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

Stephen T. Trumbo


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 hatchings against two very different types of competitors. In the first set of experiments, I presented N. quadripennis small and large male parasitoids which previously had been exposed to the field for pupation 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, not large, carrion. Carrion used by pairs also contained fewer free-flyin insects than those prepared by single females. In a second set of experiments, I examined direct competition between single females or pairs of N. orbicollis and single females of N. quadripennis. The presence of a conspecific male increased the probability that a N. orbicollis female would control the carrion. As a result, pairs of females experienced less competition for the reproductive success of single females. In addition, the injury rate of parent N. orbicollis females was 40% lower than that of single females. Nicrophorus quadripennis females that were excluded from a carrion were successful brood parasites on 30% of carrion controlled by N. orbicollis. Maternal care by N. quadripennis resulted in a decrease in the total mass of N. orbicollis broods. By providing a N. orbicollis female with heterospecific first instar larvae, one of two stages in the parental cycle, it was determined that a female will reject heterospecific young that arrive on the carrion at the expected time, but will cannibalize young that arrive more than 24 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.

S. T. Trumbo, Dept of Entomology, 120 Morrill Hall, Univ. of Illinois, Urbana, IL 61801, USA.

The ability of two individuals to raise more young than a single parent is thought to be the principal reason for the evolution of biparental cooperation and monogamy (Willmot et al. 1980, Meoli and Fujikura 1980, Clutton-Brock 1991). The superiority of two parents over one is often associated with the limited ability of a single parent to meet the nutritional needs of young (Lack 1966, Zeh and Smith 1985, Tallamy and Wood 1986, Bart and Thoresen 1989, Nolte and Jones 1991). Interspecific competition for food has been proposed 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 (Perrins 1978, B. Scott 1980, M. Scott 1990, Trumbo 1991). While interspecific competition is acknowledged to be a some-
when 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 biennial co-existence in some insects (Thomhill and Atwood 1985), 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 carcasses under a discarding model (Wilson et al. 1975) for their young while competing against exploitative or interference competitors (Ehrlich and Rougier 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 brooding 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 nestling failure by beetles (Springett 1968, Wilson 1983, Scott and Tranquillini 1987, Trumbo 1990b). Adult beetles carry phoretic mites (Puceschelus spp.) which pierce dipteran eggs that are oviposited on the carcass before and during nest preparation (Springett 1968). Puceschelus has a mildly mutistic effect on the reproductive success of its beetle host (Wilson and Knollenberg 1982). The eggs are oviposited in the soil surrounding the buried carcass and the resulting larvae hatch in 2–4 days 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 parasitize the carcass by ovipositing eggs near the nearby soil. The subadult’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 Egger 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 (Eger 1992). Both single females and pairs are nearly always successful (>80%) in producing a brood in nest-located carcasses that are not discovered by assaying beetle intruder (Wilson and Fudge 1984, Trumbo 1990a,b, Scott and Tranquillini 1991). Trumbo and Wilson (1993). The only reproductive benefits that have been attributed to parental assistance are a reduced likelihood but a conspecific will cannibalize the entire brood (Scott 1996), Trumbo 1990a,b, and slightly faster larval development (Trumbo 1991). Parental assistance has not been shown to increase the number or size of offspring in successful reproductive attempts (Hartnett 1988, Trumbo 1990a,b, 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 1992 and 1993. Before experimental trials, beetles were housed in mixed-sex groups for 5–10 days and fed a small quantity of chicken liver. Nicrophorus defloris Mannerheim, N. orbicollis Say and N. patelliferus Herbst are all woodland species at UMBS which breed in the late spring and summer on vertebrate carcasses of various sizes. Information regarding species density, phenotype 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 refrigerate before being used in experiments.

Experiment 1 – Competition with flies

Nicrophorus defloris, 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 beetle discover a carcass on the second available night, two 18–21-g Musca musca, and two 55–90-g Rattus rattus carceas were left uncovered on a board in a nearby woodland (1 km from the experimental site) from 0900 to 1800 h the day before each trial, were taken inside oversite, 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 days between 3 July and 6 August, 1991 (only large carcasses were used on 5 additional days). 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 x 15 x 30 cm container. A single female or pair, carrying a total of 4–8 Puceschelus 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 (0.5 cm mesh) was placed over the container to prevent scavengers from free-flying burying beetles from gaining access to the resource. The container was then buried flush with the soil and a rain cover was placed over the set-up. After six, 12, containers were brought back to the laboratory, wire screening was removed, and...
Fig. 1. Proportion brood failure in Experiments 1 (A) and 2 (B) by N. defoliator 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) (2x2x2 contingency test; Exp 1, G_{st} = 25.76, P < 0.001. G_{st} = 10.76, P = 0.001. G_{st} = 4.42, P > 0.2). Exp. 2, G_{st} = 7.98, P < 0.01. G_{st} = 0.04, P > 0.2). The sample sizes are shown at the base of the bars.

The parent beetles were allowed to disperse. Within 24 h of beetle larva 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. defoliator were transported, along with four carcasses, to the field. Circular plots of forest soil were dug up and filled into the base of a small plastic barrel (10 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 claw up the sides of the cup and are unable to reach to the funnel stop). Rain covers were placed over the setup. 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 congers

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 rotten 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 x 15 x 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 outset 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 larva arrived on the carcass, the non-resident female and the N. orbicollis male were removed (see Thurnherr 1991 for the rationale for removing a resident male). The resident female was removed shortly after larval emergence. 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 as adult emergence.

Experiment 4 — Vulnerability to interspecific brood parasitoids

To examine whether N. orbicollis can discriminate against heterospecific young, a female which had pre- pares a carcass for her offspring was released into a new container (the 'test' container) and presented 10 N. defo-
Results

Experiments 1 and 2 — Competition with flies

Carrion fly larvae are important competitors on carcasses which bury beetles fail to discover on the first available night. *Necrophila defoliante* failed to produce a brood on 26% 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% of their mass consumed, with 19% completely devoured). The remainder of the brood failures were attributed to fungi, ants and predate by parasitoids. In both Experiments 1 and 2, single flies 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 ANOVA). 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. 3). 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 test). Even so, on the 60 small carcasses which produced a beetle brood, the number of parents explains only 8% of the variation (adjusted r² = 0.08) for these two components of success. On large carcasses, there were no significant relationships between number of parasites and clutch size and composition of success.

Discoveries by free-flying beetles

There was considerable variation in burying beetle larvae that discovered a carcass. A single successful reproduction attempt at least one brood was dispersed from the carcass. Data from Experiments 1 and 2 were pooled (Number of larvae: effect of carcass size [CS]; F₁,₉₈ = 11.14, P < 0.001, effect of number of adults [NR]; F₁,₉₈ = 2.72, P = 0.11, CS x NR; F₁,₉₈ = 0.34, P > 0.20). More of both CS and NR had a 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. 3). 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 test). Even so, on the 60 small carcasses which produced a beetle brood, the number of parents explains only 8% of the variation (adjusted r² = 0.08) for these two components of success. On large carcasses, there were no significant relationships between number of parasites and clutch size and composition of success.
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 began 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 < 0.001, N = 26, Wilcoxon’s Matched Pairs Signed Ranks test; Fig. 3). Most discoveries (67.4%) were by heterospecific burying beetles.

Experiment 3 – Contest between N. orbicollis and N. putulatus

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 on residence in 25% 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. putulatus 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. putulatus 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. putulatus 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 exaggerated by the relatively small size of the arena and the high density of beetles in each trial.
Experiments 3 and 4 - Brood parasitism

Nicrophorus orbicollis and N. politellus females that were excluded from the carcass in Experiment 3 differed in their ability to parastitise 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. politellus. Nicrophorus orbicollis females, on the other hand, never parasitised any of the 25 carcasses which N. punctulatus 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 female treatments. N. orbicollis females had a smaller total brood mass (P = 0.07, P = 0.01, two-way ANOVAs) and produced marginally fewer larvae (F = 5.0, P = 0.08, one-way ANOVAs) when brood parasitism occurred (Fig. 3). The combined brood mass of N. orbicollis and N. politellus young did not differ in parasitised and non-parasitised broods (P > 0.01, one-way ANOVAs), suggesting that the reproductive gain of N. politellus brood parasitism was insignificant at the expense of N. orbicollis in females. In addition, the presence of a male did not appear to affect the probability that its brood would be parasitised (8 of 22 broods parasitised with the male present, 1 of 7 parasitised in the absence of a male; P > 0.01, Fisher's Exact test).

In Experiment 4, it was clear that the likelihood that N. orbicollis will accept heterospecific (N. depurator) 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 cannibalise N. depurator 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

Bouma 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 (Patnam 1983, Huisman and Cambefort 1991). Some saprophagous 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 (Dethier and Cade 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 (Polkowski 1978, Hafner et al. 1983). Such nest-building and procurement of food for young during the pre-oviposition period is highly regarded as parental investment in the broad sense (Clutton-Brock 1991). Whether or not interspecific cooperation can be a part of a strategy for dealing with interspecific competition, has not been previously explored.

Prior studies of interspecific 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 damaged by a burying beetle intruder. When carcasses are exposed to carrion flies and...
mice 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 parental 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 increase the time required to
harry a carcass in N. orbicollis (Scott 1990). Beetles also contended with flier by eating fly larvae, removing hair which likely secretes egg yolk, and depositing anal secretions which send to control the decomposition (Polowsk
ik 1953, Hafifler et al. 1983). The relative ability of pairs and single females to perform these tasks has not been investigated.

Reseaua burying beetles have a two-way system to compete against congeners. They can prevent discovery by effi

cient 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 congener 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 infactory cues used by burying 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 (Polowski 1953). 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 infantidal intruder (Scofield 1990, Trumbo 1990a). 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 con

tests with heterospecifics could have important implica
tions for understanding burying beetle species' ranges. A species with a low population density might have diffi

culty expanding its range against a species with a 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 in 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 variabilis was able to produce one brood of N. orbicollis but the reverse never occurred. Reasons for this asymmetry are not clear. Nicrophorus orbicollis will parasitize a conspecific host (Trumbo 1990a), but whether attempts are made with heterospecific hosts is unknown. Nicrophorus paludarum seems to be a formidable

able 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 heterospe

cific parasite comes at the expense of the host. Opportu

nities for potential interspecific brood parasitism may be common in the field. Heterospecifics were present near 40% of carcasses controlled by N. orbicollis on line 1 (Trumbo 1992). In Trumbo's (1982) study, however, only 1 of 35 carcasses that produced a N. orbicollis brood was apparently parasitized by a heterospecific (N. tomentosa).

Most interactions of N. orbicollis were with the much smaller N. defodiens. Parasitism may be less fre

quent among species that differ greatly in body size because a brood parasite needs some access to the carcass before ovarian growth and ejection can be triggered (Scott and Transtel 1987). As with birds, selective pressures which might have been important in the evolution of intraspecific and interspecific brood parasitism in burying beetles might include a severe shortage of available re

sources, and the ability to direct nests (Anderson and Eriksrud 1982).

Counteradaptations to brood parasitism are expected. Be

tween repelling potential parasitoids 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 definitus, N. tomentosus, and N. paludarum) 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 (Anderson and Eriksrud 1982). In this way, the host avoids trying to support two larvae a brood could either host paring and parasitism. Clearly, such considerations do not apply to species which have parentally-controlled brood reduction. Now a host reduces brood size to match resource size, as in burying beetles (Batlett 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 ad

uction. This is yet to be tested in burying beetles.

Biparental cooperation in burying beetles is well de

veloped, and includes nest building, aggregating toward young, and defense of the brood. A male also will com

pensate partially for the absence of his mate by providing additional care (Trumbo 1991, Fetherson et al. 1993), as

wells as in some birds (Wright and Callthill 1989). Among beetles, this degree of biparental cooperation is rivalled by only a few dung or wood specialists, and desert spe

cies (Schneer and Schuster 1985, Raia 1990, Hanski and Camberfort 1991), an analysis of the reproductive be

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