Ecology, 83(11), 2002, pp. 2991–2996

ON ECTOTHERM ABUNDANCE IN A SEASONAL ENVIRONMENT—STUDIES OF A DESERT ANT ASSEMBLAGE

Michael Kaspari[1,3] and Thomas J. Valone[2]

[1]*Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019-0235 USA*
[2]*Department of Biology, Saint Louis University, St. Louis, Missouri 63103 USA*

Abstract. The abundance of ectotherms should ultimately be limited by both plant productivity and the radiant energy that makes that productivity accessible. We analyzed a 21-yr data set on ant colony abundance from a North American arid grassland site. We tested the hypothesis that seed production and temperature co-limit granivorous ant abundance. We contrasted the responses of the four most common granivorous species and two omnivorous species to rainfall (summer vs. winter) and to an 8-yr seed addition experiment (summer vs. year-round seed additions). The abundance of granivorous ants was positively correlated with summer rainfall, but not winter rainfall, and was 30% higher on plots with summer vs. year-round seed additions. In contrast, the abundance of omnivorous ants was unaffected by either rainfall or the timing of seed additions. These data suggest that both the sign and size of the covariance between monthly temperature and precipitation may affect bottom-up regulation in ectotherms.

Key words: ants; desert; Dorymyrmex insanus; *ectotherm abundance;* Forelius *cf.* pruinosus; Pheidole rugulosa; Pheidole tucsonica; Pogonomyrmex desertorum; *precipitation; seasonality;* Solenopsis xyloni.

Introduction

The abundance of a taxon (individuals per unit area) is constrained by its ability to capture and store resources and to protect the resulting tissue against losses to predators, parasites, and pathogens (Lack 1954, Hairston et al. 1960, Oksanen et al. 1981, Power 1992). In ectotherms, the abiotic environment limits abundance in at least two important ways. First, temperature and rainfall co-limit net primary productivity (Rosenzweig 1968, Lieth 1975). Second, radiant heat, measured as temperature, limits behavioral and physiological access to that productivity (Andrewartha and Birch 1954, Kaspari et al. 2000). Evidence for co-limitation by productivity and temperature is limited by a lack of long-term records of a taxon's abundance, local climate, and key resources (Connell and Sousa 1983).

Ants are a model ectotherm system for testing co-limitation by productivity and temperature. Ants are important predators, competitors, and mutualists in most terrestrial habitats (Agosti et al. 2000, Kaspari et al. 2000); the factors that regulate ant populations may affect other trophic levels. Most ant colonies are sessile and can be reliably censused with quadrat counts (Agosti et al. 2000, Kaspari et al. 2000). Finally, ant abundance varies from <100 to $>60\,000$ colonies/ha from the New World tundra to rainforest (Kaspari et al. 2000). Variation in ant abundance at this geographic scale is consistent with the co-limitation of productivity and temperature (Kaspari et al. 2000).

We know less about what regulates ant abundance at local scales. For example, food addition experiments have increased (Deslippe and Savolainen 1994), marginally increased ($P < 0.055$; Ryti and Case 1988), and failed to increase (Munger 1992) reproductive output in common ant species. Thus there is sparse and conflicting experimental evidence for food limitation in ant communities despite a long-standing focus on interspecific competition for food as a process structuring these communities (Davidson 1985, Hölldobler and Wilson 1990, Kaspari et al. 2000).

We analyzed a 21-yr data set from a long-term experiment in the Chihuahuan Desert (Brown and Munger 1985, Davidson 1985, Valone et al. 1994). Rainfall limits seed production at this site (McClaran 1995, Ernest et al. 2000) and occurs in two seasonal peaks (Davidson et al. 1985). Winter rains that peak in December and January produce annuals that set seed in March and April; summer rains that peak in July and August produce a second annual seed crop in August and September. Bimodal rainfall has important consequences for access to seeds by ants. Ants are thermophilic and rarely begin foraging at temperatures $<10°C$ (Hölldobler and Wilson 1990). Desert granivorous ants studied near our study site begin foraging at 15°C (Whitford et al. 1981). Weather records from nearby Rodeo, New Mexico 1914–1978 (Western Regional Climate Center, *available online*)[4] suggest that the mean monthly temperature during the winter–spring seed set (13.1°C) is below this foraging threshold. Furthermore, granivorous ant activity is low during these months (Whitford

Manuscript received 25 March 2002; revised 16 May 2002; accepted 20 May 2002.

---

[3] E-mail: mkaspari@ou.edu

[4] URL: ⟨http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?nmrode⟩

et al. 1981; T. J. Valone, *personal observation*). In contrast, mean monthly temperature during the summer seed set (23.7°C) is well above this foraging threshold. We predict that summer seed pulses are more accessible to ants, and thus more likely to limit granivorous ant abundance. By the same logic, we predict that seeds added monthly throughout the year will be less likely to affect granivore ant abundance than if the same quantity of seed is broadcast in the warm months of August and September. Finally, we predict that the abundance of omnivorous ant species will not be strongly tied to summer seed pulses because of the availability of alternative food resources.

THE STUDY SITE AND ANT COMMUNITY

The study site is located 6.5 km east and 2 km north of Portal, Cochise County, Arizona, USA (31°55′ N, 109°09′ W) on an alluvial plain at an elevation of 1330 m. Vegetation at the site consists of upper Chihuahuan Desert scrub dominated by shrubs and scattered perennial grasses (Kelt and Valone 1995). The entire 20 ha study site is surrounded by barbed wire fence that has excluded livestock grazing since 1977 (Brown 1998).

Twenty-two ant species are common enough to be regularly noted since work began at the Portal site in 1977. Here we focus on six species that represent 82–83% of all colonies censused in 1992 and 1998 and are relatively easy to identify with field training. Over the 21 yr of this experiment, three postdoctoral fellows, and many graduate and undergraduate students helped census ant populations. Although vouchers from early in the experiment are not available, M. Kaspari checked the field identifications of T. J. Valone, who had censused the plots from 1991 to 1994 and from 1998 to the present, and found them to be accurate.

We classified four species a priori as granivores and hence most likely to respond to the natural and experimental increase in seed supplies. Species were classified as granivores based on literature descriptions (Davidson et al. 1985, Johnson 2001) and nest excavations that yielded seed caches (S. Cover, *unpublished data*; M. Kaspari, *unpublished data*). The four granivore species (*Pogonomyrmex desertorum*, *Solenopsis xyloni*, *Pheidole tucsonica*, and *Pheidole rugulosa*) are from the subfamily Myrmicinae. *Pheidole tucsonica* and *P. rugulosa* (Whitford et al. 1981) are among the smallest species with colonies of fewer than 1000 workers; *P. tucsonica* (a subspecies of *P. xerophila* raised to a full species by Wheeler and Wheeler 1986) was the numerical dominant and almost twice as abundant as the next species. *Pogonomyrmex desertorum* (Cole 1968) also has relatively small colonies and the largest workers of the six species. *Solenopsis xyloni* is the most omnivorous of the four granivores (Trager 1991), but collects and stores large quantities of seeds in the summer. It has workers of intermediate size, and likely the largest colonies of the granivores.

Two species, *Forelius* cf. *pruinosus* and *Dorymyrmex insanus* (subfamily Dolichoderinae), were classified as omnivores. Both species consume plant exudates and insect corpses and rarely visit seed baits (Creighton 1950, Hölldobler 1982, Holway 1999). *Forelius*, though one of the two smallest ants, has the largest colonies of the six species, (up to 10^5 workers; M. Kaspari, *unpublished data*).

METHODS

The Portal site contains 24 0.25-ha experimental plots: 23 were established in 1977 and 1 was established in 1979. Six-mm wire mesh fencing encloses each 50 × 50 m plot. This fencing extends 60 cm above ground and 20 cm below ground. At least 25 m separates adjacent plots (for further details see Brown and Munger 1985 and Brown 1998). From 1977 to 1987, two plots were unmanipulated controls (CONTROL treatment) and five plots excluded rodents (−RODENT treatment). One additional −RODENT plot was established in 1979. Previous studies have shown that ant abundances do not differ significantly between CONTROL and −RODENT treatment plots (Davidson et al. 1985, Valone et al. 1994). For this reason we combined −RODENT and CONTROL plots into one category and refer to these as CONTROL plots. These 7–8 plots allowed us to track ant abundance from 1977 and to correlate it with summer and winter rainfall from 1980.

Ant colonies were censused each year in July after the onset of the summer rains. Colony abundance was recorded from 49 2-m radius circles on each plot. The circles were spaced 6.5 m apart in a 7 × 7 grid. In each circle the number of colony entrances was recorded for all species except *Solenopsis*. Because a colony can have multiple nest entrances (Hölldobler 1982) multiple entrances <0.5 m apart for a given species were counted as a single colony. Because *Solenopsis* colonies often contain multiple entrances we recorded only the presence or absence of *Solenopsis* entrances for each quadrat (i.e., a maximum of one colony was recorded for each circle; Davidson et al. 1985). To ensure maximum ant activity, we conducted censuses when soil surface temperatures fell between 20° and 35°C, typically in the early morning. Census data from three years, 1995–1997, were deleted from this analysis because a different sampling protocol was used.

Precipitation was measured at the Portal site beginning in 1980. We tested the prediction that granivorous ant abundance would be correlated with the summer rainfall from the previous year. Recall that ants are censused at the outset of that year's summer rainfall and before seed set. One year should allow for the establishment of ant colonies from winged reproductives and reflect the impact of seed supply on colony survival. We predicted no effect of winter rainfall, given that seed set occurs when it is still cool (March–April). We tested for a winter effect by correlating col-

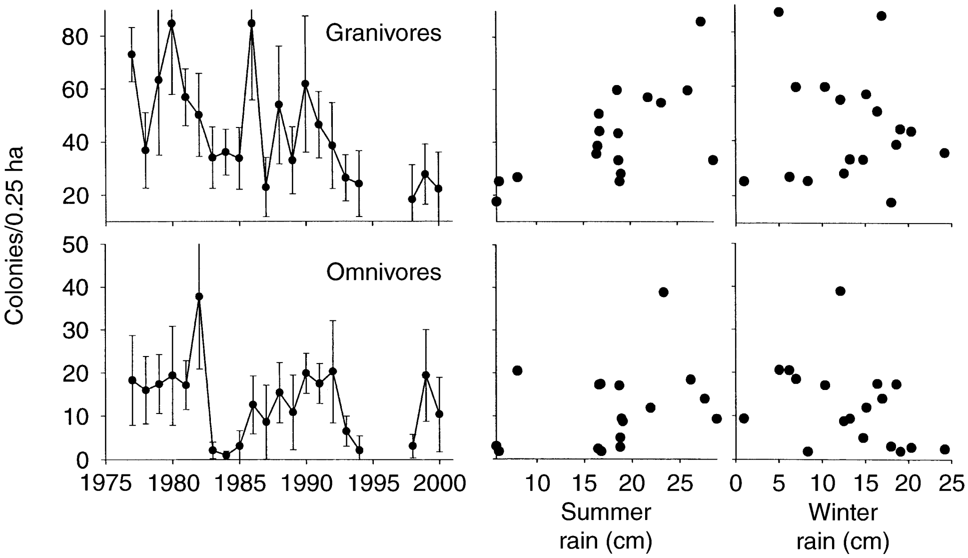

FIG. 1. July colony abundance for the four common granivorous ants and two common omnivorous ants of Portal, Arizona, USA. The left-hand plots show mean abundance (±1 SD) over the duration of this study. The center and right-hand plots show abundance from 1980 through 2000 vs. previous summer and winter rainfall.

ony abundance to rainfall from the same year and the previous year.

Seed addition experiments

Beginning in 1977 (but after the first ant census) eight plots (the +SEED treatments) were supplemented with 96 kg of milo (*Sorghum vulgare*), from September 1977 to August 1980, or millet (*Panicum miliaceium*), from September 1980 to December 1985, broadcast over the plot. Seeds were either whole (~6 mg) or cracked (~1 mg). In six plots (+$\text{SEED}_{\text{Continuous}}$ treatments) these seeds were spread in 12 equal monthly installments of 8 kg. Two plots received whole seed, two plots received cracked seed, and two plots received an equal mix by mass. In two plots (+$\text{SEED}_{\text{Pulse}}$) an equal mix of both seed sizes were broadcast in August–September.

Previous analyses (Davidson et al. 1985) suggested that granivorous ants failed to increase with seed additions. When we reexamined these data we found that in 1977, before seed addition treatments began, granivorous ant abundance on +SEED plots (93.4 colonies/0.25 ha, $n = 8$) was significantly higher than on our CONTROL plots (73.0 colonies/0.25 ha, $n = 7$, $F_{1,14} = 5.2$, $P < 0.05$), making any interpretation of CONTROL vs. +SEED difficult. We instead focus on the prediction that +$\text{SEED}_{\text{Pulse}}$ ($n = 2$) treatments will support a higher granivorous (but not omnivorous) ant abundance than +$\text{SEED}_{\text{Continuous}}$ ($n = 6$) treatments, given that pulse additions concentrate seeds in the warm months of the year when ants are most active. We used repeated-measures ANOVAs to test the null hypothesis that, while abundance may vary with time, colony abundance did not differ between +$\text{SEED}_{\text{Continuous}}$ and +$\text{SEED}_{\text{Pulse}}$ treatments.

RESULTS

Colony abundance on control plots varied considerably from year to year (Fig. 1). Annual mean granivore abundance varied 4.6-fold over time (18–85 colonies/0.25 ha); omnivore abundance varied 38-fold (1–37.8 colonies/0.25 ha). The six component species showed similar trends and covaried positively in time: Spearman rank correlations among the species (not shown) yielded only positive correlations.

Granivore abundance on CONTROL plots declined over the course of the study ($r_S = -0.58$, $P < 0.0055$, $n = 21$) whereas omnivore abundance showed no such trend ($r_S = -0.19$, $P < 0.43$). Colony abundance was neither positively ($P > 0.24$) nor negatively ($P > 0.34$) serially autocorrelated from year to year for the granivores (Durbin-Watson statistic = 2.42). In contrast, omnivore abundance was positively serially autocorrelated (Durbin-Watson statistic = 1.2, $P < 0.02$); i.e., increases or decreases in omnivore abundance tended to occur in runs.

Food limitation and rainfall

We tested the prediction that summer, but not winter, rainfall would be correlated with granivore abundance. Winter rainfall (mean = 13.3 cm) has varied 25-fold since measurements began in 1980; summer rainfall (mean = 18.1 cm) has varied fivefold in the same time period (Fig. 1). Summer and winter rainfall are not correlated ($r_S = -0.20$, $P > 0.42$).

Granivore abundance was positively correlated with

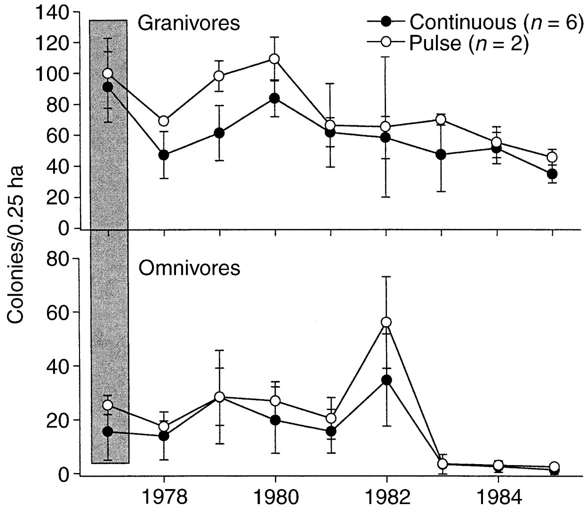

FIG. 2. Colony abundance (±1 SD) of granivorous and omnivorous ants when 96 kg of seeds were broadcast on plots in August and September (Pulse) vs. equal installments broadcast over the entire year (Continuous). The gray bar represents pretreatment abundance.

the previous summer rainfall ($r_S = 0.47$, $P < 0.03$, $n = 17$; Fig. 1), whereas omnivore abundance was not correlated with previous summer rainfall ($r_S = 0.31$, $P < 0.23$).

Granivore abundance was not correlated with preceding winter rainfall ($r_S = 0.00$, $P < 1.0$, $n = 18$). Winter rainfall was marginally negatively correlated with omnivore abundance ($r_S = -0.43$, $P < 0.08$). Similar results were obtained if winter rainfall was lagged one year (i.e., granivore $r_S = -0.11$, $P > 0.68$; omnivore $r_S = -0.35$, $P > 0.18$).

Response to pulsed vs. continuous seed additions

The abundance of granivorous ants failed to vary across the three continuous treatments (small, mixed, and large seeds) in 1977 (ANOVA: $F_{2,3} = 3.72$, $P > 0.15$) or from 1978 to 1985 (repeated-measures ANOVA treatment effect: $F_{2,3} = 0.93$, $P < 0.49$). The same was true for omnivore abundance (1977: $F_{2,3} = 1.95$, $P > 0.28$; 1978–1985: $F_{2,3} = 0.54$, $P > 0.63$). With the small sample sizes per treatment ($n = 2$), power is low. However, from 1977 to 1985, the mean colony abundance on the mixed size treatment (the same size distribution used in the +SEED$_{\text{Pulse}}$ addition) was higher in only 1 of the 9 yr for the granivores, and 4 of 9 yr for omnivores. So there is little evidence that +SEED$_{\text{Pulse}}$ plots would support more ants because the seeds themselves were more palatable. We therefore pooled the continuous treatments together under +SEED$_{\text{Continuous}}$ to compare with +SEED$_{\text{Pulse}}$ treatments.

In 1977, before the first seed additions, neither granivore abundance nor omnivore abundance differed between +SEED$_{\text{Continuous}}$ and +SEED$_{\text{Pulse}}$ treatments (Fig. 2; granivores: 92 vs. 100 colonies/0.25 ha, $F_{1,6} = 0.22$, $P > 0.65$; omnivores: 16 vs. 25 colonies/0.25 ha, $F_{1,6} = 1.5$, $P > 0.26$). Granivore abundance was, on average, 30% higher (range from +7.2% to +60.2%) on the +SEED$_{\text{Pulse}}$ treatments from 1978 to 1985 (Table 1; $P < 0.02$). Although both treatments covaried greatly from year to year (Fig. 2; year effect $P < 0.0002$), there is no interaction between time and treatment ($P > 0.49$). Although omnivore abundance also varied with time (Table 1; $P < 0.0001$), it did not differ between +SEED$_{\text{Continuous}}$ and +SEED$_{\text{Pulse}}$ treatments (Table 1; $P > 0.40$).

DISCUSSION

Net primary productivity, which ultimately limits the abundance of terrestrial consumers, is itself limited by radiant energy and rainfall (Rosenzweig 1968, Lieth 1975). However, energy and rainfall covary in different ways in different climates (Lieth 1975): lowland tropical wet rainforests are ever warm and ever wet; Mediterranean climates receive most of their rain in the cool season; many deserts receive a pulse of precipitation when it is cold and a second pulse in the heat of the summer. The nature of this covariance is important to ectothermic consumers that rely on both plant productivity and the radiant energy that promotes its harvest (Kaspari et al. 2000). Consistent with this view, the abundance of granivorous ants in the Chihuahuan Desert increases with the previous season's summer, but not winter, rain. Furthermore, seed additions concentrated in the summer increase granivorous ant abundance to levels 30% higher than year-round seed additions. The lack of such patterns among co-occurring omnivorous ants suggests that seed quantity and access limit granivore abundance in a bottom-up fashion.

Granivory is often a key population interaction in deserts (Polis 1991). At the Portal site, granivorous ants are limited by summer annual production and may also

TABLE 1. Responses of two guilds of ants to continuous vs. pulsed seed addition over eight years, analyzed with repeated-measures ANOVA.

Source	df	Type III SS†	MS	F	P
A) Granivores					
+SEED	1	3284	3284	10.3	0.0184
Error	6	1913	319		
Year	7	12 249	1750	7.7	<0.0001
Year × +SEED	7	1485	212	0.93	0.4924
Error(Year)	42	9562	2287		
B) Omnivores					
+SEED	1	283	283	0.82	0.3993
Error	6	2062	344		
Year	7	9546	1363	19.1	<0.0001
Year × +SEED	7	533	76	1.06	0.4033
Error(Year)	42	3006	72		

† Each effect is tested after all other effects are included in the model.

depress natural populations of winter and summer annuals (Davidson et al. 1985). Migratory sparrow populations also track the seeds generated by summer rains (Pulliam and Parker 1979, Dunning and Brown 1982). Rodents show a more complicated pattern, with seed additions enhancing the abundance of the largest rodent species (*Dipodomys spectabilis*; Brown and Munger 1985), but with rodent abundance failing to track precipitation or plant production (Ernest et al. 2000). It is not clear why highly mobile taxa with high metabolic costs (birds) and less mobile taxa with low metabolic costs (ants) track seed production at Portal while moderately mobile taxa with high metabolic costs (rodents) generally do not.

Winter rainfall is not correlated with granivorous ant abundance, suggesting that those seeds are relatively inaccessible at seed set due to temperature constraints (a +SEED experiment in March–April would further test this hypothesis). Furthermore, there is some evidence that winter rainfall may constrain omnivore abundance (Fig. 1). This at first seems counterintuitive; as nectarivores, both *Dorymyrmex* and *Forelius* would be expected to benefit from increases in perennial shrubs that exude nectar or the nectar-exuding insects that ants use (Wagner 1997). However, winter precipitation plus cold weather may also increase the risk of frost death (Heinze and Hölldobler 1994). The omnivores *Dorymyrmex* and *Forelius* may be especially vulnerable to frost death because both species have thin integuments (Davidson 1997).

The advantages of ectothermy (smaller possible body size, low metabolic costs, high fasting endurance; Pough 1980) come with attendant costs. Here we use long-term monitoring and an experiment to suggest that the timing of rainfall and the availability of radiant energy can combine in subtle ways to regulate access to productivity by ectotherm consumers. If true, then habitats that concentrate productivity when temperatures are low (e.g., chaparral shrublands and highly productive but cool coniferous forests) may support lower abundances of ectotherm granivores and herbivores than environments with the same annual productivity, but in which rainfall and temperature positively covary (Kaspari et al. 2000).

ACKNOWLEDGMENTS

We thank the many postdoctoral fellows, graduate students, and undergraduates who have conscientiously collected and maintained the Portal data sets. We are particularly grateful to Diane Davidson and Ed Heske. Stefan Cover, Mark Deyrup, Bob Johnson, and the students and faculty of the Ant Course 2001 provided ample constructive criticism, as did Ian Billick, Jim Brown, Nick Gotelli, and an anonymous reviewer. These data were collected with the continued support of NSF, most recently grant DEB9707406.

LITERATURE CITED

Agosti, D., J. D. Majer, L. E. Alonso, and T. R. Schultz. 2000. Measuring and monitoring biological diversity: standard methods for ground-living ants. Smithsonian Press, Washington, D.C., USA.

Andrewartha, H., and L. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. H. 1998. The desert granivory experiments at Portal. Pages 71–95 *in* W. J. Resetarits and J. Bernardo, editors. Experimental ecology. Oxford University Press, Oxford, UK.

Brown, J. H., and J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology **66**:1545–1563.

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

Connell, J., and W. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist **121**:789–824.

Creighton, W. S. 1950. The ants of North America. Bulletin Museum of Comparative Zoology Harvard University **104**: 1–585.

Davidson, D. W. 1985. An experimental study of diffuse competition in harvester ants. American Naturalist **125**: 500–506.

Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biological Journal of the Linnaean Society **61**:153–181.

Davidson, D. W., D. A. Samson, and R. S. Inouye. 1985. Granivory in the Chihuahuan Desert: interactions within and between trophic levels. Ecology **66**:486–502.

Deslippe, R. J., and R. Savolainen. 1994. Role of food supply in structuring a population of *Formica* ants. Journal of Animal Ecology **63**:756–764.

Dunning, J. B. J., and J. H. Brown. 1982. Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis. Auk **99**:123–129.

Ernest, S. K. M., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos **88**:470–482.

Hairston, N., F. Smith, and L. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **44**:421–425.

Heinze, J., and B. Hölldobler. 1994. Ants in the cold. Memorabilia Zoologica **48**:99–108.

Hölldobler, B. 1982. Interference strategy of *Iridomyrmex pruinosum* (Hymenoptera: Formicidae) during foraging. Oecologia **52**:208–213.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Belknap Press, Cambridge, Massachusetts, USA.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive argentine ant. Ecology **80**:238–251.

Johnson, R. A. 2001. Biogeography and community structure of North American seed-harvester ants. Annual Review of Entomology **46**:1–29.

Kaspari, M., L. Alonso, and S. O'Donnell. 2000. Three energy variables predict ant abundance at a geographic scale. Proceedings of the Royal Society London B **267**:485–490.

Kelt, D. A., and T. J. Valone. 1995. Effects of grazing on the abundance and diversity of annual plants in Chihuahuan desert scrub habitat. Oecologia **103**:191–195.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, UK.

Lieth, H. 1975. Primary production of the major vegetation units of the world. Pages 203–215 *in* H. Lieth and R. Whittaker, editors. Primary productivity of the biosphere. Springer-Verlag, New York, New York, USA.

McClaran, M. P. 1995. Desert grasslands and grasses. Pages 1–30 *in* M. P. McClaran and T. R. Van Devender, editors. The desert grassland. University of Arizona Press, Tucson, Arizona, USA.

Munger, J. C. 1992. Reproductive potential of colonies of desert harvester ants (*Pogonomyrmex desertorum*): effects of predation and food. Oecologia **90**:276–282.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240–262.

Polis, G. A., editor. 1991. The ecology of desert communities. University of Arizona Press, Tucson, Arizona, USA.

Pough, F. H. 1980. The advantages of ectothermy for tetrapods. American Naturalist **115**:92–112.

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

Pulliam, H. R., and T. H. Parker. 1979. Population regulation of sparrows. Fortschrift Zoologica **25**:137–147.

Rosenzweig, M. 1968. Net primary productivity of terrestrial environments: predictions from climatological data. American Naturalist **102**:67–74.

Ryti, R. T., and T. J. Case. 1988. Field experiments on desert ants: testing for competition between colonies. Ecology **69**: 1993–2003.

Trager, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). Journal of the New York Entomological Society **99**:141–198.

Valone, T. J., J. H. Brown, and E. J. Heske. 1994. Interactions between rodents and ants in the Chihuahuan Desert: an update. Ecology **75**:252–255.

Wagner, D. 1997. The influence of ant nests on *Acacia* seed production, herbivory, and soil nutrients. Journal of Ecology **85**:83–94.

Wheeler, G. C., and J. Wheeler. 1986. The ants of Nevada. Natural History Museum of Los Angeles County, Los Angeles, California, USA.

Whitford, W. G., D. J. Depree, P. Hamilton, and G. Ettershank. 1981. Foraging ecology of seed-harvesting ants, *Pheidole* spp. in a Chihuahuan Desert ecosystem New Mexico. American Midland Naturalist **105**:159–167.