The University of Chicago

COLONY SIZE AS A BUFFER AGAINST SEASONALITY: BERGMANN'S RULE IN SOCIAL INSECTS

MICHAEL KASPARI* AND EDWARD L. VARGO†

Brackenridge Field Laboratory, Department of Zoology, University of Texas,
Austin, Texas 78712-1064

Abstract.—In eusocial species, the size of the superorganism is the summed sizes of its component individuals. Bergmann's rule, the cline of decreasing size with decreasing latitude, applies to colony size in ants. Using data from the literature and our own collections, we show that colony sizes of tropical ant species are about one-tenth the average size of temperate species. This pattern holds when species or genera are sample units. Further, this trend is shown in 17 of 19 genera and five of six subfamilies. Bergmann's rule may arise if seasonal famine favors larger organisms, given their increased energy reserves. We constructed three colony sizes of the ant *Solenopsis invicta*. We deprived these colonies of food, or food and water. Queens, when surrounded by 10^2 workers or 10^4 workers, survived longer than solitary queens. When deprived only of food, days of queen survival had an allometry of $M^{0.21}$ (where M is mass), not significantly different from the predicted $M^{0.25}$ for unitary organisms. We propose that shorter growing seasons in the temperate latitudes cull small-colony species through overwintering starvation, which contributes to Bergmann's rule in social insects.

Body size plays a critical role in understanding the distribution of organisms (MacArthur 1972; Brown and Maurer 1989). One common pattern is Bergmann's rule, the cline of decreasing body size—within and between species—from the polar to the tropical latitudes (Bergmann 1847; Mayr 1956). Heat conservation was initially proposed as a mechanism for Bergmann's rule (Bergmann 1847; but see McNab 1971). The fasting endurance hypothesis has since been suggested as an alternative mechanism (Lindstedt and Boyce 1985; Millar and Hickling 1991). Since metabolic rate scales to mass (M) as $M^{0.75}$ and body reserves scale to mass as $M^{1.0}$ (Peters 1983; Calder 1984), food reserves are predicted to scale as $M^{0.25}$. Larger vertebrates may thus have the energy reserves to survive better the shortages that come with temperate winters (Lindsey 1966; Boyce 1978, 1979; Murphy 1985). Hence, the fasting endurance hypothesis is a possible mechanism for Bergmann's rule.

Less is known about the ecogeography of invertebrates. One place to start is the social insects (ants, termites, social wasps, and bees) since they are critical predators, mutualists, and competitors in the world's ecosystems (Wilson 1971;

* Present address: Lawrence Livermore National Laboratory, L-453, P.O. Box 808, Livermore, California 94550; E-mail: kaspari@targa.llnl.gov.
† E-mail: edvargo@utxvm.cc.utexas.edu.

Hölldobler and Wilson 1990). Most social insect colonies consist of a queen sur-
rounded by her sterile offspring, which feed and defend her (Wilson 1971). As a
result, the mass of a social insect colony has two components under separate
control: the mass distribution among the individuals (body size) and the total
number of individuals in that colony (colony size).

The body size of ant species in northern Europe follows Bergmann's rule
(Cushman et al. 1993). The fasting endurance hypothesis clearly predicts that
increases in body size should increase an individual ant's time to starvation (Kon-
doh 1977). But why should increasing colony size buffer a colony against famine?
Picture two single-queen colonies, one with 100 workers, the second with 1,000.
In effect, these two colonies have the same amount of reproductive tissue and
an order of magnitude difference in somatic tissue. Social insects can devour
brood and workers, catabolizing somatic tissue, under times of environmental
stress (Wilson 1971; Taylor 1978; Sorensen et al. 1983). Larger colonies thus have
more somatic tissue to catabolize to keep the same amount of reproductive tissue
alive. If so, then increasingly seasonal environments should favor larger mean
colony sizes if a population is to persist through the periodic famine.

Species in the family Formicidae produce a remarkable range of colony sizes
(from eight to 300,000,000 workers). What can cause such morphological diversity
from a single common ancestor? Here we look for evidence of Bergmann's rule
in ant colony size. Next, we test the fasting endurance hypothesis (Millar and
Hickling 1991) as one mechanism underlying Bergmann's rule in ants.

METHODS

Colony Size and Bergmann's Rule

We test a simplified version of Bergmann's rule by asking whether tropical
species have smaller colony sizes than temperate species. We do this primarily
because there is surprisingly little data on colony size in social insects (Tschinkel
1991) compared to Lindsey's 1966 exhaustive analysis of thousands of vertebrate
ectotherms. A tropical/temperate comparison seems a good starting point. We
used data from the literature combined with data from 88 species from nest collec-
tions in tropical Costa Rica and Panama (Kaspari 1993a; M. Kaspari, unpublished
data). Species means were log transformed for analysis.

We defined colony size as the total number of adult individuals serving a queen
or set of queens. We generally avoided citations that failed to provide methods (e.g.,
those having many "personal communications") or were not reviewed by peers. If
a range of colony sizes was given without the distribution, we used the mean.
Rarely, a colony size was given as "greater than x." We then used the value $2x$,
noting here that a $10x$ increase did not change any results in the following analysis.
Individuals may be distributed over a number of nests (e.g., *Formica yessensis*)
(Higashi and Yamauchi 1979). Where it was clear that species had multiple nests
per queen—and authors did not provide an average colony size—we calculated
average colony size by dividing mean nest size by the fraction of nests occupied by
queens, which yielded an average number of workers per queened nest.

We assigned species to temperate or tropical ($<23.3°$ latitude) groups on the basis of where the colonies were observed. Range maps of ants are practically nonexistent, and some species likely skirt $23.3°$, which will tend to obscure any differences. We compared colony size between these two regions using both species and genera as sample units. In addition, for 19 genera and six subfamilies of ants that have tropical and temperate species, we looked for statistical differences among the fraction of taxa with larger colonies in temperate/tropical species and the temperate/tropical means of those taxa with $n > 4$ in both regions.

The Fasting Endurance Hypothesis and Colony Size

We tested the fasting endurance hypothesis by constructing colonies of three sizes from pooled colonies of *Solenopsis invicta,* the red imported fire ant. *Solenopsis invicta* is a widespread pest species (Porter and Savignano 1990) that is abundant in central Texas in a multiple-queen form. Since multiple-queen forms of *S. invicta* readily accept other workers into their nest (Mirenda and Vinson 1982), they provide an opportunity to construct colonies of various sizes from a homogenous beginning. To do this, we dug up 10 large multiple-queen nests on the grounds of the Brackenridge Field Lab in Austin, Texas. We separated ants from soil by slowly dripping water into the bucket until the ants formed a floating mat on the water (Jouvenaz et al. 1977). In large trays coated with Fluon to prevent ant escape, we separated queens from workers through a combination of sifting and sorting with forceps. We consolidated the workers from all 10 nests to form the random pool from which experimental colonies were constructed.

We chose three colony sizes: single queen, ''small colony'' (ca. 10^2 workers), and ''large colony'' (ca. 10^4 workers). We chose these sizes for a number of reasons. First, they represent the approximate colony sizes of single-queen populations of *S. invicta* at colony founding, after 1-2 mo, and after 9 mo (Tschinkel 1988). Nine months is the growing season of *S. invicta* in southern North America (Tschinkel 1988), and thus the number of workers from this period represents the largest size the colony could attain in a single year before a period of forced inactivity. Second, 10^2 workers and 10^4 workers represent common colony sizes of tropical and temperate ant species (see below). Colony sizes were constructed volumetrically by gently tamping workers and brood into a calibrated test tube. After setting up the colonies, five counts of this volume method yielded 278–448 workers (mean = 354) for the small-colony treatment, and 9,971–14,524 workers (mean = 12,255) for the large-colony treatment.

Colonies were placed in 14-cm petri dishes with plaster bottoms and two entrance holes. These nests were placed in 26 × 16-cm plastic trays, the sides of which were coated in Fluon. The nests were placed on shelves in a room kept at 30°C, ca. 70% relative humidity, on a natural photoperiod. Queens, which move little during founding, were placed in smaller 4.5-cm cups with dental plaster bottoms.

The colonies were exposed to two types of stress. The first group (20 colonies of queen, small, and large size) was given no water. The second group (20 colonies each) was given only water (sprayed three times weekly on the nest substrate and ad lib. in test tubes plugged with cotton). We checked for queen death twice
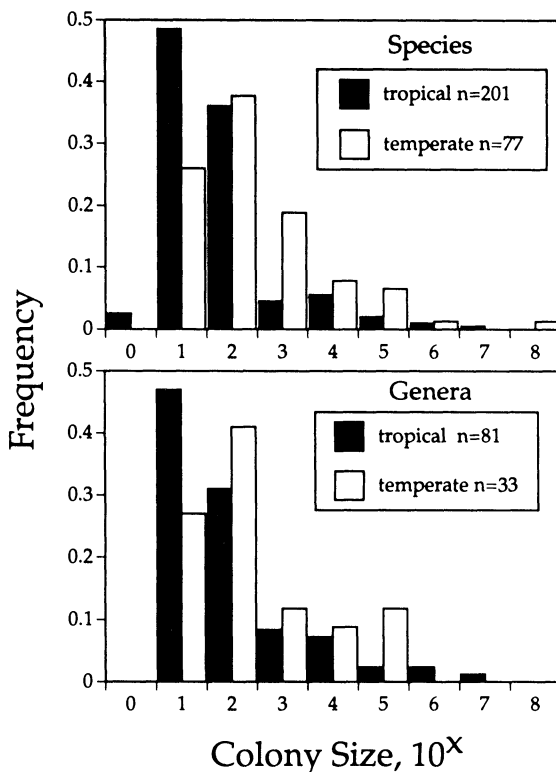
FIG. 1.—The colony sizes of temperate zone ants are larger on the average than those of tropical species, using species as sample units (*above*) and genera as sample units (*below*).

a week. Queens typically were the last ants alive in the colony. One queen each from the wet single-queen and wet large-colony treatments were crushed during observation and deleted from the analysis.

RESULTS

Our survey yielded 77 temperate and 201 tropical ant species from 14 of 16 extant ant subfamilies (Baroni Urbani et al. 1992). The family Formicidae has generated colony sizes that range over eight orders of magnitude (fig. 1; appendix). The 14 ant subfamilies differed greatly in the range of colony sizes shown by their constituent species. This is not due completely to uneven sampling. Three subfamilies in this study (Apomyrminae, Aneuretinae, Nothomyrmiciinae) are represented currently by one species. The army ants (Dorylinae, Ecitoninae, and Aenictinae) and Cerapachines are less species rich than the myrmicines, ponerines, and formicines (Hölldobler and Wilson 1990). Only the dolichoderines appear conspicuously undersampled in this study.

Weighting all species equally, the modal colony size of temperate and tropical ant species was 10^3 and 10^2 workers, respectively (fig. 1). The mean colony size

Fig. 2.—Sizes of temperate and tropical species. In 17 of 19 genera, tropical species are smaller than temperate species. The line is unity. *Triangles*, the genera in the subfamily Formicinae; *diamonds*, Cerapachinae; *squares*, Myrmicinae; *open circles*, Ponerinae; *solid circle*, Dolichoderinae.

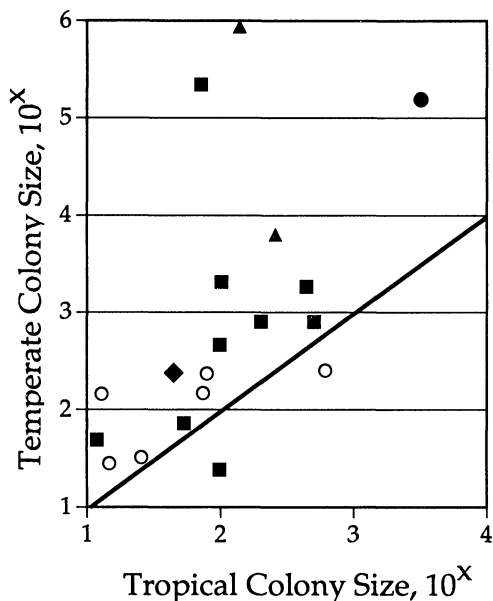of temperate species is also considerably larger ($10^{2.9}$ vs. $10^{2.2}$; Kruskal-Wallis $\chi^2_{77,201} = 27.2$, $P < .0001$; temperate and tropical sample sizes are given as subscripts, respectively). While the ranges of colony sizes were roughly equal in both groups, species with colony sizes less than 1,000 workers account for 86% of tropical species versus 64% of temperate species (fig. 1).

Since constraints on colony size may act differentially within different lineages, we performed three additional analyses to build the case for small colony sizes in the tropics. First, using the mean colony size per genus as the sample unit yielded the same statistical result: genera in the temperate zone had larger colony sizes than those in the tropics by the same magnitude ($10^{2.9}$ vs. $10^{2.4}$; Kruskal-Wallis $\chi^2_{33,81} = 5.4$, $P < .015$; fig. 1).

Six of the 14 subfamilies yield colony sizes from both tropical and temperate species. Five of these show a trend toward larger temperate colonies (binomial probability = 0.16). We compared the species means of the three subfamilies with at least $n = 4$ in both regions. The Formicinae ($P = .0001$) and the Myrmicinae ($P = .0004$), the two subfamilies with the most species and greatest size range, have significantly larger species in temperate genera. The Ponerinae show the same trend, but not significantly ($P = .14$).

Nineteen genera had tropical and temperate samples. If Bergmann's rule is true, we would expect tropical species of each genus to have smaller colony sizes. Seventeen of 19 genera (90%) had smaller average colony sizes in the tropics (binomial probability = 0.0004; fig. 2). *Pheidole*, the only genus with four
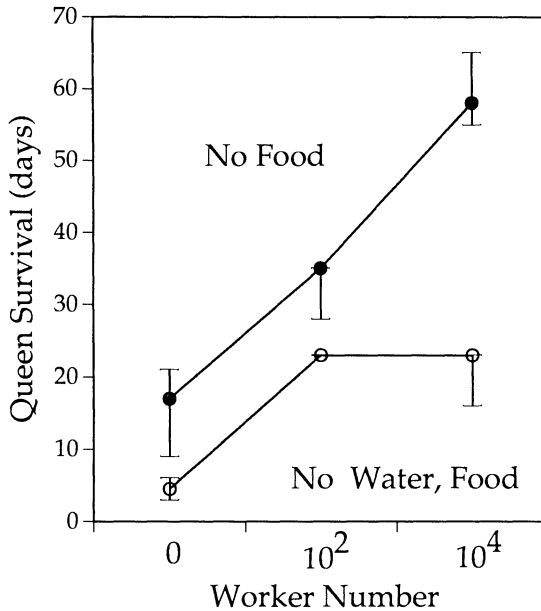
FIG. 3.—Queen survival rate in artificial colonies. Queens stressed by lack of food and water (*open circles*) and lack of food (*solid circles*) survive longer when they have more workers. Medians are given with 25% and 75% quartiles.

or more species sampled per region, had smaller colonies in tropical species ($10^{2.0}$ vs. $10^{3.3}$; Kruskal-Wallis $\chi^2_{28,4} = 10.2$, $P = .0014$).

The Fasting Endurance Hypothesis

In the test of the fasting endurance hypothesis, queens survived longer in larger colonies (fig. 3) in both water and food deprivation treatments. In colonies provided no water, all solitary queens were dead by day 6 (median = 4.5 d), while both small and large colonies survived up to 28 d (median for both = 23 d), a significant difference (Kruskal-Wallis $\chi^2_{20,20,20} = 44$, $P < .0001$).

In colonies provided water but no food there was a smooth increase in queen survival time with colony size, from medians of 16 to 31 to 57 d (Kruskal-Wallis $\chi^2_{19,20,19} = 42$, $P < .0001$). This increase follows the allometry: days of queen survival $= 1.13M^{0.214}$ (standard errors $= 0.05, 0.02$, $F = 122$, df $= 1,56$, $P = .0001$, $r^2 = 0.67$), indistinguishable by 95% confidence intervals from the predicted $M^{0.25}$ for unitary organisms.

DISCUSSION

The "size" of a social insect colony is the summed size distribution of its members. Ant species range over eight orders of magnitude in colony size. If average body size is unrelated to colony size, the family Formicidae includes half the range of mass recorded for all the animals (10^{-5}–10^{9} g) (Bonner 1988). What

factors may help us understand such variation arising from a single common ancestor?

The Pattern: Bergmann's Rule and Colony Size

Bergmann's rule, the cline of decreasing body size with decreasing latitude (Bergmann 1847; Mayr 1956), has been shown for many, but not all, unitary organisms (Lindsey 1966; Johnston and Selander 1971). Here we show that colony size in social insects follows Bergmann's rule: tropical species and genera are smaller than their temperate counterparts. The causes of Bergmann's rule are still unclear (Scholander 1955; McNab 1971). However, if there is a principal overriding mechanism, it needs to act on both colony size in social organisms and body size in unitary organisms.

Different ranges of colony size are used by different subfamilies. Colony size is thus conserved to some extent in higher taxa (fig. 2). Does Bergmann's rule hold up within lineages? Given the uncertain phylogenies even at the subfamily level (Baroni Urbani et al. 1992), we explored this question in two rather simple ways. First, five of six subfamilies show Bergmann's rule in colony size, and the two most species-rich subfamilies show it significantly. Second, and we think most convincingly, 17 of 19 genera from five subfamilies show a trend toward smaller tropical species. If genera are independent assays of this pattern, this is a highly unlikely result due to chance alone. Colony sizes of ants, from all the data currently available, seem to be generally smaller in the tropics.

Surveys of this kind are not without bias. Since there has been little emphasis on colony size as a subject of theoretical interest (Tschinkel 1991; but see Oster and Wilson 1978), colony size data are sparse and undercount inconspicuous species (e.g., subterranean and arboreal nesters). More thorough studies of these taxa, other social insects (e.g., bees, termites), and colonial organisms (e.g., bryozoans) would give us a better idea as to the generality of this pattern.

Another potential bias is that litter-nesting species, which may be constrained by nest size, may be overrepresented in tropical samples. However, we feel this bias is negligible since litter-nesting ants are the most numerous form of ground ants in the tropics (Wilson 1959; Kaspari 1993a). Further, swarm-founding polistine wasps, which build their own nests, may also show Bergmann's rule for colony size (Jeanne 1991).

Seasonality and Bergmann's Rule

Clines in body size likely arise from a number of interacting causes (for a recent review, see Cushman et al. 1993). We suggest Bergmann's rule in colony size may arise because seasonal famines in the temperate zone are longer, more severe, and more likely to cull species with small colonies. Colony sizes of around 12,000 individuals allow *Solenopsis invicta* queens to survive colony food deprivation for almost 2 mo. Colony mass scales well ($r^2 = 0.67$) with queen longevity in time of food stress, which suggests that large colonies can buffer the queen against environmental insults better than small colonies. Further, the scaling of queen longevity to colony mass ($1.13M^{0.21}$) approaches the predicted $M^{0.25}$ also found for plankton (Threlkeld 1976). We did not directly test the mechanisms behind

this increased queen survival rate, but they likely include the ability of workers in large colonies to catabolize and concentrate nutrients from workers and brood for the queen. Water is apparently less easy to shepherd and conserve, since there was no apparent difference in queen longevity from colonies of 10^2–10^4 workers.

The fasting endurance hypothesis makes predictions that may further gauge its importance underlying Bergmann's rule in social insects. First, species with small colonies will tend to accumulate in impoverished but stable environments (Millar and Hickling 1991). Second, since tropical habitats vary greatly in the duration of their dry season (Holdridge et al. 1972; Leigh et al. 1982), colony size should increase from the aseasonal to the seasonal tropics. In both cases, further tests would benefit from a more quantitative definition of seasonality than is given here (Peters 1983), since seasonal changes in cold, aridity, and other conditions likely limit growth and reproduction in different habitats.

A third prediction is that species that can store food may be able to maintain smaller colonies in seasonal environments than those that do not. Fungus-growing ants and seed harvesters are classic cases of food storage. However, even tiny omnivorous colonies may put away seeds (Kaspari 1993*a;* Levey and Byrne 1993), and the size of these stores need to be gauged against the requirements of the colony. Further, colonies may store "live" food in the form of larvae that can be consumed when necessary (see also Nonacs 1991). Thus, the economics of storage are likely complicated.

Finally, Bergmann (1947) initially pointed out clines within species. There are few samples from multiple sites for any species in this survey, but this would be a powerful test of the fasting endurance hypothesis.

Other Mechanisms for a Cline in Colony Size

What other mechanisms might favor smaller colony sizes in the tropics? Not only are the tropics less seasonal, but tropical forests tend to be humid and warm, with the humidity of the forest floor rarely dipping below 85% (Kaspari 1993*b*). Litter is the most common nest site in many Neotropical habitats (Wilson 1959; Kaspari 1993*a*), with up to 80 litter-nesting species in the same tropical habitat (M. Kaspari, unpublished data). The benign climate of a tropical rain forest may make litter accessible as a nest site, secondarily constraining colony sizes in the bargain.

Second, social insect predators (e.g., army ants) are conspicuous, periodic predators in the tropics, although their impact is largely unexplored. If predation rates increase toward the tropics, they may select for reproduction at smaller sizes (Richards 1953; Wilson 1971; Jeanne 1991; Kozlowski 1992). This old hypothesis remains untested, largely for lack of quantitative data on colony mortality in temperate or tropical habitats.

Although heat conservation was the original hypothesis for Bergmann's rule (Bergmann 1947; McNab 1971), it is difficult to see how this may work for individual insects (Scholander 1955; Cushman et al. 1993). However, large numbers of workers, massed around the queen, may provide a barrier against heat loss in the dead of winter.

Finally, perhaps the temperate latitudes, more recently freed from glacial ice, have been differentially colonized by taxa with large colonies. This idea would gain credibility if populations of large-colony taxa dispersed farther than those of small colonies. Such a situation may be possible if large colonies produce larger, hardier reproductives.

Schoener and Janzen (1968) found insects sampled from the forests of Massachusetts were smaller on the average than those collected in Costa Rica. This result runs counter to Bergmann's rule (if $n = 2$ is a representative sample). Interestingly, they also focus on seasonality in their explanation, suggesting that the longer growing seasons of the tropics allow larger maximum body sizes. This hypothesis is intriguing and may be most applicable to annual species. We, on the other hand, focus on the tactics of perennial species that need to survive the cold/dry season and reproduce over multiple years. The further exploration, and perhaps integration, of these hypotheses may yield a theory of body mass distribution for large, diverse biotas.

Bergmann's rule is a statistical pattern; there is much variation in colony size unexplained by latitude. For example, there are temperate genera with small colonies (e.g., *Leptothorax*) and tropical genera with spectacularly larger colonies (e.g., *Atta, Eciton*). Certainly other factors, including body size (Cushman et al. 1993), queen size, and dormancy, may influence the ability of a colony to found, grow, and survive the vagaries of the environment. So far, however, genera with tropical and temperate counterparts are very consistent in expressing Bergmann's rule (fig. 2), and large colonies can buffer a queen against famine better than small colonies (fig. 3). Given the fascinating range and biological importance of colony size in social organisms, exploring the historical and extant forces shaping colony size should be productive. The first author is currently collecting new colony size data to tease apart the effects of within-latitude seasonality and nest site constraints on colony size in ants.

APPENDIX

TABLE A1

MEAN COLONY SIZES OF ANT SPECIES

Subfamily and Genus	Species	Site	Mean	N	Citation
Aenictinae:					
Aenictus	currax	tr	200,000	1	Wilson 1959
	laeviceps	tr	85,000	—	Schneirla 1971
Dorylinae:					
Dorylus	wilverthi	tr	12,000,000	—	Raignier and van Boven 1955
Ecitoninae:					
Eciton	burchelli	tr	825,000	—	Schneirla 1957; Rettenmeyer 1963
	hamatum	tr	300,000	—	Rettenmeyer 1963
Labidus	praedator	tr	2,000,000	1	Rettenmeyer 1963
Neivamyrmex	nigrescens	te	110,000	—	Schneirla 1971
Leptanillini:					
Leptanilla	japonica	te	150	—	Masuko 1990
Cerapachyinae:					
Cerapachys	cf. cribrinodis	te	235	1	Villet et al. 1991
	opaca	tr	100	1	Wilson 1959
	polynikes	tr	20	1	Wilson 1959
Sphinctomyrmex	cf. steinheili	te	240	2	Buschinger et al. 1989
Ponerinae:					
Amblyopone	pluto	tr	33	3	Gotwald and Levieux 1972
	sp.	tr	89	12	Ito 1991
Anochetus	bequaerti	te	84	1	Villet et al. 1991
	diegensis	tr	13	9	BCI:odont
	faurei	te	434	2	Villet et al. 1991
	katonae	te	84	2	Villet et al. 1991
Centromyrmex	sellaris	tr	408	1	Levieux 1976
Cryptopone	motschulskyi	tr	20	1	Wilson 1959
Diacamma	rugosum	tr	40	2	Wilson 1959
Dinoponera	australis	tr	30	—	Fowler 1985
Ectatomma	ruidum	tr	105	15	Breed et al. 1990
Gnamptogenys	horni	tr	28	46	BCI:gnam2
	ingeborgae	tr	15	1	Brown 1992
	macretes	tr	40	1	Wilson 1959
	sp. 1	tr	24	1	LS:gnam1

TABLE A1 (Continued)

Subfamily and Genus	Species	Site	Mean	N	Citation
Hypoponera	?*gleadowi*	te	32	1	Villet et al. 1991
	sp. 2	tr	34	41	LS:hypo2
	sp. 3	tr	24	31	LS:hypo1
	sp. b	tr	21	27	BCI:hypob
Leptogenys	*attenuata*	te	90	4	Villet et al. 1991
	bituberculata	tr	300	1	Wilson 1959
	castanea	te	289	4	Villet et al. 1991
	chinensis	tr	367	7	Maschwitz and Schönegge 1983
	diminuta	tr	245	4	Wilson 1959
	nitida	te	595	6	Villet et al. 1991
	ocellifera	tr	32,000	1	Maschwitz and Mühlenberg 1975
	purpurea	tr	1,250	2	Wilson 1959
	sp. 2	tr	53	2	BCI:lept1
Myopias	sp. 1	tr	60	1	Wilson 1959
	sp. 2	tr	55	2	Wilson 1959
	sp. 3	tr	30	1	Wilson 1959
Odontomachus	*bauri*	tr	300	40	Jaffé and Marcuse 1983
	chelifer	tr	130	1	Medeiros et al. 1992
	laticeps	tr	15	7	LS:odonbg
Pachycondyla	*apicalis*	tr	23	1	Oliveira and Hölldobler 1990
	berthoudi	te	517	4	Peeters and Crewe 1987
	commutata	tr	800	1	Mill 1982
	foetens	tr	518	2	Levieux 1976
	obscuricornis	tr	57	1	Fresneau 1984
	pergandei	tr	19	3	BCI:hypo2
	stigma	tr	9	13	LS:pach1
	striatulus	tr	15	2	Wilson 1959
	krugeri	te	43	15	Wildman and Crewe 1988
	tarsatus	tr	600	—	Levieux 1976
Paraponera	*clavata*	tr	1,019	2	Janzen and Carroll 1983
Platythyrea	*conradti*	tr	400	—	Levieux 1976
	parallela	tr	50	1	Wilson 1959
Prionopelta	*amabilis*	tr	298	3	Hölldobler and Wilson 1986; LS: pram
	opaca	tr	20	1	Wilson 1959
Proceratium	*silaceum*	te	28	—	Kennedy and Talbot 1939
	sp. 1	tr	17	2	BCI:proc
	sp. 2	tr	13	2	LS:proc1

Genus	Species		Colony size	Samples	Reference
Rhytidoponera	*araneoides*	tr	50	3	Wilson 1959
	chalybaea	te	271	68	Ward 1981
	confusa	te	203	132	Ward 1981
	laciniosa	tr	125	2	Wilson 1959
Streblognathus	*aethiopicus*	te	26	12	Ware et al. 1990
Thaumatomyrmex	sp. 1	tr	10	1	BCI:thau1
Apomyrminae:					
Apomyrma	*stygia*	tr	53	—	Levieux 1976
Aneuretinae:					
Aneuretus	*simoni*	tr	67	7	Jayasuria and Traniello 1985
Dolichoderinae:					
Dolichoderus	*imitator*	tr	25	7	BCI:doli1
Iridomyrmex	*purpureus*	te	155,500	—	Ettershank 1971; Greaves and Hughes 1974
	scrutator	tr	3,250	1	Wilson 1959
Leptomyrmex	*fragilis*	tr	350	1	Wilson 1959
Tapinoma	*minutum*	te	239	26	Herbers 1991
Formicinae:					
Acropyga	sp.	tr	2,000	1	Wilson 1959
Brachymyrmex	sp. 1	tr	125	2	LS:PAAM
Calomyrmex	*laevissimus*	tr	250	1	Wilson 1959
Camponotus	*confusus*	tr	200	1	Wilson 1959
	herculeanus	te	12,240	1	Sanders 1970
	noveboracensis	te	8,900	1	Sanders 1970
	papua	tr	300	1	Wilson 1959
	pennsylvanicus	te	2,222	4	Pricer 1908
	sp. 1	tr	31	1	LS:CAM1
	sp. 2	tr	80	2	LS:CAMP2
	vitreus	tr	8,000	1	Wilson 1959
Formica	"*incerta*"	te	875	24	Talbot 1948
	exsectoides	te	139,938	2	Cory and Haviland 1938
	fusca	te	500	—	Wallis 1964
	japonica	te	2,495	4	Kondoh 1968
	lugubris	te	40,000	—	Breen 1979
	pallidefulva nit.	te	713	24	Talbot 1948
	rufa	te	2,005,000	—	Brian 1965
	yessensis	te	3.06E+08	1	Higashi and Yamauchi 1979
Myrmoteras	*barbouri*	tr	8	1	Moffett 1986c
	toro	tr	22	1	Moffett 1986c
Oecophylla	*longinoda*	tr	48,000	1	Way 1954

621

TABLE A1 (Continued)

Subfamily and Genus	Species	Site	Mean	N	Citation
Paratrechina	ha	tr	351	76	BCI:paha
	pallida	tr	500	1	Wilson 1959
	sp. 1	tr	200	1	Wilson 1959
	steinheili	tr	143	60	LS:PAST
	sp. 2	tr	150	1	Wilson 1959
Polyrachis	debilis	tr	325	3	Wilson 1959
	dives	te	876,096	1	Yamauchi et al. 1987
	hirsutula	tr	150	1	Wilson 1959
	limbata	tr	100	1	Wilson 1959
	omymyrmex	tr	60	1	Wilson 1959
	rufiventris	tr	200	1	Wilson 1959
Prenolepis	imparis	te	3,370	21	Talbot 1943; Tschinkel 1987
Pseudolasius	breviceps	tr	325	2	Wilson 1959
Myrmeciinae:					
Myrmecia	dispar	te	124	20	Gray 1971
	gulosa	te	887	2	Haskins and Haskins 1950
	nigrocincta	te	821	2	Gray 1971
	pilosula	te	678	2	Haskins and Haskins 1950
	vindex	te	181	2	Haskins and Haskins 1950
Nothomyrmeciinae:					
Nothomyrmecia	macrops	te	60	5	Taylor 1978
Pseudomyrmecinae:					
Pseudomyrmex	spinicola	tr	10,021	—	Janzen 1967
	termitarius	tr	200	—	Jaffé et al. 1986
Myrmicinae:					
Acanthognatus	ocellatus	tr	10	6	LS:ACEL1
Acanthomyrmex	ferox	tr	49	1	Moffett 1985
	notabilis	tr	37	1	Moffett 1985
Acromyrmex	ocotospinosus	tr	55,000	1	Weber 1972
Adelomyrmex	biroi	tr	10	1	Wilson 1959
Aphaenogaster	dromedarius	tr	100	1	Wilson 1959
	rudis	te	303	118	Headley 1949; Talbot 1951
	treatae	te	682	30	Talbot 1954
Apterostigma	angulatum	tr	155	1	Weber 1941
	GR	tr	27	1	BCI:aptegr
	SH	tr	46	1	BCI:aptesh
	SQ	tr	41	5	BCI:aptesq
Atta	columbica tonsipes	tr	1,750,000	1	Martin et al. 1967

622

Basiceros	*manni*	32	.3	tr	Wilson and Hölldobler 1986
	sp. 1	9	1	tr	LB:BASI
Cardiocondyla	*paradoxa*	50	1	tr	Wilson 1959
	thoracica	70	1	tr	Wilson 1959
Cephalotes	*atratus*	11,267	1	tr	Corn 1980
Crematogaster	BB	99	1	tr	LS:CRBB
	dohrni	28,982	2	tr	Ayyar 1937; Roonwal 1954
	elegans	300	1	tr	Wilson 1959
	KA	39	1	tr	LS:CRKA
	larreae	789	13	te	MacKay et al. 1984
	LO	221	7	tr	BCI:cremlo
	RE	125	1	tr	LS:CRRE
	subtilis	10,000	1	tr	Wilson 1959
Cyphomyrmex	*cornutas*	28	3	tr	LS:CYCO
	minutus	29	163	tr	BCI:cymimi
	rimosus	115	20	tr	Weber 1947; BCI:CYDO
Dacetinops	*cibdela*	10	1	tr	Wilson 1959
Daceton	*armigerum*	5,100	3	tr	Wilson 1962a
Eurhopalothrix	*biroi*	50	1	tr	Wilson 1959
Hylomyrma	sp. 1	16	11	tr	LS:HYLO1
Leptothorax	*acervorum*	34	7	te	Heinze and Ortius 1991
	allardycei	53	30	te	Cole 1984
	ambiguus	37	50	te	Talbot 1965
	curvispinosus	83	38	te	Headley 1943
	longispinosus	46	97	te	Headley 1943
Lordomyrma	sp.	13	—	tr	Wilson 1959
Megalomyrmex	*drifti*	9	2	tr	BCI:dibe
	ph	26	1	tr	BCI:megaph
	silvestrii	36	5	tr	BCI:mega1, megafs
Meranoplus	*spinosus*	150	1	tr	Wilson 1959
Monomorium	*rothsteini*	36,500	—	te	Davison 1982
	whitei	20,225	—	te	Davison 1982
Myrmecina	*americana*	24	5	te	Talbot 1957
	transversa	100	1	tr	Wilson 1959
Myrmica	*punctiventris*	86	63	te	Snyder and Herbers 1991
	ruginodis	1,216	12	te	Brian 1950
	schencki emeryana	255	36	te	Talbot 1945
	sulcinodis	167	224	te	Elmes 1987
Myrmicaria	*eumenoides*	19,899	2	tr	Levieux 1983
Myrmicocrypta	*buenzlii*	1,716	1	tr	Weber 1972
Neostruma	*zeteki*	30	34	tr	BCI:strummi
Ocymyrmex	*barbiger*	200	4	te	Marsh 1985
	foreli	873	2	te	Forder and Marsh 1986

623

TABLE A1 (Continued)

Subfamily and Genus	Species	Site	Mean	N	Citation
Oligomyrmex	*overbecki*	tr	400	1	Moffet 1986*b*
	nevermanni	tr	179	1	Wilson 1986
	urichi	tr	783	2	Wilson 1962*b*
Orectognathus	*versicolor*	tr	104	1	Carlin 1981
Pheidole	bic	tr	275	6	BCI:pbic
	BSH	tr	206	3	LS:pbsh
	CCC	tr	375	68	LS:pccc
	CCR	tr	134	5	LS:pccr
	cho	tr	88	40	BCI:pcho
	cramptoni	tr	172	1	LS:pbgc
	dentata	te	946	42	Calabi and Traniello 1989
	DSS	tr	22	3	LS:pdss
	eye	tr	36	4	BCI:peye
	fervida	te	4,635	43	Ito and Higashi 1990
	GLO	tr	44	1	LS:pglo
	hfb	tr	205	4	BCI:phfb
	int	tr	126	33	LS:PANN, PINT
	MGA	tr	152	4	LS:pmga
	MGS	tr	159	1	LS:pmgs
	MIC	tr	62	11	LS:pmic
	MIN	tr	80	4	LS:pmin
	morrisi	te	2,500	—	Johnson 1988
	NEB	tr	61	14	LS:pneb
	NGA	tr	62	52	LS:pnga
	NIT	tr	547	11	LS:pnit
	pallidula	te	1,600	—	Passera 1985
	PEB	tr	300	2	LS:ppeb
	pnig	tr	113	21	LS:pnig
	pnigb	tr	105	56	BCI:pnigb, ppebb
	poc	tr	58	55	BCI:ppocb
	renb	tr	60	4	BCI:prenb
	rpc	tr	60	3	BCI:prpc
	sbi	tr	42	1	BCI:psbi
	sp.	tr	150	1	Wilson 1959
	spe	tr	56	2	LS:pspe
	zeteki	tr	81	2	BCI:prsp

624

Genus	species					Reference
Pheidologeton	diversus		tr	157,000	4	Moffet 1988
	silenus		tr	72,250	4	Moffet 1988
	sp.		tr	6,000	1	Wilson 1959
Pogonomyrmex	badius		te	4,736	25	Gentry and Stiritz 1972
	barbatus		te	12,358	1	Wildermuth and Davis 1931
	californicus		te	4,533	11	Erickson 1972
	imberbiculus		te	21	10	Heinze et al. 1992
	magnacathus		te	163	—	Cole 1968
	marcusi		tr	450	2	Marcus and Marcus 1951
	montanus		te	1,665	70	MacKay 1981
	occidentalis		te	3,024	33	Lavigne 1969
	rugosus		te	7,740	20	MacKay 1981
	subnitidus		te	5,934	26	MacKay 1981
Pristomyrmex	sp.		tr	100	1	Wilson 1959
Proatta	butteli		tr	5,500	—	Moffett 1986a
Procryptocerus	scabriusculus		tr	62	1	Wheeler 1984
Rhoptromyrmex	melleus		tr	10,000	2	Wilson 1959
Rogeria	sp. 1		tr	107	1	BCI:roge1
Sericomyrmex	amabilis		tr	300	—	Wheeler 1925
	urichi		tr	946	—	Weber 1941
Smithistruma	sp. 1		tr	57	8	LS:smit2
	sp. 2		tr	55	3	LS:smit1
	sp. 3		tr	99	1	BCI:smit3
	rostrata		te	72	1	Talbot 1957
	st		tr	26	7	BCI:smitst
Solenopsis	COR		tr	47	27	LS:dicor
	GA		tr	19	4	LS:diga
	invicta		te	220,000	—	Tschinkel 1988
	MI		tr	16	1	LS:dimi
	OR		tr	140	92	BCI:dior
	PL		tr	54	12	LS:dipl
	PO		tr	185	12	LS:dipo
	SO		tr	555	14	LS:diso
	SS		tr	184	33	BCI:diss
	TT		tr	44	55	BCI:ditt
	CO		tr	42	11	LS:dico
Stenamma	diecki		te	41	7	Francoeur 1965
	brevicorne		te	70	10	Talbot 1965
	impar		te	54	8	Talbot 1957
	schmittii		te	121	4	Talbot 1957
	meridionale		te	15	2	Talbot 1957
	sp. 1		tr	12	1	LS:prug

625

TABLE A1 (*Continued*)

Subfamily and Genus	Species	Site	Mean	N	Citation
Strumigenys	*bajarii*	tr	400	1	Wilson 1959
	br	tr	15	1	BCI:strumbr
	frivaldszkyi	tr	15	1	Wilson 1959
	gl	tr	18	2	BCI:strumgl
	lj	tr	16	13	BCI:strumlj
	ljls	tr	48	2	LS:STLJLS
	loriai	tr	400	2	Wilson 1959
	mayri	tr	100	1	Wilson 1959
	mi	tr	48	30	LS:struumil
	nf	tr	26	4	LS:strunf
	sp. 1	tr	80	6	LS:strum1
	wk	tr	26	3	LS:struwk
Terataner	*alluaudi*	tr	27	7	Alpert 1992
	foreli	tr	12	9	Alpert 1992
	sp. a	tr	18	4	Alpert 1992
	sp. b	tr	39	8	Alpert 1992
	sp. c	tr	10	22	Alpert 1992
	sp. d	tr	7	3	Alpert 1992
Tetramorium	*caespitum*	te	10,975	49	Brian et al. 1967
Trachymyrmex	*ruthae*	tr	280	1	Weber 1941
	septentrionalis	te	800	99	Lenczewski 1985
	zeteki	tr	151	1	Weber 1972
Vollenhovia	*brachycera*	tr	150	1	Wilson 1959
Wasmannia	*auropunctata*	tr	839	66	LS:waau; BCI:wabf

NOTE.—N, Total number of colonies used to calculate colony size; dash (—), no sample size is given in the citation. tr, Tropical zone records; te, temperate zone records. Where no citation is listed, collections are by the first author at Barro Colorado Island, Panama (BCI), or La Selva Field Station, Costa Rica (LS). These abbreviations are followed by the code name used for the species deposited in the Museum of Comparative Zoology, Harvard University.

LITERATURE CITED

Alpert, G. D. 1992. Observations on the genus *Terataner* in Madagascar (Hymenoptera: Formicidae). Psyche (Cambridge) 99:117–127.

Ayyar, P. N. K. 1937. A new carton-building species of ant in South India, *Crematogaster dohrni artifex* Mayr. Journal of the Bombay Natural History Society 39:291–308.

Baroni Urbani, C., B. Bolton, and P. S. Ward. 1992. The internal phylogeny of ants (Hymenoptera: Formicidae). Systematic Entomology 17:301–329.

Bergmann, C. 1947. Über die Verhältnisse der Wärmeökonomie der Tiere zu ihrer Groe. Göttinger Studien 1:595–708.

Bonner, J. T. 1988. The evolution of complexity. Princeton University Press, Princeton, N.J.

Boyce, M. S. 1978. Climatic variability and body size variation in the muskrats (*Odatra zibethicus*) of North America. Oecologia (Berlin) 36:1–19.

———. 1979. Seasonality and patterns of natural selection for life histories. American Naturalist 114:564–583.

Breed, M. D., P. Abel, T. J. Bleuze, and S. E. Denton. 1990. Thievery, home ranges, and nestmate recognition in *Ectatomma ruidum*. Oecologia (Berlin) 84:117–121.

Breen, J. 1979. Worker populations of *Formica lugubris* Zett. nests in Irish plantation woods. Ecological Entomology 4:1–7.

Brian, M. V. 1950. The stable winter population structure in species of *Myrmica*. Journal of Animal Ecology 19:119–123.

———. 1965. Social insect populations. Academic Press, London.

Brian, M. V., G. Elmes, and A. F. Kelley. 1967. Populations of the ant *Tetramorium caespitum* Latreille. Journal of Animal Ecology 36:337–342.

Brown, J. H., and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. Science (Washington, D.C.) 243:1145–1150.

Brown, W. L. 1992. Two new species of *Gnamptogenys* and an account of millipede predation by one of them. Psyche (Cambridge) 99:275–286.

Buschinger, A., C. Peeters, and R. H. Crozier. 1989. Life-pattern studies on an Australian *Sphinctomyrmex* (Formicidae: Ponerinae: Cerapachyini): functional polygyny, brood periodicity and raiding behavior. Psyche (Cambridge) 96:287–300.

Calabi, P., and J. F. A. Traniello. 1989. Social organization in the ant *Pheidole dentata:* physical and temporal caste ratios lack ecological correlates. Behavioral Ecology and Sociobiology 24:69–78.

Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press, Cambridge, Mass.

Carlin, N. F. 1981. Polymorphism and division of labor in the dacetine ant *Orectognathus versicolor* (Hymenoptera: Formicidae). Psyche (Cambridge) 88:231–244.

Cole, A. C. 1968. *Pogonomyrmex* harvester ants: a study of the genus in North America. University of Tennessee Press, Knoxville.

Cole, B. J. 1984. Colony efficiency and the reproductivity effect in *Leptothorax allardycei* (Mann). Insectes Sociaux 31:403–407.

Corn, M. L. 1980. Polymorphism and polyethism in the Neotropical ant *Cephalotes atratus*. Insectes Sociaux 27:29–42.

Cory, E. N., and E. E. Haviland. 1938. Population studies of *Formica exsectoides* Forel. Annals of the Entomological Society of America 31:50–57.

Cushman, J. H., J. H. Lawton, and B. F. J. Manly. 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. Oecologia (Berlin) 95:30–37.

Davison, R. C. 1982. Seed utilization by harvester ants. Pages 1–6 *in* R. C. Buckley, eds. Ant-plant interactions in Australia. Junk, The Hague.

Elmes, G. W. 1987. Temporal variation in colony populations of the ant *Myrmica sulcinodis*. I. Changes in queen number, worker number and spring production. Journal of Animal Ecology 56:559–571.

Erickson, J. M. 1972. Mark-recapture techniques for population estimates of *Pogonomyrmex* ant colonies: an evaluation of the ^{32}P technique. Annals of the Entomological Society of America 65:57–61.

Ettershank, G. 1971. Some aspects of the ecology and nest microclimatology of the meat ant, *Iridomyrmex pupureus* (Sm.). Proceedings of the Royal Society of Victoria 84:137–152.

Forder, J. C., and A. C. Marsh. 1986. Social organization and reproduction in *Ocymyrmex foreli* (Formicidae: Myrmicinae). Insectes Sociaux 36:106–115.

Fowler, H. G. 1985. Populations, foraging and territoriality in *Dinoponera australis* (Hymenoptera, Formicidae). Revista Brasiliensis Entomologica 29:443–447.

Francoeur, A. 1965. Ecologie des populations de fourmis dans un bois de chênes rouges et d'érables rouges. Naturaliste Canadien 92:263–276.

Fresneau, D. 1984. Développement ovarien et statut social chez une fourmi primitive *Neoponera obscuricornis*. Insectes Sociaux 31:387–402.

Gentry, J. B., and K. L. Stiritz. 1972. The role of the Florida harvester ant *Pogonomyrmex badius*, in old field mineral nutrient relationships. Environmental Entomology 1:39–41.

Gotwald, W. H., and J. Levieux. 1972. Taxonomy and biology of a new West African ant belonging to the genus *Ambylopone* (Hymenoptera: Formicidae). Annals of the Entomological Society of America 65:383–396.

Gray, B. 1971. Notes on the biology of the ant species *Myrmecia dispar* (Clark) (Hymenoptera: Formicidae). Insectes Sociaux 18:71–80.

Greaves, T., and R. D. Hughes. 1974. The population biology of the meat ant. Journal of the Australian Entomological Society 13:329–351.

Haskins, C. P., and E. F. Haskins. 1950. Notes on the biology and social behavior of the archaic ponerine ants of the genera *Myrmecia* and *Promyrmecia*. Annals of the Entomological Society of America 43:461–491.

Headley, A. E. 1943. Population studies of two species of ants, *Leptothorax longispinosus* (Roger) and *Leptothorax curvispinosus* (Mayr). Annals of the Entomological Society of America 36:743–753.

———. 1949. A population study of the ant *Aphaenogaster fulva* spp. *aquia* Buckley (Hymenoptera: Formicidae). Annals of the Entomological Society of America 42:265–272.

Heinze, J., and D. Ortius. 1991. Social organization of *Leptothorax acervorum* from Alaska (Hymenoptera: Formicidae). Psyche (Cambridge) 98:227–240.

Heinze, J., B. Hölldobler, and S. P. Cover. 1992. Queen polymorphism in the North American harvester ant, *Ephebomyrmex imberbiculus*. Insectes Sociaux 39:267–273.

Herbers, J. M. 1991. The population biology of *Tapinoma minutum* (Hymenoptera: Formicidae) in Australia. Insectes Sociaux 38:195–204.

Higashi, S., and K. Yamauchi. 1979. Influence of a supercolonial ant *Formica (Formica) yessensis* Forel on the distribution of other ants in Ishikari coast. Japanese Journal of Ecology 29: 257–264.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. J. Tosi. 1971. Forest environments in tropical life zones: a pilot study. Pergamon, New York.

Hölldobler, B., and E. O. Wilson. 1986. Ecology and behavior of the primitive cryptobiotic ant *Prionopelta amabilis* (Hymenoptera: Formicidae). Insectes Sociaux 33:45–58.

———. 1990. The ants. Belknap, Cambridge, Mass.

Ito, F. 1991. Preliminary report on queenless reproduction in a primitive ponerine ant *Amblyopone* sp. (*Reclinata* group) in West Java, Indonesia. Psyche (Cambridge) 98:319–322.

Ito, F., and S. Higashi. 1990. Tests of four hypotheses on soldier production, by using wild colonies of *Pheidole fervida* F. Smith (Hymenoptera: Formicidae). Researches in Population Ecology 32:113–117.

Jaffé, K., and M. Marcuse. 1983. Nestmate recognition and territorial behaviour in the ant *Odontomachus bauri* (Emery) (Formicidae: Ponerinae). Insectes Sociaux 30:466–481.

Jaffé, K., M. E. Lopez, and W. Aragort. 1986. On the communication systems of the ants *Pseudomyrmex termitarius* and *P. triplarinus*. Insectes Sociaux 33:105–117.

Janzen, D. H. 1967. Interaction of the bull's-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. University of Kansas Science Bulletin 47:315–558.

Janzen, D. H., and C. R. Carroll. 1983. *Paraponera clavata* (bala, giant tropical ant). Pages 752–753 *in* D. H. Janzen, ed. Costa Rican natural history. University of Chicago Press, Chicago.

Jayasuria, A. K., and J. F. A. Traniello. 1985. The biology of the primitive ant *Aneuretus simoni*

(Emery) (Formicidae: Aneuretinae). I. Distribution, abundance, colony structure, and foraging ecology. Insectes Sociaux 32:363–375.

Jeanne, R. L. 1991. The swarm-founding Polistinae. Pages 191–231 in K. G. Ross and R. W. Matthews, eds. Social biology of wasps. Cornell University Press, Ithaca, N.Y.

Johnson, C. 1988. Colony structure and behavioral observations in *Pheidole morrisi* (Hymenoptera: Formicidae). Pages 371–383 in J. C. Trager, ed. Advances in myrmecology. Brill, Leiden.

Johnston, R. F., and R. K. Selander. 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. Evolution 25:1–28.

Jouvenaz, D. P., G. E. Allen, W. A. Banks, and D. P. Wojcik. 1977. A survey of pathogens of fire ants, *Solenopsis* spp., in the southeastern United States. Florida Entomologist 60:275–279.

Kaspari, M. 1993a. Removal of seeds from Neotropical frugivore droppings: ant responses to seed number. Oecologia (Berlin) 95:81–88.

———. 1993b. Body size and microclimate use in Neotropical ground ants. Oecologia (Berlin) 96:500–507.

Kennedy, C. H., and M. Talbot. 1939. Notes on the hypogaeic ant, *Proceratium silaceum* Roger. Proceedings of the Indiana Academy of Sciences 48:202–210.

Kondoh, M. 1968. Bioeconomic studies on the colony of an ant species, *Formica japonica* Motschulsky. I. Nest structure and seasonal change of the colony members. Japanese Journal of Ecology 18:124–133.

———. 1977. On the difference of vitality among worker ants under starvation. Pages 69–70 in Proceedings of the Eighth International Congress Union of Social Insects.

Kozlowski, J. 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. Trends in Ecology & Evolution 7:15–19.

Lavigne, R. J. 1969. Bionomics and nest structure of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). Annals of the Entomological Society of America 62:1166–1175.

Leigh, E. G., A. S. Rand, and D. M. Windsor. 1982. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C.

Lenczewski, B. 1985. Natural history, colonization and survival in a northern fungus-gardening ant, *Trachymyrmex septentrionalis* (Attini). M.S. thesis. Florida State University, Tallahassee.

Levey, D. J., and M. M. Byrne. 1993. Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. Ecology 74:1802–1812.

Levieux, J. 1976. Etude de la structure du nid de quelques espèces terricoles de fourmis tropicales. Annales de l'Université d'Abidjan, ser. C 12:23–33.

———. 1983. Mode d'exploitation des ressources alimentaires épigées de savanes africaines par la fourmi *Myrmicaria eumenoides* Gerstaecker. Insectes Sociaux 30:165–176.

Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. Evolution 20:456–465.

Lindstedt, S. L., and M. S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. American Naturalist 125:873–878.

MacArthur, R. H. 1972. Geographical ecology. Princeton University Press, Princeton, N.J.

MacKay, W. P. 1981. A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Psyche (Cambridge) 88:25–74.

MacKay, W. P., F. Peres-Dominiguez, L. I. Valdez, and P. V. Orozco. 1984. La biología de *Crematogaster larreae* Buren (Hymenoptera: Formicidae). Folia Entomologia Mexicana 62:75–80.

Marcus, H., and E. E. Marcus. 1951. Los nidos y los organos de estridulacion y de equilibrio de *Pogonomyrmex marcusi* y de *Dorymyrmex emmaericaellus*. Folia Universitaria, Universidad Mayor de San Simon, Cochabamba, Bolivia 5:117–143.

Marsh, A. C. 1985. Microclimatic factors influencing foraging patterns and success of the thermophilic desert ant, *Ocymyrmex barbiger*. Insectes Sociaux 32:286–296.

Martin, M. M., R. M. Carls, R. F. N. Hutchins, J. G. MacConnell, J. S. Martin, and O. D. Steiner. 1967. Observations on *Atta columbica tonsipes* (Hymenoptera: Formicidae). Annals of the Entomological Society of America 60:1329–1330.

Maschwitz, U., and M. Mühlenberg. 1975. Zur Jagdstrategei einiger orientalischer *Leptogenys*-Arten (Formicidae: Ponerinae). Oecologia (Berlin) 20:65–83.

Maschwitz, U., and P. Schönegge. 1983. Forage communication, nest moving recruitment, and prey specialization in the oriental ponerine *Leptogenys chinensis*. Oecologia (Berlin) 57:175–182.

Masuko, K. 1990. Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani (Hymenoptera: Formicidae: Leptanillinae). Insectes Sociaux 37:31–57.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10:105–108.

McNab, B. K. 1971. On the ecological significance of Bergmann's rule. Ecology 52:845–854.

Medeiros, F. N. S., L. E. Lopes, P. R. S. Moutinho, P. S. Oliveira, and B. Hölldobler. 1992. Functional polygyny, agonistic interactions and reproductive dominance in the Neotropical ant *Odontomachus chelifer* (Hymenoptera, Formicidae, Ponerinae). Ethology 91:134–146.

Mill, A. E. 1982. Emigration of a colony of the giant termite hunter *Pachycondyla commutata* (Roger) (Hymenoptera: Formicidae). Entomologist's Monthly Magazine 118:243–245.

Millar, J. S., and G. J. Hickling. 1991. Fasting endurance and the evolution of mammalian body size. Functional Ecology 4:5–12.

Mirenda, J. T., and S. B. Vinson. 1982. Single and multiple queen colonies of imported fire ants in Texas. Southwestern Entomologist 7:135–141.

Moffett, M. W. 1985. Behavioral notes on the asiatic harvesting ants *Acanthomyrmex notabilis* and *A. ferox*. Psyche (Cambridge) 92:165–179.

———. 1986a. Behavior of the group-predatory ant *Proatta butteli* (Hymenoptera: Formicidae), an Old World relative of the attine ants. Insectes Sociaux 33:444–457.

———. 1986b. Notes on the behavior of the dimorphic ant *Oligomyrmex overbecki* (Hymenoptera: Formicidae). Psyche (Cambridge) 93:107–116.

———. 1986c. Trap-jaw predation and other observations on two species of *Myrmoteras* (Hymenoptera: Formicidae). Insectes Sociaux 33:85–99.

———. 1988. Nesting, emigrations, and colony foundation in two group-hunting myrmicine ants (Hymenoptera: Formicidae: *Pheidologeton*). Pages 355–370 in J. C. Trager, ed. Advances in myrmecology. Brill, Leiden.

Murphy, E. C. 1985. Bergmann's rule, seasonality, and geographic variation in body size of house sparrows. Evolution 39:1327–1334.

Nonacs, P. 1991. Less growth with more food: how insect-prey availability changes colony demographics in the ant *Camponotus floridanus*. Journal of Insect Physiology 37:891–898.

Oliveira, P. S., and B. Hölldober. 1990. Dominance orders in the ponerine ant *Pachycondyla apicalis* (Hymenoptera, Formicidae). Behavioral Ecology and Sociobiology 27:385–393.

Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in the social insects. Princeton University Press, Princeton, N.J.

Passera, L. 1985. Soldier determination in ants of the genus *Pheidole*. Pages 331–346 in J. A. L. Watson, B. M. Okot-Kober, and C. Noirot, eds. Caste differentiation in the social insects. Pergamon, New York.

Peeters, C., and R. Crewe. 1987. Foraging and recruitment in ponerine ants: solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera: Formicidae). Psyche (Cambridge) 94:201–214.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.

Porter, S. D., and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71:2095–2106.

Pricer, J. L. 1908. The life history of the carpenter ant. Biological Bulletin of the Marine Biological Laboratory, Woods Hole 14:177–218.

Raignier, A., and J. van Boven. 1955. Etude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera: Formicidae). Annals du Musée Royal du Congo Belge, n.s. 4 (sciences zoologiques) 2:1–359.

Rettenmeyer, C. W. 1963. Behavioral studies of army ants. University of Kansas Science Bulletin 44:281–465.

Richards, O. W. 1953. The care of the young and the development of social life in the Hymenoptera. Transactions of the Ninth International Congress of Entomology 2:135–138.

Roonwal, M. L. 1954. On the structure and population of the nest of the common tree ant *Crematogas-*

ter dohrni rogenhoferi Mayr (Hymenoptera, Formicidae). Journal of the Bombay Natural History Society 52:354–364.

Sanders, C. J. 1970. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. Ecology 51:865–873.

Schneirla, T. C. 1957. A comparison of species and genera in the ant subfamily Dorylinae with respect to functional pattern. Insectes Sociaux 4:259–298.

———, ed. 1971. Army ants: a study in social organization. W. H. Freeman, San Francisco.

Schoener, T. W., and D. H. Janzen. 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. American Naturalist 102:206–224.

Scholander, P. F. 1955. Evolution of climatic adaptations in homeotherms. Evolution 9:15–26.

Snyder, L. E., and J. M. Herbers. 1991. Polydomy and sexual allocation ratios in the ant *Myrmica punctiventris*. Behavioral Ecology and Sociobiology 28:409–415.

Sorenson, A. A., T. M. Busch, and S. B. Vinson. 1983. Factors affecting brood cannibalism in laboratory colonies of the imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 56:140–150.

Talbot, M. 1943. Population studies of the ant *Prenolepis imparis* Say. Ecology 24:31–44.

———. 1945. Population studies of the ant *Myrmica schencki* spp. *emeryana* Forel. Annals of the Entomological Society of America 38:365–372.

———. 1948. A comparison of two ants of the genus *Formica*. Ecology 29:316–325.

———. 1951. Populations and hibernating conditions of the ant *Aphaenogaster (Attomyrma) rudis* Emery (Hymenoptera: Formicidae). Annals of the Entomological Society of America 44: 302–307.

———. 1954. Populations of the ant *Aphaenogaster (Attomyrma) treatae* Forel on abandoned fields on the Edwin S. George Preserve. Contributions from the Laboratory of Vertebrate Biology of the University of Michigan 69:1–9.

———. 1957. Populations of ants in a Missouri woodland. Insectes Sociaux 4:375–384.

———. 1965. Populations of ants in a low field. Insectes Sociaux 12:19–48.

Taylor, R. W. 1978. *Nothomyrmecia macrops:* a living-fossil ant rediscovered. Science (Washington, D.C.) 201:979–985.

Threlkeld, S. T. 1976. Starvation and the size structure of zooplankton communities. Freshwater Biology 6:489–496.

Tschinkel, W. R. 1987. Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. Insectes Sociaux 34:143–164.

———. 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. Behavioral Ecology and Sociobiology 22:103–115.

———. 1991. Insect sociometry, a field in search of data. Insectes Sociaux 38:77–82.

Villet, M. H., R. M. Crewe, and F. D. Duncan. 1991. Evolutionary trends in the reproductive biology of ponerine ants (Hymenoptera: Formicidae). Journal of Natural History 25:1603–1610.

Wallis, D. L. 1964. The foraging behavior of the ant *Formica fusca*. Behaviour 23:149–175.

Ward, P. S. 1981. Ecology and life history of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae). II. Colony origin, seasonal cycles, and reproduction. Psyche (Cambridge) 88: 109–126.

Ware, A. B., S. G. Compton, and H. G. Robertson. 1990. Gamergate reproduction in the ant *Streblognathus aethiopicus* Smith (Hymenoptera: Formicidae: Ponerinae). Insectes Sociaux 37: 189–199.

Way, M. J. 1954. Studies of the life history and ecology of the ant *Oecophylla longinoda* Latreille. Bulletin of Entomological Research 45:93–112.

Weber, N. A. 1941. The biology of the fungus-growing ants. VII. The Barro Colorado Island, Canal Zone, species. Revista de Entomologia 12:93–130.

———. 1947. Lower Orinoco River fungus-growing ants (Hymenoptera: Formicidae, Attini). Boletin de Entomologia Venezolana 6:143–161.

———. 1972. Gardening ants: the attines. Memoirs of the American Philosophical Society. Vol. 92. American Philosophical Society, Philadelphia.

Wheeler, D. E. 1984. Behavior of the ant, *Procryptocerus scabriusculus* (Hymenoptera: Formicidae), with comparisons to other cephalotines. Psyche (Cambridge) 91:171–192.

Wheeler, W. M. 1925. A new guest-ant and other new Formicidae from Barro Colorado Island, Panama. Biological Bulletin of the Marine Biological Laboratory, Woods Hole 49:150–181.

Wildermuth, V. L., and E. G. Davis. 1931. The red harvester ant and how to subdue it. Farmer's Bulletin, U.S. Department of Agriculture 1668:1–12.

Wildman, M. H., and R. M. Crewe. 1988. Gamergate number and control over reproduction in *Pachydondyla krugeri* (Hymenoptera: Formicidae). Insectes Sociaux 35:217–225.

Wilson, E. O. 1959. Some ecological characteristics of ants in New Guinea rain forests. Ecology 40:437–447.

———. 1962a. Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. Bulletin of the Museum of Comparative Zoology, Harvard University 127:401–422.

———. 1962b. The Trinidad cave ant *Erebomyrma (= Spelaeomyrmex) urichi* (Wheeler), with a comment on cavernicolous ants in general. Psyche (Cambridge) 69:63–72.

———. 1971. The insect societies. Belknap, Cambridge, Mass.

———. 1986. Caste and division of labor in *Erebomyrma,* a genus of dimorphic ants (Hymenoptera: Formicidae: Myrmicinae). Insectes Sociaux 33:59–69.

Wilson, E. O., and B. Hölldobler. 1986. Ecology and behavior of the Neotropical cryptobiotic ant *Basiceros manni* (Hymenoptera: Formicidae: Basicerotini). Insectes Sociaux 33:70–84.

Yamauchi, K., Y. Ito, K. Kinomura, and H. Takamine. 1987. Polycalic colonies of the weaver ant *Polyrachis dives.* Kontyû, Tokyo 55:410–420.

Associate Editor: Nancy A. Moran