

Chapter 7

Tropical Arboreal Ants: Why So Abundant?

Diane W. Davidson and Linda Patrell-Kim

ANTS ARE AMONG the most numerous and readily observed arthropods of tropical forests. Indeed, based on their standing biomass and many effects on other species, ants (Formicidae) are arguably the dominant arthropod family in the canopies of lowland rain forest trees (Tobin 1995).

Others have tried to account for the remarkable abundances of arboreal ants in canopy arthropod samples (see especially the works of Majer 1990 and Tobin 1991, 1994), and we attempt to extend these explanations here using stable isotopes to diagnose the trophic specializations of the most abundant ant taxa. We begin with a review of ant diversity and abundance in the tropical arboreal zone.

cidal fogging of forest canopies in lowland tropical rain forests has yielded remarkably high levels of species richness (Table 7.1). Almost a decade ago, Wilson (1987) noted that a single tree in western Amazonia contained generic and species diversity approximately equal to that of the British Isles, and even his records were subsequently eclipsed. Nevertheless, the diversity of tropical arboreal ants is just modest by comparison with that of certain non-social insect taxa, including Coleoptera, Diptera, and parasitic Hymenoptera, especially the Chalcidoidea, in which the ratio of species to individuals is especially high (Erwin 1983; Stork 1988, 1991; Hammond 1990; Askew 1990; Kitching et al. 1993). In retrospect, the relatively low ratio of species to individuals in ants might have been anticipated for these eusocial insects.

Diversity and Abundance of Tropical Arboreal Ants

Diversity

Together with other sampling techniques, insecti-

Tropical arboreal ants show relatively low species turnover across host trees within a site (e.g., Wilson 1987), but high turnover among forests differing in productivity (Erwin 1983; Adis et al. 1984; Wilson 1987). Nevertheless, based on existing studies, ant abundances rank inconsistently across productivity gradients (Erwin 1983 versus Adis et al. 1984), and more sampling will be needed

Table 7.1. Some record high diversities of arboreal ants in lowland tropical rain forests. For a comprehensive summary of published data, see Tobin (1995).

Numbers of ant		Source, location	Reference
Species	Genera		
77	20	One fogged tree, central Amazonia	Harada and Adis (1994; <i>fide</i> Tobin 1994)
43	26	One fogged tree, western Amazonia	Wilson (1987)
44	21	One tree, eclectors, western Amazonia	Verhaagh (1990)
56	49	One tree, first fogging, Borneo	Floren and Linsenmair (1996)

to define the effects of productivity on ant abundance.

Abundance

A number of investigators have noted that tropical arboreal ants of lowland rain forests are more remarkable for their summed abundances in canopy samples than for their overall diversity (e.g., Erwin 1983; Stork 1988, 1991; Stork and Brendell 1990; Tobin 1991, 1994; Floren and Linsenmair 1996; Table 7.2 vs. Table 7.1). The same need not, and probably does not hold for all taxonomic subgroups of the Formicidae. In estimates from various studies throughout the tropics, ants comprised between 9% and 94% of all arthropods sampled by insecticidal fogging (mainly) and other techniques, and approximately 17-50% of arthropod biomass (Table 7.2; Tobin 1995). Ants dominated both the numbers and biomass of arboreal arthropods in all ten samples from three forest types fogged by Erwin (1983) in central Amazonia. They were also numerically dominant in each of 19 first-time fogging samples from individual trees in Borneo, where they contributed an average of 56% of all arthropod individuals in aggregate samples (Floren and Linsenmair 1996).

Table 7.2. Some record high numbers (or biomasses) of arboreal ants, as a percentage of all arthropods sampled. Data are from lowland tropical rain forest. For a comprehensive summary of published data, see Tobin (1995). In studies of Bassett et al. (1992), not used here, ants comprised on average 44% of individuals in canopy samples, but, as the authors admitted, their sampling technique was biased against highly active and volant arthropods.

Number (Biomass)	Forest type, location	Reference
94-42 (?)	Current and older flood-plain, western Australia	Tobin (1995)
? (86)	Mango plantation, western Australia	Majer (1990)
? (72)	Cocoa plantation, Ghana*	Majer (1976b)
69.7 (50)	Older (higher) terraces, western Australia	Tobin (1991)
53.4 (24.6)	Terra firme, central Amazonia	Adis et al. (1984)
52.2 (46.9)	Varzea, central Amazonia	Adis et al. (1984)
46 (?)	Lowland rain forest, central Amazonia	Harada and Adis (1994; <i>fide</i> Tobin 1996)
42.7 (?)	Various lowland forest types, central Amazonia	Erwin (1983)
42.5 (?)	Lowlands, Seram, Indonesia	Stork (1988)
56 (?)	Lowland rain forest, Borneo	Floren and Linsenmair (1996)

* Data for the dominant species only.

Calculations by Stork (1988) offer additional perspective on ant abundance. First, ants made up just a marginally greater fraction of arboreal arthropod diversity in tropical than in temperate samples, but they exhibited much higher proportionate abundance in the former than the latter regions. Second, when arthropods were sampled

from the "five principal biotopes" of lowland rain forest in Seram, Indonesia, ants dominated the faunas to a much greater extent in the canopy than in the other four biotopes (tree trunks, ground vegetation, leaf litter and soil; see also Adis and Schubart 1985). Over all five biotopes, Stork estimated 42.5 million arthropods per hectare. The canopy alone accounted for 12.0 million individuals, about 50% of which were ants.

In summary, tropical ants are more outstanding for their abundance than for their diversity, and their remarkable numbers and biomass are principally a phenomenon of the tropical arboreal zone.

Tobin's "Ant-Biomass Paradox"

The exceptional abundance of ants in tropical forests led Tobin (1991, 1994) to question how ants, which have been presumed to feed mainly as secondary consumers, can possibly be so abundant, often more abundant than their prey. Although inverted trophic pyramids are a frequent occurrence when based on numbers, inverted biomass pyramids are rare and based on special circumstances (e.g., Phillipson 1966). Unfortunately, reports of ant numbers are more common than those of biomass, which bears more directly on Tobin's "ant-biomass paradox" (Tobin 1994), but Adis et al. (1984), Majer (1990), and Tobin (1991) all report samples in which ants comprise 46% or more of the biomass of canopy arthropods. In two canopy studies of plantation crops, single species of numerically dominant ants accounted for 72% and 86%, respectively, of arthropod biomass (Majer 1990).

Of four possible explanations proposed by Tobin (1991) to resolve this paradox, one was methodological: fogging methods may grossly underestimate the biomass of the (often volant) herbivores on which ants feed. However, in some respects, it seems more likely that ants could be undersampled relative to herbivores. Although fogging retrieves many insects in flight and most insects from leaf and branch surfaces, it may miss those, e.g., leaf-rollers, leaf miners, and several

categories of Homoptera, with certain lifestyles or fixed attachments to leaves (Stork 1991). Quite likely, it could also undersample ants, whose brood, sexuals, and young workers are often recessed under bark, inside hollow branches, and in highly modified nest structures where they might either survive the fogging or die *in situ*. Consistent with the possibility of survival is the observation that ants recover from fogging more rapidly than do most other arthropods (Stork 1991). On the whole then, it seems likely that ants are at least as abundant as data in Table 7.2 would suggest, and perhaps even more so.

If we accept the high abundances as real, workers might still be oversampled relative to their ecological roles in the canopy due to an influx of ants from places where they normally feed (Tobin 1991). By this hypothesis, many of the ants could be "tourists" (*sensu* Moran and Southwood 1982), as apparently are various Diptera and Carabidae (Stork 1991). Because most of the ants sampled by fogging are representatives of the worker (foraging) caste, this explanation also seems unlikely.

Two other hypotheses appear more promising. The explanation given most credence by Tobin is that ants feed mainly as herbivores rather than as predators and scavengers. He brings together numerous convincing observations to support the view that workers in particular, as contrasted with brood, feed mainly as primary consumers (see also Holldobler and Wilson 1990), and that herbivory contributes both to large colony sizes and to the general abundance of canopy ants. Finally, and considered only peripherally by Tobin, is the hypothesis that ant biomass could exceed prey biomass if prey populations were very productive but experienced high turnover rates. For example, the explanation commonly given for an excess of zooplankton over phytoplankton biomass in some aquatic ecosystems is that of high plant productivity with rapid turnover but low standing biomass (Phillipson 1966). Applied to arboreal ants, such a theory might posit high productivity but low standing crop of ant-tended Homoptera. We consider this hypothesis to be plausible, though we know of no data to test it.

The theory that ants feed mainly as herbivores is more complicated than would appear at first glance. Protein building blocks needed for colony growth and reproduction are relatively poorly represented in plant resources generally, as well as in the plant and homopteran exudates widely used by "herbivorous" ants (Auclair 1963; Baker et al. 1978). Consequently, protein acquisition would appear to depend on the processing of extremely large exudate volumes. Alternatively, or in addition, large colony size could result from the use of plant resources to expand the protein carrying capacity, for example, by subsidizing rapid motion that allows ants to discover more prey and reduce prey densities to exceptionally low levels (see below). A third possibility is that significantly longer individual life spans in ants may allow large populations of (mainly carbohydrate-dependent) workers to accumulate over the longer term, despite a shortage of protein. By this line of reasoning, it might be argued that only larval ants should be considered in pyramids of biomass for canopy arthropod samples, because only they are heavily protein-dependent. Finally, ants relying mainly on relatively nitrogen-poor plants as a source of protein might make flimsier workers, with lower protein costs for chitinous exoskeleton. Thus, works as old as Wheeler (1910) include observations that exudate-dependent formicine and dolichoderine ants have flimsier exoskeleton than do other, more predatory ant taxa.

Refining the Question

Within canopy arthropod samples, most ant species occur at low-to-moderate abundances, and the extraordinary abundances of one or a very few ant species account for most of the relative "excess" of ants. Records of the same genera appear repeatedly in different parts of the world (Table 7.3; Davidson, in preparation). Thus, our question can be revised to ask how *these particular* ants can be so common. Shared characteristics of these ants provide clues. All of the abundant taxa except *Paraponera clavata* Fabricius regularly nest arboreally in the proximity of plant and homopteran exudates on which they are heavily reliant (Davidson, in preparation). Moreover,

those genera for which internal anatomy has been carefully studied have digestive systems adapted to process large volumes of liquid food (Eisner 1957; DeMoss 1973; Davidson, in preparation). *Paraponera clavata*, which carries large droplets of exudates between its mandibles, will likely prove exceptional in lacking such digestive modifications, and digestive functions of *Dolichoderus* bear further scrutiny (Davidson, in preparation).

In canopy samples, taxa best represented in numbers, biomass, or frequency belong to four of the five ant subfamilies in which at least some species depend directly and substantially on plant resources (Table 7.3); missing are only the Pseudomyrmecinae (see Davidson, in preparation, for a possible explanation). Formicines and especially dolichoderines (Tobin 1994) figure very prominently in the list. The Ponerinae, which include many specialized predators, are poorly represented here, as among obligate plant-ants (Davidson and McKey 1993). The list includes only *P. clavata*, an atypical ponerine characterized by obligate arboreal foraging and strong reliance on plant exudates and even fruit (Young and Hermann 1980), as well as by occasional arboreal nesting (Breed and Harrison 1989). Taken together, these observations seem to support Tobin's claim that plant resources subsidize the remarkable abundance of ants in canopy arthropod samples.

Although plant and homopteran exudates contain some amino acids and peptides (Table 7.4), carbohydrates (CHOs) are the main nutritive components of these secretions (Auclair 1963; Baker et al. 1978; Harborne 1982). Davidson (in preparation) argues that high ratios of CHO:protein in the diets of these ants may provide CHOs in excess of quantities that can be paired with limiting protein for colony growth and reproduction as first priorities. Perhaps at little cost then, these "excess" CHOs can serve as ready energy sources to fuel activities and functions that increase access to growth-limiting nitrogenous resources. For example, in the taxa represented in Table 7.3, excess CHO in exudate-rich diets may be used for (1) nitrogen-free offensive and defen-

Table 7.3. Ants dominating individual canopy samples (or local faunas, where data not by sample) in numbers, biomass, or frequency, and reference or unpublished source of the observation. Some of the cited studies found secondary and tertiary dominants, but these were often considerably less common than was the primary dominant, and we standardized the data by reporting only the primary ant species. Two species are listed from Wilson (1987), but given his system of reporting (number of tray records or frequency in trays) and the wide discrepancy in body sizes of the two species, it was difficult to judge which species would have been the primary dominant. From Wilson, we omitted *Solenopsis (Diplorhoptrum) parabiotica*, which parasitizes broods of ant-garden ants and has tiny workers.

Ant taxa	Reference ^{''}
Formicinae	
<i>Camponotus femoratus</i>	Wilson 1987 ^{''A1}
<i>Camponotus</i> sp.	Stork (1991) ^b
<i>Camponotus</i> sp. (two samples)	Floren and Linsenmair (1996) ^b
<i>Oecophylla longinoda</i>	Majer (1976a) ^{At13}
<i>O. smaragdina</i>	Majer (1990) ^{As,3}
<i>Plagiolepis</i> sp.	Floren and Linsenmair (1996) ^b
Dolichoderinae	
<i>Azteca</i> sp. (4 samples)	Adiset al. (1984) ^{*TM}
<i>Azteca</i> sp.	Tobin (unpublished) ^{CA,3}
<i>Dolichoderus bispinosus</i>	Tobin (1991, unpublished) ^{Am,3}
<i>D. lutosus</i> (2 samples)	Adis et al. (1984) ^{Am}
<i>Dolichoderus</i> sp.	Tobin (unpublished) ^{oA}
<i>Dolichoderus</i> sp. (2 samples)	Floren and Linsenmair (1996) ^b
<i>Dolichoderus</i> sp. (6 samples)	Floren and Linsenmair (1996) ^b
<i>Dolichoderus</i> sp.	Floren and Linsenmair (1996) ^b
<i>Technomyrmex albipes</i>	Room (1975) ^{''o}
<i>Technomyrmex</i> sp.	Room (1971) ^{At}
Myrmicinae	
<i>Crematogaster brevispinosa</i> (2 samples)	Adis et al. (1984) [^]
<i>Crematogaster</i> cf. <i>limata</i> var. <i>parabiotica</i>	Wilson (1987) ^{''A11}
<i>C. striatula</i>	Majer (19768) [^]
<i>Crematogaster</i> sp. (4 samples)	Stork 1991 ^b
<i>Crematogaster</i> sp. (2 samples)	Floren and Linsenmair (1996) ^b
<i>Myrmicaria</i> sp., (2 samples).	Stork (199J) ^b
Ponerinae	
<i>Paraponera clavata</i>	Tobin (unpublished) ^{CA,b}

¹ Superscripts = geographic regions: Af = Africa; Am = Amazonia; Au = Australia; B = Borneo; CA = Central America; NG = New Guinea; WA = western Amazonia.

² Superscripts = type of sample: b = biomass; f = frequency in samples; otherwise (no superscript) = numbers.

sive weaponry, (2) level HI territoriality, i.e., patrolling/maintenance of absolute territories (Vepsalainen and Pisarski 1982), and (3) "high tempo" activity (Oster and Wilson 1978), correlated with high "dynamic densities" and rapid resource discovery rates (Vepsalainen and Pisarski 1982).

Do exudates contribute to ant abundance only indirectly, by fueling protein-gathering activities, or do colony growth and reproduction depend directly and substantially on the nitrogen present at low concentrations in exudates? Anecdotal evidence suggests the latter, at least in some ant species. Thus, some ants are known to tend Homoptera or Lepidoptera preferentially on plant species or plant parts (new leaves, fruiting and flowering pedicels) that are relatively rich in nitrogen (Nixon 1951; Maschwitz and Hanel 1985; Davidson 1988). This is weak evidence at best, and, as seen next, we employed mass spectrometry and ratios of stable nitrogen isotopes in a preliminary, but stronger, test of the potential for nitrogenous constituents of exudates to subsidize the abundances of exudate-feeding ants.

A Preliminary Test

Methods. ¹⁴N and ¹⁵N are stable isotopes that fractionate differently in biological processes due to slight variations in their physical and chemical properties. Although disparities in the equilibrium and kinetic properties of these two isotopic species are usually small, even minor disparities can lead to measurable differences in ⁸¹⁵N values between biological samples and a standard, in this case the ¹⁵N:¹⁴N ratio in atmospheric air (Ehleringer and Rundel 1988), which contains just 0.366% of ¹⁵N (Nier 1950; Sweeney et al. 1978). Relative to plant values, animal tissues are almost always enriched in ¹⁵N, and this enrichment is enhanced at successive trophic levels (Miyake and Wada 1967; DeNiro and Epstein 1981; Minegawa and Wada 1984;

Table 7.4. Essential amino acids reported from extrafloral nectaries and homopteran exudates. On a subjective scale, amount is summed for 21 different plant species reported by Baker et al. (1978). Coccid data were obtained from Ewart and Metcalf (1956), and mealy bug data on honeydew (HD) were from Salama and Rizk (1969) or Gray (1952); these were recorded as presence (+)/absence (-) data, respectively.

	Argenine	Isoleucine	Histidine	Leucine	Lycine
Amount	40	29	6	24	23
% Absent	0	10	76	29	38
Coccid ^{HD}	+	-	-	-	-
Mealy bug ^{HD}	+/-	+/+		+/	
	Methionine	Phenyl- alanine	Threonine	Tryptophan	Valine
Amount	10	23	28	20	24
% Absent	62	38	10	38	14
Coccid ^{HD}	-	-	+/+	-	+
Mealy bug ^{HD}	-/+	+/+	-/+	+/+	

Schoeninger and DeNiro 1984) by catabolic pathways favoring the heavier over the lighter isotope (Gaebler et al. 1966; Macko et al. 1986, 1987). When sample values are expressed relative to the atmospheric-air standard,

$$\delta^{15}\text{N} = \left(\frac{R^{\text{sample}}}{R^{\text{standard}}} - 1 \right) \times 1000,$$

$\delta^{15}\text{N}$ increases on average about 3 per mil per trophic level (Schoeninger and DeNiro 1984). Therefore, if exudate-feeding ants obtain a significant fraction of their nitrogen from their liquid diets, and if physiological, anatomical and enzymatic processes involving nitrogen are more or less similar across ants as a whole, then the $\delta^{15}\text{N}$ values of exudate-feeders should be lower than values for predatory ants.

We tested this hypothesis by analyzing the $\delta^{15}\text{N}$ values of several ant species collected in lowland moist evergreen tropical forest on Barro Colorado Island in Panama. Included in our sample (Table 7.5) were four representatives of the exudate-feeding genera in Table 7.3 (three dolichoderines and one formicine), to be compared with four predatory ponerines and one predatory army ant (Ecitoninae). We also sampled two species of leaf-cutters (*Atta*, Myrmecinae), which feed on plant sap from cut leaves (Littleddyke and Cherrett 1976) and are hypothesized by Tobin to feed mainly as

herbivores. Samples were collected in January, 1996, near the end of a prolonged wet season. Ants were crushed and placed in silica desiccant, and the desiccant was changed as often as the color indicator revealed its hydration.

After their return to the laboratory, sampled workers and their sometimes detached body parts were separated from the desiccant and ground (in aggregates of 2-10 workers per colony) in liquid nitrogen with a mortar and pestle. The resultant fine powders were dried to constant weight at 40°C in a Precision drying oven, and stored within a desiccator. Prior to analysis, each sample was placed in a pre-weighed tin cup, and cups plus samples were weighed again on a Perkin-Elmer AD-4 Autobalance, calibrated for 2.0 mg and 5.0 mg weights and set to a range of 20 mg. Ground sample weights were small, and none exceeded 1.5 mg. The tin cups were then folded to seal the samples inside and to remove atmospheric nitrogen. The elemental analyzer (Carla Erba 1108 CHN) combusted samples and then transferred the gaseous nitrogen to a Finnigan MAT 252 mass spectrometer, where the two isotopes were separated and measured. Prior to each multi-sample run, the mass spectrometer was calibrated by first running a blank to obtain background values for atmospheric nitrogen. After entering the value for an acetanilide standard, both this

Table 7.5. Nitrogen isotope ratios (8^{15}N) and % dry weight nitrogen for exudate-feeding, predatory, and leaf-cutting ants on Barro Colorado Island, Panama. Values are individual measurements (*Azteca* sp. 1 and *Leptogenys*, where sample material limited) or means of multiple runs. In parentheses, sample size (number of runs from a single collection, the same for both 8^{15}N and % nitrogen values), followed by % difference between extreme measurements for the sample [(Max - Min)/ \bar{x} , where \bar{x} is the mean of the sample]. The exception is *Eciton hamatum*, for which we repeated the analyses sufficiently for a standard deviation (s) to be meaningful. See text for comparisons of 8^{15}N values with those for plant values on BCI."

Species	Sample size	8^{15}N (% difference)	% dry weight N (% difference)
EXUDATE FEEDERS			
Formicinae			
<i>Camponotus sericeiventris</i>	4	1.82(3.8%)	11.36(4.8%)
Dolichoderinae			
<i>Azteca</i> sp. 1	1	3.04 (-)	10.39 (-)
<i>Azteca</i> sp. 2	2	3.99 (3.3%)	9.62(2.8%)
<i>Dolichoderus</i> sp.	2	1.79(1.7%)	11.05(0.3%)
PREDATORS			
Ponerinae			
<i>Ectatomma tuberculatum</i>	2	6.37 (0.6%)	14.07(1.1%)
<i>Leptogenys</i> sp.	1	7.08 (-)	13.69 (-)
<i>Odontomachus</i> sp.	2	9.34 (1.3%)	13.25(1.2%)
<i>Pachycondyla apicalis</i>	2	8.48 (1.1%)	13.15(0.8%)
ARMY ANTS			
Ecitoninae			
<i>Eciton hamatum</i>	6	3.76 (s=0.20)	13.77 (s=0.08)
LEAF-CUTTERS			
Myrmicinae			
<i>AttaspA</i>	2	1.97(1.5%)	13.38 (2.54%)
<i>Atta</i> sp. 2	2	1.63 (1.8%)	13.57(0.6%)

"Unfortunately, values for herbivores are available only for a different rain forest site, La Selva Biological Station on the Atlantic coast of Central America. For material collected there three weeks after the BCI collections, mean $5^{15}\text{N}_{\text{herbivores}} = 4.06$ (n = 6; s = 2.08), and mean $8^{15}\text{N}_{\text{herbivores}} = 3.15$ (n = 6; s = 0.51). Measurements for *Dolichoderus* sp. and *Camponotus sericeiventris* were lower than those for five of the six herbivores. Among the herbivores sampled were two adult moths and one caterpillar (Lepidoptera), one adult cricket (Orthoptera), and one adult and one larval beetle (Coleoptera). The mean 8^{15}N for herbivores was computed as the mean of the mean values for each (equally weighted) species. Although, the herbivore values provide some context in which to interpret 8^{15}N values for ants, caution is necessary because our sample sizes are too small to accurately characterize the variety of herbivores in these forests, and because actual means may differ between the forests.

standard and a known lab standard were processed to assure that the machine was functioning properly. Our ant samples were set up on a sequencer with the lab standard placed every four or five samples, and 8^{15}N values were corrected according to the variance of the lab standard from its known value.

Results and Discussion. 8^{15}N in **exudate-feeders and predators.** Table 7.5 gives the 8^{15}N values for the ants in our study. In the comparisons that follow, we took the conservative view that the two *Azteca* species might have similar 8^{15}N values due to common ancestry, and we averaged the values for two species to give a single value representative of this genus. 8^{15}N values for the

typically exudate-feeding dolichoderine and formicine ants were significantly lower than those of all predatory ponerines (Mann Whitney U -tests, $T(3,4) = 0$, one-tailed $P = 0.0028$) and those of all predators including army ants ($T(1,5) = 0$, $P = 0.018$). Not surprisingly, the $\delta^{15}\text{N}$ measurement for *Ectatomma tuberculatum* was lower than values for the other ponerines. Atypically for a ponerine, this ant forages extensively for nectar, which it transports in droplets held by the mandibles. Relatively low $\delta^{15}\text{N}$ values for two leaf-cutter ants (*Atta* spp.) in our sample may support Tobin's view that these ants feed at a lower trophic level than do predatory ants, though we currently lack data on $\delta^{15}\text{N}$ values of cultivated fungi.

The army ant, *Eciton hamatum*, was exceptional among the predators for its low $\delta^{15}\text{N}$ value. Why should the $\delta^{15}\text{N}$ value of this species be so low? Interestingly, data of Rettenmeyer et al. (1983) on the diets of *E. hamatum* show the species feeding mainly on brood of either attines (on BCI) or dolichoderines and formicines (in Ecuador, where they also retrieved certain Homoptera tended by *Pheidole* ants). If our army ants from BCI had fed mainly on the brood of attines, such as those we sampled, or, indeed, of the dolichoderines and formicines sampled, then the measured $\delta^{15}\text{N}$ value of *E. hamatum* is within the range of values ($\delta^{15}\text{N} = 1.3 - 5.3$) likely for predators with that trophic specialization (Table 7.5; Minagawa and Wada 1984). Based on these data, it is interesting to speculate that *E. hamatum* may specialize on abundant ant species feeding at relatively low trophic levels.

Remarkably, values for *Dolichoderus* sp. and *Camponotus sericeiventris* are lower than those of most plants studied in various sites across BCI (Virginia et al. 1988; Rundel, unpublished data). In total, Rundel and colleagues sampled leaves of 32 plant species, including a variety of plant life forms and 20 species in the family Fabaceae (legumes). Because many species in this family form symbiotic relationships with N-fixing microbes, they tend to have lower $\delta^{15}\text{N}$ values than do other plant species, at least within very local forest areas where $\delta^{15}\text{N}$ values tend to be relatively homogeneous (Virginia et al. 1988). Nevertheless,

8 N values of *Dolichoderus* sp. and *C. sericeiventris* were lower than 55% of Fabaceae (11 of 20 spp.) and 83% of species (10 of 12 spp.) in other families. Some caution should be exercised in interpreting these data, since the species overlap between Rundel's plants and the resource plants of our ants cannot be estimated, and because plants and ants were sampled at different times. Though seasonal variation in microbial processes might be correlated with seasonal variation in the $\delta^{15}\text{N}$ values of soils, effects of such variation on foliar $\delta^{15}\text{N}$ might be expected to be buffered in the mature leaves sampled (Rundel, personal communication). Similarly, $\delta^{15}\text{N}$ values of ants might reflect the $\delta^{15}\text{N}$ values of ant resources, integrated over worker life spans.

How can we account for the remarkably low $\delta^{15}\text{N}$ values of some exudate-feeders? Directly or indirectly, through Homoptera, these ants may obtain a significant fraction of their nitrogen from plant exudates, plant parts (directly or indirectly through Homoptera; D. Wagner, in preparation), and plant species that are relatively depleted in $\delta^{15}\text{N}$. Compared with foliar $\delta^{15}\text{N}$ values, stem tissues may be ^{15}N depleted (Shearer and Kohl 1986). However, if observations of Bergersen et al. (1988) prove to be general, phloem may be ^{15}N enriched, possibly due to selective removal and transport of ^{15}N from aging leaves. With regard to the question of host specialization, Fabaceae is one of three plant families with large numbers of myrmecophytic species (McKey and Davidson 1993), and ant-garden ants (*Camponotus femoratus* and *Crematogaster* cf. *limata* var. *parabiotica*, Table 7.3) are known to favor hosts in the genus *Inga* (Fabaceae; Davidson 1988). However, *Inga* may also be preferred for their extrafloral nectaries, and more and better data will be required to properly test the hypothesis that the dominant arboreal ants rely disproportionately on N-fixing host species.

Exoskeleton in exudate-feeders and predators.

One additional factor may contribute to differences in the $\delta^{15}\text{N}$ values of exudate-feeders and predators. If protein-rich exoskeletons were ^{15}N -enriched relative to internal protein and non-

protein nitrogen (but see DeNiro and Epstein 1981, for the opposite result in non-social insects), relatively low investment in exoskeleton by exudate-feeders might also lead to ^{15}N depletion in these ants. This is a significant consideration, since some amino acids, e.g., tyrosine, are more important than others in the sclerotization and melanization of exoskeleton (Chapman 1982), and because isotopic fractionation can vary among the biosynthetic pathways producing different amino acids (Macko et al. 1987). Our $^{8^{15}}\text{N}$ analyses produced measurements of % (of dry weight) nitrogen in the bodies of worker ants, and these values were significantly lower in exudate-feeders than in predatory ponerines ($t_{[1,4]}=0$, one-tailed $P = 0.028$), as well as in all predators including army ants ($U_m = 0$, $P = 0.018$). If this trend holds under the much larger sample sizes needed to define such a pattern confidently, the simplest explanation may be that protein-rich insect cuticle is thinner and flimsier in dolichoderines and formicines than in ponerines (Wheeler 1910). Much larger samples will be needed to determine if dolichoderines and formicines invest more than ponerines in protein-rich cuticle.

At least three factors might contribute to such a pattern. First, flimsy exoskeleton might have adaptive value to ants carrying large volumes of liquid food. Favoring this hypothesis is the observation that leaf-cutter ants, which may masticate leaf fragments primarily in the confines of the nest rather than transporting large volumes of liquid over long distances, have %N values more similar to predators than to exudate-feeders. Second, if protein is more limiting to growth and reproduction in exudate-feeders than in predators (Davidson, in preparation), the former species may invest less than do the latter species in this form of individual worker protection. Finally, relatively short worker life spans, perhaps correlated with "high tempo" activity in exudate feeders (Davidson, in preparation), would predict investment in "reclaimable," rather than "non-reclaimable," defenses, as appears to be the case for foliar defenses of plants (McKey 1984). Thus, substantial one-time and non-reclaimable investment in costly exoskeleton would be warranted only if the costs could be amortized over rela-

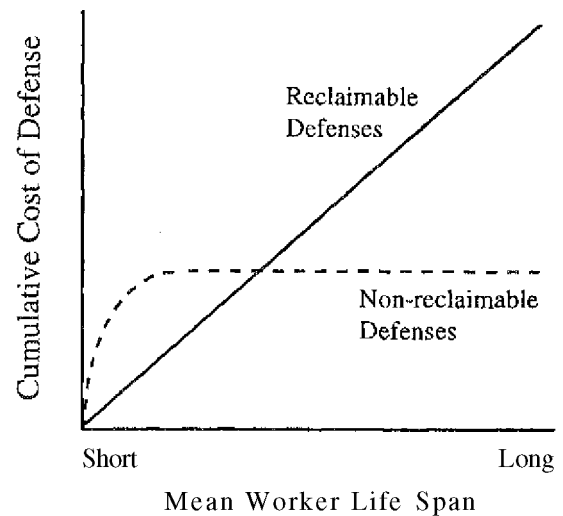


Figure 7.1. Proposed scaling of cumulative costs of defense as a function of worker life span for reclaimable (e.g., formic acid) versus non-reclaimable defenses (e.g., exoskeleton). Based on McKey's (1984) analysis of plant defenses in relation to leaf life span. Individual workers should be defended by reclaimable defenses where mean worker life spans are short, but by non-reclaimable defenses where life spans are long.

tively long mean worker life spans (Fig. 7.1). For shorter life spans, it should be cheaper to deploy defenses, e.g., behaviors, chemical sprays, etc., whose constituents or precursors might be easily shunted from aging to new workers.

Bacterial upgrading of nitrogen. Because our data appear to show that exudate-feeders derive a significant fraction of their nitrogen from plant resources, we must return to the question of how the abundant canopy ants might thrive on resources offering only low concentrations of the essential amino acids (Auclair 1963; Baker et al. 1978; Harborne 1982). Bacterial "upgrading" of nitrogenous compounds, e.g., from non-essential amino acids (Prosser et al. 1992), is well documented (Douglas 1989; Prosser et al. 1992; Baumann et al. 1995), and might be crucial to the capacities of exudate-feeders to obtain much of their nitrogen from sources low in the food chain. Bacterial symbionts also live within the mycetocytes of some species of *Camponotus* and *Formica* species, and perhaps other taxa where

they have yet to be ruled out. Their function in ants remains a mystery. Curiously, many *Camponotus* and some other exudate-feeding formicines, including *Oecophylla* (Table 7.3) and species of *Dendromyrmex* and *Polyrachis*, have secondarily lost their metapleural glands (Holldobler and Engel-Siegel 1984), known to secrete anti-microbial compounds in other species (Maschwitz et al. 1970; Maschwitz 1974; Mackintosh et al. 1995). Further work will be needed to determine whether these losses are evolutionary responses to nutritional dependency on microbial symbionts.

If Homoptera or their bacterial symbionts discriminate between stable isotopes of nitrogen, such discrimination could influence the ^{15}N signatures of exudates. The most likely scenario might be that both bacterial upgrading of nitrogen, and uptake and use of amino acids by bacteria and Homoptera, discriminate in favor of ^{15}N . If this were so, ^{15}N depletion in essential and non-essential amino acids passed on to tending ants might contribute to the very low ^{15}N signatures in some exudate-feeding ants.

Conclusions

Our preliminary test lends support to Tobin's hypothesis that the extraordinary abundances of tropical canopy ants may be funded to a significant extent by nitrogen from plant and homopteran exudates. Based on nitrogen isotope ratios, representatives of the ant genera dominating canopy samples in numbers, biomass, or frequency appear to obtain their nitrogen from lower trophic levels than do predatory species. Canopy dominants may rely substantially on nitrogen parasitized, directly or via Homoptera, from plants and upgraded by bacterial symbionts of ant-tended Homoptera or (quite speculatively) of the ants themselves. Although amino acids and peptides are minor components of plant and homopteran exudates (Auclair 1963; Baker et al. 1978; Harborne 1982), the capacities of formicines, some dolichoderines, and also *Crematogaster* (Table 7.3) to process large quantities of liquid foods efficiently because of

modifications to the digestive system (Eisner 1957; DeMoss 1973) may grant these taxa disproportionate abilities to benefit from such weakly concentrated nitrogen sources (Davidson, in preparation). Strangely, however, these same digestive modifications do not appear to be characteristic of *Dolichoderus*, the most frequent dominant in canopy samples (Table 7.3; Eisner 1957; Davidson, in preparation), and it will be important in the future to scrutinize the handling and processing of fluids by these ants. More detailed studies of nitrogen fractionation in plants and Homoptera (e.g., those of D. Wagner, in preparation) will also be needed to distinguish among a variety of factors potentially contributing to the very low ^{15}N values of *Camponotus* and *Dolichoderus* species. Such studies might also shed light on the dietary contributions of ant-harvested Homoptera (e.g., Way 1954; Pontin 1978).

Although our results suggest that the nitrogen budgets of some abundant, exudate-feeding canopy ants are subsidized at lower trophic levels than those of predatory ants, such subsidies may not be sufficient, in and of themselves, to account for the extraordinary abundances of these ants. Also contributing to abundance may be a reduction in the protein content of individual workers (Table 7.5) and the use of excess dietary CHOs as fuel to power activities, e.g., high tempo foraging, that increase protein harvesting from predation and scavenging (Davidson, in preparation). In the latter context, it is interesting to note that studies of tropical ant mosaics in crop plantations have documented pronounced effects of particularly abundant arboreal ant species on populations of other insects (e.g., Leston 1969, 1973; Majer 1976b).

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