Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles

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The potential impact of interspecific competition on mating systems has received limited attention. In this study, I examine the ability of single females and pairs of burying beetles (*Nicrophorus* spp.) to secure and prepare carrion resources for their brood when matched against two very different types of competitors. In the first set of experiments, I presented *N. defodiens* small and large rodent carcasses which previously had been exposed in the field to oviposition by carrion flies. Pairs experienced significantly fewer brood failures than single females (25% vs 51%). In successful reproductive attempts (at least one beetle larva produced), the presence of a male marginally increased the number and mass of the brood on small, but not large, carcasses. Carcasses prepared by pairs also attracted fewer free-flying congeners than those prepared by single females. In a second set of experiments, I examined direct contests between single females or pairs of *N. orbicollis* and single females of *N. pustulatus*. The presence of a conspecific male increased the probability that a *N. orbicollis* female would control the carcass. As a result, paired females experienced four times the reproductive success of single females. In addition, the injury rate of paired *N. orbicollis* females was 40% lower than that of single females. *Nicrophorus pustulatus* females that were excluded from a carcass were successful brood parasites on 31% of carcasses controlled by *N. orbicollis*. Parasitism by *N. pustulatus* resulted in a decrease in the total mass of *N. orbicollis* broods. By presenting a *N. orbicollis* female with heterospecific first instar larvae at one of two stages in the parental cycle, it was determined that a female will accept heterospecific young that arrive on the carcass at the 'expected' time, but will cannibalize young that arrive more than 20 h before her own eggs hatch. These results suggest that interspecific competition can promote the origin of biparental cooperation in organisms which prepare a discrete and valuable resource for young.

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The ability of two individuals to raise more young than a single parent is thought to be one of the principal reasons for the evolution of biparental cooperation and monogamy (Wittenberger and Tilson 1980, Mock and Fujioka 1990, Clutton-Brock 1991). The superiority of two parents over one is often associated with the limited ability of a single parent to meet the nutrional needs of young (Lack 1968, Zeh and Smith 1985, Tallamy and Wood 1986, Bart and Tornes 1989, Nalepa and Jones 1991). Intraspecific competition for food has been pro-

posed as an ecological mechanism which can maintain monogamy (Wilson 1975, Tallamy 1984), and the potential advantages of biparental care have been demonstrated in direct competition with conspecifics (Perrone 1978, D. Scott 1980, M. Scott 1990, Trumbo 1991). While interspecific competition is acknowledged to be a sometimes potent force in other ecological contexts (Connell 1983, Schoener 1983), its relationship to mating systems is largely neglected (Thornhill 1987). This neglect has occurred, in part, because interspecific competition is

often diffuse (Bock et al. 1992), and difficult to manipulate in many experimental situations. While it has been suggested that interspecific competition might be important in maintaining biparental cooperation in some insects (Thornhill and Alcock 1983, Tallamy and Wood 1986), there have been no demonstrations of its importance. In this study of burying beetles (*Nicrophorus*), I examine the relative ability of single females and pairs to secure and prepare a discrete 'bonanza' resource (sensu Wilson 1975) for their young while competing against exploitative or interference competitors (Ehrlich and Roughgarden 1987). I also report the occurrence of facultative interspecific brood parasitism.

Natural history of burying beetles

Adult male and female burying beetles independently search for a suitable vertebrate carcass to use as a breeding resource. The carcass is prepared for brood by burial, removal of hair or feathers, rounding into a ball, and deposition of anal secretions which affect the decomposition (Pukowski 1933). Competition with carrion flies can be intense, and may result in nesting failure by beetles (Springett 1968, Wilson 1983, Scott and Traniello 1987, Trumbo 1990b). Adult beetles carry phoretic mites (*Poecilochirus* spp.) which pierce dipteran eggs that are oviposited on the carcass before and during nest preparation (Springett 1968). *Poecilochirus* has a mildly mutualistic effect on the reproductive success of its beetle host (Wilson and Knollenberg 1987). Beetle eggs are oviposited in the soil surrounding the buried carcass and the resulting larvae hatch in 2–4 d and make their way to the carcass where they are cared for by one or both parents. When more than one same-sex conspecific or heterospecific discovers a small carcass, fights reduce the resident population to a single pair (Pukowski 1933, Wilson and Fudge 1984). Excluded (subordinate) females often attempt to parasitise the brood of a conspecific by ovipositing in the nearby soil. The subordinate's young will be accepted by the conspecific if the young arrive on the carcass within a window of time that corresponds to the dominant's oviposition period (Müller and Eggert 1990, Müller et al. 1990). When a male fails to discover the resource, a female will attempt to breed on her own, utilizing sperm stored from previous inseminations (Eggert 1992). Both single females and pairs are nearly always successful (>90%) in producing a brood on non-fly infested carcasses that are not discovered by a burying beetle intruder (Wilson and Fudge 1984, Trumbo 1990a,b, Scott and Traniello 1991, Trumbo and Wilson 1993). The only reproductive benefits that have been attributed to paternal assistance are a reduced likelihood that a conspecific will cannibalize the entire brood (Scott 1990, Trumbo 1990a,b), and slightly faster larval development (Trumbo 1991). Paternal assistance has not been shown to increase the number or size of offspring in successful reproductive attempts (Bartlett 1988, Trumbo

1990a,b,c, 1991), and in some cases, might lower reproductive output (Scott 1989, Scott and Gladstein 1993). The methods that have been employed, however, used carcasses presented to beetles either in the laboratory or under temporary covers in the field. The impact of carrion competitors, thus, was greatly reduced.

Methods

Burying beetles were caught in pitfall traps baited with carrion at The Univ. of Michigan Biological Station (UMBS, described in Wilson et al. [1984]) during June and July of 1991 and 1992. Before experimental trials, beetles were housed in mixed-sex groups for 5–10 d and fed a small quantity of chicken liver. *Nicrophorus defodiens* Mannerheim, *N. orbicollis* Say and *N. pustulatus* Herschel are all woodland species at UMBS which breed in the late spring and summer on vertebrate carcasses of various sizes. Information regarding species density, phenology and niche partitioning are provided in Anderson (1982), Wilson et al. (1984) and Trumbo (1990, 1992). Mouse and rat carcasses were obtained from university or commercial breeding facilities, and immediately frozen until needed. Carcasses were thawed 12–16 h in a refrigerator before being used in experiments.

Experiment 1 – Competition with flies
Nicrophorus defodiens, the smallest species of burying beetle at UMBS, was used to assess the ability of single females and pairs to compete with carrion flies. Six transects, spaced 50 m apart, were established in a secondary woodland of mixed composition (four points/transect with 50-m intervals between points). To simulate a situation in which beetles discover a carcass on the second available night, two 18–24-g *Mus musculus* and two 50–90-g *Rattus rattus* carcasses were left uncovered on a board in a nearby woodland (3 km from the experimental site) from 0900 to 1800 h the day before each trial, were taken inside overnight, and then re-exposed the following day from 0900 to 1400 h. These four carcasses, along with beetles (separately transported in soil), were taken to the experimental site on each of 18 d between 3 July and 6 August, 1991 (only large carcasses were used on 5 additional d). At four randomly chosen transect points, a rectangular section of soil was dug from the forest floor and trimmed to fit snugly into an 8 × 15 × 30 cm container. A single female or pair, carrying a total of 4–8 *Poecilochirus* mites, was placed into a container holding either a small or large carcass. Leaf litter (which had been removed during digging) was replaced, and wire screening (0.3 cm mesh) was placed over the container to prevent scavengers and free-flying burying beetles from gaining access to the resource. The container was then buried flush with the soil and a rain cover was tilted over the set-up. After six d, containers were brought back to the laboratory, wire screening was removed, and
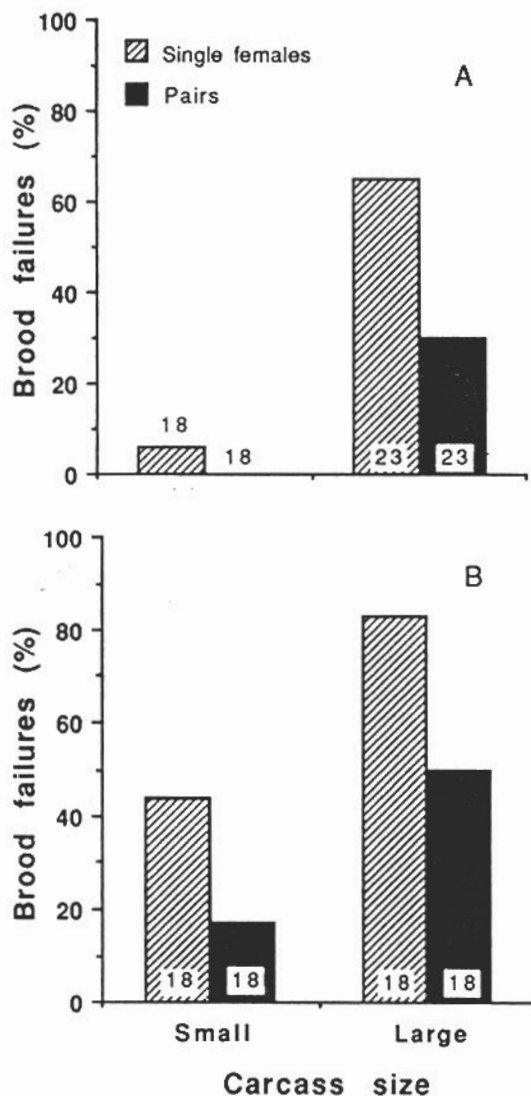
Fig. 1. Percent brood failures in Experiments 1 (A) and 2 (B) by *N. defodiens* single females and pairs on carcasses previously exposed to flies. The rate of brood failure (BF) was related significantly to carcass size (CS) and the number of residents (NR) ($2 \times 2 \times 2$ contingency tests; Exp. 1, $G_{CS \times BF} = 26.19$, P < 0.001, $G_{NR \times BF} = 6.69$, P < 0.01, $G_{CS \times NR \times BF} = 0.42$, P > 0.20; Exp. 2, $G_{CS \times BF} = 10.76$, P < 0.001, $G_{NR \times BF} = 7.98$, P < 0.01, $G_{CS \times NR \times BF} = 0.04$, P > 0.20). The sample sizes are shown at the base of the bars.

the parent beetles were allowed to disperse. Within 24 h of beetle larvae crawling away from the carcass, the number and mass of the brood were determined.

Experiment 2 – Competition with flies and discoveries by free-flying burying beetles

At a distance of 5 km from the field site in Experiment 1, two transects were established 100 m apart (four points/ transect with 60-m intervals between points). Small (24–30 g) and large (90–120 g) carcasses were exposed to

fly oviposition as before. On each of 13 d in 1991 and 5 d in 1992, single females and pairs of *N. defodiens* were transported, along with four carcasses, to the field. Circular plugs of forest soil were dug up and fitted into the base of a small plastic barrel (36 cm height, 29 cm diameter). A single female or pair was placed into the barrel, along with a small or large carcass, as in Experiment 1. The barrel was buried such that its rim was flush with the soil surface. The top of the barrel was covered with fine mesh wire screening (0.2 cm) which had a circular hole cut into it. A cup was inserted into the circular hole and a funnel was placed into the cup such that free-flying beetles that were attracted to the carcass fell into the cup via the funnel and were prevented from escaping (beetles attempt to crawl up the sides of the cup and are unable to reach the funnel spout). Rain covers were tilted over the set-up. Free-flying beetles that were trapped were removed each day for six d, after which time the barrel was taken to the laboratory, the wire screening was removed, and resident beetles were allowed to disperse. Brood number and mass were determined as in Experiment 1.

Experiment 3 – Competition with congeners

Laboratory populations of two larger species of burying beetle, *Nicrophorus orbicollis* and *N. pustulatus*, were used to examine interference competition on newly discovered carcasses. These populations were derived from wild-caught beetles at UMBS and were maintained on a 15:9 light-dark cycle at 22°C. A single female or male-female pair of *N. orbicollis* was matched against a single female of *N. pustulatus* on a 60–80 g *Rattus* carcass. A male and female of *N. orbicollis* that were paired differed in mass by less than 5%; each female *N. pustulatus* weighed 5–15% less than the smaller *N. orbicollis* in each particular trial. Beetles were placed into a soil-filled container ($8 \times 15 \times 30$ cm) during their inactive period and covered with loose dirt. Each carcass was placed on top of the soil and partially covered by a paper towel. Both species emerge at the onset of darkness and generally discover an available carcass within 10 min. On days 5–7, the carcass was checked and the identity of resident beetles recorded. On the third day after larvae arrived on the carcass, the non-resident female and the *N. orbicollis* male were removed (see Trumbo 1991 for the rationale for removing a resident male). The resident female was removed shortly after larvae dispersed. All adults were checked for injuries to legs and antennae (partial or complete severance) before and after experimental trials. Beetles with more than one injury were not used in experimental trials. The number, mass and species identity of offspring were determined at adult emergence.

Experiment 4 – Vulnerability to interspecific brood parasitism

To examine whether *N. orbicollis* can discriminate against heterospecific young, a female which had prepared a carcass and oviposited was transfered to a new container (the 'test' container) and presented 10 *N. defo-*
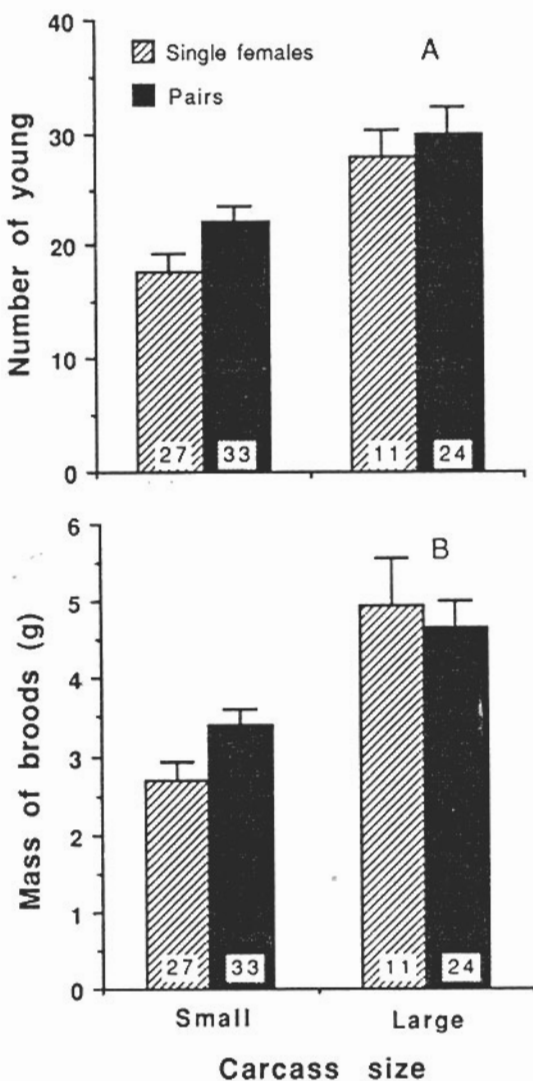
Fig. 2. Number of young (A) and mass of broods (B) produced by *N. defodiens* in successful reproductive attempts (at least one larva dispersed from the carcass). Data from Experiments 1 and 2 were pooled (Number of larvae: effect of carcass size [CS], $F_{1,91} = 21.14$, $P < 0.001$, effect of number of residents [NR], $F_{1,91} = 2.72$, $P = 0.10$, CS × NR, $F_{1,91} = 0.34$, $P > 0.20$; Mass of broods, CS, $F_{1,91} = 27.95$, $P < 0.001$, NR, $F_{1,91} = 0.34$, $P > 0.20$, CS × NR, $F_{1,91} = 2.35$, $P > 0.10$). Group means are plotted with error bars denoting 1 SE. The sample sizes are shown at the base of the bars.

diens first instars. First instar *N. defodiens* were presented to a *N. orbicollis* female at one of two times: 20–30 h before hatching of the *N. orbicollis* female's own larvae in the oviposition chamber, or 0–8 h after the female's own larvae hatched.

To ascertain whether foster parents accepted or rejected the experimental brood, test chambers were checked 2 and 4 d after the presentation of heterospecific larvae. The presence of larvae at both of these checks was scored as an acceptance by the foster parent. The absence of larvae at these two checks, and the presence of a replacement brood at a later time was scored as a rejection. Young that dispersed from the carcass were identified at adult emergence.

When data from two treatments or experiments were pooled, it was first determined that standardized scores of the pooled values did not depart significantly from normality (P > 0.05, Lilliefors' test). Statistical analyses were carried out using SYSTAT (Wilkinson 1989).

Results

Experiments 1 and 2 – Competition with flies

Carrion fly larvae are important competitors on carcasses which burying beetles fail to discover on the first available night. *Nicrophorus defodiens* failed to produce a brood on 29% and 49% of the carcasses in Experiments 1 and 2, respectively. The majority of carcasses on which beetles failed were completely consumed by fly larvae (88% had more than 30 dipteran larvae [predominantly *Phaenicia* spp.] of greater than 1.5 mm diameter). The remainder of the brood failures were attributed to fungi, ants and premature abandonment by parents. In both Experiments 1 and 2, single females were significantly more likely to experience brood failure than pairs (Fig. 1). Carcass size also had a significant impact on the likelihood of brood failure, reflecting the greater difficulty of preparing larger resources.

To examine other components of reproductive success (brood number and total brood mass in 'successes' [at least 1 beetle young produced]), data from Experiments 1 and 2 were pooled (see Methods; there were no significant differences between Experiments 1 and 2 for either of these measures of reproductive success on either small or large carcasses [P > 0.05, 1-way ANOVAs]). Carcass size had a highly significant effect on both the number of beetle larvae that dispersed from the carcass and the total brood mass. The number of parents tending the brood was not related to either measure of reproductive success (two-way ANOVA, Fig. 2). Results from small and large carcasses were then analysed separately. On small carcasses, pairs produced 25% more young and a 26% larger brood mass than single females (P < 0.05, Tukey-Kramer tests). Even so, on the 60 small carcasses which produced a beetle brood, the number of parents explains only 8% of the variation (adjusted $r^2 = 0.08$) for these two components of success. On large carcasses, there were no significant relationships between number of parents and either component of success.

Discoveries by free-flying beetles

There was considerable variation between replicates in the number of free-flying burying beetles that discovered
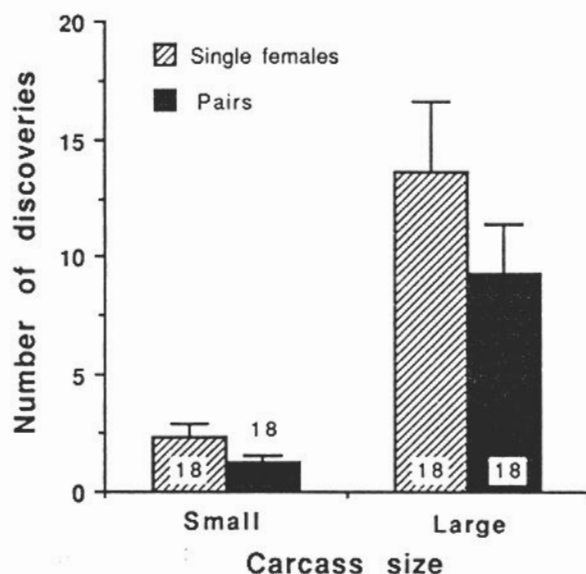
Fig. 3. Mean (±SE) number of free-flying beetles that discovered carcasses prepared by single females or pairs of *N. defodiens*. Sample sizes are shown at the base of the bars.

carcasses in Experiment 2. For example, 31% of large carcasses were discovered by 3 or fewer beetles while 47% were discovered by 10 or more potential intruders. Much of this variation likely can be attributed to differences in temperature and humidity during the beetles' active period (Wilson et al. 1984). To reduce the effect of weather, trials from replicates begun on the same day were paired (a single female vs a male-female pair, separately for small and large carcasses). The presence of a male significantly reduced the number of potential competitors that discovered the carcass ($P < 0.01$, $N = 36$, Wilcoxon's Matched Pairs Signed Ranks test; Fig. 3). Most discoveries (67.4%) were by heterospecific burying beetles.

Experiment 3 – Contests between N. orbicollis and N. pustulatus

There was a dominant female in residence on 54 of the 56 carcasses in Experiment 3 (the subordinate was not observed on the carcass on days 5–7). In two trials both females were seen on the carcass; one of these trials resulted in a brood failure, and the other in a mixed brood. The presence of a *N. orbicollis* male significantly altered the outcome of contests. The *N. orbicollis* female was in residence in 85% of trials with a male but in only 25% of trials without a male ($P < 0.001$, $N = 56$, Fisher's Exact test). Since the dominant female produced more young than the subordinate in 51 of 54 cases ($P < 0.001$, Sign test), the difference in residency had a sizable effect on reproductive success. The *N. orbicollis* female produced more young and a greater total brood mass in trials

with a *N. orbicollis* male than in trials without a male; the reproductive success of *N. pustulatus* females was significantly less when the *N. orbicollis* male was present (Fig. 4).

Fights were severe as evidenced by the prevalence of injuries sustained during trials; 80%, 75% and 50% of *N. orbicollis* female, *N. orbicollis* male and *N. pustulatus* females, respectively, were injured. The presence of a male reduced the likelihood that the *N. orbicollis* female would be injured from 100 to 61% ($P < 0.001$, Fisher's Exact test). In trials employing males, the injury rates for *N. orbicollis* males and females did not differ significantly ($P = 0.17$). The overall injury rate of *N. pustulatus* females did not differ between treatments ($P > 0.2$), but the probability of severe injury (3 or more limbs or antennae damaged) was greater in trials with *N. orbicollis* males than in trials without males (50 vs 14%, $P < 0.01$). Although high rates of injury are indicative of intense contests for the resource, injury rates were likely exag-
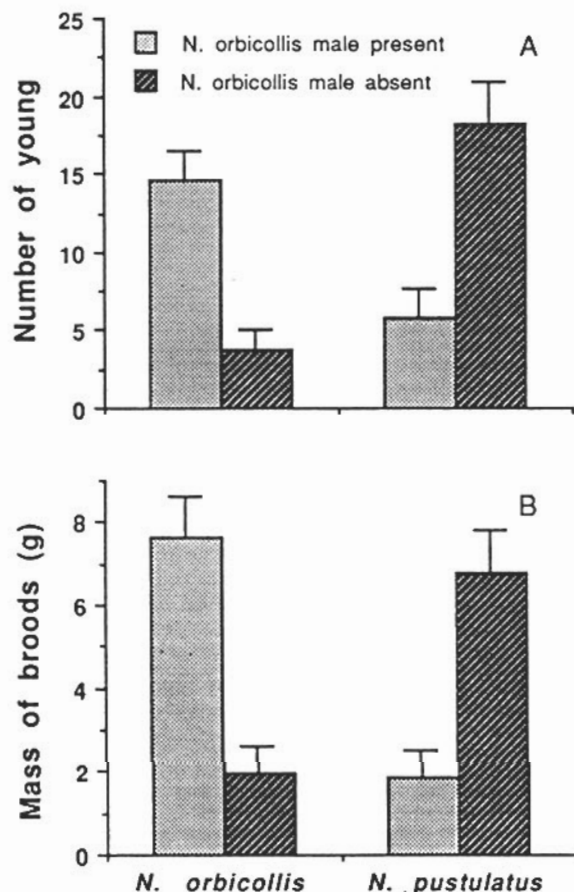

Fig. 4. Mean (±SE) number of young (A) and mass of broods (B) produced by *N. orbicollis* and *N. pustulatus* females in the presence ($N = 28$) or absence ($N = 28$) of a *N. orbicollis* male (Mann Whitney U-tests on the effect of the male: *N. orbicollis*, $U_{number} = 158$, $U_{mass} = 152$, P's < 0.001; *N. pustulatus*, $U_{number} = 575$, $U_{mass} = 587$, P's < 0.005).
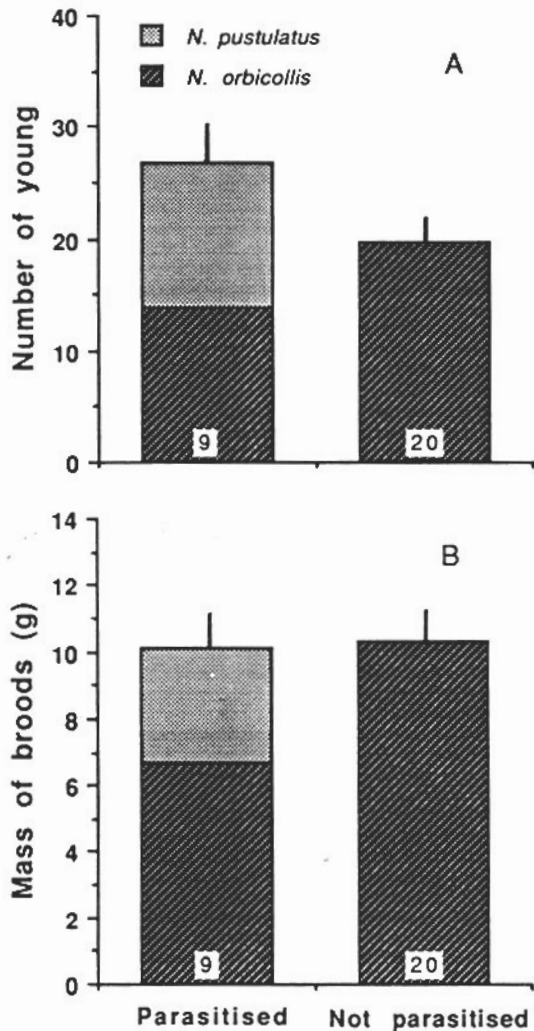
Fig. 5. Number of larvae (A) and mass of broods (B) produced by *N. orbicollis* females for parasitised and non-parasitised broods when *N. orbicollis* was the dominant resident female. Results for *N. pustulatus* are shown for parasitised broods. Error bars denote 1 SE for the entire brood (*N. orbicollis* + *N. pustulatus* young). Sample sizes shown at the base of the bars.

gerated by allowing repeated contact between competitors over a number of days. In the field, subordinates usually depart by the end of the oviposition period.

Experiments 3 and 4 – Brood parasitism

Nicrophorus orbicollis and *N. pustulatus* females that were excluded from the carcass in Experiment 3 differed in their ability to parasitise the brood of the resident. Of the 29 trials in which the *N. orbicollis* female was in control of the carcass, 9 (31%) were successfully parasitised by *N. pustulatus*. *Nicrophorus orbicollis* females, on the other hand, never parasitised any of the 25 car-

casses which *N. pustulatus* controlled ($P < 0.01$, Fisher's Exact test). To examine the effect of brood parasitism on the reproductive success of *N. orbicollis*, trials in which *N. orbicollis* controlled the carcass ($N = 29$) were pooled from male and no-male treatments. *N. orbicollis* females had a smaller total brood mass ($F_{1,27} = 7.10$, $P = 0.013$) and produced marginally fewer larvae ($F_{1,27} = 3.86$, $P = 0.06$; one-way ANOVAs) when brood parasitism occurred (Fig. 5). The combined brood mass of *N. orbicollis* and *N. pustulatus* young did not differ in parasitised and non-parasitised broods ($P > 0.20$, one-way ANOVA), suggesting that the reproductive gain of *N. pustulatus* brood parasites was directly at the expense of *N. orbicollis* females. In addition, the presence of a male did not appear to affect the probability that his mate would be parasitised (8 of 22 broods parasitised with the male present, 1 of 7 parasitised in the absence of a male; $P > 0.20$, Fisher's Exact test).

In Experiment 4, it was clear that the likelihood that *N. orbicollis* will accept heterospecific (*N. defodiens*) larvae depends on the timing of their arrival on the carcass. If heterospecific larvae arrived 20–30 h earlier than 'expected', they were always rejected and replacement broods of *N. orbicollis* larvae were eventually produced ($N = 9$). Several *N. orbicollis* females were observed to cannibalize *N. defodiens* larvae. If heterospecific larvae arrived 'on time', however, they were usually accepted (9 of 10 trials) and no replacement broods were produced ($P < 0.01$, Fisher's Exact test).

Discussion

Bonanza resources (Wilson 1975) such as carrion, dung and dead wood attract a diverse group of organisms, many of which are specialized to exploit the resource rapidly before competitors become established (Putnam 1983, Hanski and Cambefort 1991). Some sarcophagid flies, for example, deposit first instar larvae rather than eggs on a carcass and thereby decrease the time it takes for their offspring to exploit the resource (Denno and Cothran 1976). The burying beetle strategy is to quickly conceal carrion underground, and then to eliminate microbial and dipteran competitors that may have had a head start (Pukowski 1933, Halffter et al. 1983). Such nest-building and procurement of food for young during the pre-oviposition period is rightly regarded as parental investment in the broad sense (Clutton-Brock 1991). Whether or not biparental cooperation can be a part of a strategy for dealing with interspecific competition, has not been previously explored.

Prior studies of biparental cooperation in burying beetles have severely limited competition for carcasses during the critical first 24 hours, and thus have found that both single females and pairs rarely experience brood failure unless a carcass is discovered by a burying beetle intruder. When carcasses are exposed to carrion flies and

microbes before being presented to beetles (the typical order of discovery), paternal assistance clearly enables females to win a higher proportion of carcasses. Other components of reproductive success (number of larvae and brood mass) are less affected by paternal cooperation, but male help might be important when resources are limited (on smaller carcasses). Why two parents are more effective than a single parent is not clear. The presence of a male may not decrease the time required to bury a carcass in *N. orbicollis* (Scott 1990). Beetles also contend with flies by eating fly larvae, removing hair which likely destroys fly eggs, and depositing anal secretions which seems to control the decomposition (Pukowski 1933, Halffter et al. 1983). The relative ability of pairs and single females to perform these tasks has not been investigated.

Resident burying beetles have two ways to compete against congeners. They can prevent discovery by efficient burial and maintenance, and they can attempt to repel individuals that manage to discover the resource. In both respects, pairs do better than single females. Fewer congeners discovered a resource that was prepared by pairs rather than by single females. It is likely that pairs were either faster at preparing the carcass or better able to control the decomposition, thereby decreasing olfactory cues used by flying beetles. Pairs also were superior to single females in direct contests with a heterospecific, and the male's presence decreased the probability that the female would be injured. Previously, it has been found that at the time of discovery, fights among conspecifics are entirely intrasexual (Pukowski 1933). Pairs only do better against a conspecific intruder when there is a brood on the carcass and both the male and female resident have a stake in expelling an infanticidal intruder (Scott 1990, Trumbo 1990b). This study suggests a very different interaction when individuals of two species discover a resource, with both sexes contesting heterospecifics.

The superiority of two parents over one in direct contests with heterospecifics could have important implications for understanding burying beetle species' ranges. A species with a low population density might have difficulty expanding its range against a species with higher population density. For a rare species, a higher proportion of carcasses will likely be buried by a single female since females have no mechanism for attracting a male. This will put the rare species at a competitive disadvantage since there is a greater probability that at least one male and female of a more common species will discover the resource.

A female that is excluded from a carcass and cannot raise her own brood has options to increase her fitness. *Nicrophorus pustulatus* was able to parasitise broods of *N. orbicollis* but the reverse never occurred. Reasons for this asymmetry are not clear. *Nicrophorus orbicollis* will parasitise a conspecific host (Trumbo 1990a), but whether attempts are made with heterospecific hosts is unknown. *Nicrophorus pustulatus* seems to be a formidable brood parasite. It produces the largest clutches, by far, of any *Nicrophorus* species (Trumbo 1992), and thus could potentially swamp the clutch produced by the host. Because of its rarity, however, this species' reproductive biology is poorly understood.

As with intraspecific brood parasitism in this group (Müller et al. 1990), reproductive success of a heterospecific parasite comes at the expense of the host. Opportunities for potential interspecific brood parasitism may be common in the field; heterospecifics were present near 50% of carcasses controlled by *N. orbicollis* on Day 1 (Trumbo 1992). In Trumbo's (1992) study, however, only 1 of 35 carcasses that produced a *N. orbicollis* brood was apparently parasitised by a heterospecific (*N. tomentosus*). Most interactions of *N. orbicollis* were with the much smaller *N. defodiens*. Parasitism may be less frequent among species that differ grossly in body size because a brood parasite needs some access to the carcass before ovarian growth and oviposition can be triggered (Scott and Traniello 1987). As with birds, selective pressures which might have been important in the evolution of intra- and interspecific brood parasitism in burying beetles might include a severe shortage of available resources, and the ability to detect nests (Andersson and Eriksson 1982).

Counteradaptations to brood parasitism are expected. Besides repelling potential parasites and limiting their access to the resource, hosts would profit from killing young. Burying beetles do not appear to have an absolute mechanism to discriminate against heterospecific larvae (*Nicrophorus defodiens*, *N. tomentosus* and *N. pustulatus* also will accept heterospecific first instars [Trumbo 1987]). The only apparent mechanism that burying beetles have to discriminate against heterospecific young is the same mechanism described by Müller et al. (1990) to combat intraspecific parasitism (killing young that do not come to the carcass at the 'expected' time). It also has been suggested that hosts should produce a smaller clutch in response to brood parasitism (Andersson and Eriksson 1982). In this way, the host avoids trying to support too large a brood which could expose both host and parasite young to starvation. Clearly, such considerations do not apply to species which have parentally-controlled brood reduction. When a host reduces brood size to match resource size, as in burying beetles (Bartlett 1987, Trumbo 1990c), one would expect the host to increase clutch size when confronted with possible parasitism, thus diluting the contribution of the parasite before brood reduction. This is yet to be tested in burying beetles.

Biparental cooperation in burying beetles is well developed, and includes nest-building, regurgitating to young, and defense of the brood. A male also will compensate partially for the absence of his mate by providing additional care (Trumbo 1991, Fetherston et al. 1993), as occurs in some birds (Wright and Cuthill 1989). Among beetles, this degree of biparental cooperation is rivalled by only a few dung or wood specialists, and desert species (Schuster and Schuster 1985, Rasa 1990, Hanski and Cambefort 1991). An analysis of the reproductive bene-

fits that maintain extended paternal care and monogamy, however, may not address the origin of biparental associations (Barlow 1988). Two mechanims which can promote associations between a male and a female are mate guarding and females' withholding copulations from males that do not make an investment in young (Thornhill and Alcock 1983, Barlow 1988). It has been suggested that female burying beetles might not mate off a carcass (Thornhill and Alcock 1983) or that they might delay mating until nest-building is underway (Zeh and Smith 1985). There is little evidence to support either speculation. Females mate away from carcasses (Eggert 1992) and mate repeatedly with little courtship soon after the discovery of a resource (Pukowski 1933, Müller and Eggert 1989). It also does not seem necessary to invoke mate guarding to explain the evolutionary origin of associations during the burial and preparation of the carcass (although changes in male behavior following the arrival of a second male would be of interest). When a male discovers a carcass before a female, he conceals it beneath the leaf litter and initiates burial, even before advertising for a mate (Pukowski 1933). The most detailed accounts of the discovery stage in burying beetles (Fabre 1919, Pukowski 1933) comment on the looseness of the association and the independent action of the male and female (excepting interruptions for copulation). Males do not guard a female, but guard the resource; they pair with any resident female that has excluded her rivals (Pukowski 1933). Any mechanism, such as mate guarding or withholding copulations, which depends on monitoring the activity of the other member of the pair might take time away from competitive activities and thus be counterproductive on an attractive resource such as carrion. This study suggests that interspecific competition can promote the evolution and maintenance of biparental cooperation in organisms which prepare a discrete and valuable resource for young.

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