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Joint breeding in female burying beetles

Anne-Katrin Eggert[1] **and Josef K. Müller**[2]

[1] Department of Biological Sciences, Illinois State University, Normal, IL61761, USA
[2] Institut für Zoologie, Albert-Ludwigs-Universität, Albertstrasse 21a, W-7800 Freiburg, Federal Republic of Germany

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Summary. Burying beetles (*Nicrophorus*) exhibit advanced parental care, by feeding and guarding their offspring on buried vertebrate carrion. Till now, interactions between two conspecific females on a carcass have been thought to be mostly competitive, and parental care was thought to be provided by single females or male-female pairs exclusively. Here we demonstrate that cooperative brood care occurs in this species, and that its incidence is contingent on carcass size. Small carcasses are usually monopolized by one female; typically the larger of two female combatants secures the carcass for her offspring (Figs. 1 and 2). On large carcasses fights still occur, but in most cases both females stay on the carcass long enough to provide care for the brood. The use of genetic markers revealed that the maternity of offspring is shared evenly among joint breeders (Figs. 3, 4). We hypothesize that cooperative breeding is an adaptive response to a situation that arises partly as a consequence of a physical constraint.

Introduction

Cooperative breeding, a "reproductive system in which one or more members of a social group provide care to young that are not their own offspring" (Stacey and Koenig 1990), occurs in several animal taxa, e.g. mammals, birds (Brown 1987; Stacey and Koenig 1990), and also in parasocial insects, where it is regarded as one of a number of plausible antecedants to the evolution of eusociality in insects (Michener 1969; Wilson 1971; Lin and Michener 1972; Eickwort 1979). Not surprisingly, most studies on cooperative breeding in insects have focussed on the Hymenoptera (e.g. Noonan 1981; Evans and Hook 1982; Rissing and Pollock 1987; van der Blom and Velthuis 1988); in this groups, parental care is widespread and eusociality has evolved in several independent lineages (Wilson 1971; Andersson 1984). Nonetheless, advanced parental care has also evolved in a number of other insect orders (von Lengerken 1954; Wilson 1971; Eickwort 1979; Andersson 1984; Tallamy and Wood 1986; Nalepa 1984; Hanski and Cambefort 1991). Such groups offer an important advantage in identifying the ecological factors that may have favored the evolution of cooperative breeding: they lack the haplodiploid genetic structure that characterizes the Hymenoptera and which appears to have predisposed this group to social evolution (Hamilton 1964, 1972; Trivers and Hare 1976).

Parental care in burying beetles (*Nicrophorus*[1]: Coleoptera, Silphidae) is manifest in a suite of highly specialized behaviors, and is considered the most advanced in the Coleoptera (von Lengerken 1954; Tallamy and Wood 1986; but see Rasa 1990). Adult beetles bury small vertebrates carcasses in the soil, feed their larvae from the carcass, and guard them from predators and intruding burying beetles (Pukowski 1933; Bartlett 1988; Fetherston et al. 1990; Trumbo 1990a, b). Eggs are deposited in the soil near a buried carcass; while a female buries a carcass, her ovarioles undergo rapid maturation and increase two- to three-fold in weight within 24–48 h (Wilson and Knollenberg 1984; Scott and Traniello 1987).

Carcasses are nutrient-rich but rare "bonanza" resources (Wilson 1971; Hanski and Cambefort 1991) for which competition is intense (Wilson and Fudge 1984; Wilson et al. 1984; Trumbo 1990a). On carcasses suitable for reproduction, adults engage in intense inter- and intraspecific fights (Pukowski 1933; Bartlett and Ashworth 1988; Otronen 1988; Müller et al. 1990a). Between conspecifics, these fights are exclusively intrasexual while the carcass remains unburied. Fights can even occur after burial when the buried carcass is detected by other burying beetles that attempts to usurp it for their own reproduction (Scott 1990; Trumbo 1990a, b).

Correspondence to: J.K. Müller

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[1] The genus that is referred to in this paper as *Nicrophorus* is equivalent to the genus referred to as *Necrophorus* in the authors' earlier papers

In burying beetles, reproductive success is dependent on carcass size, because the number of larvae that survive increases with resource size (Wilson and Fudge 1984; Bartlett 1987; Scott and Traniello 1990). Adult *N. vespilloides* Herbst exhibit behaviors that probably evolved as adaptive responses to this situation: they adjust the number of eggs laid (Müller et al. 1990b), as well as the number of larvae eventually accorded parental care (Bartlett 1987), to the size of the carcass. However, the clutch sizes produced on large carcasses do not allow an optimal utilization of these carcasses because the number of eggs females are able to produce in a single clutch is typically smaller than the number of larvae a large carcass can support (Bartlett 1988; Müller et al. 1990b). Such circumstances might reduce competition between two females on a large carcass or their offspring, as suggested by Trumbo (in press), and favor joint reproduction. We tested this hypothesis by placing pairs of inseminated females on mouse carcasses of different sizes, and using genetic markers (Müller and Eggert 1989; Müller et al. 1990a) to determine the maternity of offspring produced. The reproductive success of two females on a carcass was compared with that of females rearing a brood in the absence of other females.

Methods

Experiments were carried out in the laboratory using individuals of *N. vespilloides* from laboratory strains. These strains originated from beetles trapped no further than 15 km from the University of Bielefeld in northern Germany. The beetles were kept at 20° C under a 16L/8D light regime and, when used in an experiment, were between 20 and 50 days old. Adults were fed dead mealworms; for reproduction, they were supplied with frozen and rethawed laboratory mouse carcasses.

The experiment was designed to stimulate the situation in which two females have detected the same carcass. Two sexually mature females from two laboratory strains that differ in wing cover coloration were measured to the nearest 0.02 mm (pronotum width) and placed on a carcass in small transparent containers in the late afternoon (1600 hours, "lights off" at 1800 hours). The females used were large and the size differences between them relatively small (range 0–17.5%, mean 4.2% difference in pronotum width between the two females).

When both females had become active and were on the mouse, the carcass and the females were transferred into a larger plastic flower-pot (16 cm high, 16 cm diameter) filled almost to the rim with moist peat. The carcasses we used weighed 5.0–5.3 g, 15.0–15.3 g, 25.0–25.3 g, or 35.0–35.3 g. The pot was covered with a transparent plastic disk until the females had buried the carcass. In 86% of the replicates, the beetles had buried the carcass before the following morning. The disk was then removed and the pot covered with the reversed lower half of a second pot. From this time on, the beetles were given the opportunity to leave the container through a transparent plastic tube that was flush with the peat surface. Beetles leaving the carcass were trapped in a *Drosophila* tube with a moist plaster bottom; these tubes were checked and emptied every 12 h. Beetles were checked for injuries; those with minor injuries such as the loss of the pretarsi on one leg, or small indents in the elytra, were not recorded as injured.

In this experiment, the sample size for different variables presented is not always equivalent. For example, there were some replicates in which there was no measurable difference in body size (pronotum width) between the two females. Also, those cases in which injuries had not been determined carefully enough were not considered.

The same experimental design was used to obtain measures of the reproductive success of females that singly buried a large carcass; 5-g carcasses were not used in these replicates.

For direct observations on large carcasses, 13 pairs of females were each offered a 25-g or 35-g carcass in a transparent plastic container (20 × 20 × 10 cm) half-way filled with moist peat moss. After burial, the containers were stored in the dark and checked daily under dim red light.

Results

Aggressive interactions between females occurred on carcasses of all sizes and frequently resulted in injury to one of the combatants. The injury rate, measured as the proportion of all-female pairs in which at least one female was injured when she left the container, was highest (44% of 48 pairs) on 15-g carcasses (injury rates for 5-g, 25-g, and 35-g carcasses were 17% ($n=40$), 17% ($n=42$), and 25% ($n=40$), respectively). The effect of carcass size on injury rates was statistically significant (contingency table analysis, $\chi^2=11.36$, $P<0.05$).

Aggressive interactions in burying beetles typically are resolved in favour of the larger individual (Pukowski 1933; Otronen 1988; Bartlett and Ashworth 1988; Müller et al. 1990a), and we would thus expect the smaller individual to abandon the carcass first. However, our experiments revealed that this was true only for carcasses of small size (Fig. 1): on small (5- or 15-g) carcasses, the smaller female left first significantly more often than the larger one. Although females also fight on large (25- and 35-g) carcasses, the larger and the smaller female were equally likely to leave first from these carcasses. Even when the data from 25-g and 35-g carcasses are combined, smaller females were not significantly more likely to leave first (binomial test, $P>0.05$). A comparison of the pooled data from 5- and 15-g carcasses and the pooled data from 25- and 35-g carcasses showed that the two pooled groups differed significantly in the proportion of smaller females leaving first (Chi-square test, $\chi^2=9.126$, $P<0.01$). These results indicate that the females that left first from small carcasses were

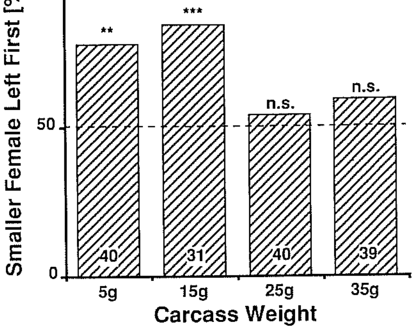

Fig. 1. Proportion of replicates in which the smaller female was the first to leave on carcasses of different size. Statistics: binomial test, *** $P<0.001$, ** $P<0.01$. The *numbers* inside the bars indicate the sample sizes

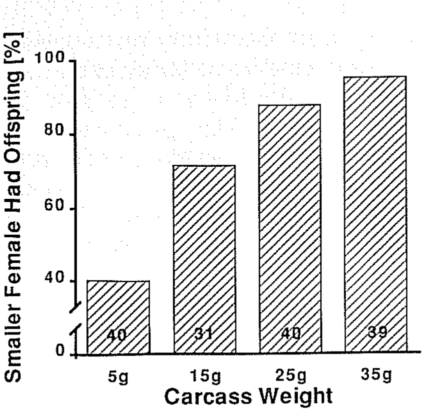

Fig. 2. Proportion of replicates in which the smaller female had one or more offspring surviving to adult emergence on carcasses of different size

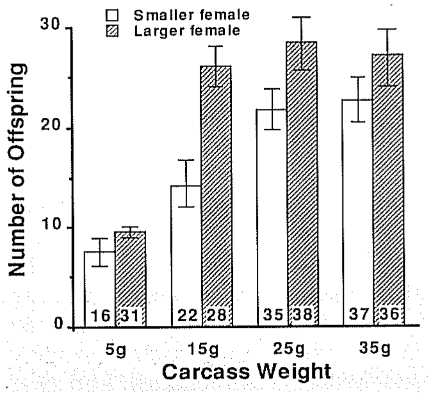

Fig. 3. Number of offspring surviving to adult emergence (mean ± SE) for both females on carcasses of different size. Only those females that produced at least one offspring were considered. *Numbers* in bars indicate sample sizes. *Open bars*, smaller female; *shaded bars*, larger female

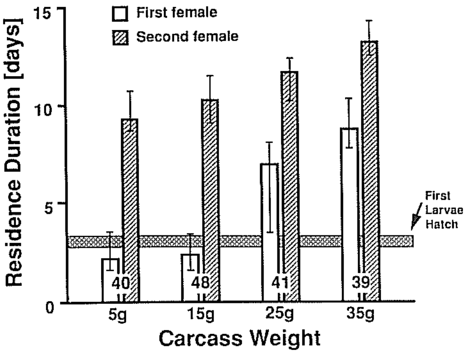

Fig. 4. Residence times in days (median and interquartile range) for females that were the first to leave the carcass (first female, *open bars*) and females that were the last to leave the carcass (second female, *shaded bars*) on carcasses of different size. Data on the time when the first larvae hatch were obtained in a separate experiment in which eggs were collected from the substrate and checked for the hatching of first instars every 2 h

Table 1. Number of offspring surviving to adult emergence for inseminated females reproducing alone or in the presence of a smaller female on 15, 25 and 35 g carcasses (means ± SE, sample size in parentheses). Statistics: *t*-test

Carcass size	Single ♀	The larger of two ♀♀	*P*
15 g	30.3 ± 3.9 (9)	26.0 ± 2.0 (28)	>0.05
25 g	37.7 ± 1.8 (19)	26.8 ± 2.4 (40)	<0.01
35 g	38.7 ± 2.8 (8)	25.0 ± 2.4 (39)	<0.05

evicted, whereas females leaving first from large carcasses were not evicted but rather left voluntarily to search for other reproductive opportunities.

The size of the carcass also affected the chances of the smaller female leaving at least some offspring. Our experiment showed that as the size of the carcass increased, smaller females experienced a higher probability of producing at least some offspring (contingency table analysis, $\chi^2=36.17$, $P<0.0001$; Fig. 2). Additionally, the females that were successful at producing some offspring also produced a greater number of offspring on larger carcasses (Fig. 3). Both of these effects resulted in the smaller female having fewer offspring than the larger female on 5- and 15-g carcasses (Wilcoxon MPSR test, 5 g: $z=2.57$, $P<0.05$; 15 g: $z=2.33$, $P<0.05$), wheras on 25- and 35-g carcasses, there was no significant difference in the offspring numbers of the smaller and the larger female (Wilcoxon MPSR test, 25 g: $z=1.86$, $P>0.05$; 35 g: $z=1.08$, $P>0.05$).

On small carcasses, one female usually abandoned the carcass before the larvae began to hatch; on large carcasses, both females usually remained long enough to provide care for the brood (Fig. 4). The second female to leave also stayed longer on larger carcasses; however, the effect of carcass size on the residence time of second females was less pronounced. Presumably second females stay longer on larger carcasses because they extend the period of feeding when more food per larva is available.

Direct observations revealed that females, at least on some occasions, jointly feed broods on large carcasses. In six pairs, both females were still present on the carcass on the 6th day after burial, and in four of these cases the two females were observed regurgitating to the larvae side by side. The two females' broods on these carcasses were not physically separated, as there was only one hole in the carcass that contained both females' larvae. On 15-g carcasses, joint parental care by two females may also occur in rare instances (Fig. 4, see also Müller et al. 1990a). This shows that although joint breeding can occur on carcasses of various sizes, it is far more likely to occur on large carcasses.

We found no positive effect of joint breeding on the superior female's reproductive success (Table 1). In our laboratory experiment, single females had more offspring than the larger of two competing/cooperating females on 25-g and 35-g carcasses, but on 15-g carcasses, the difference was not significant.

Discussion

Female *N. vespilloides* cohabiting on large carcasses jointly care for the brood, and each obtains a similar share of the carcass for their offspring. Following the current terminology used by researchers of vertebrate breeding systems, this situation could be classified as "cooperative breeding" (Stacey and Koenig 1990). Social-insect terminology would describe the organisms involved as facultatively "quasisocial" or "parasocial" (Michener 1969). However, these labels to not help us understand the evolution and maintenance of the phenomenon; only some of the effects of the joint breeding attempt on each female's reproductive success are known, and some of those seem deleterious rather than beneficial. Our laboratory study indicates that the larger female's reproductive success is negatively affected by the presence of a second female on the carcass, which clearly creates a conflict of interest between the two females. Each female would probably do better if the other female were not present. Even our initial assumption that the presence of a co-resident female on a large carcass would be less deleterious than on a small carcass was not supported. On 25- and 35-g carcasses, the reduction in offspring number for the larger female through another female's presence was greater than on 15-g carcasses. We do not know whether these results would hold true in the field. However, the injuries incurred by females on carcasses clearly show that the interactions of females on large carcasses are not entirely peaceful, which suggests a conflict of interest between the two females.

The females are also unlikely to experience an increase in inclusive fitness through the other female's presence because it is highly improbable that two females meeting on a carcass are related: emerging adults cover distances of several kilometers in search of carcasses (unpublished data).

Trumbo (in press) frequently observed more than one male and female of the same species (*N. orbicollis, N. defodiens*) on large carcasses in the field. He hypothesized that several same-sex *Nicrophorus* individuals cooperate in burying and maintaining large carcasses because this is their only opportunity to utilize these carcasses for reproduction in the face of intense interspecific competition from scavenging mammals and carrion flies.

Fights occurred on carcasses of all sizes. We can envision two general benefits that females might acquire by attacking consexuals arriving on the carcass simultaneously. Since ovarian development is completed only on carcasses (Wilson and Knollenberg 1984; Scott and Traniello 1987), keeping the oher female away from the carcass might delay or prevent the other female's ovarian development. This would benefit the attacker because a reduction in the number of unrelated larvae on the carcass reduces competition for food to her own larvae. Secondly, because females show infanticidal behavior for several hours after oviposition prior to parental care (Müller and Eggert 1990), attacks against the female that oviposited last might be required to prevent her from killing and eating larvae during this time.

Injuries were observed more frequently on carcasses of 15 g weight than on either smaller or larger carcasses. One possible explanation for the lower injury rate on 5-g carcasses is the lower value of these small carcasses to the beetles. In laboratory experiments, broods from a single female had an average of 8.8 offspring surviving to adulthood on 5-g mice (Müller et al. 1990b), but an average of 31.9 adult offspring on 15-g mice (Müller et al. 1990a). The smaller amount of larval food represented by a smaller carcass may make it a less valuable prize to the competing females.

Although joint parental care occurred on large carcasses, fights also occurred, which leads us to believe that the beetles do not simply tolerate each other. Instead, we suggest that joint breeding results from a simple constraint. Oviposition takes place in the soil off the carcass, so that the superior female cannot possibly monopolize the actual oviposition site, but has to attempt to prevent ovarian development in her competitor by excluding her from the carcass. This is undoubtedly more difficult to achieve on larger carcasses of greater surface area. We hypothesize that carcass size affects the defensibility of the carcass: larger females can effectively defend small carcasses through aggressive behaviors; on large carcasses, however, the smaller female can secure enough time on the carcass to fully develop her ovaries, whether the superior female shows aggressive behaviors or not. If this is true, further attacks on the inferior female are ineffective as a means of preventing her from laying a large number of eggs near the carcass.

There is only one other situation in which there may be a conflict of interest between the females, and that is with respect to the onset of parental care. If there is an interval of more than 4 h between the time each of the two females started oviposition, one of the females may still be in the infanticidal state (Müller and Eggert 1990) by the time the other female's larvae come to the carcass. In this situation, the female that oviposited first would benefit from keeping the other female away from her larvae for a limited period of time. A lack of synchronization and the infanticidal behavior of females last to oviposit may account for the reduced number of offspring of jointly reproducing females relative to singly reproducing females. However, this effect could also arise if both females perceive the joint brood as "too large" and kill some of the larvae that come to the carcass when parental care has already begun (Bartlett 1987).

Once females have started to care for larvae, they do not discriminate against unfamiliar or unrelated offspring if the entire brood is exchanged (Müller and Eggert 1990), or in mixed broods (unpublished data). Therefore, both females will feed and guard their own and the other female's larvae indiscriminately once they have started to feed larvae. At this point in time, there should no longer be a conflict of interest between the two females.

There are a number of positive effects that joint breeding might have on the costs and benefits of parental care to each female. These effects could have contributed to the more tolerant behavior of females on large carcasses. Shared parental care might reduce the energetic expenses of feeding the large brood for each parent and thus confer positive effects on the survival of the caregivers, as seems to be the case for some cooperatively breeding birds (Stacey and Koenig 1990). However, burying beetles differ from birds in the nature of the resource that is utilized to provision the young. The carcass does not require any effort on the part of the feeding parents except for the actual behavior of feeding and the production of enzymes for the predigestion of carrion before regurgitation, and thus energetic expenses may not be the most important costs of parental care.

Tolerating an inferior female on the carcass might also create an opportunity for the superior female to leave early and search for new reproductive opportunities. The fact that males in male-female pairs as well as one of the females in all-female pairs leave several days before the larvae disperse from the carcass suggests that from this point on, a single parent is sufficient to feed and defend the brood from predators. The remaining parent is likely to care for the brood until the larvae disperse.

Whether it is the lack of further costs through the other female's presence, or a reduction of the energetic expenses of feeding that had selected for tolerant behavior in the superior female, it does not explain the inferior female's participation in brood care. If one female can provision and protect the mixed brood as effectively as two, and larvae are cared for indiscriminately, one of the females might be expected to leave shortly after oviposition. This is exactly what happens on smaller carcasses (Müller et al. 1990a). However, on large carcasses, the number of larvae is much greater than on a small carcass and the joint brood may be too large to be effectively fed and defended by one female. If an additional female's contribution has a positive effect on the survival or growth of the larvae, both females should be selected to stay and tolerate each other, because both contribute a large number of larvae to the brood. A similar positive effect of feeding by additional adults on the number of young surviving to independence has been demonstrated in some cooperatively breeding birds (e.g., Reyer 1990).

Several authors have also suggested that in the field, two burying beetles (a male-female pair) may be more efficient than one (a single female) at handling the carcass, burying and maintaining it (Pukowski 1933; Wilson and Fudge 1984; Scott 1990; Trumbo 1990a, 1991, in press). However, a field study by Scott (1990) failed to demonstrate a significant difference between single females and male-female pairs in the time taken to bury a carcass. Additionally, our results show that in the laboratory single females effectively maintain 25- and 35-g carcasses and rear large broods on them. Carcass burial and maintenance could, however, have quite different effects in the field. Large carcasses may be more attractive to intruders and thus subject to more predation by congenerics, and even more so if the carcass is poorly maintained (Trumbo 1990a). At high population densities, male-female pairs are more effective than solitary females at defending the carcass, or concealing it from infanticidal congeners (Trumbo 1990a, 1991); at moderate to low densities, however, such intrusions appear to be rare (Scott 1990).

We think that the "cooperative" or "mutualistic" interactions between the two females (joint regurgitation, presumably joint defense of the brood) can probably be characterized as "maintained by ordinary selfish behavior incidentally benefitting neighbours" (West Eberhard 1975).

As an alternative to adaptive explanations for the behavior of helpers in cooperatively breeding birds, the "misdirected parental care" hypothesis or "unselected hypothesis" (Jamieson 1991) has been proposed. It suggests that strong selection for parental care behavior has led to a situation in which individuals that encounter nestlings other than their own accidentally care for these (Jamieson and Craig 1987; Craig and Jamieson 1990; Jamieson 1991). In burying beetles, it is not likely that parental care provided by inferior females is incidental or "unselected". Females exhibit parental care behavior indiscriminately within a certain time interval after oviposition (Müller and Eggert 1990). However, females that have oviposited near a carcass can, and on small carcasses often do, simply abandon the carcass before the larvae actually hatch (Müller et al. 1990a, and this paper). Therefore, it is more likely that the prolonged stay of the second female on a large carcass is selectively advantageous for this female.

There are two aspects in which burying beetles apparently differ from many other cooperatively breeding vertebrate and insect species. The collaborating females are not closely related, and cooperation occurs in a situation with apparent intense reproductive competition. It appears that female interactions on carcasses follow the rule "If you can't beat them, join them!"; once parental care has begun, jointly provisioning and defending the brood may benefit both of the breeding females.

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