multiplying a constant quality of service by quantity (as proposed by Herrera 1987, 1989). Instead, we must multiply the quantity of service by a quality of service that is a nonlinear function of quantity. Here, we quantify the nonlinear relationship between the quality and quantity of mutualistic service, and offer an integrated measure of total service provided by different partner species.

We expect differences among partners to be particularly pronounced for mutualists that offer rewards accessible to a variety of members of the surrounding community. For example, extrafloral nectar (hereafter, EFN) can be eaten by ''practically any ant that encounters it'' (Carroll and Janzen 1973), and the average EFN-bearing plant species is visited by six to nine ant genera (Oliveira and Brandão 1991). EFN-visiting ants often protect plants from herbivores, although interspecific differences among the ant partners can have significant effects on plant fitness (Horvitz and Schemske 1984, Rico-Gray and Thien 1989, Djieto-Lordon et al. 2004) and perhaps on selection pressures fostering the mutualism (Rudgers 2004). Here, we use our integrated measure of total service to assess how the quality and quantity of protection provided by different ant species contribute to their effectiveness as bodyguards.

We focus on the ant assemblage associated with *F*   (Cactaceae), an EFN-bearing cactus of the Sonoran Desert. Although EFN-bearing cacti are common in desert ecosystems (Lloyd 1908, Pemberton 1988) and the diversity of ants attracted to individual species has been noted to be quite high (Blom and Clark 1980, Oliveira et al. 1999), little is known about the benefits that EFN visitors confer (but see Pickett and Clark 1979, Oliveira et al. 1999). The *F*.   system has several characteristics that make it amenable to studying the links between the quality and quantity of protection provided by different ant species. Extrafloral nectaries are spatially concentrated due to the plant's simple architecture (making it possible to observe ant
l75;avirs eectureacea-268.3(.7e5;ayas(thei6obs51Ra)-256.1(on99284.7(the)-446.3(pl);rt.)-24obs51Ra)6334.8(species)]TJ0-1.2266TD.

able to the presence of one another. We monitored a subset of control plants without caterpillars added, to clarify that any change in ant abundance was due to the presence of caterpillars rather than observers. We also added 10 caterpillars to plants without ants, to estimate the rate that caterpillars might abandon the plants or be removed by other predators in the absence of ants.

For each ant species, we computed a measure of total protection service that integrates the quantity and quality components of service. For each observation of a given ant species in the 2003 surveys, we substituted the observed number of workers and that ant's maximum likelihood estimate of   into Eq. 1 to obtain a measure of potential herbivore removal for that observation. We then averaged these values over all observations of that ant species. As Eq. 1 is a nonlinear (convex) function of the number of workers, the alternative procedure of substituting the average number of workers observed across surveys into Eq. 1 would overestimate the average protection a plant would receive when the ant species is present. Because the survey describes the number of ants present prior to any herbivore-induced response, we used the values of   derived from abundance data before caterpillars were added. To gauge the likely range of total protection, we also estimated average protection as described previously but using the upper and lower 95% confidence limits of   for each ant species. Because the observed number of workers on occupied plants was less in April–June than in July–September (see   ), estimates for those two periods were separated.

A

We counted the numbers of floral buds, flowers that failed to produce fruits, and mature fruits on each of the 259 plants on 1–3 October 2004. To measure plant reproductive success during the bud maturation phase (April–June), we computed the survival of buds to flowering as the ratio of the observed number of floral buds that flowered (i.e., the sum of senesced and/or abscised flowers and mature fruits on each plant in October) to the number

by the ants. We used the ratio of surviving fruits produced to the number of buds expected based on plant size as the dependent variable. As before, we used linear regressions to compare how mean reproductive success changed with mean protection by ants.

RESULTS

A   :   ‗   .

Plants were occupied by only one ant species at a time in 94% and 95% of the inspections at which ants were observed in 2003 and 2004, respectively. Ant turnovers were common, and 92% of the plants hosted more than one ant species over the course of the 2003 survey (3.3 ϭ 1.4 species/plant, mean ϭ SD; maximum = 8 species/ plant). *C   * was the ant most commonly observed at EFN (55% and 44% of the plant censuses in which ants were found in 2003 and 2004, respectively).

variance, = 3.51, df = 83, = 0.0004). During those surveys, phytophagous hemipterans, including _C_ -, , _, and sp., were five times more abundant on untended plants, relative to plants with ants at the time of inspection (0.02 ᵹ 0.001 and 0.12 ᵹ 0.06 individuals/plant/survey, mean ᵹ ꜱᴇ;

one-sided = 1.65, df = 275, = 0.049). Hemipterans were less abundant on plants tended by only . _ at

buds increased with plant protection by ants, whether plants were grouped by integrated measures of protection (simple linear regression, $F = 31.2$, df $= 1, 9$, $= 0.0004$) or by their most common attendant ($F = 33.4$, df $= 1, 4$, $= 0.004$). Those relationships were best described by decelerating power functions (Fig. 3a, d, respectively).

Plants tended by ants in July–September matured a greater proportion of buds into mature fruits, relative to untended plants (0.89 ∂ 0.03 fruits/bud, $= 227$ plants and 0.52 ∂ 0.22 fruits/bud, $= 4$ plants, respectively); one-sided t test assuming unequal variance, $= 1.79$, df $= 4$, $= 0.07$). Differences in the mean proportion of buds surviving to fruit were accurately predicted (^{2} 0.9) whether plants were grouped by integrated measures of protection (simple linear regression, $F = 28.4$, df $= 1, 5$, $= 0.003$) or by their most common attendant ($F = 5.73$, df $= 1, 4$, $= 0.07$). Those relationships were best described by logarithmic (Fig. 3b) and decelerating power functions (Fig. 3e), respectively.

Ultimately, the production of mature fruit differed among plants with different ant tending histories from April to September. The magnitude of these differences was accurately predicted (^{2} 0.8) whether plants were grouped by integrated measures of protection (simple linear regression, $F = 13.5$, df $= 1, 7$, $= 0.008$; Fig. 3c) or by their most common attendant ($F = 14.5$, df $= 1, 4$, $= 0.02$; Fig. 3f). The relationships were best described by logarithmic and decelerating power functions, respectively.

<center>DISCUSSION</center>

The overall effect of the interactions between mutualists is determined by both interaction frequency and net effects per interaction event. In cases such as the interaction between ants and EFN-bearing plants, where each event may involve multiple individual ants from the same colony interacting with an individual plant, the net effect for the plant may depend on both the number of ants and their per capita effect. In our study, we found evidence of variation among potential mutualist species in their numbers of individuals per interaction event, per capita effects, and in the frequency of those interactions. Recognizing these several ways that ant partner species can differ helped us to predict variation in the reproductive output among plants based on their different histories of interactions.

Although it is well appreciated that prospective partner species can differ in their effectiveness as mutualists, the components of this variation are rarely dissected. For example, the ant bodyguards of plants are often ranked by a gestalt approach, one that combines observations of clearly aggressive behaviors (bites and sprays) with more ambiguous behaviors, such as recruitment to disturbance (e.g., Buckley and Gullan 1991, Itioka et al. 2000, Michelangeli 2003). A more quantitative approach involves adding surrogate herbivores that are available in abundance but do not damage plants to explore the degree of protection conferred by ant attendants (e.g., Inouye and Taylor 1979, Koptur 1984, Cronin 1998). This technique standardizes trials with respect to herbivore size, condition, and abundance, although it is uncertain whether the interactions between an ant and these surrogates mimic interactions with the natural herbivore communities. We used the Michaelis-Menten function to quantify the per capita effectiveness of ants in finding and attacking surrogate herbivores, and to describe those species on a continuous (rather than ordinal) scale. This technique allowed us to assess the functional significance of differences among ant species, and facilitated accurate predictions regarding the protection these ants provide in the wild. Further, it illustrates that relatively few aggressive individuals and a larger number of milder ants can provide similar protection (Janzen 1972), particularly if the latter are more likely to discover herbivores (Koptur 1984). Last, this technique recognizes that the protective services conferred by ants saturates with increasing ant abundance (e.g., Inouye and Taylor 1979, Rocha and Bergallo 1992). Although our methodology places a ceiling on these benefits, because we only added 10 caterpillars per plant for the ants to subdue, this caterpillar density exceeds the density of native herbivores observed in the wild (McIntosh 2002). We chose to add surrogate herbivores at higher densities for ecological and methodological reasons. First, a surrogate herbivore may be easier for bodyguards to deter or kill than is a natural, and perhaps ant-adapted, herbivore (e.g., Freitas and Oliveira 1996). Second, because the Michaelis-Menten function relates the species-specific to the proportion of a service completed, can be estimated with greater accuracy when (1) the criteria for "complete service" (here, incapacitating all caterpillars) is more stringent, and (2) the proportions can be distinguished in progressively smaller increments.

Because the four ant species that interact most frequently with $F.$ at our site are found in different abundances, and differ in their per capita effectiveness when challenged to remove herbivores, we can describe a hierarchy of protection offered by these ant species when visiting the plants: . _ . . $= C.$. F sp. (Appendix B). However,

of returning to the plant (as in Inouye and Taylor 1979, Koptur 1984, Rocha and Bergallo 1992), in situations where new herbivores continually attack the plant, or where the presence of ants discourages oviposition by adult herbivores (Freitas and Oliveira 1996). Against these herbivores, the protection that ants provide the plant may saturate with the quantity of workers on the plant at any one time (a ''visit'') yet still increase continually with the frequency of visits.

Whether a visit by a given ant species truly confers protection to the plant may also be influenced by the correspondence between the phenologies of a plant's bodyguards and its natural enemies, because bodyguards may provide little benefit when plants do not need protection. Analogously, two pollinators can differ in quality simply because they visit flower stages of differing receptivity to pollen (e.g., Herrera 1987). We distinguished two three-month periods to account for the variation *F*.   may experience in vulnerability, worker abundance per interaction, and interaction frequency over time. Our results (Fig. 3) suggest that plants benefited from ant tending in both April–June and July–September, although estimated protection was greater in the later season, due to an increase in visit frequency, workers per visit, and more frequent visitation by . . Many EFN-bearing plants, including a congener of *F.*   (Rufner and Clark 1986), can change the nectar rewards they offer among seasons, perhaps explaining some of the temporal variation in interaction frequency, worker abundance, and partner identity observed in this system (Morris et al. 2006). We note, however, that even if a greater proportion of plants are tended by *C.*   in one season or . in another, that distinction may be of negligible importance to an individual plant if those species provide similar levels of protection. Further, the saturating relationship we find between ant protection and plant benefit suggest that the importance of variation in plant protection decreases as plants become progressively better defended.

We view the strong correlations between the protection provided by ants and the successful production of flowers and fruits by plants as evidence that the ant–cactus interaction is in fact a mutualism, in which ants benefit from a carbohydrate food source and cacti benefit by protection from natural enemies. An alternative hypothesis is that the relationship between plant reproduction and ant tending is coincidental rather than causal. Interestingly, reproduction by the subset of plants tended by rarer ant species (i.e., *C*   , *D* _ _   , _   . _   , and   spp. as a group) in greater than half of the inspections was similar to that by untended plants (60 6 20% of buds predicted from plant size, and 61 6 12.4% of buds became mature fruits;   = 4 plants in April–June, 7 plants in July–September, respectively). The fact that a particular subset of ant-tended plants reproduce no better than do untended plants suggests that variation among ant species influences plant reproduction. This

variation may be due to among-ant differences in both the costs and benefits plants can incur by participating in the mutualism. Our current study explores how bodyguards deter herbivores and increase flower and fruit production, two positive effects on plant fitness components. A companion study (Ness 2006) explores whether the more aggressive ant species may also deter pollinators, perhaps thereby altering the quantity of pollen delivered to, or donated by, host plants, as well as seed production arising from those individual flowers. Although spatiotemporal variation in the relative magnitudes of these costs and benefits may be considerable (e.g., due to fluctuating herbivore and pollinator populations), we believe the net effects of this ant–plant interaction are typically positive.

If we view quantity and quality as the two axes along which multiple partner species in generalized mutualisms may differ, we must recognize that these two axes often will not be independent. Although we expect in general that resource limitation will cause quality to decline as quantity increases, details are likely to differ for different types of mutualism (Holland et al. 2002). Mutualisms may also differ in the components that constitute the quantity of interaction. For example, when animal partners forage singly, as in most pollination and seed dispersal mutualisms, the quantity of service is simply the number of individual partners arriving at a plant per unit time. In most ant protection mutualisms, both the proportion of time ants are present and the number of workers when present contribute to the quantity of interaction. We found evidence that the quality of protection service may saturate with an increasing quantity of service measured at both of these levels: herbivore removal saturates as the number of workers increase, and plant reproduction saturates as overall protection (which incorporates the proportion of time

re-23po

generalize mutualisms
tvhepr53.68.8chxes we   ausnd
quantity   seand service may

soft scales and mealybugs (Homoptera: Coccidae, Pseudo-coccidae). Biotropica **23**:282–286.

Carroll, R. C., and D. H. Janzen. 1973. Ecology of foraging by ants. Annual Review of Ecology and Systematics **4**:231–257.

Cronin, G. 1998. Between-species and temporal variation in *A*   –herbivore interactions. Biotropica **30**:135–139.

Del-Claro, K., and P. S. Oliveira. 2000. Conditional outcomes in a neotropical treehopper–ant association: temporal and species specific variation in ant protection and homopteran fecundity. Oecologia **124**:156–165.