ANTS

STANDARD METHODS FOR MEASURING AND MONITORING BIODIVERSITY

EDITED BY DONAT AGOSTI, JONATHAN D. MAJER, LEEANNE E. ALONSO, AND TED R. SCHULTZ

FOREWORD BY EDWARD O. WILSON
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STANDARD METHODS FOR MEASURING AND MONITORING BIODIVERSITY
Biological Diversity Handbook Series

Series Editor: Don E. Wilson

This series of manuals details standard field methods for qualitative and quantitative sampling of biological diversity. Volumes focus on different groups of organisms, both plants and animals. The goal of the series is to identify or, where necessary, develop these methods and promote their adoption worldwide, so that biodiversity information will be comparable across study sites, geographic areas, and organisms, and at the same site, through time.
This book is dedicated to the memory of William L. Brown Jr., with affection, respect, and gratitude. For the inspiration you provided, for the firm foundation you built for ant systematics, and especially for your generous soul and irreverent good humor, we will never forget you, Bill.
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Ecological assemblages are in a constant state of flux. Individuals reproduce and die. Populations cycle and are buffeted by factors ranging from random to predictable. Species are introduced and go extinct. Parts of the landscape are disturbed and recover. The role of human perturbation in this dynamic is not new, nor is it restricted to advanced industrial societies. But the availability of cheap energy combined with human population pressures has produced agriculture, urbanization, and resource extraction on a grand scale. As a result, habitats are increasingly changed and fragmented. Introduced species invade these disturbed areas and infiltrate pristine habitats. Waste products that result from the production and use of this "cheap" energy accumulate in the soil, water, and atmosphere.

The Challenge

Society calls upon the ecologist and resource manager primarily to do two things. First, we are asked to monitor extant, pristine environments and warn society of looming change. But ecosystems naturally vary in almost every property. We require a detailed "baseline" so as not to cry wolf every time a population dips or becomes locally extinct. In other words, ecologists need an expectation of normalcy and a protocol to achieve it. Second, ecologists and resource managers are presented with degraded ecosystems in various stages of recovery and asked to evaluate the reconstruction of these ecosystems.

Central to both endeavors is an understanding of the variability inherent in ecosystems. But
ecosystems are complex, dynamic things, with countless taxa exhibiting an array of interactions between organisms and the abiotic environment. As described in Chapter 6, selected taxa are often used as indicators of the diversity or ecological responses of other taxa and sometimes even as representatives of an entire ecosystem. In monitoring environmental change, taxa that are hypersensitive to perturbations (Kareiva et al. 1993) are most often chosen. Spellerberg (1991) suggests a set of criteria for including taxa in a monitoring program.

Ants are an ideal indicator group for inclusion in such a program. Many ant species have narrow tolerances and thus respond quickly to environmental change. Ants' small size and reliance on relatively high temperatures make them especially sensitive to climate and microclimate change. In addition, some ant colonies are long lived and have permanent nests that can be marked and revisited. Long-lived species thus allow us to monitor the health of a colony as the environment changes around it. In contrast, short-lived ant species may show high turnover and immediate responses to a stressor. Ant assemblages, therefore, allow a monitoring program that is sensitive to change on a number of temporal scales. (See Chapter 6 for other attributes of ants as an indicator taxon.)

Here we explore the potential role for ground-dwelling ant assemblages in programs aimed at monitoring environmental change and evaluating remediation (recovery) efforts. We first review the evidence for long-term stability in ant assemblages. We then review how ant assemblages have been used to study remediation efforts after perturbation. We conclude with modest suggestions—based on our best evidence and a fair bit of conjecture—of the properties of ant assemblages that would be most valuable for a successful environmental monitoring program.

Baseline Change: Variable Ant Populations in a Changing World

The assumption of any monitoring program is that a pristine ecosystem is sensitive to changing conditions. Remediation programs attempt to reconstruct ecosystems that behave, to some degree of accuracy, like pristine systems. The point of baseline monitoring studies, as controls for remediation or as worthy endeavors in themselves, is to determine the degree to which ecosystem properties (e.g., productivity, biomass, species composition and richness) vary naturally. Even if populations fluctuate wildly, such a “fuzzy target” becomes our expectation of normalcy and should temper our interpretation of any remediation effort.

To assess this variability, we need long-term data sets, ideally greater than the average lifespan of our longest-lived organism (Connell and Sousa 1983). Such data sets are rare. This section summarizes a few studies that followed ant populations or assemblages for at least four years. In each, we look for evidence of stasis in population trends and community dominance. We find, instead, dynamic populations and assemblages. At least one study points to long-term trends in climate as a potential cause for these ecosystem changes.

A Neotropical Ant Guard Assemblage

In a Neotropical second-growth rainforest, ants were monitored attending *Calathea ovandensis*, an understory herb (Horvitz and Schemske 1990). The flowers of *C. ovandensis* produce a sugary solution that attracts ants. These ants, in turn, remove herbivores from *Calathea*. Four plots, from 25 to 64 m² in area and from 80 to 250 m apart, were monitored every two weeks from 1983 through 1986. Inflorescences were surveyed for ants. In effect, Horvitz and Schemske report data from a four-year bait study. Their results are sobering.
Such fluctuations in insect numbers are common (Andrewartha and Birch 1954). For example, in a 14-year light trap sample on Barro Colorado Island, Panama, one in five Homoptera species showed a 10% change in numbers (Wolda 1992). Do these changes represent normal variation around an equilibrium (hence “baseline” variation)? Or are the Homoptera “indicating” subtle changes in the forest? This is, as we shall see, a basic problem in interpreting monitoring data. Interestingly, even as individual species waxed and waned, Wolda found that two measures of species richness were rather constant.

Two Northern Harvester Ants
The remaining studies all come from arid North America. All resulted from counts of large, soil-nesting species that build conspicuous nest mounds. Two population studies come from northern desert-grasslands, two from southern desert-grasslands. The former two feature the genus _Pogonomyrmex_, harvester ants that construct nest disks and mounds of fine gravel. These harvester ants store large quantities of seeds in underground middens.

A population of _Pogonomyrmex salinus_ was monitored in a Great Basin sagebrush habitat in Idaho (Porter and Jorgensen 1988). Mounds were censused on three plots (two of 0.25 ha and one of 2.72 ha) three times over 9 years. The populations varied little from 1977 to 1986, although there was considerable population turnover (Fig. 7.2).

In shortgrass prairie of Nebraska a population of _Pogonomyrmex occidentalis_ was monitored in a 1-ha plot (Keeler 1993). Mounds were marked and censused yearly for 15 years. In contrast to those of _P. salinus_, _P. occidentalis_ densities at this site increased 41% from 1977 to 1991, during a period of no apparent change in grazing pressure or site characteristics but higher than average rainfall (K. Keeler, pers. comm.). The causes of this increase are unknown.
Two Studies from the Chihuahuan Desert

Two more long-term studies reflect how different investigators focusing on different species may achieve complementary results. Chew and De Vita (1980) studied three species (Aphaenogaster cockerelli, Myrmecocystus depilis, and M. mexicanus) in Chihuahua desert scrub. A 9.3-ha cattle exclosure was censused six times over 23 years. One species, the diurnal M. depilis, varied in density about 50%, while the numbers of its congener M. mexicanus increased 11-fold (Fig. 7.3a). A. cockerelli, in contrast, was locally extirpated over the same time period. The increase of M. mexicanus, given its negative association in space with the other two species, suggested competitive release from A. cockerelli, but there was little to suggest why the assemblage had changed.

A second experiment nearby found evidence for major reorganization of species composition over 18 years (Brown et al. 1997). Brown and colleagues followed the responses of plants, rodents, ants, and birds to various experimental treatments on a set of 0.25-ha plots. On the site’s control plots, the numbers of two harvester ants, Pogonomyrmex rugosus and P. desertorum, decreased over the 18 years (Fig. 7.3b). P. rugosus, like A. cockerelli in the previous study, went locally extinct. A third species, Pheidole xerophila, though showing threefold variation in density, had no downward trend. These changes in ant composition occurred at the same time as a threefold increase in shrub cover and shifting abundance of a number of dominant rodent species. Changes in ant and rodent densities appeared to ramify throughout the desert community, affecting horned lizards (which prey on P. rugosus) and burrowing owls (which nest in rodent burrows).

Brown et al. (1997) link these community changes to an increase in winter rainfall from four El Niño years. The increased winter rainfall favors shrubs at the expense of desert grasses, and it may wet and ruin the stored seeds of harvester ants such as Pogonomyrmex and Aphaenogaster. As in Wolda’s study of Panama light traps, such profound changes in species composition in this ecosystem yielded little change in species richness (Valone and Brown 1995). In both cases, the loss of some species may be compensated by the arrival of others.

Recovery from Perturbation: Inertia, Resilience, and Nonlinearities

We now turn to studies of ecosystems recovering from stressors. For our purposes, a stressor is anything that alters the ecosystem properties of a site relative to a control site. Stressors create a perturbation; the site recovers to some degree once the stressor is removed. Given the inherent variability of ecosystems (as we have seen previously), monitoring site recovery
Figure 7.3. Changes in two Chihuahuan desert ant assemblages as reported by (a) Chew and De Vita (1980) and (b) Brown et al. (1997). In both systems, over roughly the same time period, populations of seed-harvesting ants decreased.

requires the simultaneous monitoring of multiple control sites. Over time, one accumulates data on the trajectories of both control and perturbed sites with the goal of determining when those trajectories have converged.

The trajectory taken by each disturbed ecosystem is by definition unique. However, all have a number of features that can be quantified by a monitoring program and measured against control sites. To discuss these features, we use the metaphor of a spring stretched and allowed to recoil. The resulting terminology has been elegantly set forth by Westman (1986), and we develop some of his terminology in the following sections (Fig. 7.4).

Inertia

Inertia reflects the ability of an ecosystem to retain its properties in the face of a stressor. Some ecosystem properties are highly sensitive to certain stressors. For example, in response to chemical pollution, a lake’s species richness is likely to change more rapidly than its produc-

Figure 7.4. Model illustrating the response of an ecosystem to perturbation using the terminology of Westman (1986). A number of control assemblages (with error bars) are compared with two disturbed assemblages, before and after the stressor. One assemblage (labeled High inertia) has high inertia and resilience—responding less to the stressor and quickly attaining properties of the control assemblages. The other (labeled Low inertia) has low inertia and resilience and fails to recover control conditions completely. It is considered more malleable and may have reached an alternate equilibrium point.
tivity (Schindler 1990). In this case, species richness has low inertia and may be an important property to monitor, as it is often the harbinger of more profound and irreversible ecosystem changes.

Properties of ant assemblages show different degrees of inertia relative to similar stressors. For example, an Australian mallee ant assemblage retained its entire species complement following a hot woodland fire (Andersen and Yen 1985). An ant assemblage in an English heathland, in contrast, was dramatically changed by fire (Brian et al. 1976). Likewise, logging will likely have a greater impact on insect diversity in a Neotropical forest, where the canopy is rich with insects (including ants), than in a temperate pine woodland, where insect diversity may be concentrated on the ground (Jeanne 1979; Erwin 1986; Blackburn et al. 1990). Thus one of the first steps in a remediation program is to determine the actual impact of the stressor.

Resilience

Resilience reflects an ecosystem’s ability to recover the properties of matched control sites. Resilient ecosystems recover quickly and converge on original ecosystem properties. What properties of ant assemblages yield high resilience?

One important factor appears to be rainfall (Fig. 7.5). Species richness on six 3-year-old mine sites increased most rapidly in sites with the highest amount of rainfall (Majer 1992). In tropical rainforests, wetter sites with higher productivity and higher levels of ant activity recovered ant density and diversity on 1-m² plots more quickly than drier sites (Kaspari 1996a). Ant density and diversity in rainforests may be quite resilient to drought. A severe El Niño drought in a seasonal Panama rainforest decreased ant densities to their lowest recorded values (as measured by Berlese funnels), yet the drought’s signature had disappeared only a few weeks into the wet season (Wheeler and Levings 1988). Recovery of drier sites may be much slower without extra remediation efforts.

A second factor that must enhance resilience is proximity of the disturbed area to sources of new immigrants, or “propagules” (MacArthur and Wilson 1967). Large-scale perturbations should recover species richness more slowly than small-scale perturbations embedded within pristine habitat. Species richness of ants in recovering bauxite mines decreased with increasing distances from the forest border (Majer 1980). The processes by which species richness—and other properties such as productivity and biomass—may recover from perturbation deserve further investigation.

Malleability

Some disturbed ecosystems may never recover to control levels. Instead, they may reach a different, stable set of properties. Malleability is the difference between the disturbed ecosystem’s final properties and those of the control plots. The greater the difference, the more malleable the ecosystem (Westman 1986).
Malleability is a function of the stressor and the ecosystem. In one study, ant colonization was followed over 30 rehabilitated bauxite mines (Majer et al. 1984). One site had been accidentally cleared and revegetated with pines, with no mining having taken place. Ten years after restoration the species richness of ants in this plot was high relative to that of mined plots of similar age that had also been planted with pines (means of 12 and 10.5 species per transect respectively). Preservation of the original soil profile may have reduced that site’s malleability.

Yet who is to say that temporary periods of stasis will not give way to further convergence of disturbed sites on control sites? Data cited in the next section should make one view short-term dynamics with caution.

**Oscillations and Other Nonlinear Behavior**

Just as a perturbed spring may oscillate before reaching an equilibrium, so may an ecosystem’s properties fluctuate following a perturbation. Species richness in particular may be highest at intermediate time periods following perturbation (Connell 1978). If so, then remediation projects that use species richness alone to gauge success may end prematurely.

Ant assemblages in postmining ecosystems commonly show sharp fluctuations in species richness, as dominant species are lost and replaced. In the next two examples, species richness on recovering mining sites shows opposite yet symmetric relationships between age and species diversity.

One site, a dune system in Queensland, Australia, increased in species richness from the cessation of mining up to year 8 (Fig. 7.6). In that year there was an abrupt increase in the population of the multiple-queen tramp ant *Pheidole megacephala*. Like other introduced species (see Chapters 2 and 4), *P. megacephala* frequents disturbed ecosystems and can have major effects on the local ant assemblage. The arrival of *P. megacephala* at this site was accompanied by an equally abrupt decrease in species richness and the introduction of new species into the newly depauperate assemblage (Majer 1985).

In another dune-heath system in New South Wales, Australia, Fox and Fox (1982) found a gradual decrease in species diversity after the cessation of mining. The cause was another dominant ant, a territorial *Iridomyrmex* that gradually increased in abundance for 8 years. Then, in year 9, this species was replaced by another *Iridomyrmex* species. This dramatic switch was accompanied by an increase in species diversity. In both cases, species diversity seemed to hinge on the identity of the dominant species. Succession in ant assemblages, then, may not always represent the gradual accumulation of species (Haskins and Haskins 1988).

Oscillations and nonlinearities in ecosystem properties create problems for the design of
remediation studies. In addition to oscillations in species richness, the assemblage can exhibit nonlinear trends in species composition during succession. A study of ants in rehabilitated mine sites at Richard's Bay, South Africa, illustrates this phenomenon. Here a mosaic of cleared and pristine coastal dune forest is being mined for mineral sands. The company is attempting to rehabilitate much of the area to coastal dune forest by planting forest species and species that follow shifting cultivation-type farming. Ordination—which collapses species lists into fewer, descriptive, variables—was used to study succession in plots ranging from 0.3 to 13 years old (plus three forest controls). The first part of the succession was not "directed" toward the original forest assemblage. Rather, only in the older plots does the ant assemblage start to resemble that of the original forest. Again, introduced species played a role. Early stages were dominated by *P. megacephala*, which progressively attains massive densities in the youngest rehabilitation. As the tramp ant declines to negligible levels from years 6 to 13, species composition approaches that of the control plots (Majer and de Kock 1992).

we are far from understanding ecosystem dynamics, a series of control plots is vital to creating a realistic target for remediation. Such control plots, aside from allowing the monitoring of a remediation program, will also provide society with much-needed long-term baseline ecological data (Palmer et al. 1997).

2. Stressors come in many spatial scales. Apart from local perturbation, such as timber harvesting or mining, large-scale changes in the environment, such as the accumulation of greenhouse gases, may be changing the abiotic environment. Hence control plots will also likely change, albeit at a slower rate.

3. A key strategy for enhancing remediation may be the control of introduced ant species such as *Pheidole megacephala* and *Solenopsis wagneri* (=*S. invicta*). On the other hand, if those hardy species are able to modify the environment (e.g., through soil preparation), they may be valuable remediation tools.

4. Arid ecosystems may take longer to reconstruct.

### Lessons from Baseline and Perturbation Studies

The emerging picture from long-term studies of ant assemblages in both disturbed and pristine ecosystems is one of flux. A close study of Fig. 7.6 should give any ecologist pause—a progress report written in year 6 would look dramatically different from one written two years later.

Some tentative lessons from these case histories include the following:

1. Populations and assemblages are dynamic entities and may be highly sensitive to the way in which they are constructed. Since

### What to Measure?

#### A Cautious Assessment

One admonition in conservation biology is to "save all the parts." That is, in something as complex as an ecosystem the loss of any part may have unintended consequences. A conservative approach would therefore be to try not to lose any species.

Ecologists monitoring an ecosystem face a similar problem. We are asked to define an expectation of normalcy for an ecosystem when the critical elements that hold an ecosystem together—if indeed there is such a class of elements—are still poorly known. Little wonder that Spellerberg's (1991) first rule of ecosystem
monitoring is “Any variable or process which can be readily measured and dated may be valuable in detecting changes in ecosystems.” A corollary to “save all the parts” thus seems to be “monitor everything you can.” However, all monitoring programs are limited by time, money, and taxonomists.

Given the sensitivity of ant assemblages outlined in this chapter, we argue that ants would be an ideal animal group to monitor in an ecosystem. But what aspects of an ant assemblage should be monitored? We suggest a set of three parameters—those of individuals, populations, and diversity.

**Individual-Based Changes in Ant Assemblages**

Individual organisms can be collected and assessed for physiological responses to environmental change. In long-lived colonies (e.g., the harvester ant *Pogonomyrmex*) the same colony can be monitored over many years. This might be especially useful if early warnings of stressors are first reflected at the individual level.

Thus far such studies in ant ecology have been rare. However, there are a number of properties of individual colonies that might be monitored. One is colony activity. If it is sampled at the same time every year, in similar weather, a concerted decline in the numbers of foragers recorded outside a colony may suggest pathology long before the colonies die.

A second possibility is deformation of individual workers. A promising new field in conservation biology is the study of fluctuating asymmetry (Palmer and Strobeck 1986; Leary and Allendorf 1989). Organisms tend to develop symmetrically (i.e., their right and left sides are mirror images of each other). Environmental stressors can disturb this development and cause asymmetry. Yearly samples of large, long-lived species may thus detect changes in symmetry in colonies exposed to stressors compared to controls. Working on social insects has the added benefit of holding the genotype constant as the environment changes.

**Population-Based Changes in Ant Assemblages**

Within any diverse assemblage there are likely to be species that are acutely sensitive to a variety of stressors (Carpenter et al. 1993; Tilman 1996). A monitoring program focusing on the population responses of these species stands a good chance of picking up the effects of stressors on ecosystem function long before permanent damage is done (Schindler 1990).

Measurements of colony density—based on quadrat sampling, coupled with hand, Winkler, or Berlese extraction (Chapter 9)—probably remain the best foundation on which to build an ant population monitoring program, because of the quadrat’s lack of ambiguity. The more indirect and relative the estimate of abundance (e.g., that arrived at using baits or pitfall traps), the harder it is to interpret changes in numbers (see Fig. 7.1).

Large-colony species like the harvester ants may be relatively easy to detect and should be part of any monitoring program. Small-colony species, such as those that nest in the litter, are also readily sampled using a quadrat-based method. Combined, the two groups of species would monitor for change on a variety of spatial and temporal scales.

Certain species may characterize pristine ecosystems (Chapter 6). If so, the abundance of those species should be an index of an ecosystem’s recovery from perturbation. Such an index (percentage recovery of target species) may be used to gauge recovery. Ordination methods, which can detect trends in (or add weighting to) target species, might be used to detect such trends (see Chapter 13).

**Diversity-Based Changes in Ant Assemblages**

Monitoring has often focused on some measure of diversity, be it the number of species (species
richness), the makeup of the species in the assemblage (species composition), or some index reflecting a combination of these two values.

Species richness (the number of species in a given area and time), as we have seen, is a tricky measure upon which to base a monitoring program for at least two reasons. First, species richness is often a nonlinear function of time and is expected to overshoot the control plots during the course of recovery. As a result, remediation programs may be halted prematurely when control species richness equals that of the recovering plots. For example, recovering bauxite and manganese mines may yield ant assemblages whose species richness approaches that of control sites after 7.5 years. But these sites can have quite different species (Majer 1984). Second, species richness may remain constant even while the assemblage undergoes major restructuring (Brown et al. 1997).

The use of species richness has its advantages, including its relative lack of ambiguity and its already wide use. We suggest that it be incorporated, but not relied upon solely, as one index among many in a monitoring program. Andersen (Chapter 3; 1997b) advocates ant functional groups (collections of species based on an amalgam of phylogeny, habitat, and microclimate) as another potential index.

Conclusion

The study of ecology, although it has made great strides in the past hundred years, is still coming to grips with the complexity of ecosystems—a complexity manifest in the intricate dynamics we have reviewed in this chapter. We feel that the three sampling approaches just highlighted—based on individuals, populations, and diversity—will likely capture much of the phenomena required to describe and reconstruct ecosystem structure and function. We also foresee that attempts at ecosystem remediation, and the monitoring they require, will only increase our understanding of these dynamics and point to relationships yet unknown. Many, if not most, of the profound advances in ecosystem and community ecology will come from these tentative applications of our current understanding (Palmer et al. 1997).
Literature Cited

———. 1991. Revision of the oriental ant genus Cladomyrma, with an outline of the higher classification of the Formicinae (Hymenoptera:


———. 1970. Review of the ant genus Myrmica (Hymenoptera, Formicidae) in the European part of the USSR. Zoologicheskii Zhurnal 49:1829–1844. [In Russian.]


Balazy, S., A. Lenoir, and J. Wisniewski. 1986. Aegeriella oussillonensis n. sp. (Hyphomycetes, Blastosporae), une espèce nouvelle de champignon epizoïque sur les fourmis Cata-


———. 1978b. Materiali per una revisione dei Lepothorax neotropicali appartenenti al sotto-


———. 1978b. Materiali per una revisione dei Lepothorax neotropicali appartenenti al sotto-


———. 1976. The ant tribe Tetramorini (Hymenoptera: Formicidae). Constituent genera, review of smaller genera and revision of Triglyphothrix


---. 1978. Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe


on ant diversity and distribution on Santa Cruz Island, Galapagos. Biotropica 14:196–207.


Dlussky, G. M. 1964. The ants of the subgenus Coptoforimmica of the genus Formica (Hymenoptera, Formicidae) of the USSR. Zoologicheskii Zhurnal 43:1026–1040. [In Russian.]


Erickson, J. M. 1971. The displacement of native ant species by the introduced Argentine ant Iridomyrmex humilis Mayr. Psyche (Cambridge) 78:257–266.
Gadagkar, R., P. Nair, K. Chandrasekhar, and D. M. Bhat. 1993. Ant species richness and diver-
sity in some selected localities in Western Ghats, India. Hexapoda 5:79–94.


Huxley, C. R. 1978. The ant-plants Myrmecodia and Hydrophytum (Rubieaeae), and the relationships between their morphology, ant occupants, physiology and ecology. New Phytologist 80:231–268.


Linnaeus, C. 1758–1759. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis (10th ed.). Homiae, Salvii. 2v.


Ogata, K. 1982. Taxonomic study of the ant genus Pheidole Westwood of Japan, with a description


———. 1989b. Ants of the *Plagiolepis* genus of the European part of the USSR. Zoologicheski Zhurnal 68(9):153–156. [In Russian.]


———. 1979a. Three new species of the Palaeotropical arboreal ant genus *Cataulacus* (Hyme-


Tillyard, R. J. 1926. The Insects of Australia and New Zealand. Angus and Robertson, Sydney.


———. 1990. The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): Generic revi-
—. 1993. Systematic studies on *Pseudomyrmex* acacia-ants (Hymenoptera: Formicidae: Pseudo-
—. 1994. *Adetomyrma*, an enigmatic new ant
genus from Madagascar (Hymenoptera: Formicidae), and its implications for ant phylogeny. Systematic Entomology 19:159–175.
—. 1977. The species and subspecies of *Noma-
—. 1982. The army ants of Mexico (Hyme-
Weber, N. A. 1943. Parabiosis in Neotropical “ant


———. 1957. A second look at the ants of the *Camponotus herculeanus* group in eastern Asia. Journal of the Faculty of Agriculture, Kyushu University 11:45–51.


