

Reproductive benefits of infanticide in a biparental burying beetle *Nicrophorus orbicollis*

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Summary. Single females and pairs of *Nicrophorus orbicollis* Say were established as residents on carcasses to investigate interactions with intruders under natural conditions. When carcasses were exhumed 10–12 days later, one or more intruders were found on 19% of nests. Intruders expelled one or both of the residents and sometimes paired with a resident or another intruder of the opposite sex. An intruder tended to be larger than the same-sex adult it replaced on a carcass. A male intruder that joined a single female, on the other hand, was not necessarily larger than the resident female. There was indirect evidence that intruders committed infanticide and then started their own reproductive attempt on the carcass. Follow-up experiments in the laboratory indicated that interactions between intruders and residents were agonistic and that infanticide regularly occurred as a consequence of a takeover. Use of a genetic marker demonstrated that male and female intruders obtained reproductive benefits from infanticide. However, intruders sometimes cared for mixed broods consisting of their own young and young of a prior resident.

Introduction

Reports on the occurrence and possible causes of infanticide increased substantially once this behavior began to be viewed from evolutionary perspectives (Hrady 1974; Wilson 1975). Reviews of infanticide make it clear that it occurs across a wide variety of taxonomic groups and is regular and normal behavior in many species (see Hrady and Hausfater 1984a). Although it is increasingly believed that infanticide can be adaptive, assessment of its importance for social systems has been slow. This has occurred because infanticide may be difficult to observe and because it is difficult to measure direct reproductive benefits that infanticidal individuals obtain. The

determination of parentage of offspring produced subsequent to infanticide is less of a problem for species in which all copulations can be observed and eggs can only be fertilized for a short period of time. The use of genetic markers, however, is essential for most species. This includes all insects which are able to store sperm for long periods of time.

A male-female pair of burying beetles (*Nicrophorus Fabricius* spp.) will bury a small vertebrate carcass which is used as a resource for their brood. The ovaries of the female increase about three-fold in a short period and eggs are oviposited in the soil surrounding the burial crypt within 48 h (Wilson and Knollenberg 1984; Scott and Traniello 1987). A male that pairs with a female fathers a large proportion of the offspring although a lone female will use stored sperm to produce a clutch if no male discovers the carcass (Bartlett 1988; Müller and Eggert 1989). When present, both parents help prepare the carcass, regurgitate to larvae, and defend the brood against intruders (Pukowski 1933; Milne and Milne 1976; Trumbo 1987; Scott 1990; Trumbo 1990).

This study attempts: (1) to document that takeovers and infanticide are common occurrences under natural conditions in *Nicrophorus orbicollis* Say; (2) to examine interactions between residents and intruders; and (3) to examine parentage of offspring produced subsequent to infanticide by employing a genetic marker. The results are discussed in relation to three hypotheses that have been proposed to explain why adults kill unrelated conspecific young (Hrady 1979).

Methods

Occurrence of takeovers – experiments in the field. This study was conducted at The University of Michigan Biological Station near Pellston, Michigan (described in Wilson and Knollenberg 1984). *Nicrophorus orbicollis* was collected in pitfall traps that were located at least 2 km from experimental sites and baited with rat carcasses. Mixed-sex groups of 10–20 beetles were housed in plastic containers for 10–20 days before being used in field trials. Body length was measured as the distance from the tip of the mandibles to

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the edge of the elytra. Beetles were marked by clipping off a small part of the posterior edge of one of the elytra. All carcasses were laboratory *Mus musculus* L. that were killed with CO₂, frozen until needed, and thawed overnight in a refrigerator prior to trials.

Ten transects, separated by a minimum of 100 m, were established in a birch-beech-aspen secondary forest (12 points/transect with 15 m intervals between points). Either a pair or a single female was placed on a mouse carcass (10–33 g) at randomly chosen transect points on 17 days between 29 June and 3 August, 1985 and on each day from 24 June to 13 July, 1986. A total of 339 experimental placements were made.

Opposite ends of a 1 m length of dental floss were tied to a stake and to the hind leg of the mouse to assist in locating the carcass after burial. Leaf litter which had been removed from the site during the procedure was then replaced. The set-up was covered with an inverted plastic container (23 cm diameter) for 1 day to prevent rivals from contesting the resource during interment. Carcasses which were moved away from the stake within 24 h were categorized as accepted and were subsequently left uncovered for the remainder of the trial.

Nests were exhumed after 10–12 days by sorting through the leaf litter in the vicinity of the nest, removing soil overlying the burial crypt and searching the surrounding soil within a 30 cm radius. At exhumation, the number and size of larvae and adults were determined. Marked adults were classified as residents and unmarked adults as intruders.

Observations of infanticide. All laboratory experiments were conducted at The Mason Farm Biological Reserve in Chapel Hill, North Carolina with beetles descended from The University of Michigan Biological Station population. Beetles were kept at 21° C and 15L:9D. To make direct observations of possible infanticide in the laboratory, 6 females were each provided with a mouse carcass (20–30 g) in a 8 × 15 × 30 cm container filled with soil. Two days after larvae appeared, a larger male or female intruder was introduced into the container. After the intruder discovered the carcass, observations began for 3 h. The set-up then was reinspected 24 h after the intruder had discovered the carcass.

Genetic marker. A genetic marker, 'spotless', was employed to examine reproductive benefits following takeovers. Spotless adults lack the two orange basal markings on the elytra that wild type individuals possess. A spotless × spotless cross produces all spotless offspring and a spotless × wild type cross produces offspring which all show some degree of basal marking on the elytra (unpublished results).

Seven spotless females were each paired with a spotless male (females were never housed with wild type males) and provided with a carcass (21–24 g) in containers in the laboratory. Carcasses were examined on the fourth day and the resident male was removed. Carcasses were checked once a day thereafter. When larvae were detected on the carcass an intruder male (wild type, pronotum 5%–15% wider than the female) was placed in the corner of the container farthest from the burial crypt and then covered with soil. During daily checks it was determined if larvae were on the carcass and whether the resident and/or intruder were on the carcass. Any larvae that dispersed from the carcass to pupate were weighed and reared to the adult stage to determine parentage. At dispersal, the resident and intruder were checked for leg and antennal injuries not present at the beginning of the trial.

Seven additional trials were carried out, reversing the genetic marker for the resident and intruder male. Results for the two subsets of trials involving intruder males were similar and were combined for analysis.

A similar experimental procedure was used to investigate the effect of a female intruder. A large wild type intruder female ($N=7$, all prior mates wild type) or a large spotless intruder female ($N=7$, all prior mates spotless) was introduced to a resident female possessing the alternate genetic marker. Subsequent procedures were the same as outlined above.

Additionally, seven wild type female × spotless male crosses and seven spotless female × spotless male crosses (males removed on day 4) were made using 21–24 g carcasses. In these trials no intruders were introduced.

Results

Occurrence of takeovers – experiments in the field

Twenty-three of the 339 carcasses used in the study conducted in the field were either scavenged by vertebrates or were not accepted by the experimentally placed beetles. Of the remaining 316 carcasses, 251 had residents or large third instar larvae at exhumation, 59 had an unmarked intruder present and 6 were abandoned after burial. There were never an intruder and a resident of the same sex on the carcass at the end of the trial. Every other possible combination of an intruding and resident beetle occurred (Table 1). The intruder was found paired with a resident of the opposite sex on 43% of the carcasses on which the appropriate mate was available ($N=51$).

The body size of beetles established on a carcass was related to their ability to retain ownership. In a large proportion of cases a male intruder was larger than the male resident replaced (0.79, $N=14$, $P<0.05$, Wilcoxon's matched pairs signed ranks test). The proportion was similar for female intruders and residents (0.77, $N=31$, $P<0.01$). Male intruders were not significantly longer than resident single females they joined ($N=15$, $P>0.20$) or single females that left the carcass after the intrusion ($N=12$, $P>0.20$).

Staying on the carcass during brood development is not without risks. Remains of 6 burying beetles (2 residents, 2 intruders and 2 unidentified) were found in or near crypts at exhumation. Additionally, 21 residents that retained ownership of their resource (no intruder present) received a leg or antennal injury during the trial. On carcasses established with pairs, 8% of residents that were present at exhumation on large carcasses (30–33 g) had been injured while 3% of residents on small carcasses (10–18 g) had been injured ($N_S=71$, $N_L=120$, $\chi^2=2.11$, $0.20 < P < 0.10$).

Table 1. The number of carcasses accepted by the resident adults that were found at exhumation with an intruder, and the proportions of each type of intrusion. I = Intruder, R = Resident

	<i>N</i>	Intruder present	I male I female	I male only	I female only	I male R female	I female R male
Singe females	123	35	0.23	0.11	0.23	0.43	(–)
Pairs	193	24	0.21	0.21	0.29	0.17	0.12

Over 95% of nests without an intruder contained larvae ($N=257$), while only 42% of nests with an intruder had larvae ($N=59$, $\chi^2=104$, $P<0.001$). Additionally, of the 25 nests with an intruder and larvae, the mean mass of individual larvae of 24 of these broods was less than the median mean mass of individual larvae of the appropriate reference group (median test, $\chi^2=22.66$, $P<0.001$). This provides indirect evidence that intruders kill larvae they find on the carcass and then initiate their own reproductive attempt (Trumbo 1987; Scott 1990).

Single females that were joined by a male intruder also suffered costs. Only forty percent of females that were joined ($N=15$) had larvae on the carcass by exhumation, a figure significantly different from single females that were not joined (92%, $N=88$, $\chi^2=21.41$, $P<0.001$). In the 6 cases in which larvae were present, the mean mass of larvae was less than the median mean mass of the appropriate reference group (median test, $P<0.05$).

Observations of infanticide in the laboratory

An encounter with an intruder triggered attack and pursuit from the resident female. In the most intense bouts a leg is held firmly in the mandibles while the attacker jerks its head rapidly to the side and twists the leg. When the larger intruder was a female, the roles of attacker and the pursued reversed as the encounter proceeded. A male intruder, on the other hand, rarely initiated aggression with the resident female. Instead, he alternated between attempting to copulate with the resident and counterattacking. Although aggression by the female gradually declined, sporadic attacks and counterattacks continued even after the male was well established on the carcass. In all 3 cases the resident female attacked the intruder male in the last 30 min of observation. Whether the intruder was male or female, infanticide began shortly after the carcass was discovered (within 30 min in 4 of 6 cases; Table 2). Once infanticide began, larvae were not killed all at once but opportunistically as the intruder inspected the carcass. Intruders pierced the integument of larvae with their mandibles and handled larvae for 3–72 s. Those held the longest were almost entirely consumed while those held for only a few seconds were dropped, immobilized but alive, and later consumed by the intruder or the resident.

Table 2. Observations of larvae that were killed within 3 h of an intruder discovering the carcass

Sex of intruder	Number of larvae before intrusion	Number of larvae killed within 3 h	Number of larvae after 24 h
Male	9	2	0
Male	15	13	0
Male	11	5	0
Female	11	8	0
Female	12	1	0
Female	6	4	0

Table 3. Results of experiments employing a genetic marker to determine paternity or maternity of offspring. All residents were females that were smaller than the introduced intruder

	Male intruder	Female intruder	No intruder
<i>N</i>	14	14	14
Resident injured (dead)	8 (3)	11 (7)	0 (0)
Intruder injured (dead)	9 (4)	5 (1)	–
Initial brood survived	4	2	13
Mean (SD) number of young	4.5 (2.6)	4.0 (4.2)	10.3 (3.5)
Replacement brood produced	7	9	0
Replacement brood survived and dispersed	5	7	–
Mean (SD) number of young	5.2 (4.5)	4.0 (2.4)	–
Proportion of mixed replacement broods	0.40	0.14	–
Proportion of replacement young attributed to intruders	0.85	0.93	–

Genetic marker

In 22 of 28 trials in which an intruder was introduced into a container with a resident female and her brood, all the larvae in the initial brood died. In 16 trials a replacement brood was produced and 12 of these replacement broods produced third instar larvae which dispersed from the carcass (Table 3). Initial and replacement broods that were produced when an intruder was present contained significantly fewer larvae than initial broods when an intruder was not present (Mann-Whitney U -tests, $P<0.05$).

There was a greater likelihood that the smaller resident and not the larger intruder would die when the intruder was a female ($\chi^2=4.37$, $P<0.05$), but no difference in the likelihood of death when the intruder was a male ($\chi^2=0.00$, $P>0.20$).

Successful male intruders (at least 1 larva in a replacement brood) fathered 85% of offspring in replacement broods (range, 60%–100%). Two of the 28 offspring produced in replacement broods after the introduction of a female intruder were attributed to the smaller resident. This occurred despite the fact that in every case the intruder was the only female seen on the carcass during daily checks.

Discussion

In this study, 59 of 316 carcasses placed in the field with established *N. orbicollis* were discovered and taken

over by conspecific intruders. In a similar field study of *N. orbicollis*, Scott (1990) reported no takeovers under natural conditions, seven takeovers when density was increased by releasing beetles in the study area and numerous takeovers when intruder beetles were placed adjacent to the burial crypt and confined to the area. Intrusions by congeners are even more frequent when the smaller *N. defodiens* is established on carcasses (Wilson et al. 1984; Trumbo 1990). Intrusions and takeovers, therefore, appear to be a regular feature of the breeding system of *Nicrophorus* in the field.

The mating association appears to be quite flexible. Single females are fully competent to produce a brood without the assistance of a male (Trumbo 1987; Bartlett 1988; Scott 1989; Scott and Traniello 1990), and either mate can accept and pair with an intruder of the opposite sex. Intruders can pair with either a resident or another intruder. There are two findings which suggest that interactions between same-sex resident and intruders are different from interactions between opposite-sex residents and intruders. A resident female normally repels a smaller intruder female but is less successful against a smaller intruder male (Trumbo 1987; Scott 1990). In addition, a female intruder attacks and attempts to drive a female resident from the crypt. A male intruder, on the other hand, rarely initiates an attack against a female although he often becomes aggressive as the encounter proceeds.

Intruders of both sexes kill larvae they find on the carcass and attempt to use the resource for their own reproduction. One other observation of infanticide following a takeover in *Nicrophorus* has been reported (Scott and Traniello 1989) and there is indirect evidence that infanticide is common (Trumbo 1987; Scott 1990; Trumbo 1990). Takeovers by intruders are more common on large rather than small carcasses and are more likely to occur when a single female rather than a pair is resident on the carcass (Trumbo 1987; Scott 1990; Trumbo 1990). Infanticide might be an important determinant of the social system of *Nicrophorus*. The only benefit of paternal care that has been demonstrated is that it reduces the probability of takeovers by congeneric intruders (Trumbo 1987; Scott 1990; Trumbo 1990).

The use of a genetic marker demonstrates that direct reproductive benefits accrue to infanticidal individuals of both sexes. However, the offspring produced subsequent to infanticide were not all attributed to the infanticidal individual. In some trials, both male and female intruders cared for young that were not their own. In a different context, Müller et al. (1990) demonstrated that dominant females sometimes care for young of subordinate females ("brood parasites") that are displaced during the initial competition for the carcass.

Injury rates were quite high in the experiment involving the genetic marker. This might have occurred because subordinates were confined to the container and the number of interactions was thereby increased. In addition, the ability of male intruders to produce a brood following infanticide is likely to be underestimated in the laboratory because the resident female is sometimes killed, injured or attempts to disperse. In such

cases in the field, an unpaired male likely will advertise for a mate (Pukowski 1933; Müller and Eggert 1987).

The regular occurrence of infanticide following a takeover and the substantial reproductive benefits that are obtained suggest an adaptive explanation for infanticide in *Nicrophorus*. Hrdy (1979) proposed three hypotheses which might explain why adults kill unrelated conspecific young. Exploitation occurs when individuals kill young and directly benefit from the use of the victim, usually by cannibalism. Cannibalism may be especially important for species with low protein diets such as herbivorous and wood-feeding insects (Polis 1984; Linsenmair 1987). Exploitation does not appear to be the primary explanation for infanticide in *Nicrophorus* because well-fed beetles commit infanticide on a superabundant high-protein resource and do not always eat the young that are killed.

Sexually selected infanticide results when individuals improve their opportunity to breed by killing dependent young of a prospective mate. Although well documented in other taxa (Hrdy 1977; Stephens 1982; Brooks 1984; Hayssen 1984; Packer and Pusey 1984; Mock 1984; Freed 1986), no clear-cut examples exist among insects (Polis 1984). The scenario of an infanticidal takeover in *Nicrophorus* is consistent with the sexual selection hypothesis. A male or female intruder defeats the resident of the same sex (if present), kills any larvae, mates with the resident of the opposite sex, and produces its own brood while obtaining parental investment from the mate. Müller (1987) has shown that artificial brood reductions cause females to oviposit a replacement clutch if the carcass remains suitable. Presumably, infanticide by a male manipulates female reproduction in a similar way. A female intruder that kills young of a resident male not only obtains a carcass but also may obtain his cooperation in protecting the brood. There are three reasons however why infanticide following takeovers in *Nicrophorus* cannot be explained solely by sexual selection: (1) In over half of the trials in the field, an intruder did not pair with a resident but was found either alone at exhumation or with another intruder. (2) Female intruders kill young of resident females when no male is present, and (3) Both *N. orbicollis* and *N. sayi* regularly commit larvicide following interspecific takeovers in which there is not prospect of manipulating the reproductive or parental investment of a potential mate (Trumbo 1990).

Resource competition can select for infanticide if killing young increases access to a limiting resource for the infanticidal individual. Although widely reported, it is often difficult to demonstrate that reproductive benefits accrue to the infanticidal individual and not simply to all individuals in the population (Hrdy and Hausfater 1984b; Leyland et al. 1984). Females practice this form of infanticide more commonly than males (Pardi 1948; Wilson 1971; Mumme et al. 1983; Polis 1984; Mock 1984; Whitmore 1986). *Nicrophorus* competes inter- and intraspecifically for a discrete, defensible and valuable resource (Milne and Milne 1976; Wilson and Fudge 1984; Wilson et al. 1984). The nature of agonistic contests and the risks that are taken, both before (Pukowski

1933; Bartlett and Ashworth 1988) and after the carcass is buried, attest to the necessity of obtaining a carcass for breeding. Infanticide is a normal consequence of a takeover of a carcass by either sex. It appears to prevent time, energy and resources from being wasted on unrelated young and allows a replacement brood to be produced. I suggest that infanticide following a takeover is adaptive primarily because of resource competition, and secondarily as a result of exploitation and sexual selection.

The ability to employ genetic markers and to make direct observations of *Nicrophorus* suggests that subtle differences in interactions can be explored. Further studies can manipulate variables including the relative body size of residents and intruders, time of arrival on the carcass, whether residents are paired or unpaired, and resource size in order to determine how reproductive success and parentage vary in different contexts. It then will be possible to ascertain whether intruders and residents adjust their infanticidal and defensive behavior as the social and abiotic environment is altered.

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