Blackwell Scientific, Oxford, England.

COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. Annu. Rev. Ecol. Syst. 27: 305–335.

CROAT, T. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California.

DAVIDSON, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biol. J. Linn. Soc. 61: 153–181.

———, AND L. PATRELL-KIM. 1996. Tropical arboreal ants: why so abundant? In A. C. Gibson, (Ed.) Neotropical biodiversity and conservation. UCLA Botanical Garden No. 1, Los Angeles CA, USA.

DUDGEON, D., H. MA, AND P. LAM. 1990. Differential palatability of leaf litter to four sympatric isopods in a Hong Kong forest. Oecologia 84: 398–403.

HÖLLDOBLER, B., AND E. O. WILSON. 1990. The ants. Belknap Press, Cambridge, Massachusetts.

KASPARI, M. 1996. Litter ant patchiness at the m^2 scale: disturbance dynamics in three Neotropical forests. Oecologia 107: 265–273.

LEIGH, E. G., JR., A. S. RAND, AND D. W. WINDSOR. 1996. The ecology of a tropical forest. Smithsonian Institution Press, Washington, DC.

OKSANEN, L., S. FRETWELL, J. ARRUDA, AND P. NIEMELA. 1981. Exploitation ecosystems in gradients of primary productivity. Am. Nat. 118: 240–262.

PERRY, D. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155–157.

PIMM, S. L., M. L. ROSENZWEIG, AND W. MITCHELL. 1985. Competition and food selection: field tests of a theory. Ecology 66: 798–807.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. 28: 289–316.

Powers, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73: 733–746.

Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? In R. E. Ricklefs and D. Schluter (Eds.). Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois.

Savolainen, R., and K. Vepsäläinen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51: 135–155.

Stork, N. E., and T. M. Blackburn. 1993. Abundance, body size, and biomass of arthropods in tropical forest. Oikos 67: 483–489.

Swift, M., O. Heal, and J. Andersen. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, California.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.

Tobin, J. E. 1994. Ants as primary consumers: diet and abundance in the Formicidae. In J. H. Hunt and C. Napela (Eds.). Nourishment and evolution in insect societies. Westview Press, Boulder, Colorado.

White, T. 1978. The importance of a relative shortage of food in animal ecology. Oecologia 33: 71–86.

Whitmore, T. C. 1962. Studies in systematic bark morphology. I. Bark morphology in Dipterocarpaceae. New Phytol. 61: 191–207.

Yanoviak, S. P., and M. Kaspari. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos. In press.

Michael Kaspari[2] and **Stephen P. Yanoviak**

Department of Zoology
University of Oklahoma
Norman Oklahoma 73019-0235, U.S.A.

[2] Corresponding author: E-mail: mkaspari@ou.edu