COMPETITION BETWEEN *NICROPHORUS ORBICOLLIS* AND *N. DEFODIENS*: RESOURCE LOCATING EFFICIENCY AND TEMPORAL PARTITIONING

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ABSTRACT — The larger-bodied burying beetle, *Nicrophorus orbicollis,* competes with the smaller *N. defodiens* for valued, protein-rich, carrion resources. We tested four hypotheses of this competitive relationship. We found support for the hypotheses that *N. defodiens* locates fresh carcasses more quickly than *N. orbicollis* and that carcasses placed under the leaf litter are more difficult for *Nicrophorus* to locate than carcasses placed above the leaf litter. By shifting the photocycle of *N. defodiens* we were able to manipulate this normally crepuscular species into beginning its active period 3 h later, during the active period of the nocturnal *N. orbicollis*. This clock-shift eliminates the 3 h head start that *N. defodiens* typically experiences in the field. We did not find support for the hypothesis that clock-shifted *N. defodiens* would suffer in competition compared to non-clock-shifted beetles. We did find support for the hypothesis that the presence of *N. defodiens* on a carcass provides clues to searching *N. orbicollis*. We suggest that the presence of efficient carrion searchers such as *N. defodiens* may significantly increase the numbers and success of the *Nicrophorus* guild.

INTRODUCTION

Species that coexist are expected to be separated by space, time, or resource use. Measurements of niche differences are insufficient to evaluate the importance of competition in shaping life history; direct experimental manipulation provides more convincing evidence that competition can lead to ecological displacement (Connell 1980). While controversy continues over the importance of competition in some systems (e.g., herbivorous insects; Denno et al. 1995; Hairston et al. 1960; Lawton and Strong 1981), there is little doubt that competition can be a selective force for insects exploiting discrete, protein-rich resources such as carrion and dung (Hanski and Cambefort 1991, Trumbo 1990a, Wilson et al. 1984).

Species differ in their physical ability to monopolize resources. Dominant species (scroungers) may obtain a disproportionate share of resources relative to their searching effort by exploiting the searching

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effort of subordinate species (producers) (Barnard 1984). The use of cues from other individuals may be most important when resources are highly ephemeral (Pulliam and Millikan 1982). Subordinate species are therefore expected to attempt to locate resources at times or places where the dominant is not active, or to conceal the location of resources that have been discovered ("finders advantage," Mangel 1990).

One manipulative method for demonstrating the potential of competition is to experimentally bring isolated species into closer contact. For example, Hairston (1983) transplanted geographically isolated populations of a montane salamander species to bring it into sympatry with a congener, demonstrating that the competitive dominant limited the range of the competitive subordinate. This provided strong evidence that past competition was responsible for the present-day altitudinal separation of these species. In the present study, we manipulated the photoperiod of a temporally isolated subordinate species to examine how temporal separation might affect competition. There have been few such manipulations, despite the ease of manipulating photoperiod of insects (Saunders 1976) and despite evidence that temporal separation can minimize competition among insects (Inbar and Wool 1995).

Interference or contest competition (Gill 1974) is common in insects which utilize a discrete, protein-rich "bonanza" resource (Wilson 1971). Among burying beetles (Coleoptera: Silphidae: *Nicrophorus*), interspecific competition is generally asymmetrical (Lawton and Hassell 1981); body size chiefly determines which individuals win carcasses, bury them under the soil, and prepare these resources for their young (Otronen 1988; Pukowski 1933). The carcass and brood must then be protected for 10 - 20 days from congeners, which can fly long distances in search of resources to colonize or usurp (Robertson 1993; Scott 1994; Trumbo 1990a, 1990b). While burying is thought to make it more difficult for competitors to find a carcass (Fabre 1899; Trumbo 1990a), beetles can use odor cues from the carcass or from resident beetles to aid in locating the resource (Müller and Eggert 1987).

The competitive relationship between the larger *Nicrophorus orbicollis* Say and the smaller *N. defodiens* Mannerheim has been particularly well studied. Both species coexist in forests throughout the northern U.S. and southern Canada (Anderson 1982; Anderson and Peck 1985). Some niche partitioning has been documented. Although there is wide overlap in the size of carcasses used for reproduction (*N. defodiens*: 3 - 100 g; *N. orbicollis*: 7 - 200 g), *N. defodiens* will use very small carcasses that *N. orbicollis* rejects (Trumbo 1990a). In addition, *N. defodiens* becomes active several weeks before *N. orbicollis* (early June vs. mid-June in northern Michigan) (Wilson et al. 1984). For most of the breeding season, however (mid-June to early August), the two species are in direct competition. Finally, the smaller *N. defodiens* becomes active several hours before sunset while *N. orbicollis* becomes active at sunset (Wilson

et al. 1984). It has been hypothesized that this diffeence allows *N. defodiens* to control carcasses on days when falling temperatures in the evening prevent *N. orbicollis* from being active. This interpretation is supported by the poorer relative performance of *N. orbicollis* on nights when the temperature at sunset is below 14 ºC (Wilson et al. 1984). On warm nights it is not known if the head start of *N. defodiens* also provides time to conceal carcasses before *N. orbicollis* becomes active, thereby reducing the ability of *N. orbicollis* to monopolize carcasses.

There is evidence that *N. orbicollis* limits the abundance of *N. defodiens*. *Nicrophorus defodiens* is not found in geographic areas where the nocturnal *N. orbicollis* is active almost continually through-out the summer (Wilson et al. 1984). *Nicrophorus defodiens* is also extremely abundant on small islands where *N. orbicollis* is not estab-lished (Trumbo and Thomas 1998).

In the present study we tested four hypotheses. The first three hy-potheses attempt to explain why *N. defodiens* might have a competi-tive advantage over the larger *N. orbicollis*. Hypothesis 4 proposes that *N. orbicollis* benefits by exploiting cues from *N. defodiens*. (1) The smaller-bodied congener, *N. defodiens*, locates fresh carcasses more quickly than the larger *N. orbicollis*. (2) Carcasses are more difficult to locate once taken under the leaf litter. (3) The temporal head start of *N. defodiens* provides time to conceal a carcass from *N. orbicollis*. (4) Once a carcass is hidden under the leaf litter, the presence of *N. defodiens* provides cues that attract *N. orbicollis*.

METHODS

Carcass discovery

The relative ability of *N. orbicollis* and *N. defodiens* to discover fresh and aged carcasses was examined in a woodland at the University of Michigan Biological Station (UMBS) in Pellston, Michigan, USA. On 7 days between 22 July and 8 August, 1996, 8 - 12 mouse carcasses (30 - 33 g) were placed along transects above or below the leaf litter. Carcasses were thawed at 8:00, placed in the field by 12:00, and avail-able to *Nicrophorus* at the beginning of their active period (19:00 for *N. defodiens*). Transect points were spaced 10 m apart. The treatment (above or below the leaf litter) for the first transect point was deter-mined randomly. Treatments were then alternated for subsequent transect points. Dental floss was tied to a stake at one end and to the hindleg of the carcass at the other to facilitate locating the carcass after displacement by burying beetles. Between 9:00 and 11:00 the following day each carcass was inspected and all beetles were removed. Carcasses were left in the field for 4 days. Because the rate of decomposition may be affected by the position above or below the leaf litter, a carcass

placed above the leaf litter on one night was placed below the following night, and vice-versa. A total of 73 carcasses were used over 4 days for a total of 229 trap-nights. The sample size decreased over the 4 days because some carcasses were removed by scavengers or deteriorated to the point where they were removed by the investigator.

Manipulation of photocyclic behavior of *N. defodiens*

To bring *N. defodiens* into more direct competition with *N. orbicollis*, it was necessary to manipulate the photoperiod of *N. defodiens*. To determine whether this was feasible, 66 wild-caught *N. defodiens* males were kept in the laboratory in covered containers (17 x 31 x 8 cm) half-filled with soil. Each male was provided a 21 - 24 g mouse carcass and a rock to use as a pheromone-emitting perch beginning on 22 June, 1996 (sunset: 21:27; end of twilight: 22:05). For the following nine nights, each male was checked for the pheromone-emitting posture (Eggert and Müller 1989) every 15 min from 19:00 until 2:00 the next morning. The males were placed in one of three treatments: (1) control beetles were kept at the natural photoperiod (lights on at sunrise, lights off at sunset); (2) clock-shifted beetles were kept on a photoperiod in which lights on and lights off were delayed 3 h; (3) a second group of clock-shifted beetles were kept on a 3 h delay for 6 days, and were then shifted back to the natural photoperiod for the last 3 days. Twenty-two males were used for each treatment. Carcasses were replaced after days 3 and 6. Female *N. defodiens* were also monitored for flight activity (indicative of searching behavior) under clock-shifted and normal photoperiod conditions.

Field manipulation of competition

A field experiment was conducted to bring clock-shifted *N. defodiens* (7 days of photoperiod manipulation of a 3 h delay) into direct competition with *N. orbicollis* by eliminating the normal temporal separation in their activity periods. *Nicrophorus defodiens* adults were trapped in Colebrook, Connecticut, USA in the Algonquin State Forest. To increase the probability of *N. orbicollis* activity during the competition experiment, *N. defodiens* were placed on carcasses in the Naugatuck State Forest, Cheshire, Connecticut, where *N. orbicollis* is the only woodland species that utilizes carrion for reproduction during mid-summer (approximately 5 km south of the geographic range of *N. defodiens*; unpublished result). The temperature at sunset was > 20°C during experimental trials. Carcasses were tied to a stake with dental floss and placed at transect points spaced 20 m apart. On 28 and 29 July, 1999, 27 carcasses (27-30 g), aged for 2 days in the laboratory, were provided to both control and clock-shifted pairs of *N. defodiens*. At the beginning of

the beetles' active period (17:30 for control beetles, 20:30 for clock-shifted beetles), the pairs were placed directly underneath carcasses and covered briefly (15 min) with an inverted plastic pot. After 15 minutes, the pot was removed for the remainder of the night. Carcasses were checked the following morning to determine whether the established residents or other *Nicrophorus* spp. were in possession of the resource.

Discovery by *N. orbicollis* in different geographical areas

The success of the *Nicrophorus* guild in geographical areas with and without *N. defodiens* was investigated by placing carcasses in two locations: (1) Naugatuck State Forest, Cheshire, Connecticut, approximately 5 km south of the range limit of *N. defodiens*; and (2) Algonquin State Forest in Colebrook, Connecticut where *N. defodiens* is very active. In Naugatuck State Forest, ten fresh carcasses were placed on transect points separated by 20 m on each of 2, 6, 10 and 14 August, 1999, and on 21 and 25 June, and 15 and 20 July, 2000. The carcasses were checked on each of the following four mornings and all beetles were removed. In Algonquin State Forest 10 fresh carcasses were placed on the leaf litter along transects on each of 12, 19, 26 July, and 2 August, 1999. Each carcass was inspected between 9:00 and 11:00 for 4 days and beetles were removed.

Cues from *N. defodiens* and discovery by *N. orbicollis*

To determine whether the presence of *N. defodiens* affects the ability of *N. orbicollis* to locate carcasses already under the leaf litter, 62 carcasses (31 - 34 g), aged for 3 days, were placed between 18 July and 5 August, 1997 in Naugatuck State Forest in Connecticut. In half of the trials, a male-female pair of *N. defodiens*, kept on a normal photocycle, was placed under the carcass at the beginning of the active period of *N. defodiens*. The other half of the carcasses were left under the leaf litter without beetles. Carcasses were inspected the following morning.

RESULTS

Carcass discovery

At the University of Michigan Biological Station, the placement of carcasses below or above the leaf litter, and the age of the carcass affected the rate of discovery by *Nicrophorus* spp. (Fig.1; $G_{placement}$ = 56.8, P < 0.001, G_{day} = 56.4, P <0.001). Of the carcasses buried by *Nicrophorus* spp., 91% were possessed by the two most common species, *N. defodiens* and *N. orbicollis*. The number of carcasses held by *N. defodiens* was greater for carcasses aged for 1 or 2 days as compared to carcasses aged 3 or 4 days (Fig. 1; G_{day} = 17.6, P < 0.001).

Manipulation of photocyclic behavior of *N. defodiens*

Male *N. defodiens* responded very quickly to a shift in photoperiod. Beetles on a 3 h clock-shifted delay had completely shifted their phero-mone-emitting period by the third day (Fig. 2). Males that were initially clock-shifted responded more slowly to having their photoperiod pushed forward 3 h. Similar to pheromone-emitting males, *N. defodiens* females initiated searching behavior (flight and movement over the soil) 3 h later under clock-shifted conditions.
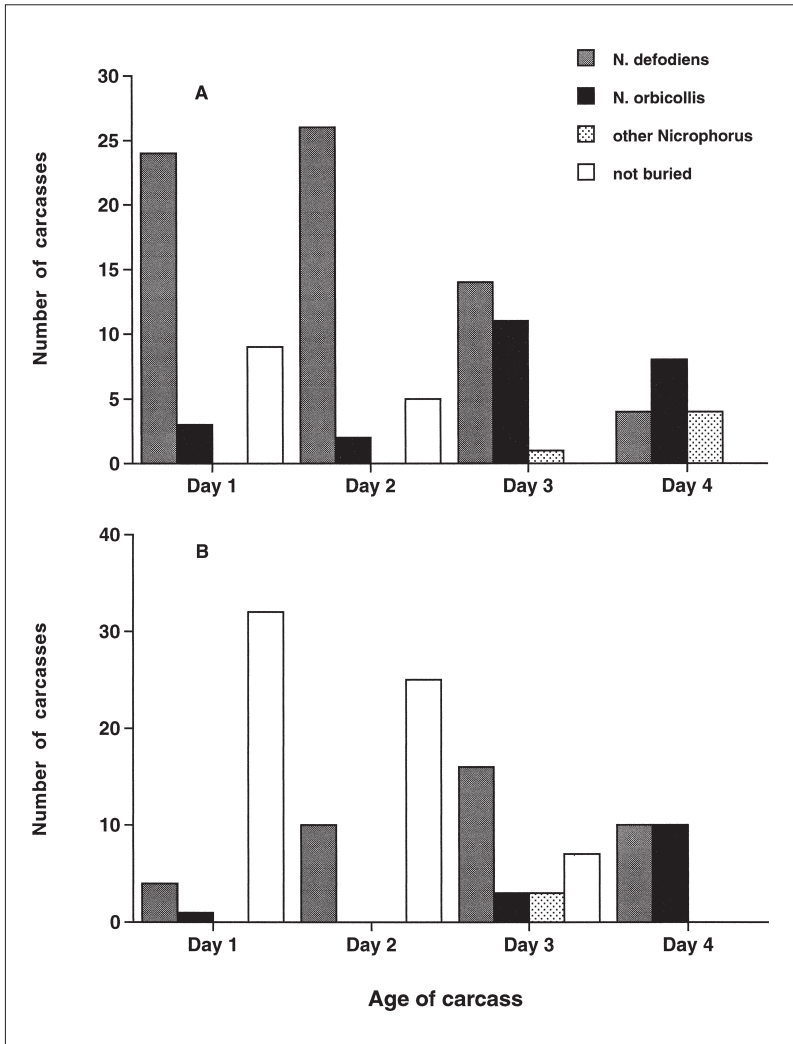
Figure 1. The number of carcasses placed above (a) or below (b) the leaf litter and aged for 1, 2, 3 or 4 days which were buried by *N. defodiens*, buried by *N. orbicollis*, buried by other *Nicrophorus* spp., or were not buried at UMBS.

Field manipulation of competition

In the Naugatuck State Forest, Connecticut, the proportion of car-
casses discovered by *N. orbicollis* was not affected by whether the
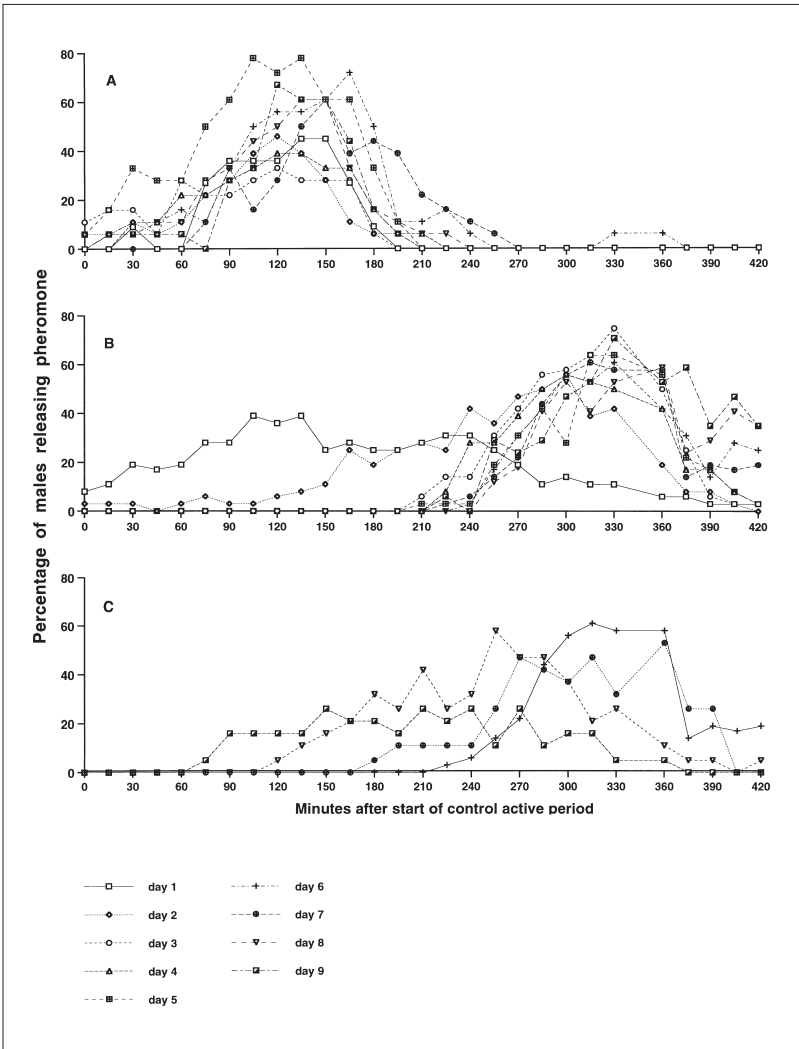resident *N. defodiens* pairs were on a clock-shifted or normal photope-

Figure 2. The percent of *N. defodiens* releasing pheromone for (a) control males
on the natural photoperiod; (b) males which were clock-shifted by a 3 h delay in
photoperiod; and (c) males which were initially clock-shifted by a 3 h delay for
days 1-6, and then shifted forward to the normal photoperiod for days 7-9. For
(c) results for only days 6 - 9 are shown to prevent graphical overlap during the
initial clock-shifting and re-setting periods.

riod (Fig. 3; G = 0.2, P = 0.64). The proportion of carcasses discovered by *N. orbicollis* was low, suggesting that *N. orbicollis* rarely discovers carcasses on the first night even in areas where *N. defodiens* is absent.

Discovery by *N. orbicollis* in different geographical areas

Nicrophorus orbicollis discovered a low percentage of carcasses on the first night even in the absence of its competitor, *N. defodiens*, which is not present in the Naugatuck State Forest. Of 80 fresh carcasses, only 12 (15%) were discovered by *N. orbicollis* on the first night, despite favorable temperatures for searching. The ability of *N. orbicollis* to discover carcasses increased with the number of days the carcass was in the field (G_{day} = 33.6, P < 0.001, 4 x 2 contingency test, Fig. 4a).

In Algonquin State Forest in Connecticut, the number of carcasses placed above the leaf litter that were possessed by all *Nicrophorus* spp. did not vary with the number of days the carcass was in the field (G_{day} = 1.08, P > 0.20, 4 X 2 contingency test, Fig. 4b). Of carcasses buried by *Nicrophorus* spp., 98.6% were held by *N. defodiens* or *N. orbicollis*. *Nicrophorus orbicollis* was more likely to have held carcasses aged for more days (Fig. 4b; G_{day}= 15.2, P = 0.002, 4 x 2 contingency test), discovering only 10% of carcasses on the first night. In both forests, *Nicrophorus* spp. discovered a similar percentage (60 - 65%) of available carcasses on days 3 and 4.
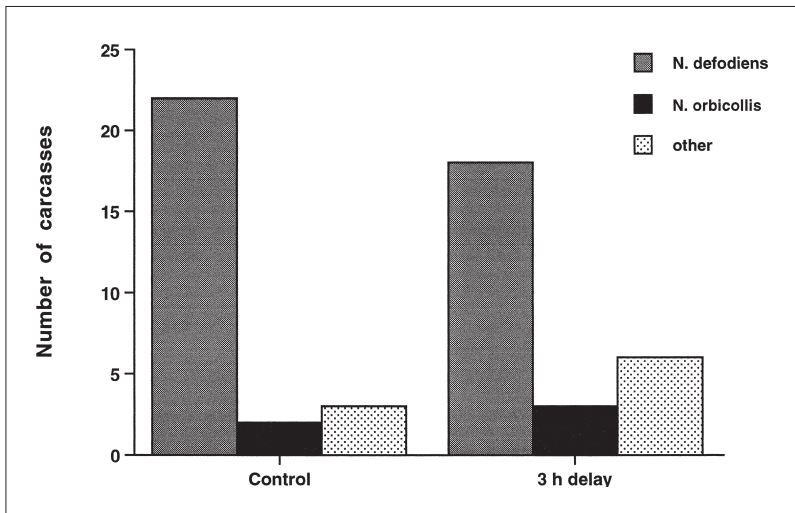

Figure 3. The number of carcasses occupied by *N. defodiens*, occupied by *N. orbicollis*, or "other" (scavenged carcasses or carcasses held by other species of *Nicrophorus*) in Connecticut in which clock-shifted (3 hour delay) or control photoperiod pairs of *N. defodiens* were placed on carcasses in the field.

Cues from *N. defodiens* and discovery by *N. orbicollis*

Nicrophorus orbicollis discovered a greater number of aged carcasses (3 days) placed under the leaf litter when *N. defodiens* was established on the carcass (41.9%, N = 31) than when the carcass was not experimentally colonized by *N. defodiens* (12.9%, N = 31, G = 6.2, P = 0.01; Fig. 5). It was evident that *N. defodiens*, in the 3 h it had access to the carcass prior to the active period of *N. orbicollis*, was not
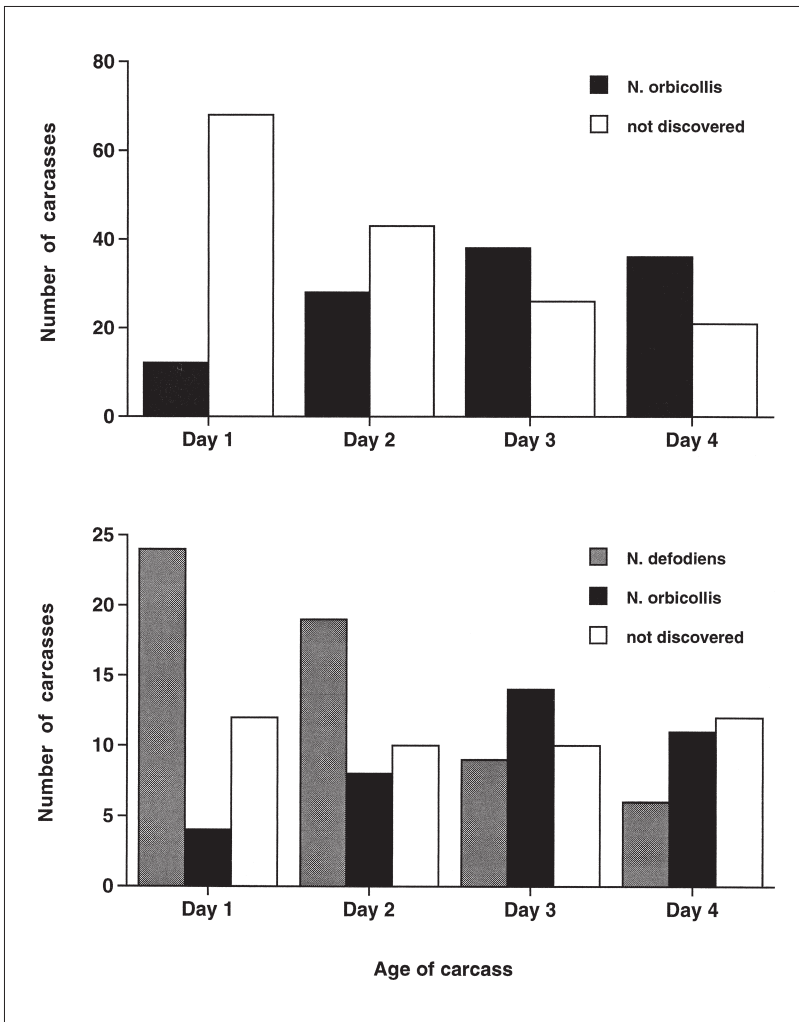

Figure 4. The number of carcasses occupied by *Nicrophorus* on days 1, 2, 3, and 4 in (a) a Connecticut forest where *N. defodiens* is absent; and (b) a Connecticut forest where *N. defodiens* is present.

manipulating the resource in a way that prevented discovery by *N. orbicollis*, and instead, may have been providing cues that *N. orbicollis* exploited.

DISCUSSION

Previous field work has demonstrated a wide niche overlap between *N. orbicollis* and *N. defodiens*. *Nicrophorus orbicollis* is a competitive dominant which usurps small vertebrate carcasses from *N. defodiens* (Scott 1994; Trumbo 1990a, 1992; Wilson and Fudge 1984; Wilson et al. 1984). Much of the evidence comes from comparing carcass owner-ship on Day 1 with carcass ownership much later (Day 6-10), noting the increasing proportion of carcasses occupied by *N. orbicollis*. The tim-ing of these takeovers and the behaviors that *N. defodiens* may employ to reduce takeovers have been little studied. The present study examined four hypotheses. We found support for hypothesis 1, that *N. defodiens* locates carcasses more quickly than *N. orbicollis*. This is a statement about population, not individual ability, since population estimates are not available. It is known, however, that at both UMBS (Wilson and Knollenberg 1984) and in Connecticut (Trumbo, unpublished results), as well as at additional sites near these latitudes (Anderson 1982; Beninger and Peck 1992; Scott 1994), that *N. orbicollis* is trapped more frequently than *N. defodiens* early in the breeding season (June and July) in pitfall traps baited with a large quantity of well-rotted carrion. The
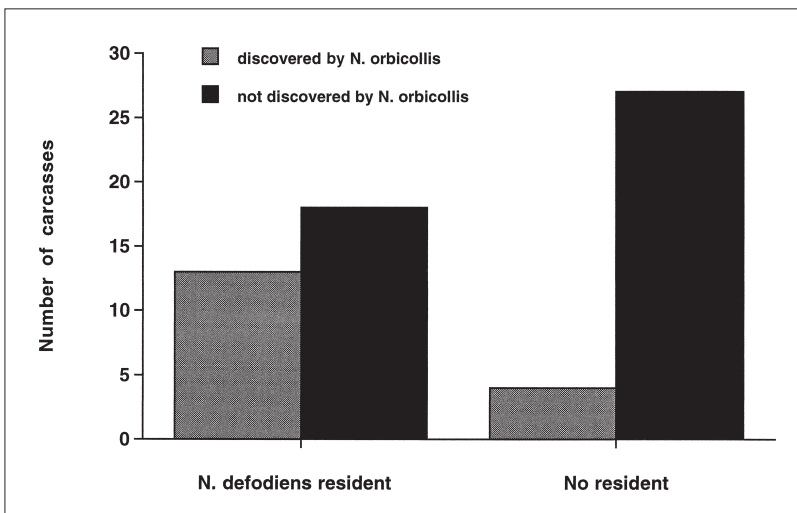

Figure 5. The number of carcasses (aged 3 days) placed under the leaf litter and occupied by *N. orbicollis* when *N. defodiens* was established as a resident or not on the carcass in Connecticut.

over-representation of *N. defodiens* on fresh carcasses on Day 1 (relative to numbers in pitfall traps), also noted by Wilson et al. (1984) and Beninger and Peck (1992), suggests a much superior searching ability of individuals of this species.

There was clear support for hypothesis 2, that carcasses placed under the leaf litter would be more difficult for *Nicrophorus* to locate than carcasses placed above the leaf litter. Previous work demonstrated that carcasses placed under 2 cm of soil were more difficult for *Nicrophorus* to locate (Shubeck 1985; Shubeck and Blank 1982). These results can best be explained by the reduction in olfactory cues available to flying *Nicrophorus*.

Hypothesis 3, that the temporal head start of *N. defodiens* would provide time to conceal a carcass from *N. orbicollis* was not supported. This hypothesis was based on the knowledge that *N. defodiens* becomes active several hours before *N. orbicollis* and will maneuver a carcass beneath the leaf litter quickly (Wilson et al. 1984), and that a hidden carcass is not found as quickly. Results from the present study suggest two explanations why Hypothesis 3 was not supported. The head start of *N. defodiens* typically occurs on a fresh carcass that *N. orbicollis* has difficulty locating anyway, and additional odor cues from resident beetles may provide cues to aid searching *N. orbicollis*. Preliminary work from UMBS utilizing clock-shifted *N. defodiens* in habitats where *N. defodiens* is normally found, also suggests that the 3 h head start provides no competitive benefit (Trumbo and Bloch, unpublished result).

Hypothesis 4, that the presence of *N. defodiens* provides clues to searching *N. orbicollis,* was supported. A study of a distinct species assemblage of *Nicrophorus* in Japan produced a different result (Suzuki 1999). The presence of *N. vespilloides* L. on fresh carcasses substantially reduced the probability that two congeners, *N. maculifrons* Kraatz and *N. quadripunctatus* Kraatz, would discover the resource. In that study, however, the resident used was *N. vespilloides*, a competitive dominant. Suzuki (1999) therefore suggested that congeners may have detected but avoided carcasses which had previously been discovered by the dominant *N. vespilloides*. It is possible that searching beetles will respond to olfactory cues from congeners, as well as from carrion. In a prior study, Müller and Eggert (1987) demonstrated that *Nicrophorus* spp. respond to male pheromone emission of congeners and that dominants were more likely to respond to pheromone of subordinates than subordinates to pheromone of dominants. While pheromone emission may indicate the location of a carcass, searching beetles may avoid carcasses which have been discovered by species which are competitively dominant. Our work and Suzuki's (1999) also suggest that search-

ing burying beetles can respond to the presence of congeners, irrespective of pheromone emission. Since *N. defodiens* is a competitive subordinate to *N. orbicollis*, it is possible that *N. orbicollis* is attracted to *N. defodiens* on the ground, as suggested by the finding that carcasses placed under the leaf litter with *N. defodiens* were more attractive than carcasses without beetles.

The more efficient searching ability of the smaller *N. defodiens* and the usurpation of resources by *N. orbicollis* suggest that this interaction might be modeled as a producer-scrounger relationship (Barnard 1984). It is not clear why *N. orbicollis* is less able to locate this key resource. A possible tradeoff of better searching ability is the greater energetic cost associated with searching. A more sensitive response to carrion stimuli would lead to more false positives, including visits to residual odor cues left on the substrate and to carrion too small to exploit. These energetic costs may be higher for a larger beetle searching during a cooler time of the day.

The ability of *N. orbicollis* to use cues from congeners when searching for a carcass may explain why the diurnal head start of *N. defodiens* provides little benefit which can be measured in the field. Previously, the low percentage of fresh carcasses discovered by *N. orbicollis* in habitats without *N. defodiens* was explained by low population density (Trumbo 1990c; Wilson and Fudge 1984). In light of the present study, we now believe that *N. orbicollis* is relatively poor at locating a newly available resource. We also suggest that there may be abrupt differences in the success and numbers of the *Nicrophorus* guild on either side of the border of *N. defodiens*' geographic range. Information "sharing" among individuals will increase the rate of resource discovery (Clark and Mangel 1984). The presence of *N. defodiens* will not only increase the number of carcasses discovered by the *Nicrophorus* guild, but by reducing carrion fly and microbial populations, may preserve resources eventually usurped by larger congeners (Pukowski 1933).

ACKNOWLEDGMENTS

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