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The Role of Ants and Termites in Desert Communities

5

William P. MacKay

Ants and termites are among the most abundant animals in most terrestrial habitats and may be the dominant insects in many ecosystems (MacKay 1981; MacKay, Zak, and Whitford 1989). Wilson (1985) estimated that one-third of the animal biomass of the Amazonian terra firma rain forest is composed of ants and termites. One ha of soil in such regions may contain more than eight million ants and one million termites. It is not only their dominance in numbers and biomass that makes these insects important in ecosystems, but also their activity. These groups can concentrate more energy at critical points than can any single competitor; they use sheer numbers to construct nests in suboptimal habitats as well as defend young and retrieve food efficiently (Wilson 1985).

Ants are one of the major components in desert ecosystems (Pisarski 1978; Crawford 1981; Briese 1982c; Reyes Lopez 1987), yet most information on their importance is purely descriptive (Baroni Urbani and Aktac 1981) and few studies have documented the relative abundance of species within a community (Marsh 1985a). Ants are the leading predators of other insects and invertebrates in many habitats (Wilson 1985). Seed harvesters are especially abundant and important in arid habitats (Briese 1982c). Schumacher and Whitford (1976) estimated ant colony densities of up to 4,000 colonies/ha in the northern Chihuahuan Desert of North America. In the Ivory Coast dry savanna there are 20 million ants/ha with a single species (*Camponotus acvapimensis*) accounting for 2 million (Levieux 1981). In the western Sahara, individual ants account for 75 percent of the whole fauna (in numbers) (Bernard 1972).

The ecology of termites has received little attention (Lee and Wood 1971b), but has recently been summarized (Krishna and Weesner 1969, 1970; Brian 1978). The

limitations in knowledge about desert termites must be stressed (Harris 1970); however, they have been shown to be important in nutrient cycling and organic matter processing, and for the effects of their tunnels on soil properties and chemistry (Holt 1987; Nutting, Haverty, and La Fage 1987; MacKay, Zak, and Whitford 1989). Termites are by far the most important invertebrate decomposers in semiarid Australia (Holt 1987) and the northern Chihuahuan Desert of North America (MacKay, Zak, and Whitford 1989). *Heterotermes aureus* and *Gnathamitermes perplexus* are the dominant organisms involved in soil turnover, litter decomposition, and nutrient cycling in the Sonoran Desert of North America (Nutting et al. 1987).

Desert termites are especially difficult to study because most species are primarily subterranean. In addition to the lack of knowledge concerning the habits of termites, the taxonomy is in a state of chaos. Due to intraspecific variability and the importance of obtaining soldiers and winged reproductives for proper identification, it is difficult to identify termites and thus to study their ecology.

Both ants and termites are very important in terms of biomass (Table 5.1). In many desert locations the mass is an order of magnitude greater than the mass of the mammalian herbivore population (Lee and Wood 1971b; Wood and Sands 1978; MacKay, Zak, and Whitford 1989). The biomass of *Gnathamitermes tubiformans* exceeds that of cattle in the northern Chihuahuan Desert (MacKay, Zak, and Whitford 1989). The termite biomass in a Sahel savanna site (0.96 g/m²) exceeds that of all other dominant aboveground arthropods (0.3 g/m²) and birds (0.3–0.6 g/m²), but is less than the biomass of domestic stock and herbivorous mammals (2.0–3.0 g/m²) (Lepage 1974, cited in Wood and Sands 1978). Few estimates are available on the biomass of social insects in arid ecosystems, but apparently social insects are important in arid ecosystems and biomass of termites is higher than that of ants (Table 5.1).

It has been suggested that the struggle to exist in the harsh physical environments of deserts so dominates the ecology of desert organisms that interactions between species are insignificant (Brown, Reichman, and Davidson 1979). This chapter will show this is clearly not the case with social insects: interspecific interactions are very important in desert ecosystems.

Species Richness and Diversity of Social Insects in Arid Regions

Although some authors conclude that ant species richness is low in desert ecosystems (Pisarski 1978), recent studies show an amazingly diverse fauna in arid regions. Chew (1977) found 23 species in a 30.3-m² grid in the Chihuahuan Desert of Arizona. More than 50 species were collected along a 3-km-long transect in the Chihuahuan Desert of New Mexico, including three undescribed species (MacKay, Van Vactor, and Whitford n.d.). Wheeler and Wheeler (1973) collected 59 species of ants in a single desert canyon in California. Ant species richness is especially high in arid regions of Australia. Anderson (1983, 1986) collected 150 species in an area of less than 1 ha. Australian deserts have more than double the species richness of North American deserts, although the within-habitat diversity in Australian arid zones is about the same (Morton 1982). High species richness may be due to the low density

Table 5.1 Maximum estimates of biomasses of ants and termites in terrestrial ecosystems.

Species	Habitat	Biomass (g/m²)	Source
ANTS			
Pogonomyrmex californicus	Chihuahuan Desert (U.S.)	0.001	Whitford 1972
Pogonomyrmex californicus	Chaparral (U.S.)	0.003	Erickson 1972
Pogonomyrmex montanus	Pine forest (U.S.)	0.01	MacKay 1981
Pogonomyrmex occidentalis	Grassland (U.S.)	0.025	Rogers, Lavigne, & Miller 1972
Pogonomyrmex rugosus	Chihuahuan Desert (U.S.)	0.028	Whitford, Johnson, & Ramirez 1976
Pogonomyrmex rugosus	Arid grassland (U.S.)	0.137	MacKay 1981
Pogonomyrmex subnitidus	Chaparral (U.S.)	0.016	MacKay 1981
Tetramorium caespitum	Heath (England)	0.193	Brian, Elmes, & Kelly 1967
TERMITES[a]			
Cubitermes exiguus	Steppe savanna (Congo)	0.19	Bouillon 1970
Cubitermes fungifaber and spp.	Rainforest (Congo)	1.10	Maldague 1964
Gnathamitermes tubiformans	Arid grassland (U.S.)	2.22	Bodine & Ueckert 1975
Gnathamitermes tubiformans	Chihuahuan Desert (U.S.)	0.30	MacKay, Zak, & Whitford 1989
Nasutitermes costalis	Rainforest (Puerto Rico)	0.01	Wiegert 1970
Nasutitermes exitiosus	Dry sclerophyll forest (Australia)	0.30	Lee & Wood 1971b

[a]Termite values were converted from wet mass to dry mass by multiplying the values by 0.1.

of rodents or other important seed predators, to the high rate of turnover between habitats, to the between-habitat diversity (Morton 1982), or even to microtopographical differences, which affect the composition of assemblages of ants in the Chihuahuan Desert of North America (Chew 1977). Australian harvester ant communities also contain a much higher diversity of polymorphic ant species (Morton 1982), the significance of which is not clear. Ants clearly play a major role in arid ecosystems due to their numerical abundance; this is especially so for the seed predators (Marsh 1986b).

Many studies have shown that precipitation indirectly determines the richness and diversity of desert ant communities (Davidson 1977b; Greenslade and Halliday

1983; Marsh 1986a). Ant species richness in the central gravel plains of the Namib Desert is strongly correlated with mean annual precipitation (Figure 5.1A). Ant species diversity is highly correlated with the amount of precipitation in North American deserts (Figure 5.1B), explaining 69 percent of the variation in species diversity among ant communities (Davidson 1977b). Mean annual precipitation is an index of primary production in arid ecosystems (Davidson 1977b; MacKay and MacKay 1984; Marsh 1986a). All desert ants depend on plants either directly or indirectly as a source of food. Harvesters and nectar feeders depend directly on plants; those that tend Homoptera, and predators, depend on plants indirectly. Rodent species diversity also is correlated with precipitation (Figure 5.1B), which explains 64 percent of the variation in species diversity among rodent communities. The slopes for rodents and ants (Figure 5.1B) are statistically indistinguishable and the intercepts differ by less than 2 percent (Davidson 1977b). Data sets for other continents suggest that species diversity in arid regions is also largely determined by the amount of rainfall. Morton (1982) found that Australian communities and North American communities with similar amounts of rainfall had similar numbers of species, although Australian communities with lower amounts of precipitation tend to be more diverse than similar communities in North America (Morton and Davidson 1988). Ant species richness of the arid Guajiran Peninsula of Colombia also is correlated with amount of precipitation (personal observation).

Unfortunately, we do not have similar data sets for desert termites. Termites are primarily a tropical group, although subterranean termites are diverse and abundant in warm arid and semiarid regions of the world (Wood and Sands 1978). There are 4 relatively common genera (4 species, one species in each genus) in the northern Chihuahuan Desert (MacKay personal observation), 6 genera in the Sonoran Desert (Haverty and Nutting 1975; MacKay personal observation), 9 species in the Coachella Valley of California (Polis this volume), 14 genera in the Kalahari Desert of southern Africa (Coaton 1963), and up to 12 genera (48 species) in central Australia (Watson, Barrett, and Lendon 1978). Termite densities actually increase with increasing aridity in tropical Australia (Holt 1987; Morton and James 1988) and Madagascar (Paulian 1970). Emerson (1955) suggested that species richness decreases with a decrease in temperature, which seems to be true based on the distribution of termites in the United States (Weesner 1965). There are fewer termite species at higher altitudes in the highlands of southwestern Kenya (Kooyman and Onck 1987).

Biogeography of Social Insects in Arid Regions

Ants arose in the tropics and remain predominantly tropical (Brown 1973). None of the genera found in deserts occurs exclusively in arid regions and all were apparently derived from tropical ancestors. Those that are most speciose in arid regions (*Pheidole, Solenopsis, Pogonomyrmex, Messor* [= *Veromessor*; see Bolton 1982], *Crematogaster, Camponotus, Aphaenogaster* [= *Novomessor*; see Brown 1974], *Conomyrma, Forelius, Ocymyrmex, Leptothorax, Cataglyphis, Tetramorium, Mono-*
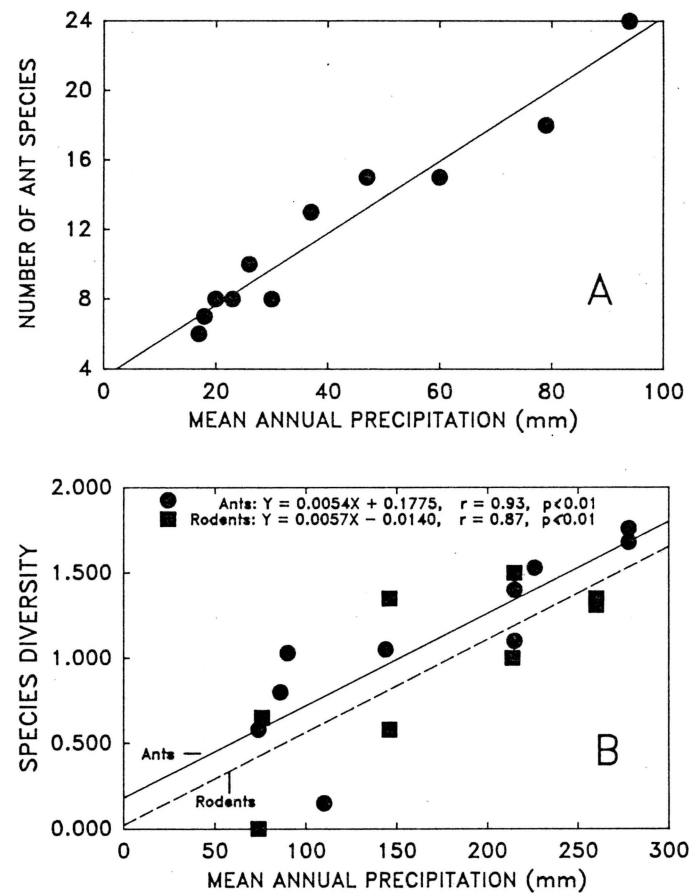

Figure 5.1. Effect of mean annual precipitation on desert ant species richness *A*, along a climatic gradient in the Namib Desert (Marsh 1986a); and *B*, on the species diversity in the deserts of southwestern United States (from Davidson 1977a), where species diversity = H = Σ p_i ln p_i, where p_i are the proportions of each species.

morium, Chelaner) have representatives in mesic habitats. Most of these genera are more common in certain deserts than in others. For example, *Pogonomyrmex, Pheidole, Aphaenogaster, Messor*, and the subfamily Dolichoderinae (especially *Forelius* and *Conomyrma*) are most common in North American deserts, *Pheidole, Meranoplus, Chelaner*, and *Tetramorium* are common in Australian deserts, *Pheidole, Messor, Monomorium, Tetramorium*, and *Leptothorax* are most common in African deserts. *Pheidole* occurs in all major deserts; the common New World genus *Pogonomyrmex* does not occur in the Old World.

The composition of the African deserts is especially interesting. The fauna of the Namib Desert is similar in overall composition to that of the Sahara (Marsh 1986b).

Both deserts are dominated by the subfamilies Myrmicinae and Formicinae, but differ from North Amerian deserts as the subfamily Dolichoderinae is poorly represented. This may be because Africa separated from Gondwanaland before the subfamily Dolichoderinae had speciated to any extent (MacKay n.d.). There are some interesting differences between the two African deserts (Marsh 1986b). *Ocymyrmex* (subfamily Myrmicinae) in the Namib is replaced by *Cataglyphis* (subfamily Formicinae) in the Sahara. Although they have completely different phylogenetic origins, both are active during the heat of the day and have similarities in their foraging behavior and speed of locomotion. *Leptothorax* and *Tetramorium* have converged to occupy similar granivorous niches in two African deserts (Marsh 1986b). *Tetramorium* is rare in the Sahara where *Leptothorax* is common; in the Namib, *Tetramorium* is common and *Leptothorax* does not occur. Neither of these genera are common in North American deserts, although both occur. Perhaps they are replaced by *Pogonomyrmex*, although *Pogonomyrmex* is generally common wherever these two genera occur. Little is known of the biologies of these two genera in North American arid habitats, but *Leptothorax* is probably omnivorous. North American and Australian deserts show some similarities (Marsh 1986b). The subfamilies Formicinae and Myrmicinae dominate arid (and most other) habitats on both continents, but the subfamily Dolichoderinae is also important. Predacious ants of the subfamilies Dorylinae and Ponerinae are found in both deserts, but are uncommon in arid zones of Africa (Marsh 1986b).

Termites are predominantly tropical (Emerson 1955; Lee and Wood 1971b), although distinct faunas have evolved in the southwestern deserts of North America and in the arid regions of Madagascar (Weesner 1965, 1970; Paulian 1970). Termites are so important in arid ecosystems that the pharaohs imported termite-resistant timbers from Syria for mummy cases (Harris 1970). *Amitermes* is particuarly important in desert ecosystems throughout the world (Emerson 1955; Harris 1970), especially in North Africa (Harris 1970), Australia (Gay and Calaby 1970; Lee and Wood 1971b; Holt 1987), the Arabian Peninsula (Cowie 1989), and North America (Weesner 1970). It often constructs large mounds on the soil surface in mesic habitats (Harris 1970; Holt 1987; MacKay and Whitford 1988); in arid regions it is predominantly subterranean (Gay and Calaby 1970; Harris 1970). Other common genera in arid regions of North Africa include *Anacanthotermes* (restricted to deserts; also occurs in Indian deserts), *Microcerotermes*, and the sand termites *Psammotermes* (Harris 1970). *Psammotermes* are found in areas of complete desertification where they apparently feed on subfossil relics of the humid pleistocene flora, notably trunks of large *Tamarix* (Harris 1970). The termite fauna of Madagascar is especially interesting. Most species live in the specialized xerophytic vegetation of southern arid or semiarid regions (Paulian 1970). The rain forest of Madagascar is relatively poor in species.

Most termite species in Australia are found in tropical savanna woodlands (Lee and Wood 1971b; Braithwaite, Miller, and Wood 1988). Species in arid regions are members of the genera *Anacanthotermes* and *Psammotermes* (Emerson 1955) as well as of *Drepanotermes* and *Tumulitermes* (Gay and Calaby 1970; Lee and Wood 1971b; Morton and James 1988). The family Termitidae is especially abundant in North American deserts (Weesner 1970). Common termitid genera include *Anoplotermes*, *Gnathamitermes*, and *Tenuirostritermes*; the kalotermitids include *Paraneotermes* and *Pterotermes* (Weesner 1970; Jones, La Fage, and Wright 1981). Except for *Reticulitermes* and *Zootermopsis*, Nearctic termites have a Neotropical origin (Emerson 1955). The common *Gnathamitermes* of the North American deserts was undoubtedly derived from *Amitermes*.

Abiotic Factors in Community Patterns

Abiotic factors, especially soil temperature and moisture, are very important for desert arthropods (MacKay et al. 1986; Abushama and Al-Houty 1989). Desert ants respond to temperature and evaporative stresses in one of two major ways. They may be physiologically adapted to tolerate extremes and hence are active even at high temperatures and vapor pressure deficits, or they may avoid extremes by being active only at night, at twilight, or on cooler days (Whitford, Kay, and Schumacher 1975; Whitford 1978c; Briese and Macauley 1980; Briese 1982b; Marsh 1988; Cloudsley-Thompson 1989). Desert seed harvesters are exposed to high temperatures and desiccation stress while searching for seeds on the soil surface (Heatwole and Harrington 1989). Such ants have very low desiccation rates and high thermal maxima, especially the seed harvesters *Pogonomyrmex* spp. and the omnivore *Aphaenogaster cockerelli* (Whitford, Kay, and Schumacher 1975). Some Australian species, such as *Melophorus* spp., forage at extremely high temperatures when other ants are inactive, and are inactive during the cooler times of the day and during the cooler months (Anderson 1984). *Ocymyrmex barbiger* is a diurnal scavenger of arthropods that have succumbed to thermal and desiccation stress in the Namib Desert (Marsh 1985b; Wehner 1987). It forages in one of the hottest and most barren habitats in the world. Activity increases when the ambient temperature passes 45°C and the ant continues to forage until surface temperatures reach 70°C (Wehner 1987). The number of successful foraging excursions actually increases with higher vapor pressure deficits (Marsh 1985b). The ants are able to radiate heat by resting in the shade and by maintaining a high speed of locomotion, up to 1 m/sec (Wehner 1987). The genus *Cataglyphis* of the Saharan desert is similar in many respects to *O. barbiger* (Wehner 1987), although the colonies are much larger (Marsh 1985b). *Melophorus* has a similar "thermal niche" in Australia, although it is a seed harvester (Marsh 1985b).

Some desert ants are not physiologically adapted for extremes of temperature and low vapor pressures. *Solenopsis xyloni*, a common species in North American deserts, does not differ physiologically from the tropical *S. geminata* (Francke, Potts, and Cokendolpher 1985; Braulick, Cokendolpher, and Morrison 1988). The crepuscular exudate feeder *Formica perpilosa* has water loss rates similar to ants from more mesic environments (Whitford, Kay, and Schumacher 1975). Many diurnally active ants become nocturnal during summer, due to higher temperatures and also due to the increase in abundance of nocturnal insects used as prey (Whitford and Ettershank 1975). For example, ants in the Namib Desert tend to be diurnal in the
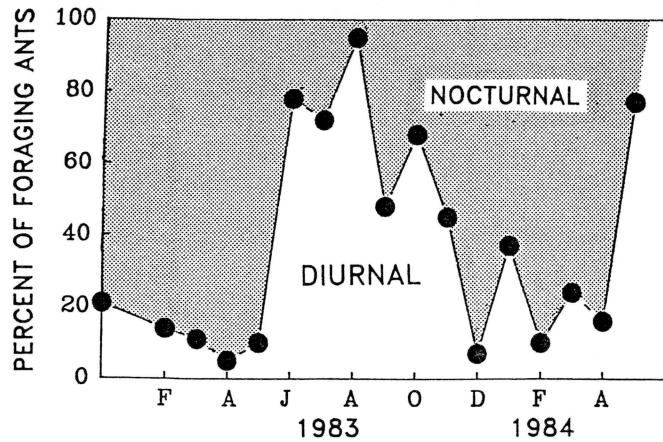
Figure 5.2. Proportion of foraging ants that were diurnally and nocturnally active over a 17-month period in the Namib Desert (from Marsh 1985b).

winter and nocturnal in the summer (December to April–May) (Marsh 1985b; Figure 5.2).

Of all the factors affecting ant foraging activity, soil temperature is the most important (Briese and Macauley 1980; Bailey and Polis 1987; Davison 1987; Porter and Tschinkel 1987; Marsh 1988; MacKay and MacKay 1989). Many diurnal desert ants demonstrate a bimodal diurnal aboveground activity pattern (Whitford 1978c; Lynch et al. 1980; Marsh 1988; MacKay and MacKay 1989), with activity reduced during the hottest part of the day (Figure 5.3). MacKay and MacKay (1989) demonstrated that ambient temperature explained most or all of the variation in foraging activity of *Pogonomyrmex rugosus* and *P. subnitidus*, but had little effect on *P. montanus*, which occurs in more mesic environments.

Seasonal foraging patterns also can be related to seasonal changes in temperature (Heatwole and Muir 1989). Lynch, Balinsky, and Vail (1980) studied seasonal foraging patterns of three common ants in Maryland hardwood forests. They found a bimodal seasonal pattern in *Aphaenogaster rudis* (Figure 5.4A), with reduced activity during the hotter summer months. *Paratrechina terricola* and *Prenolepis imparis* were active during these hotter months. Ant activity was correlated with preferred temperature. *Aphaenogaster rudis* was most active at surface temperatures below 20°C, *Pa. terricola* and *Pr. imparis* at temperatures of nearly 30°C (Figure 5.4B). Several authors have discussed reductions in foraging activity of ant species during the summer (Bernstein 1974; Davidson 1977a). One must be careful as the numbers of hours that nests are active during a particular season may not be correlated with forager effort. Reduced hours of nest activity during the summer occur during the seasonal foraging peaks (MacKay 1981), when energetic costs of the nest are higher due to the higher ambient temperature and the presence of brood (MacKay 1985). The ants are simply very active for a short period each day. Activity of desert ants
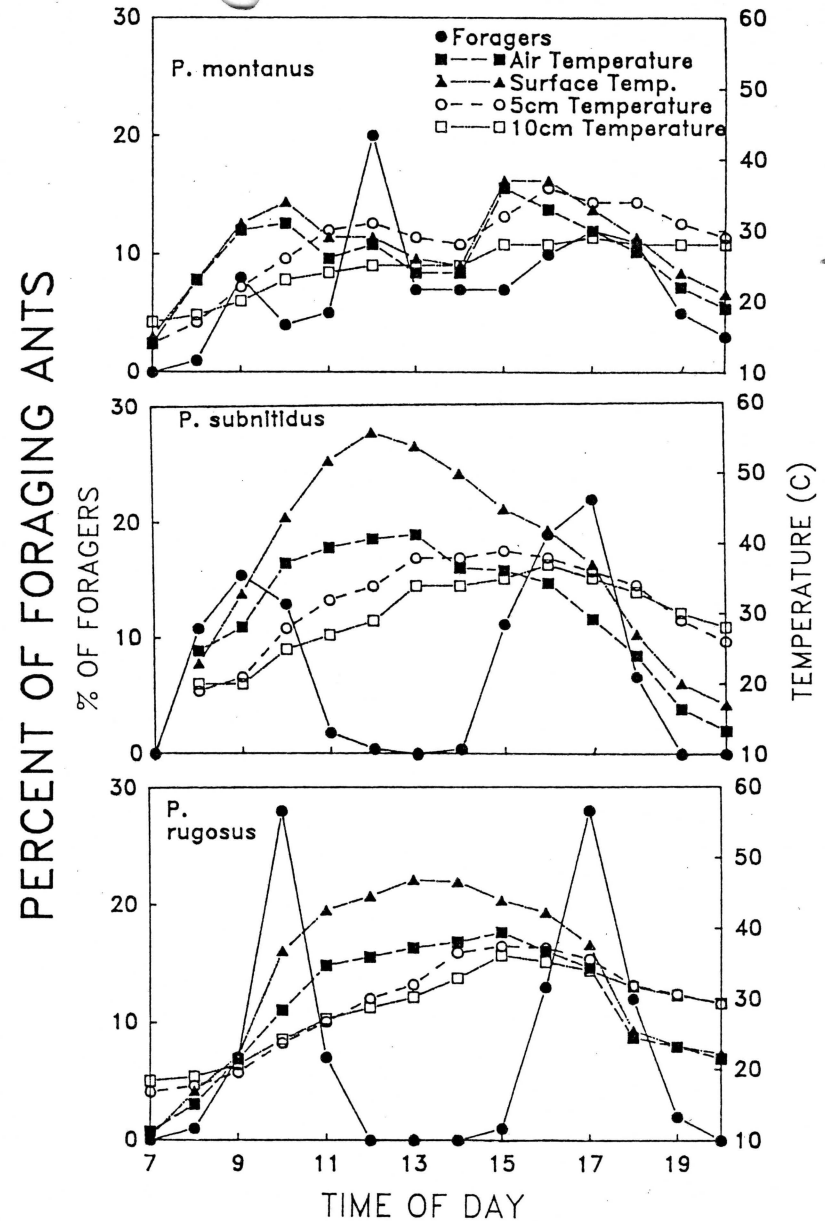

Figure 5.3. Diurnal foraging patterns of three species of *Pogonomyrmex* harvester ants, the ambient temperatures in the nest at 5-cm and 10-cm levels, the surface temperature, and the air temperature directly above the nest surfaces (data from MacKay & MacKay 1989).

generally increases after a rain, and nocturnal ants become diurnal when temperatures drop (Marsh 1988).

Unfortunately, we do not have many data on the diel and seasonal activity of desert termites. The desert termites *Gnathamitermes tubiformans*, *Heterotermes aureus*, *Anacanthotermes* sp., and *Psammotermes hybostoma* have unimodal seasonal foraging patterns, with most foraging occuring in the late summer and fall during the seasonal rains (Jones, Trosset, and Nutting 1987; Abushama and Al-Houty 1988; Salman et al. 1988; MacKay, Zak, and Whitford 1989). Aboveground activity is considerably reduced during the hottest periods of summer days (MacKay, Zak, and Whitford 1989). Termites are not active aboveground during the winter months in North American deserts (MacKay personal observation). Soil moisture is extremely important (together with soil temperature) for desert termites (MacKay. et al. 1986; Abushama and Al-Houty 1988; Salman, Morsy, and Sayed 1988), possibly due to high rates of water loss (Collins 1969). MacKay et al. (1986) experimentally demonstrated that soil moisture at the 5-cm level was the most important factor regulating aboveground activity in *G. tubiformans* in the Chihuahuan Desert. Reducing soil temperature had no effect on termite activity. In other experiments, MacKay, Fisher et al. (1987) verified the importance of water in termite activity and showed that increased activity resulted in an increase in mass loss of fluff grass (*Erioneuron pulchellum*) litter. Soil temperatures act as an on-off switch in spring and autumn, while soil moisture regulates activity during summer (MacKay et al. 1986). Temperature may be important in other termite species. *Heterotermes aureus* attacks organic matter primarily at sites having the most vegetative cover (Jones, Trosset, and Nutting 1987). This may be due to lower temperatures as termites respond to thermal shadows (Ettershank, Ettershank, and Whitford 1980).

Activity of other desert arthropods, especially soil mites, does not depend on soil moisture (MacKay, Fisher et al. 1987; MacKay, Silva, and Whitford 1987). Soil temperature may play a more important role for such arthropods. Cooler soil temperatures had no effect on positions of ant nests, contrary to results of other studies which demonstrated that shade causes ants to move their nests (MacKay et al. 1986). However, numbers of colonies in watered plots were reduced. This may be due to soil moisture facilitating growth of brood pathogens, especially fungi.

In general, rates of ecological processes in the northern Chihuahuan Desert are not limited by water (MacKay et al. 1986; MacKay, Fisher et al. 1987; Whitford 1986). However, Strojan, Randall, and Turner (1987) suggest that, at least in the Mojave Desert, the amount of precipitation may limit decomposition rates. Primary production of natural vegetation in deserts is limited by nitrogen (Whitford 1986). Decomposition in the northern Chihuahuan Desert is not limited by nitrogen (MacKay, Zak, and Whitford 1989) and termites actually show an aversion to nitrogen-impregnated wood (Zak and MacKay n.d.).

Ants and termites are very important in soil processes. Both taxa move subterranean soil to the surface. Soil turnover by ants in arid regions ranges from 350 to 420 kg · ha^{-1} · y^{-1} in Australia (Briese 1982c) to 842 kg · ha^{-1} · y^{-1} in the Chihuahuan Desert (Whitford, Schaefer, and Wisdom 1986). These rates result in a deposition of from 3 mm to 2 cm of soil on the surface every century (Briese 1982a;
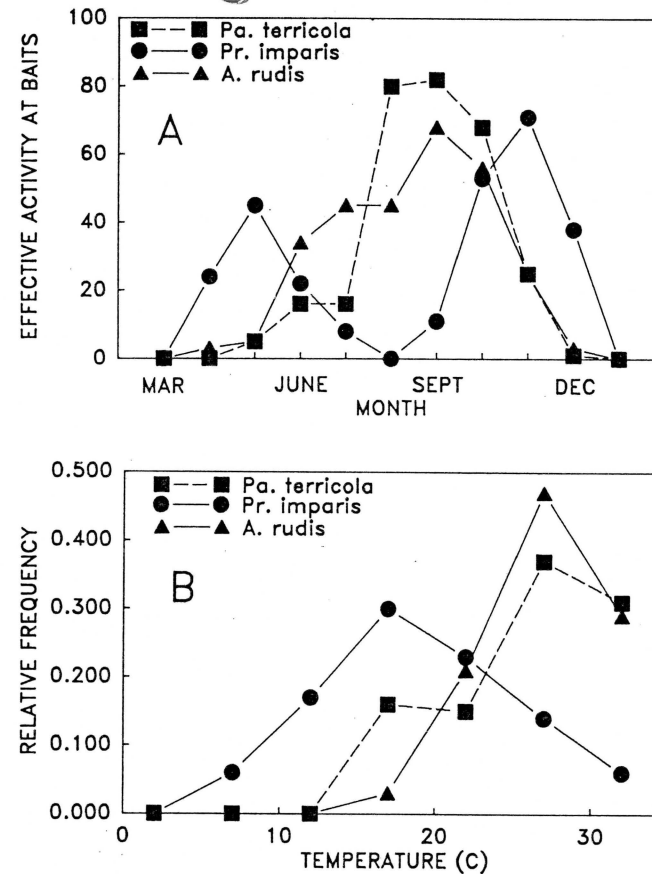

Figure 5.4. *A*, Seasonal activity patterns of three ant species (*Paratrechina terricola*, *Prenolepis imparis*, and *Aphaenogaster rudis*) in a Maryland hardwood forest; and *B*, the air temperatures at which the ants were most active (based on Lynch, Balinsky, & Vail 1980).

Whitford, Schaefer, and Wisdom 1986). Deposition rates for termites vary from 0.25 to 0.5 cm/century in North Queensland (Holt, Coventry, and Sinclair 1980), 4 cm/century (Williams 1968, Lee and Wood 1971a) to 7.5 to 10 cm/century in the Ivory Coast (Lepage 1984). This mixing of plant and animal matter with soil results in more nutrients being available to plants (Briese 1982a) and influences plant species composition (Whitford, Schaefer, and Wisdom 1986).

Termites are also important in other soil processes (Nutting, Haverty, and La Fage 1987), possibly more important than ants. Galleries of subterranean termites in the northern Chihuahuan Desert are very important in increasing water infiltration rates (Elkins et al. 1986; MacKay, Zak, and Whitford 1989). Plots without termites
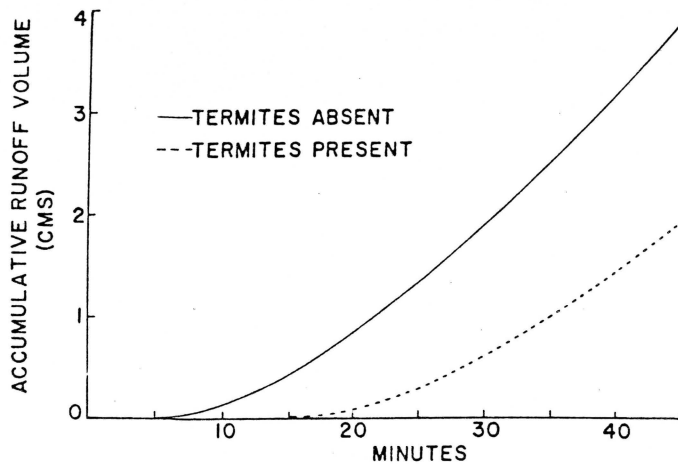
Figure 5.5. Accumulative runoff volumes from plots with and without termites in the northern Chihuahuan Desert (from MacKay, Zak, & Whitford 1989).

in the northern Chihuahuan Desert began to have sheet flow within 5 minutes of initiation of artificial irrigation, whereas plots with termites began to "run" only after 15 minutes (Figure 5.5). The total volume of runoff was much greater in plots without termites (MacKay, Zak, and Whitford 1989). Bed load concentration was three times greater from termite-free plots due to the increased bulk density of the soils after the collapse of subterranean galleries (Elkins et al. 1986).

Biotic Community Processes

Three biotic processes may be important in structuring social insect populations in deserts: competition, predation, and interactions with plants. Competition will be discussed in the first section.

Competition

Competition is well documented in social insect populations (Levings and Traniello 1981). It includes territorial conflicts and "food robbing" in which a forager of one species removes a food item from the mandibles of a forager of another species (Hölldobler 1986; Carroll 1988). For example, *Myrmecocystus mimicus* waylays returning foragers of *Pogonomyrmex* spp., *Aphaenogaster cockerelli*, and *Pheidole desertorum*, and robs food from their mandibles. *Myrmecocystus navajo* robs prey from *A. cockerelli*. This behavior may be important in the structure of desert ant communities (Hölldobler 1986).

Interspecific competition could be either less important (Brown, Reichman, and

Davidson 1979) or more important (Anderson 1986) in arid regions than in other regions. Ant species tend to be generalists with strongly overlapping resource requirements. Therefore, competition between species of desert ants would be expected to be intense, and should result in partitioning of resources (López Moreno and Díaz Betancourt 1986), although Davidson (1977b) concluded that microhabitat partitioning, interspecific aggression, and territorial defense are relatively unimportant in desert ant communities. Many ant species are unlikely to coexist locally within relatively uniform habitat types (Whitford, Johnson, and Ramírez 1976; Davidson 1977a). Thus we would expect to see patterns of resource partitioning among ant species, involving microhabitat differences, differences in food type, quality, and size, and differences in temporal foraging patterns. Ants may even compete with desert shrubs for water (Rissing 1988).

Ants of the genus *Pogonomyrmex* are especially abundant in New World arid ecosystems (MacKay 1981). Most species primarily use seeds as a food source (Figure 5.6), especially in the most arid ecosystems. *Pogonomyrmex montanus* is exceptional as it uses dead insects and vertebrate fecal material to a large extent, but occurs in somewhat more mesic habitats in clearings in pine forests. This trend also occurs in *P. occidentalis* and *P. subnitidus*, which are often found at higher elevations in somewhat more mesic environments. *Pogonomyrmex rugosus* in the Chihuahuan Desert frequently includes subterranean termites in its diet, a resource which is not as common in grasslands in Southern California, where *P. rugosus* primarily uses seeds of a single plant species, *Erodium cicutarium* (MacKay personal observation).

There is some evidence that ants are food limited. Bernstein (1974) concluded that harvester ants are seed limited, although there are large reserves of seeds in the soil even after several years during which no seeds were produced (Tevis 1958; but see Chew 1977). Davidson (1977b) found a strong correlation between ant diversity and primary production, which suggests that the number of species present in a community in an arid ecosystem is limited by the food source. This may not be true in Australia, although dominant species have a substantial impact on the remainder of the ant community, presumably due to interspecific competition (Fox and Fox 1982). Species richness in ants has also been shown to be limited by primary production (Figure 5.1), but Briese (1982b) found that areas with different seed production rates supported similar populations of ants. This suggested to Briese that some other factor limited population density of desert ants below levels set by food availability.

Ants partition resources in a number of ways. Harvester ants partition seeds on the basis of size and nutritional quality (Chew 1977; Davidson 1977a,b, 1978; Hansen 1978; Whitford 1978c). We can usually find differences in the sizes of ants in a guild of desert ants. For example, ants in a Chihuahuan Desert community were grouped within three feeding guilds (Chew 1977; Chew and De Vita 1980). The body masses within a feeding guild differed by an average ratio of 1.66; between categories the average ratio was 1.28. Davidson (1977b) demonstrated that seed size preference was highly correlated with worker body size in a number of desert harvester ants (Figure 5.7). Larger ants harvest medium and larger sized seeds, which maximizes net energy intake (Bailey and Polis 1987). Hansen (1978) found that seed size was correlated with worker mass in a group of *Pogonomyrmex* harvester ants.

The largest species (*P. rugosus*) used the largest seeds, the inter·diate-sized species (*P. maricopa*) used medium-sized seeds, and the smallest species (*P. desertorum*) used the smallest seeds. Kelrick et al. (1986) were able to show the importance of nutritional quality of seeds, and pointed out that nutritional quality has been overlooked as an important characteristic in ecological studies. Omnivores may also divide resources on the basis of size (Whitford 1978c).

Seed size may be important to desert ants only in the North American deserts, and only under certain circumstances. Ants in Australian deserts tend to be smaller (Morton 1982; Morton and Davidson 1988), and differences in size among coexisting ants are not nearly as marked as they are in North America (Briese 1982b). Therefore, Australian ants presumably cannot partition seeds on the basis of size (Morton 1982). Two species in the Namib, *Tetramorium rufescens* (4.0–5.1 mm total
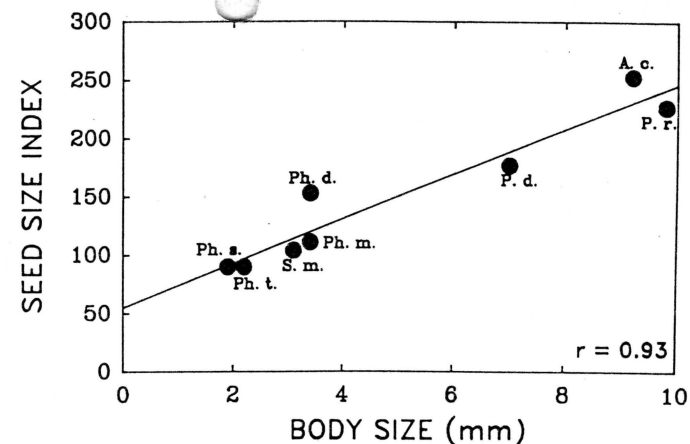

Figure 5.7. Relationship between mean worker body length and seed size index for eight species of harvester ants in the Chihuahuan Desert of North America (modified from Davidson 1977b). Seed size indices were calculated as $\Sigma\, p_i d_i$, where p_i is the proportion of seeds chosen from the ith size class and d_i is the median diameter of seeds in that class (see Davidson 1977b for further details). The abbreviations for the ant species are: Ph. s. = *Pheidole* sp., Ph. t. = *P. tucsonica*; Ph. d. = *P. desertorum*; Ph. m. = *P. militicida*; S. m. = *Solenopsis maniosa*; P. d. = *Pogonomyrmex desertorum*; P. r. = *P. rugosus*; A. c. = *Aphaenogaster cockerelli*.

length) and *Messor denticornis* (5.5–11 mm total length), are very different in size, yet both species utilize the same size of food items (Marsh 1987). In addition, the two species are active at the same time diurnally and have similar seasonal foraging patterns. Thus, interspecific competition for food is not important in these two species (Marsh 1987). These data support the notion that interspecific competition for food is not of major importance to ants in unpredictable arid environments (Briese 1982c). Under certain circumstances (where there is an abundance or a scarcity of seeds), North American desert harvesters collect seeds as they are encountered, without regard to mass, size, or chemical composition (Whitford 1978b). Rissing and Pollock (1984) concluded that there was no correlation between body size of the polymorphic species *Messor pergandei* and seed size. They state that statistically significant correlations may have little biological impact. Although worker size and seed size may not be correlated in all species, correlations as strong as those shown with the variables in Figure 5.7, and which also have a reasonable biological explanation, are difficult to refute.

Coexistence in a large community of ecologically similar desert harvester ant species may be made possible by partitioning the times of day during which foragers are active aboveground (Whitford, Johnson, and Ramírez 1976; Chew 1977; Hansen 1978; Briese and Macauley 1980; Baroni Urbani and Aktac 1981; Ryti and Case 1984). Baroni Urbani and Aktak (1981) demonstrated that two species of *Messor*
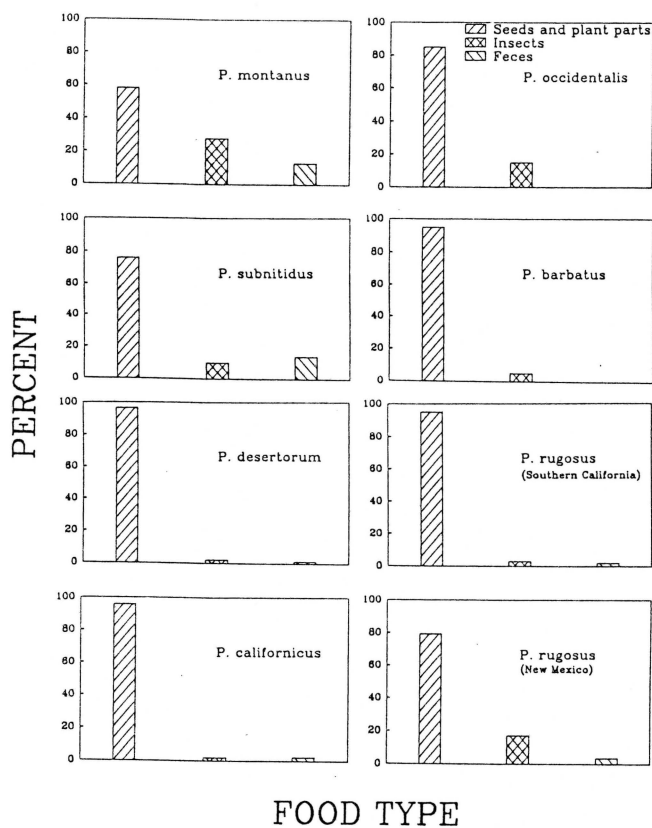

FOOD TYPE

Figure 5.6. Food types of ants of the genus *Pogonomyrmex* from arid and semiarid regions in southwestern United States. All except *P. montanus*, *P. occidentalis*, and *P. subnitidus* occur in deserts. (Data from Lavigne 1969; Whitford, Johnson, & Ramírez 1976; Whitford 1972, 1978b; MacKay 1981.)
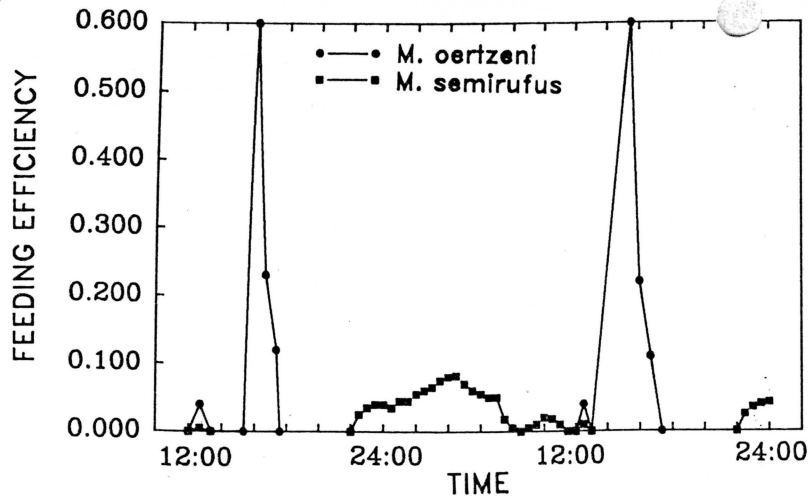
Figure 5.8. Circadian foraging patterns and feeding efficiency (E_a) in two species of *Messor* harvester ants in the desert of Turkey, where E_a = the total number of individuals of one species at one time on baits divided by the total number of ants observed on the baits (from Baroni Urbani & Aktac 1981).

harvester ants were active at different times of the day (Figure 5.8). *Messor pergandei* and the large desert *Aphaenogaster* (= *Novomessor*) spp. are usually nocturnal or crepuscular, whereas the common *Pogonomyrmex* spp. are primarily diurnal in North American deserts. *Pogonomyrmex barbatus* often forages at night, whereas *P. rugosus* never forages at night (MacKay 1981), or forages at night only occasionally (Whitford, Johnson, and Ramírez 1976; Mehlhop and Scott 1983). Temporal displacement of foraging patterns may not be important in seed harvesters, as seeds are available at all times of the day, but species active at different times would avoid aggressive encounters and could thus coexist.

Ants also exhibit differences in seasonal foraging patterns (Whitford, Johnson, and Ramírez 1976; Hansen 1978; Whitford 1978b; Briese and Macauley 1980; Anderson 1984). For example, *P. barbatus* is more active in early summer; *P. rugosus*, in midsummer (Whitford, Johnson and Ramírez 1976). *Pogonomyrmex californicus* avoids competition with its congeners by foraging in the early spring and late autumn (Whitford 1978c). It also climbs into the canopy of desert plants to harvest seeds, as do other species of desert ants (Chew 1977). *Pogonomyrmex* spp. in an upper Sonoran grassland partitioned the foraging season in a similar way (Hansen 1978). Common North American desert omnivores such as *Conomyrma insana* and *C. bicolor* co-occur and also are active at different times during the season (Whitford 1978c). Omnivores of the Australian deserts, such as ants of the *Iridomyrmex agilis* species complex, are active in the summer, and are inactive in winter when the *I. itinerans* species complex predominates (Anderson 1984). A third group, ants of the *I. dromus* species group, are active at night throughout the year, thus avoiding the other two

species, which ___ diurnal. This may partition food resources, as omnivores may encounter different prey or foods at different times. Food type changes seasonally in harvester ants (MacKay 1981). For example, *P. subnitidus* increases the proportion of seeds in its diet in late summer. Briese (1982b) showed that niche breadth and niche overlap between species pairs continually change in response to overall availability of food resources, although it is difficult to interpret the significance of niche overlap. Ants both specialize and become generalist feeders when the opportunity occurs (Briese 1982b).

Some ants also are able to partition seed resources on the basis of the distribution and density of seeds (Chew 1977; Davidson 1977a,b, 1978; Hansen 1978; Brown, Reichman, and Davidson 1979; Kelrick et al. 1986), which are clumped in deserts (Henderson, Peterson, and Redak 1988). Species that specialize on low-density seed patches are usually individual foragers, whereas species that specialize on high density seed patches are group foragers (Davidson 1977a). (Note that Traniello [1989] objects to the use of the label "individual forager," as no ant is ever completely independent of the others, but I will continue to use the term until we have a better one.) In group foraging species, individuals locate seeds and recruit others to the source using trail pheromones or tandem running. To some degree, species tend to be characterized as either individual foragers or group foragers (Brown, Reichman, and Davidson 1979). Often the type of foraging of a nest changes depending on the situation (Curtis 1985), or some colonies of a species in an area are group foragers, whereas others are individual foragers (Whitford, Johnson, and Ramírez 1976). *Messor pergandei* may be a group forager only when high density patches of seeds are available (Davidson 1977a). *Pogonomyrmex rugosus* may group forage in areas of dense vegetation and individually forage in open areas, even along the same trunk trail (MacKay personal observation). In some assemblages of harvester ants, species of similar body sizes tend to coexist only if they differ in foraging behavior, with one being a group forager and the other an individual forager (Davidson 1977b). Group foraging species are somewhat more successful in locating food and tend to be considerably more specialized in terms of the food source (Davidson 1977a; MacKay 1981). Group foraging is metabolically more expensive due to the production of costly trail pheromones and the higher rates of predation by specialized sit-and-wait predators such as *Phrynosoma* spp. lizards, which harvest ants along trunk trails.

We can compare the costs and benefits of the two types of foraging as a function of seed density (Figure 5.9). Benefits outweigh costs at a relatively low seed density for species that forage individually, due to the lower costs involved in foraging. Seed density must be considerably higher in group foraging species before benefits outweigh costs. The benefit to group foraging species is considerably higher at high seed densities, and they may be able to outcompete individually foraging species, if food were limiting under such conditions. Species that adjust foraging behavior to seed density are probably at an advantage.

Desert harvester ants typically store seeds in their nests. Seed storage may be favored in habitats with short, infrequent pulses of primary production (Marsh 1986a), in which it serves to ensure survival during droughts (Marsh personal communication; Polis personal communication). When granaries are full, foraging ceases
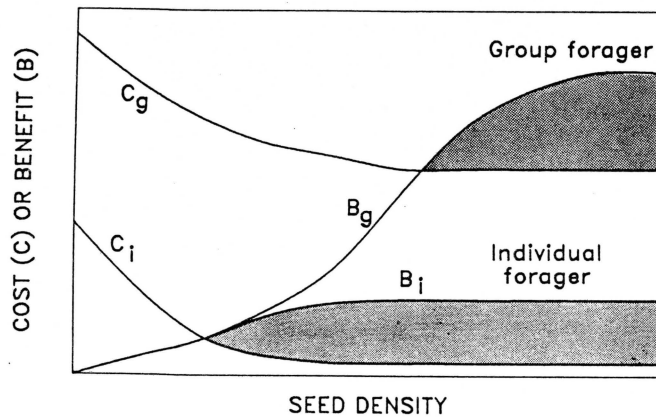
Figure 5.9. The hypothetical costs and benefits of individual foraging and group foraging vs. seed density (modified from Davidson 1977a).

in some *Pogonomyrmex* species (Whitford and Ettershank 1975; Bailey and Polis 1987). Many authors have assumed that seeds are eaten during the winter or are a form of "insurance" in an unpredictable environment. The available data do not support either of these "obvious" hypotheses (MacKay and Mackay 1984). Seed storage, in at least some *Pogonomyrmex* species, appears to be a form of protection against predation, especially by spiders. When a nest is under siege, foragers stop aboveground activity until the spiders leave.

The storage of liquids in specialized replete ants is also common in deserts. We encounter repletes in the common *Myrmecocystus* in North America, *Melophorus* in Australian deserts, *Camponotus* in the Sahara, and *Anoplolepis* in the Namib (Marsh 1986a).

Interactions between ant species can result in the formation of well-integrated communities (Davidson 1977b; Anderson 1984). Competition is especially important in some assemblages (Whitford and Ettershank 1975; Fox, Fox, and Archer 1985) and may result in habitat partitioning and variation in foraging behavior, food type preference, and worker body sizes. The outcome of competition may be difficult to predict. It undoubtedly changes as local densities of species change. Further, it can be shifted by the presence of a parasitic phorid fly, which interferes with the defensive behavior of one of the members of a species pair (Feener 1981). Even if competition can be demonstrated, it does not necessarily have a major role in community organization (Shorrocks, Rosewell, and Edwards 1984).

Other evidence for the importance of competition in desert ants is that colonies tend to be more widely spaced in more arid habitats (Davidson 1977b), although nest overdispersion may not always be a result of competition (Levings and Traniello 1981). Harvester ants are intraspecifically overdispersed and interspecifically aggregated in arid regions (Ryti and Case 1984, 1986). The spacing is due to competition between adults and expulsion (predation) on founding colonies (Ryti and Case 1986,

1988). Nests of the honeypot ants *Myrmecocystus* sp. are evenly spaced in the Chihuahuan Desert; establishment of new nests is inversely related to the existing density of nests (Chew 1987). There is some evidence for interspecific competition between *Messor pergandei* and *Pogonomyrmex californicus* in the Colorado Desert (Ryti and Case 1988). A series of nest removal and food supplementation experiments demonstrated no changes in foraging activity or diet breadth, but nests with an augmented food supply produced proportionally more reproductives.

Territoriality is common in desert ants, especially *Pogonomyrmex* (De Vita 1979), *Pheidole* (Creighton 1966), and *Myrmecocystus* (Hölldobler 1981), and can result in mortality between colonies. Apparently ant colonies can "come to an agreement" as to the boundaries of their territories. Adjacent colonies of *Pogonomyrmex barbatus* and *P. rugosus* were not observed to fight in New Mexico (Whitford, Johnson, and Ramírez 1976). Whitford et al. (1976) concluded that territoriality was relatively unimportant in relations between the two harvester ant species, although this may have been a case of "competition past." The two species rarely occur together, which would be expected of ecological equivalents (Davidson 1977b). There is a sharp boundary between the distributions of the two species in New Mexico (Whitford, Johnson, and Ramírez 1976), with *P. barbatus* occurring in slightly more mesic habitats (MacKay personal observation). *Myrmecocystus mimicus* defends territories against neighboring colonies and engages in complex display tournaments (Hölldobler 1981). Colonies also forage in different directions and avoid contact between foragers. Competitive exclusion can occur in ants (MacKay and MacKay 1982), although most examples involve displacement of native or introduced ants by other introduced ants. Some ants can be very innovative in their interactions with other species. *Tetramorium caespitum* drops soil down the nests of the alkali bees to eliminate them from the ants' territories (Schultz 1982).

Ants and rodents also compete for seeds, although to some extent they specialize on different sized seeds (Davidson, Inouye, and Brown 1984). Many species of ants, rodents, and birds may all prefer the same foods. Kelrick et al. (1986) found that all three preferred the same seeds in the Great Basin Desert, especially millet seeds, which are particularly high in percentages of soluble carbohydrates and free water. This may not be biologically meaningful, as millet does not naturally occur in the habitat. A number of investigators have studied competitive interactions between ants and rodents in arid regions. In one study in the Chihuahuan Desert, the populations of most common harvester ants initially increased in response to rodent removal (Davidson, Inouye, and Brown 1984) (Figure 5.10). Within 12 months the populations in the rodent-free plots began to decline as small-seeded plant species were competitively replaced by large-seeded annuals. After 30 months the ant populations had returned to pretreatment levels and were not different from plots with rodents present. Rodents in the ant-free plots increased slightly in density and biomass, but the long-term and short-term responses were not detectably different (Davidson, Inouye, and Brown 1984). In a similar study, Brown and Munger (1985) found the elimination of *P. rugosus* alone or of all species of granivorous ants had no effect on the granivorous rodent population in the Chihuahuan Desert of southeastern Arizona. Galindo (1986) has questioned the conclusions of Davidson, Inouye,

and Brown. He states there is no firm statistical basis for the conclu___ that rodents increased in density when ants were removed. See Brown and Davidson (1986) for a rebuttal. Thus, it is unclear how extensively ants and rodents compete for seeds. In fact, the net interaction of these two consumers at the same trophic level is mutualistic, as each consumer specializes on a different class of resources and those resources are in competition (Davidson, Inouye, and Brown 1984). The presence of both ants and rodents is necessary to establish moderately productive food resources for each. The selection pressure on plants to avoid predation by ants by producing larger seeds makes the seeds more attractive to rodents, and the reverse also occurs as a result of rodent predation (Mares and Rosenzweig 1978). Clearly we have not heard the last word on interphyletic competition between ants and rodents.

There is evidence of intraspecific competition between termite colonies and between different species. Some termite species are highly territorial and can eliminate competitors around their nests (e.g., Levings and Adams 1984 for tropical species); others coexist peacefully (Bouillon 1970). Territoriality can be used to define the limits of a termite colony. Termites from several parts of a study area can be mixed; if fighting occurs, the termites are from different colonies (Schaefer and Whitford 1981).

Resources may be partitioned between termite species in several ways. For example, *Gnathamitermes tubiformans* constructs galleries into the canopies of dead vegetation, whereas *Amitermes wheeleri* forages only below or at the soil surface (MacKay et al. 1985). Very subtle resource partitioning may occur in termites. Several species may attack a single piece of wood. Some may be in the hardwood, others in the wood buried by soil, others on the surface of the wood, others in partially decomposed sections of the wood, etc. Hocking (1965) found that eastern African
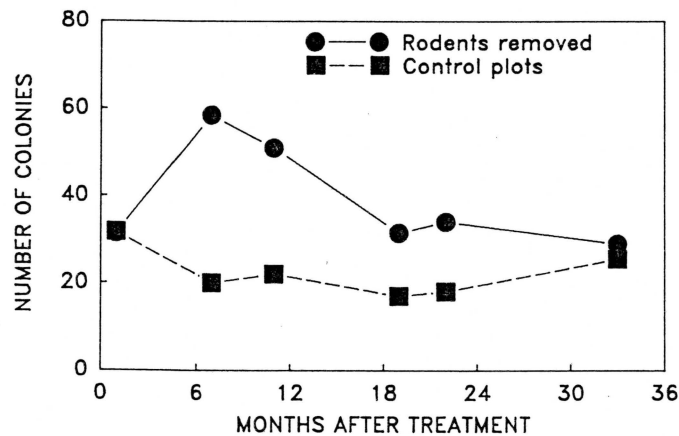

Figure 5.11. Populations of soil microarthropods in fluffgrass litter (*Erioneuron pulchellum*) in plots with and without subterranean termites in the Chihuahuan Desert of North America (from MacKay, Zak, & Whitford 1989).

termite species utilize different food sources such as dead stumps, dead branches, earth-filled stumps, the base of the stump, etc. Some species specialize in cattle droppings, especially in North American arid pastures. Different diurnal foraging patterns, seasonal differences, behavioral differences, and other characteristics allow coexistence of five species of *Trinervitermes* (Bouillon 1970).

Some evidence suggests that termites compete with soil microarthropods for organic matter (Silva, MacKay, and Whitford 1989.) Plots in the Chihuahuan Desert in which termites had been excluded had higher densities of microarthropods (Figure 5.11). This should be expected, since mites, collembola, psocoptera, and termites are in competition by feeding either directly or indirectly on litter (Silva, MacKay, and Whitford 1985).

Predation

Predation is an important process in social insect populations. Such insects may be preyed upon, especially by lizards (Munger 1984), and ants themselves are abundant and important predators (Feener 1988). Predation, especially by lizards, may

Figure 5.10. Changes in density of *Pheidole* spp. (*P. tucsonica, P. sitarches*, and *P. gilvescens*) on plots with and without rodents in the Chihuahuan Desert of southeastern Arizona (from Davidson, Inouye, & Brown 1984).
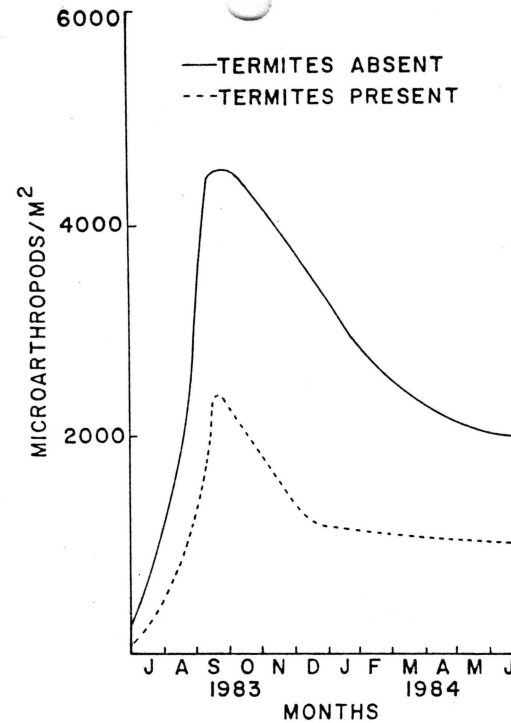
have been important in the morphological and behavioral evolution of ants (Hunt 1982).

Lizards, especially the horned lizards (*Phrynosoma* spp.) of North American deserts, are major predators of ants (Whitford and Bryant 1979; Rissing 1981; Shaffer and Whitford 1981; Munger 1984). *Phrynosoma cornutum*, a larger species of horned lizard in the Chihuahuan Desert, specializes on larger *Pogonomyrmex* harvester ants, usually foraging at the nest entrance or along the foraging trails of the ants (Whitford and Bryant 1979). They may consume an estimated 72 percent of the standing crop of the ants. *Phrynosoma modestum*, a smaller species of horned lizard in the Chihuahuan Desert, specializes on foragers of the smaller *Myrmecocystus depilis* and *M. mimicus* ants (Shaffer and Whitford 1981). *Phrynosoma modestum* may consume 50 percent of the early summer standing crop. These lizards also eat other ant species that become active after summer rains. *P. modestum* apparently partitions the ant fauna with *P. cornutum* (Shaffer and Whitford 1981). *Phrynosoma platyrhinos* in the Mojave Desert also feeds on harvester ants (Rissing 1981). It apparently prefers solitary foraging *Pogonomyrmex californicus* and avoids group foragers (*P. rugosus* and *Messor pergandei*), which "mob" lizards as a response to predation. Juveniles feed on the smaller *Pheidole gilvescens* workers in addition to the larger *Pogonomyrmex* spp. workers (Rissing 1981). Juveniles of *P. cornutum* have essentially the same diet as the adults (Whitford and Bryant 1979). Under some circumstances horned lizards may behave as "prudent predators" (preying on weaker individuals of prey populations) (Whitford and Bryant 1979; Munger 1984), although Rissing (1981) doubts this is possible. *Phrynosoma* spp. are generally not aggressive to other lizards and do not defend territories and thus could not protect themselves from "cheaters" (predators that prey on any individual of the prey population).

Other animals, such as birds (Gentry 1974) and spiders (MacKay 1982; MacKay and Vinson 1989; Porter and Eastmond 1982), are important ant predators. Spider predation on harvester ant nests may become so intense that the ants close the nest entrance with pebbles (MacKay 1982). The proportion of the nest population removed by the spiders under such circumstances may actually be low, less than 0.2 percent of the nest population per day (MacKay 1982). If spiders are removed from the vicinity of such nests, ants open the entrance and foraging resumes within 24 hours (MacKay 1982). Mammals may also be important predators of ants in desert ecosystems, especially in African deserts (Smithers 1983; Earlé and Louw 1988; Marsh personal communication). Heteromyid rodents (*Dipodomys* spp.) open harvester ant nests and remove the seed caches (Clark and Comanor 1973).

As suggested above, ants usually respond to predation. *Pogonomyrmex* harvester ants usually become immobile when nearby foragers are preyed on by horned lizards. Whitford and Bryant (1979) interpreted this behavior as avoidance of detection, but Rissing (1981) concluded that the ants are locating the predator and are preparing to attack during such times. Artificial or natural removal of part of the forager population usually causes a nest to stop aboveground activity (Gentry 1974; Whitford and Bryant 1979; MacKay 1982), although foraging activity may increase under such circumstances (Whitford and Bryant 1979). The cessation of foraging may prevent the entire nest from being destroyed by predation (Gentry 1974). Other responses of ants to predators include moving the nest entrance and the posting of guards (MacKay 1982).

Termites are also eaten by ants, lizards, birds, and humans in desert ecosystems (Smithers 1983; Redford 1984; Nkunika 1986), especially during the nuptial flights (MacKay personal observation; Marsh personal communication). During flights, termites may become the major food source for predators, even seed-harvesting ants (MacKay personal observation). The aardwolf feeds almost exclusively on termites and occurs in the eastern parts of the Namib as well as the Kalahari (Marsh personal communication). The aardvark has a similar distribution and feeds on both ants and termites. Bat-eared foxes consume considerable numbers of termites and are widespread in the Namib, occurring as far west as Gobabeb (Marsh personal communication). Termites compose up to 85 percent of the diet of *Lygodactylus* lizards in Zambia. A number of ant genera, such as *Palothyreus* and *Megaponera* (Nkunika 1986), are termite specialists. Termites are a major food source for *Myrmecocystus mimicus* (Hölldobler 1981), *Pogonomyrmex* spp. (Hölldobler 1986), and *Pheidole titanis* (Feener 1988) in North American deserts.

Interactions Between Social Insects and Plants

Mutualism between ants and plants has been extensively investigated in tropical and temperate ecosystems (Buckley 1982; Beattie 1985), but we know little about these interactions in desert ecosystems. The few data available suggest that social insects are very important for desert flora. Myrmecochory (seed dispersal by ants) is common in drier areas of Australia and South Africa, especially in areas with poor soils (Milewski and Bond 1982). More than 1,000 species of plants of the Cape Flora of South Africa are dispersed by ants (Giliomee 1986). Ants also have been shown to be important in the structure of desert plant communities (Inouye this volume). Ants may affect desert plant communities in several ways: (1) seed harvesters remove (and move) seeds; (2) ants move tremendous amounts of subsoil to the surface during nest construction; and (3) many species clear vegetation from their mounds, or the vegetation which grows on mounds is considerably different from the surrounding vegetation. Another factor that has not been investigated is the importance of subterranean galleries on water infiltration. Presumably ant galleries would be similarly important to those of termites.

Harvester ants collect between 2 and 10 percent of the total annual seed production in the Chihuahuan Desert (Whitford 1978a), up to 20 percent in the semiarid deserts of Australia (over 20,000 seeds/m^2 produced) (Briese 1982c). The selective removal and consumption of seeds of certain species affects the relative abundance of species in a desert community (Whitford 1978b). Plants that produce seeds not consumed by ants could increase in abundance. *Filago california* (a small-seeded composite) increased to dominate habitats when ants were excluded from plots (Inouye et al. unpublished, cited in Brown, Reichman, and Davidson 1979). There was also a decrease in species diversity of the plants within such plots. In some instances, ants may exert no effect on the plant community. Briese (1982c) found little effect

of ants on the plant community in semiarid New South Wales where ₃ are not seed limited.

Harvester ants could also change the spatial distribution of desert plants by moving seeds to other locations. Survival of the offspring of a plant could be increased by myrmecochory away from the parent plant where competition with the parent may reduce survivorship. A number of plant species have propagules made up of diaspores (seeds with protective covering) and elaiosomes (appendages that contain oils and fats and are very attractive to ants), which are collected by ants (Drake 1981). Often the elaiosome is eaten and the diaspore with seed is discarded intact. Myrmecochory is found in at least 223 genera in 61 families of plants (Nesom 1981). The majority of the herbs in a mesic forest community in New York are dispersed by ants (Handel, Fisch, and Schatz 1981). Myrmecochory was once believed to be limited to forests, but has been shown to be common in arid regions, at least in Australia (Davidson and Morton 1981b), where ants disperse the seeds of *Acacia* spp. (Mimosaceae), *Sclerolaena convexula* and *S. divaricata* (Chenopodiaceae), and *Dissocarpus biflorus* (Chenopodiaceae) (O'Dowd and Hay 1980). Although seeds are destroyed (Maddox and Carlquist 1985), myrmecochory is very important for most plant species involved. Plants compete for dispersion of seed by ants (Davidson and Morton 1981b). Myrmecochory has also been shown to assist seeds in escaping predation by rodents (Heithaus 1981). O'Dowd and Hay (1980) have shown that desert harvester ants are very important in the transportation of the seeds of *Datura discolor*. Ants collect the seeds and carry them to the nest. Ants remove the fleshy structure and discard the seed. The rate of predation by rodents is considerably reduced due to the action of the ants.

Many studies have demonstrated the importance of ant mounds in changing the
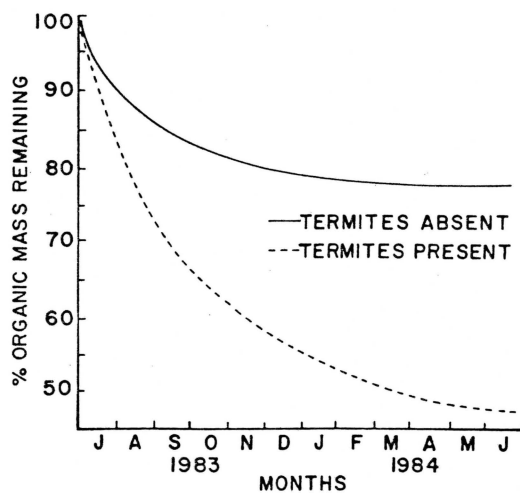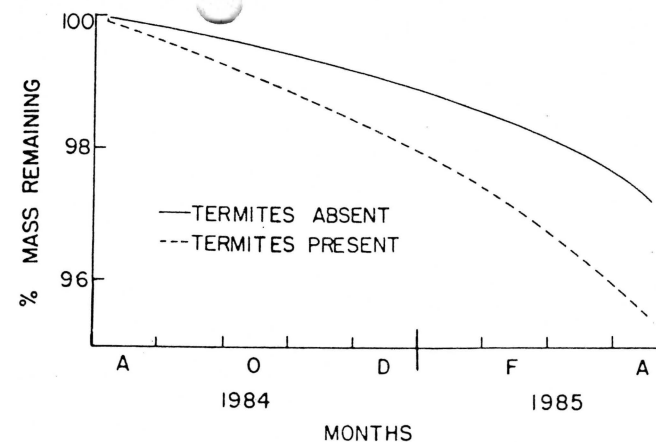

Figure 5.13. Effect of termites on mass loss of creosotebush wood (*Larrea tridentata*) in the northern Chihuahuan Desert of North America (from MacKay, Zak, & Whitford 1989).

vegetation in an area (Petal 1978). Soils from mounds are higher in nutrients and organic matter due to the concentration of resources by ants at a specific point (Breckle 1971; Davidson and Morton 1981b; Beattie and Culver 1983). The highly directional dispersal of diaspores by ants to nests where nutrients are concentrated and possibly more accessible (Davidson and Morton 1981b) greatly enhances the survival of the seedlings (Beattie and Culver 1983). As a consequence of harvesting of seeds and the change in the chemical composition and physical properties of the soil of the nest by the ants, floras around ant nests are quite different from floras of surrounding areas. For example, significant differences exist between the flora on *Myrmica* mounds versus that of control areas (Elmes and Wardlow 1982). There are clear qualitative and quantitative differences in the floras of mounds of *Cataglyphis bicolor* compared to surrounding areas in east Afghanistan (Breckle 1971). Each nest has a narrow band of rich flora surrounding it. Some plant species grow exclusively on ant mounds (Davidson and Morton 1981b).

Social insects, especially termites, can be considered to be keystone species in North American deserts (Whitford, Steinberger, and Ettershank 1982; Nutting, Haverty, and La Fage 1987; MacKay, Zak, and Whitford 1989). Termites are responsible for up to 100 percent of the mass loss from organic matter in the Chihuahuan Desert (Whitford, Steinberger, and Ettershank 1982) and can reduce the half-life of ocotillo wood in the Colorado Desert from 29 to 17 years (Ebert and Zedler 1984). Silva, MacKay, and Whitford (1985) were able to demonstrate that decomposition rates of fluffgrass litter on plots with termites present were much higher than plots where termites were excluded (Figure 5.12). Termites are also important in the mass loss of wood of the dominant shrub in North American deserts, creosotebush (*Larrea tridentata*), but not in mass loss of leaf litter (MacKay, Silva, Loring et al. 1987). Wood grazed by termites lost significantly more mass than ungrazed wood (MacKay, Zak, and Whitford 1989) (Figure 5.13).

Figure 5.12. Mass loss of fluffgrass (*Erioneuron pulchellum*) in plots with and without termites in the northern Chihuahuan Desert (from Silva, MacKay, & Whitford 1985).

Termite activity appears to be controlled by abiotic factors acting directly on the individual and by those factors that affect the rate of dead wood and litter production (MacKay, Zak, and Whitford 1989). Dead wood is added to the system from the effects of wind, snowfall, and insect damage (Figure 5.14). Litter falls to the soil surface as a result of drought or nutrient stress, changes in temperature, wind action, and by the browsing of mammals, especially rabbits (Steinberger and Whitford 1983). Lack of precipitation and temperature extremes also kill roots.

The effects of termites, water, and nitrogen in the composition of the Chihuahuan Desert plant community were examined by Gutierrez and Whitford (1987). Changes in the dominance of annual plant species were obtained within 3 years after termite removal (MacKay, Zak, and Whitford 1989). While some species, such as *Eriastrum diffusum*, were not affected by the treatments (Figure 5.15), others (e.g., *Baileya multiradiata*, *Descurainea pinnata*, *Eriogonum rotundifolium*, and *Lepidium lasiocarpum*) became more common in plots with termites removed. The growing period of some species (*Eriogonum tricopes* and *Tidestromia lanuginosa*) was reduced on plots without termites. Fluffgrass, the preferred food source of *Gnathamitermes tubiformans*, virtually disappeared from plots without termites by the fourth year following eradication of the termites (MacKay, Zak, and Whitford 1989). These
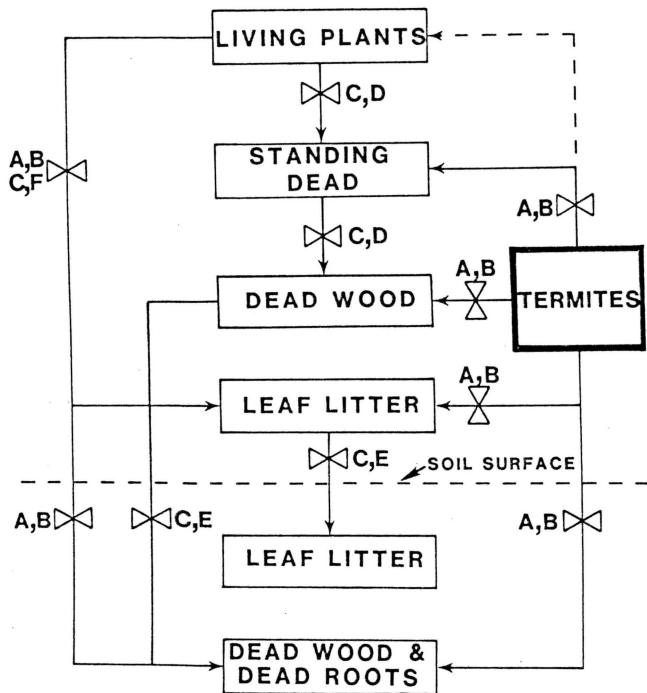

Figure 5.15. Comparison of the effects of termites, water and/or nitrogen on the phenology of a Chihuahuan Desert plant community. BAMU = *Baileya multiradiata*; DEPI = *Descurainea pinnata*; ERDI = *Eriastrum diffusum*; ERRO = *Eriogonum rotundifolium*; ERTR = *Eriogonum tricopes*; LELA = *Lepidium lasiocarpum*; and TILA = *Tidestromia lanuginosa*; T − = termites absent; T + = termites present; W = 0.6 cms of water applied to plots per week; N = nitrogen applied to plot at rate of 2.5 g/m^2 in a single application (from Gutierrez & Whitford 1987).

Figure 5.14. A schematic representation of the role of termites in the breakdown of organic matter in the northern Chihuahuan Desert (from MacKay, Zak, & Whitford 1989).
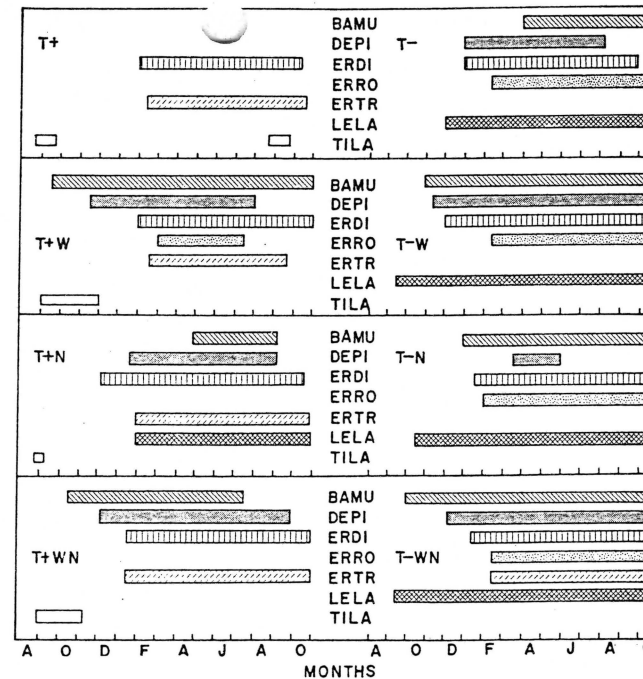
results demonstrate that termites have an important effect on the composition and dynamics of desert plant communities. The interactions between termites, water, and nitrogen on plant growth appear to be complex and dependent on the plant species examined. The type of vegetation in an area also has considerable influence on the termite fauna in semiarid woodlands of North Queensland (Holt and Coventry 1988).

Convergent Evolution among Deserts

There is considerable evidence that convergent evolution occurs in the fauna and flora of the world deserts. We must be careful in the interpretation of the data, as Australia, Africa, and South America were connected during the Cretaceous, and similarities could be due to common phylogenies (Milewski and Bond 1982).

Certain taxa compensate in diversity for the lack of other taxa. This especially obvious with regard to granivory. Patterns of granivory in other deserts may differ from the pattern in North American deserts, although the Israeli desert seems to be similar (Abramsky 1983). Rodents are more efficient than ants at finding and harvesting seeds. Rodents find seeds below the soil surface, which may be one mechanism of coexistence, as the Israeli ants forage only on the surface. Seeds are consumed much less readily in the Monte Desert of Argentina (Mares and Rosenzweig 1978). There are apparently fewer species of granivorous ants in South American deserts than in North American deserts (Mares et al. 1977; Brown and Ojeda 1987), although the genus *Pogonomyrmex* is best represented in South America (MacKay 1981). There are also fewer seed-eating mammals in South America due to recent extinctions (Pleistocene; especially the marsupial family Argyrolagidae), and other rodents and ants have not yet responded to this reduction via species radiation (Mares and Rosenzweig 1978; Brown and Ojeda 1987). Ants are dominant seed predators in Australian deserts (Morton 1985; Morton and Davidson 1988). Birds are also important in Australian deserts, but are unimportant in the New World deserts (Mares and Rosenzweig 1978). Rodents are relatively scarce in Australian deserts, but this has not resulted in intensified seed predation by ants (Morton 1985). Birds may compensate to some extent for the lack of rodents (Morton and Davidson 1988). The high intensity of seed predation in North American deserts may be due to a more dependable precipitation regime, adequate nutrient supplies, and perhaps the rapid recycling of nutrients (Morton 1985). Thus, convergence may not occur between deserts, and North American deserts may even be peculiar when compared to others (Morton 1985). Morton (1985) concluded that the seed removal rates are highest in North America, less in Australia, and least in South America.

Conclusions

Evidence clearly shows that ants and termites are very important components of arid ecosystems. They are among the dominant organisms in terms of numbers and biomass. Yet we know little about these social insects. For example, we have only a few good estimates of populations. We might assume that certain taxa (e.g., *Pogonomyrmex*, *Pheidole*) are all seed harvesters, but this is not the case. Several species in both genera feed on other insects or vertebrate feces (MacKay personal observation). We know little of factors that influence termite species richness in arid ecosystems. These insects are important in nutrient cycling and energy flow, but again few data are available to evaluate how important they actually are. The basic biology of most species is completely unknown, including what they eat and when they are active. Systematics of ants and especially termites is in a poor state. Thus, it is always difficult and sometimes impossible to identify common species or even to put generic names on some. We need to understand the processes of evolution from studies of the convergence between different regions. What effect do social insects have on other organisms? Are mutualisms between desert plants and ants common, and if not, why not? Is the environment too dry to allow many species to

nest in shrubs and trees? Are myrmecochores common in all deserts, but we simply don't know it? Morton and James (1988) have suggested that the abundance of termites in arid regions of Australia has led to a remarkable radiation of lizard species. The abundance of termites in the region may be due to the general infertility of the soils. What effect has the abundance and diversity of social insects had on the vertebrate fauna in other deserts of the world? Has the high ratio of sclerotized chitin to digestible biomass of ants (Redford and Dorea 1984) hindered predatory specialization on them? How common are chitinases in ant predators? They commonly occur among ants, even "seed predators" (MacKay personal observation). Do termites have an important effect on the vegetation in all deserts, as they do in the Chihuahuan Desert? Clearly an immense amount of work remains to be done. Unfortunately we will not understand the structure and function of arid ecosystems until we understand the roles of ants and termites in desert ecosystems.

Summary

Ants and termites are abundant in arid ecosystems of the world, both in terms of biomass as well as species numbers. They are keystone species in many ecosystems. Both ants and termites arose in the tropics and the genera present in arid regions today presumably had tropical ancestors. Primary production is the principal factor determining the number of ant species in a given habitat. Termite species richness may be determined by temperature: warmer habitats have more species. Also, areas with poorer soils have higher species richness. Ants and termites either avoid temperature extremes and vapor pressure deficits by being active during the cooler times of the day or night, or are physiologically adapted to the harsh conditions. These two taxa are especially important in altering the chemical and physical properties of the soil. Interactions between species, especially competition, are very important in structuring communities. Resources are partitioned according to differing activity patterns (seasonal or diurnal), by microhabitat differences, or based on size or quality of the food item. Both ants and termites are important in determining the composition of the plant community in a specific habitat. Termites are especially important as they greatly affect the chemical and hydrological properties of the soil, and because they also harvest and recycle plant materials.

Acknowledgments

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Patterns of Heterogeneity in Desert Herbivorous Insect Communities

6

Charles S. Wisdom

Herbivorous insects in desert regions face considerable environmental obstacles to successful growth and reproduction. These organisms must deal directly with the excessively high temperatures, vapor pressure deficits, and drought found in the arid regions of the world. Many studies have demonstrated the physiological and behavioral traits that desert-adapted arthropod herbivores use in dealing with these environmental variables, such as temperature tolerance (Edney 1967; Cloudsley-Thompson 1975; Mares et al. 1977), behavioral thermoregulation (Stower and Griffiths 1966; Cloudsley-Thompson 1975; Casey 1976, 1977; Mares et al. 1977; Anderson, Tracy, and Abramsky 1979; May 1979; Parker 1982), morphological adaptations (Cloudsley-Thompson 1975; Willmer and Unwin 1981), regulation of evaporative water loss (Edney 1967; Cloudsley-Thompson 1975; Edney 1977; May 1979; Toolson 1987), and mechanisms to prevent water loss (Edney 1967; Cloudsley-Thompson 1975; Edney 1977; Massion 1983).

Community organization of herbivorous insects is also affected indirectly by the environmental extremes of desert habitats through the responses of their host plants. Plants in desert climates face similar conditions of high temperature and irradiance and the unpredictable availability of water (Neales, Patterson, and Hartney 1968; Balding and Cunningham 1974; Beatley 1974; Caldwell 1985; Ehleringer 1985; Nobel 1985). Additionally, plants must deal with the occasional scarcity of some elements (e.g., nitrogen and phosphorus) (Turner et al. 1966; West and Skujins 1978) or overabundance of others (e.g., salts) (Moore, Breckle, and Caldwell 1972; Goodman 1973; Caldwell 1985).

Consequently, the community composition of herbivorous insects results directly