COMPETITION FOR PREY BETWEEN ANTS AND BURYING BEETLES (*NICROPHORUS* SPP): DIFFERENCES BETWEEN NORTHERN AND SOUTHERN TEMPERATE SITES.

BY MICHELLE P. SCOTT, JAMES F. A. TRANIELLO, AND ISABELLE A. FETHERSTON

Department of Biology, Boston University, Boston, Massachusetts 02215

INTRODUCTION

Burying beetles (Silphidae: *Nicrophorus*) utilize small vertebrate carcasses which can be quickly buried or rolled down a hole and concealed. Because carrion is also used by other invertebrates and vertebrates, burying beetles may be in competition with species of a wide variety of taxa for access to carcasses. For example, calliphorid flies are often first to oviposit on carrion and if the eggs are not detected and destroyed by *Nicrophorus* the carcass may be consumed by developing fly larvae, causing the beetles to abandon the resource.

One aspect of resource competition in *Nicrophorus* that has not been examined concerns interactions between burying beetles and ants (Arnett 1946). Ants are abundant, omnivorous scavengers in many habitats; ant colony size is often large and many species have swift recruitment systems that would allow them to occupy and defend small vertebrate prey. Ant species diversity and abundance are known to follow a latitudinal gradient (Kusnezov 1957, Wilson 1971, Jeanne 1979), and therefore the predatory or scavenging habits of ants may exert different effects on the ability of northern and southern temperate *Nicrophorus* species to control small vertebrate carrion. In this paper we report on the results of a study examining competitive interactions between burying beetles and ants at northern and southern sites in North America.

MATERIALS AND METHODS

The natural history of burying beetles (*Nicrophorus* spp.) and their ecological relationships have been well described (Pukowski

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1933, Milne and Milne 1976, Anderson 1982, Wilson 1983, Wilson et al. 1984, Wilson and Knollenberg 1984, Wilson and Fudge 1984). Males and females are attracted to carrion, and intrasexual competition occurs within each sex until usually only one male and female remain. The pair may then move the corpse; both sexes dig beneath to bury it, remove the fur or feathers of the carcass, and roll it into a ball treated by both male and female with anal and oral secretions. Following burial, the female's ovaries rapidly complete development (Scott and Traniello 1987) and she lays approximately thirty eggs in the soil nearby which hatch into altricial larvae that are fed regurgitated food by both parents. The larvae are soon capable of feeding from the corpse directly, but may also receive food from their parents throughout development. About two weeks after burial, the larvae leave the burial chamber and pupate in the soil nearby. Usually, at least one parent remains with the brood until larval dispersal.

Ant and burying beetle competition was studied in a mixed hardwood (maple/birch/beech) and softwood (pine/hemlock/spruce) forest at Jaffrey, New Hampshire (Cheshire County) and in a pine/oak forest and two field sites at Wimauma, Florida (Hillsborough County). *Nicrophorus sayi, N. orbicollis, N. defodiens,* and *N. tomentosus* are common at the northern site, and *N. orbicollis* and *N. carolinus* were trapped in Florida. In order to study abundance and diversity of ants and burying beetles, a transect of 10–25 pitfall traps (0.95 liter jars) located 10 m apart was set out on each site. In New Hampshire these were baited with aged beef kidney and in Florida with previously frozen whole chicks (*Gallus gallus*) which did not dry out in the heat and were more effective in attracting all invertebrates. Pitfall traps were censused after 24 h. To examine competition between ants and beetles for the utilization of small vertebrate carrion, previously frozen mice (*Mus musculus*), 8–60 g, or chicks, 45–55 g, were placed over 0.95 liter jars or 11.4 liter pots filled with potting soil and sunk into the ground at 25-m intervals. These traps were censused every 24 h and the ultimate fate of each carcass (buried by beetles, overrun by ants until the carcass was consumed or was no longer attractive, removed by vertebrates, or utilized primarily by flies) was recorded. The traps containing carcasses buried by beetles were retained and adults leaving the brood chamber, and either eclosing flies or teneral

beetles were captured. Studies were conducted June–August 1984, 1985 in New Hampshire and May–July 1986 in Florida.

RESULTS

Burying beetles were readily caught in pitfall traps at both locations. In New Hampshire, 662 beetles of all four above-mentioned common species were trapped in 525 trap-nights in 1984 and 457 beetles were trapped in 525 trap-nights in 1985. Ants (*Camponotus novaboracensis, Acanthomyops* sp. and *Aphaenogaster* spp) were found in less than 2% of the pitfall traps and always in low numbers (less than 10). At the southern site 441 beetles were trapped in 794 trap-nights. Ninety-five percent of these were *N. carolinus* which were trapped in equal numbers in the forest and in the field. *N. orbicollis* were captured primarily in the forest. Ant/burying beetle interactions were related to habitat also, reflecting the primarily open-field distribution of the imported fire ant *Solenopsis invicta.* In the forest *S. invicta* was found in 33% of the pitfalls and other ant species in 9% (N = 360); in the field 61% of the pitfalls were occupied by fire ants and 6% by other ant species (N = 434). Information on ant abundance from the pitfall traps at the two study sites similarly indicates a greater potential for ant interference at the Florida site. When ants were present in pitfalls, 94% of traps contained more than approximately 100 workers. Other ant species (*Camponotus abdominalis floridanus, Crematogaster clara*) were found in pitfall traps in small numbers (less than 10). *Pheidole dentata, P. moerens, Crematogaster ashmeadi* and *Conomyrma* sp. were found at baits in the same habitat but not in the pitfall traps.

There were striking differences between sites in New Hampshire and Florida in the percentage of mice or chicks available that were successfully buried by *Nicrophorus* spp. (42% vs 10%, N = 172 and 48, respectively, $t_S = 4.70$, $P < 0.001$, angular transformation test for the equality of two percentages). In New Hampshire, *N. orbicollis* was the dominant species and accounted for 55% of the carrion buried. In Florida, only *N. carolinus* successfully buried prey items experimentally offered. Only 12% of all prey were ultimately utilized by ants at the northern site. Generally, only a few ants were present at a time with the exception of two or three small prey which were completely overrun with *Acanthomyops.* In contrast, significantly more (77%) of the prey at the southern site were utilized by ants,

primarily *Solenopsis* ($t_S = 8.79$, $P < 0.001$). Other ant species collected in pitfall traps were not observed on these prey placed on the surface, perhaps due to displacement by fire ants. Flies were more successful in utilizing prey in New Hampshire ($t_S = 7.23$, $P < 0.001$) perhaps also due to displacement by fire ants in Florida.

At both sites, prey size affected its ultimate utilization. In New Hampshire, ants were significantly more successful at utilizing small prey (< 30 g, $t_S = 5.34$, $P < 0.001$) and flies were significantly more successful utilizing large prey ($t_S = 5.45$, $P < 0.001$). In Florida, beetles were less successful in burying small prey ($t_S = 2.30$, $P < 0.02$) but ants were equally successful with large or small prey ($t_S = 0.96$, $P = 0.33$; Table 1).

Discussion

The wide range of feeding habits of ants produce considerable dietary overlap with members of other, unrelated taxa utilizing the same resources (see for example Brown and Davidson 1976). Because many ant species are opportunistic and scavenge for a wide variety of sizes and types of animal prey, it is not unusual that carrion may be used as a food source when available. Such a large, concentrated resource will induce an extraordinary recruitment response from a colony, perhaps exhausting all foragers within the nest. Although the sensitive chemoreceptors of *Nicrophorus* permit them to locate carrion over long distances, the high density of foragers of ant species with well-developed trail communication and chemical or aggressive defense of resources may bring burying beetles and ants into competition for small vertebrate carcasses. Even if prey are first found by *Nicrophorus,* the time during which intrasexual competition occurs and burial is completed could increase the time period in which the carcass might be located by ants and thus increase the probability that they would displace the beetles. In the present study the lack of success of Florida *Nicrophorus* on carcasses was apparently due to interference from fire ants rather than to a lack of beetles in the study area because 416 *N. carolinus* were collected from pitfall traps but only five prey (N = 48) were buried. The nocturnal activity of some *Nicrophorus* species might favor early detection of carcasses and successful utilization, but this advantage would depend upon the temporal pattern of vertebrate mortality. Carcasses could also be lost to ants following burial, as

Table 1. Ultimate use of prey of different sizes in New Hampshire and Florida. Prey unaccounted for in the table (17%, 12%, 33%, and 5% for small and large prey, NH and FL, respectively) disappeared and were presumed to have been taken by vertebrates. N = sample size.

	Prey size (grams)	N	Use by: beetles	ants	flies
New Hampshire	8–29	69	45%	28%	10%
	30–60	103	41%	2%	46%
Florida	20–25	12	0	67%	0
	45–55	36	14%	81%	0

many species have subterranean as well as epigaeic foraging habits.

In addition to loss to ants, *Nicrophorus* will abandon carcasses that are infested with fly larvae. The mutualism between burying beetles and *Poecilius* mites that are predators of fly eggs appears to have evolved in the context of reducing competition with dipterans (Wilson 1983). Also, the cooperative burial shown by the diurnal *Nicrophorus tomentosus* may function in accelerating carcass concealment, thereby reducing prey availability to flies during the warmer periods of the day when fly activity is greater (unpublished data). We observed no behaviors in *Nicrophorus* that could be interpreted as specific to ant/beetle competition, although their coordinated carcass movement (Pukowski 1933, Milne and Milne 1976) could have the effect of decreasing the chance of ant utilization. Moving the carcass to a site suitable for burial might involve selection of appropriate soil conditions and lower ant abundance. The few direct interactions we observed between ant and burying beetles were characterized in New Hampshire (between one beetle and less than 10 ants) by indifference or removal of the ant which had come in contact with the beetle's leg. In Florida, however, *Nicrophorus* avoided carcasses occupied by ants.

There are 85 species of *Nicrophorus* worldwide, most being European and Asian in distribution, and there is a decrease in species diversity at southern latitudes in both the Old and New World (Peck and Anderson 1985). In the New World, fifteen species occur in the United States and Canada, nine in Latin America, three of which are endemic to South America and two endemic to Central America (Anderson and Peck 1985). The biogeography of silphids in general indicates that they are less prominent members of tropical

carrion-feeding insect guilds than in temperate regions (Carnaby 1974, Jirón and Cartin 1981). It has been suggested that their lower abundance in the tropics is due to the increased loss of carrion to bacteria, fly larvae, carrion-scavenging vertebrates and ants (Arnett 1946, Peck and Anderson 1985). It would be tempting to assume that the inverse correlation between ant and burying beetle species diversity is a causal factor in the distribution of silphids. However, our limited study of competition between ants and burying beetles allows us to conclude only that ants may exert at least a strong, local effect on the ability of burying beetles to secure carrion. This effect does not appear dependent only on interactions with the imported species *Solenopsis invicta;* the native *S. geminata* also dominates carrion placed out at other sites in Florida (Lloyd Davis, pers. comm.). Although there is a difference in ant species diversity between the two sites in our study (approximately twelve species total in New Hampshire and sixteen to thirty in Florida; Jeanne 1976, Calabi 1986, Trager, pers. comm., Traniello, pers. obs.), we cannot conclude that there is a direct cause-and-effect relationship between ant diversity and the ability of ants to control prey potentially available to burying beetles. In fact Jeanne's (1979) data show that predation rate by ants was higher on the ground than on vegetation although ant species diversity was higher in the latter microhabitat. Although very little is known about the use of small vertebrate carrion in the tropics, such resources may be exploited by ants, and the presence of only a few dominant ground species may reduce burying beetle reproductive success. Given the information available on the patterns of distribution and abundance of ants, it can be inferred that carrion may be approached more frequently by ants in the tropics than in the temperate zone. A relatively small number of omnivorous genera having species with large colony size and rapid recruitment communication may effectively restrict the use of carrion by burying beetles, perhaps producing patterns in the tropics similar to what we have described in Florida. In New Hampshire and Florida the relative importance of ants in *Nicrophorus* ecology seems dramatically different, but the relative importance of the distribution of ants, flies, and microbes in the biology of burying beetles remains to be determined.

SUMMARY

By sampling the diversity and abundance of burying beetles and ant species utilizing small vertebrate carcasses with pitfall and burial traps and recording the success of *Nicrophorus* spp. in securing carrion for reproduction, we found that ant interference was more prevalent in a population in central Florida than in southern New Hampshire. Carrion placed along transects in central Florida was occupied by the imported fire ant *Solenopsis invicta,* and although burying beetles were abundant in the area, few prey were successfully utilized. It is concluded that some ground-dwelling ant species may have a significant local impact on burying beetle reproductive ecology.

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