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Interference competition among burying beetles (Silphidae, *Nicrophorus*)

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Abstract. 1. This study investigated the impact of intraspecific and interspecific competition on the reproductive success of a biparental burying beetle, *Nicrophorus defodiens* Mannerheim.

2. Marked pairs or single females were placed on small and large mouse carcasses in the field in 1985 and 1986. Carcasses were exhumed after 9–10 days to determine the identity of the resident adult(s) and the production of young.

3. Competition was assessed by the prevalence of takeovers by intruders (unmarked adults). For *N.defodiens*, after the initial colonization of the carcass, interspecific competition from larger *N.orbicollis* Say and *N.sayi* Laporte was substantial and more intense than intraspecific competition. Competition was also greater in the middle of the breeding season and on large as opposed to small carcasses.

4. Successful takeovers resulted in the expulsion of the prior resident(s), killing of any offspring present on the carcass, and oviposition of a new clutch by the intruder.

5. Females aided by males were more likely than single females to avoid takeovers but did not produce larger broods or larvae of larger mass.

6. An additional laboratory experiment in 1985 and a field experiment in 1986 suggest that *N.defodiens* is able to reproduce on very small carcasses despite intense heterospecific activity.

Key words. *Nicrophorus*, competition, interference, reproductive success, parental care, larvicide.

Introduction

Male and female burying beetles (Silphidae, *Nicrophorus* Fabricius) compete for small vertebrate carcasses until a single dominant pair remains. Carcasses are then buried and protected from aggressive intruders for 10–15 days (Pukowski, 1933; Scott, 1989). Smaller species bury carcasses just below the leaf litter while larger species take carcasses to greater depths so that the resource is completely covered by soil (Pukowski, 1933; Wilson & Knollenberg, 1987). A nest is prepared by rounding the carcass into a brood ball, removing hair or feathers, and depositing faecal secretions which may control the decomposition (Halffter *et al.*, 1983). Extensive biparental care which includes regurgitation of liquefied carrion is provided to young

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(Pukowski, 1933; Milne & Milne, 1976). On smaller carcasses, parents reduce the size of the brood to reduce competition for food (Bartlett, 1987).

Apart from the social taxa, interference and interspecific social dominance have received limited study as mechanisms of competition in insects (Morse (1974), but see Rathcke (1976), Zwolfer (1979) and reviews by Lawton & Hassell (1981, 1984)). Wilson *et al.* (1984) examined competition among species of *Nicrophorus* by placing mouse carcasses in the field and allowing colonization by free-flying beetles. A comparison of carcass ownership at days 1 and 10 provided indirect evidence that two dominant species, *N.orbicollis* Say and *N.sayi* Laporte, tended to displace the smaller *N.defodiens* Mannerheim from carcasses and appropriated resources for their own reproductive benefit. *N.defodiens*, however, is active prior to sunset while its competitors are nocturnal. Wilson *et al.* concluded that *N.defodiens* is able to coexist with its larger competitors because of its success on nights when temperatures fall rapidly after sunset.

I studied competition that occurs during the parental period of *N.defodiens*. The purpose was fourfold: (1) determine the frequency of conspecific and heterospecific takeovers when *N.defodiens* is established on a carcass; (2) re-examine resource partitioning based on temperature-dependent competition and resource size; (3) describe larvicide as a mechanism of competitive interference in *Nicrophorus*; (4) determine how paternal care increases male reproductive success in *N.defodiens*.

Materials and Methods

This study was conducted at The University of Michigan Biological Station (UMBS) near Pellston, Michigan (described in Wilson & Knollenberg, 1984). All carcasses were laboratory *Mus musculus* L., killed with CO_2 and frozen until used. During May and June of 1985 and 1986, *N.defodiens* was collected in baited pitfall traps at least 2 km from experimental sites, maintained in plastic containers, and fed chicken livers *ad libitum*. Beetles were marked by clipping off a small part of the posterior outer edge of one elytra. Prior to being placed in the field, the size of adult beetles was measured as the length from the mandibles to the edge of one of the elytra.

Reproductive success – field experiments. Ten transects, separated by a minimum of 100 m (ten points per transect with 15 m intervals between points) were set up in a secondary hardwood forest. On 20 days between 4 June and 27 June 1985, on every transect, I placed a pair of beetles on each of four large mice (27–30 g), a pair on each of four small mice (10–15 g), a single female on a large mouse, and a single female on a small mouse. The order in which transect points were used was determined randomly and each transect point was used twice in the course of the experiment. One end of a 1.0 m length of dental floss was tied to a stake and the other end to the hind leg of the mouse in order to locate the carcass after burial. Carcasses and beetles were covered with an inverted plastic container (23 cm diameter) for 1 day to prevent rivals from contesting the resource during internment. Carcasses accepted by beetles within the initial 24 h period (95%) were subsequently left uncovered and exhumed after 9 or 10 days to determine the presence of marked and unmarked beetles as well as the number and mean mass of larvae. In order that the number of larvae could be measured accurately, carcasses were exhumed before larvae had completed feeding and dispersed. Therefore, mean larval mass at exhumation in field experiments reflects larval development rather than larval size at dispersal.

To obtain additional comparative information on reproductive success of pairs and single females in the field, a short-term experiment was conducted in 1986. From 26 June to 1 July, along three transects, eighteen pairs and forty-two single females were each provided with a 15–18 g mouse carcass and protected from competitors for 48 h. Subsequent procedures were similar to the preceding field experiment described.

Reproductive success – laboratory experiments. No single female produced a brood on a large carcass in the field. Therefore, brood production for this class was measured in the laboratory during July 1985. Ten *N.defodiens* females working without the help of a male were each provided with a large carcass (27–30 g) in a plastic container filled with topsoil and leaf litter, maintained at room temperature, and exposed to the natural photoperiod. The number of larvae and mass of the brood were measured a full day after larvae dispersed from the nest.

To examine the effect of an intruder on reproductive success, each of six pairs of *N.defodiens* were established on 20–30 g mice in separate containers during July 1985. On the first day that larvae appeared, a female of *N.orbicollis* was introduced. The carcass subsequently was examined each day for the presence of larvae. Larvae that eventually dispersed from the carcass were collected and species identification was made upon their emergence as adults.

Resource size – laboratory experiment. To examine differences among species in the use of carcasses of different sizes, two experiments were conducted. In the laboratory, twenty-two pairs of *N.defodiens* and twenty of *N.orbicollis*, fed *ad libitum* prior to experiments, were each provided with a very small (4–7 g) or small (7–9 g) mouse carcass on which to breed during mid-July 1985. The number of larvae and mass of the entire brood were measured a full day after larvae dispersed from the nest.

Resource size – field experiment. Resource use by free-flying beetles was examined in the field in 1986 on a 200 × 200 m grid (25 m between adjacent grid points). From 25 June to 15 July, eighty-one mice in one of two size classes (4–6 g and 33–36 g) were placed on randomly selected grid points so that ten undiscovered carcasses were present on the grid each night. Grid points were not used a second time until all points had been selected. Carcasses were examined daily until discovered. Eight days after discovery and burial, carcasses were exhumed and the following data were recorded: species, number, sex, and size of adult beetles on the carcass, and number and mass of the entire brood.

Results

Reproductive success – field experiments.

In the studies where I established *N.defodiens* on carcasses, only 11% (1985) and 22% (1986) of 120 nests with intruders (unmarked adults) were occupied by conspecifics. The remaining nests with intruders were occupied by the larger *N.orbicollis* and *N.sayi*. Table 1 summarizes intrusions by species, sex and number of intruders present at exhumation. An intrusion by a conspecific did not mean that both established adults were necessarily displaced. On six occasions a *N.defodiens* intruder was found with the opposite sex adult that originally was placed

Table 1. The proportion of each class of intrusion on carcasses established with *N.defodiens*.

	N.defodiens	*N.orbicollis*	*N.sayi*
Small carcasses[*]			
Intruding female only	0.02	0.24	0.16
Intruding male only	0.00	0.04	0.04
Intruding pair	0.12	0.22	0.10
Intruding male, established female	0.02	–	–
Intruding female, established male	0.06	–	–
Large carcasses[†]			
Intruding female only	0.01	0.00	0.07
Intruding male only	0.00	0.03	0.00
Intruding pair	0.00	0.30	0.20
Intruding male, established female	0.01	–	–
Intruding female, established male	0.04	–	–
2 intruding adults, same sex	0.00	0.00	0.03
3 intruding adults	0.00	0.07	0.15
4+ intruding adults	0.00	0.03	0.04

[*] Proportions based on twenty-eight takeovers in 1985 (10–15 g carcasses) and twenty-three takeovers in 1986 (15–18 g carcasses).

[†] Proportions based on sixty-nine takeovers in 1985 (27–30 g carcasses).

on the carcass. In twenty-two takeovers by heterospecifics on large carcasses there were two intruders of the same species and sex present at exhumation. In all but two of these cases the larger beetle was found on the carcass and the smaller beetle was found in the leaf litter (N= 22, P<0.001, Wilcoxon's Matched Pairs Signed Ranks test). The size of *N.defodiens* residents that successfully held their carcass did not differ from those that lost their carcass in a takeover (P>0.1, Mann-Whitney U test).

The presence of an intruder on the carcass had important consequences for the reproductive success of the established residents. 98% of nests without an intruder (N=101) contained larvae, while only 12% of nests with an intruder (N=121) did (χ^2=161, P<0.001). Every nest with an intruder and larvae contained only first or second instar larvae while the majority of nests without intruders contained third instar larvae (82%).

Pairs of *N.defodiens* retained fewer carcasses that they had colonized as the season progresged in 1985 (χ^2=13.61, P<0.01, 2 df, 2×3 Contingency test; Fig. 1). *N.defodiens* pairs also found it more difficult to hold large rather than small carcasses (χ^2=41.58, P<0.001, 2×2 Contingency test). As a result, pairs produced twice the number of larvae per breeding attempt on small rather than large carcasses even though the number of larvae produced per successful attempt (no intruder) was related positively to carcass size (t=5.16, P<0.001) as well as to female size (t=3.35, P<0.01, Regression analysis). Pairs were significantly more likely to retain their resource than were females working alone on both small (χ^2=12.77, P<0.001, 2×2 Contingency test; Fig. 2) and large carcasses (P= 0.019, Fisher's Exact test) in 1985. At the time of exhumation 71% of males established with a female were present on small carcassess (N= 55, 1985), 83% were present on large carcasses (N=18, 1985) and 67% were present on 15–18 g carcasses (N=9, 1986, nests with intruders excluded). The established female was found on 95% of carcasses at exhumation (N= 101, nests with intruders excluded).

On successful nests the presence of a male on the carcass did not affect the number of larvae produced nor the mean mass of individual larvae at exhumation in 1985 or 1986 (all P>0.2, Mann-Whitney U tests; Fig. 3). For pairs in 1985, mean mass of individual larvae was greater on small carcasses than on large carcasses for trials terminated on day 10 (n_S=31, n_L=6, z= 1.96, P<0.05, Mann-Whitney U test).

Reproductive success – laboratory experiments

Although *N.defodiens* females working alone were never able to reproduce successfully on large carcasses in the field in 1985, all ten

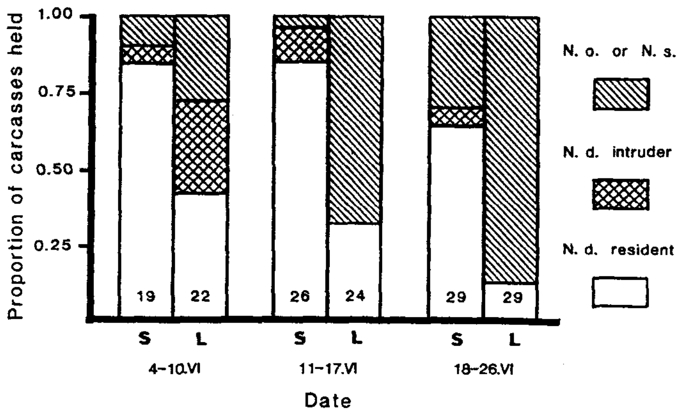

Fig. 1. Proportion of small and large carcasses experimentally colonized by pairs of *N.defodiens* in 1985 that were held at the end of the trial by resident *N.defodiens*, by *N.defodiens* intruders, and by heterospecific intruders (*N.orbicollis* or *N.sayi*). The number of small (S) and large (L) carcasses held by species of *Nicrophorus* during each time period is shown at the base of the bar graphs. During the study, 3% of carcasses were scavenged by vertebrates and are not included in the analysis.

females that were provided mice in the laboratory nested successfully. All mice were buried the first night and the number of larvae produced was comparable to pairs reproducing on large mice in the field (Fig. 3).

The outcome of an interspecific takeover in the laboratory was clear. In all six cases the resident pair was displaced from the carcass, larvae that were present when the intruder was introduced died within 48 h, eggs were oviposited by the intruder and larvae of *N.orbicollis* were eventually produced. Observations during these trials confirmed that intruders kill larvae found on the carcass.

Resource size — laboratory experiment

N.orbicollis buried all but one of the 4–9 g carcasses the first night, rounded them into nest-balls, oviposited eggs, and were attentive to the nests for variable periods of time. Many of these reproductive attempts, especially on

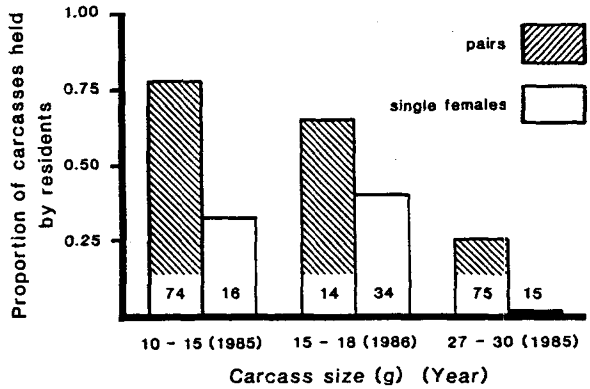

Fig. 2. Proportion of carcasses successfully held by resident pairs and single females of *N.defodiens*. Sample sizes are shown at the base of the bar graphs.

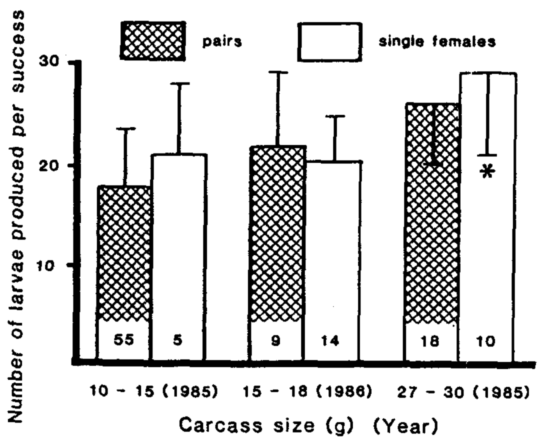

Fig. 3. Number of larvae produced (mean ±SD) on successful nests of pairs and single females. Sample sizes are shown at the base of the bar graphs. *Results for single females placed on large carcasses in 1985 are from laboratory experiments.

Table 2. The use of very small (4–7 g) and small (7–9 g) carcasses by pairs of *N.orbicollis* and *N.defodiens* in the laboratory.

	Carcass size (g)	
	4–7	7–9
N.orbicollis		
N	9	11
Buried, prepared, eggs oviposited	8	11
Produced third instars	1	8
Mean (±SD) number of larvae	3 (–)	3.7 (1.6)
Mean (±SD) mass of individual larvae (g)	0.42 (–)	0.36 (0.15)
N.defodiens		
N	11	11
Produced third instars	11	11
Mean (±SD) number of larvae	9.9 (4.9)	16.4 (4.4)
Mean (±SD) mass of individual larvae (g)	0.11 (0.02)	0.11 (0.02)

very small carcasses, were abandoned and did not produce a brood (Table 2). Such incomplete reproductive attempts are rare when *N. orbicollis* is supplied a carcass larger than 10 g (Wilson & Fudge, 1984).

N.defodiens, on the other hand, readily accepted all carcasses and was able to maintain a consistent mean mass of individual larvae for broods raised on 4–9 g carcasses by rearing fewer larvae on smaller mice (Table 2). Mean mass of individual larvae was unaffected by mouse or female size (F=1.56; Regression analysis). The number of larvae produced was related to mouse size (t=4.65, P<0.001) but not to female size (t=1.75, P=0.10). As anticipated, *N.defodiens* produced more larvae per gram of resource than the larger *N.orbicollis* (1.9 *v*. 0.5).

Resource size – field experiment

During the 1986 study in which unoccupied carcasses were placed on grid points in the field, sixty-two of eighty-one carcasses were exploited by *Nicrophorus*. Free-flying *N.defodiens* utilized very small (4–6 g) and large (33–36 g) carcasses quite differently than *N.orbicollis* (Table 3; *N.sayi* is less active by late June and was found on only two carcasses). *N.orbicollis* was the dominant species on large carcasses as it was during mid-summer in the extensive study

Table 3. Free-flying *N.defodiens* use of two carcass sizes in the field.

	Carcass size (g)	
	4–6	33–36
No. of carcasses occupied by *Nicrophorus*	33	29
% occupied by *N.defodiens*	91	38*
Mean (±SD) adult length	14.2 (1.1)	14.7 (0.8)†
Mean (±SD) number of larvae/success	8.0 (2.1)	22.8 (9.5)‡
Mean (±SD) mass of individual larvae (g)	0.10 (0.03)	0.07(0.03)†
Male present on carcasses with larvae	1/26	6/9

* P<0.0001, 2 × 2 Contingency test.

† P<0.05, Mann-Whitney U test.

‡ P<0.001, Mann-Whitney U test.

by Wilson *et al.* (1984). In the present study, *N.defodiens* exploited very small carcasses during a period of intense activity by *N.orbicollis*. In addition, males of *N.defodiens* were notably absent from 4–6 g carcasses. Apparently, males never arrived or they deserted before the trials were terminated.

Discussion

Interference, or alpha selection (Gill, 1974; Hairston, 1983), is often important in communities with limiting resources that have achieved a high degree of exploitation efficiency (Miller, 1967; MacArthur, 1972; Roughgarden, 1979; Vance, 1985). Small vertebrate carrion is a highly contested resource (Putnam, 1983). In an earlier study over 90% of mouse carcasses not found by scavengers were discovered by burying beetles on the first available night, most being discovered by more than one potential competitor (Wilson & Fudge, 1984). The present study demonstrates that *N.defodiens* is highly vulnerable to takeovers even after carcasses are buried and incorporated into a nest beneath the leaf litter. The large majority of these takeovers is by heterospecific burying beetles.

Interspecific competition among burying beetles appears to be highly asymmetrical (Milne & Milne, 1944; Easton, 1979; Wilson *et al.*, 1984), as has been found in the majority of studies that demonstrate competition in insects (Lawton & Hassell, 1981). In experiments in which I established *N.orbicollis* (Trumbo, 1987) or *N.sayi* (Trumbo, unpublished data) on carcasses in the field, *N.defodiens*, never displaced these larger species. *N.defodiens*, however, probably has an indirect negative effect on *N.orbicollis* and *N.sayi* by taking carcasses beneath the leaf litter and thereby reducing the number that are discovered by its larger competitors.

Subordinate species can persist by restricting themselves to activity periods or resources for which interference is unprofitable for dominants (Case & Gilpin, 1974) or by the more efficient exploitation of resources (Vance, 1984, 1985; Persson, 1985). As in Wilson *et al.*'s (1984) study, the present investigation determined that *N.defodiens*' reproductive success was greater early in the season when nocturnal temperatures were lower and *N.orbicollis* was less active. Further evidence of the importance of temperature-dependent competition is the altitudinal segregation of *N.orbicollis* and *N.defodiens* in montane habitats near the southern limit of *N.defodiens*' range (Lumpkin, 1971; pers. collections).

A better understanding of the abundance of smaller species of *Nicrophorus* is possible once their success on small carcasses is considered. Small carcasses experimentally colonized by *N.defodiens* were less likely to be discovered by *N.orbicollis* than were large carcasses. Small carcasses (<15 g) were manipulated into nearly spherical balls so that the head and rear of the mouse became unrecognizable. On large carcasses the head was simply folded toward the abdomen and the carcass laid on its side. Larger species of burying beetles show similar variation, making well-shaped brood balls with carcasses up to 50 g and more crudely constructed brood balls with larger carcasses (Bartlett & Ashworth, 1988). These findings suggest that large carcasses are more difficult to handle and conceal from competitors than small carcasses.

In addition, *N.defodiens* has nearly uncontested access to very small carcasses (4–6 g), both because *N.orbicollis* has difficulty locating these carcasses and because *N.orbicollis* sometimes rejects very small carcasses that they discover. Smaller species have less reason to reject very small carcasses since they produce more offspring per gram of resource than larger species (Easton, 1979; Wilson & Fudge, 1984).

N.defodiens' ability to regulate brood size supports earlier findings that *Nicrophorus* adjusts the number of offspring to match carcass size (Wilson & Fudge, 1984; Bartlett, 1987; Trumbo, 1987; Bartlett & Ashworth, 1988). It is known that female size is positively related to clutch size in *Nicrophorus* (Bartlett & Ashworth, 1988). In the present study, female size did not have an effect on brood size on 4–9 g carcasses but did produce a significant effect on 10–30 g carcasses. Perhaps there is less of an effect for smaller carcasses because females reduce brood size to a similar level despite variation in clutch sizes. A positive relationship between female size and brood size may become more apparent on larger carcasses where brood reduction is less likely to be employed.

The most plausible explanation for interspecific larvicide is to prevent depletion of a scarce resource while the usurping female begins oviposition. Although it was evident that usurpers kill larvae found on a carcass, it was less clear how they respond when no larvae are present but when eggs of the subordinate species have been oviposited in the surrounding soil just prior to a takeover. This problem is addressed in Trumbo (1987).

This study identified the prevention of interspecific takeovers as the primary contribution of *N.defodiens* males. Since body size of an *N.defodiens* adult that was experimentally established on a carcass did not affect its ability to hold a carcass, active defence does not appear to explain this finding. It can be assumed, therefore, that *N.orbicollis* and *N.sayi* have more difficulty locating carcasses manipulated by a pair than by a female working alone. Perhaps a pair buries its carcass faster and is better able to control the decomposition than a female working alone.

The ability to win a carcass by fighting in *Nicrophorus* is related to body size (Wilson & Fudge, 1984; Bartlett & Ashworth, 1988). In the field experiment allowing colonization by free-flying beetles, the greater body size of *N.defodiens* on large carcasses suggests that more individuals arrived on large carcasses and that intraspecific as well as interspecific competition was greater than on small carcasses. Although all small carcasses may not have been colonized by a male, the absence of males warrants additional study. In some cases, social systems of subordinate species can be adjusted facultatively to cope with the activity of dominants (Thornhill, 1987). If extended paternal care by subordinate species of *Nicrophorus* primarily serves to reduce interspecific interference competition, then males should desert sooner on smaller carcasses for which dominant species compete less vigorously. This prediction can be tested by establishing marked pairs on very small and small carcasses in the field.

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