Ecological Entomology (2000) **25**, 262–266

Benefits of communal breeding in burying beetles: a field experiment

ANNE-KATRIN EGGERT[1,2] and SCOTT K. SAKALUK[1] [1]Behavior, Ecology, Evolution and Systematics Section, Department of Biological Sciences, Illinois State University, U.S.A. and [2]Institut für Zoologie der Albert-Ludwigs-Universität, Freiburg, Germany

Abstract. 1. The ultimate causes of communal breeding and joint parental care in various species of *Nicrophorus* burying beetles have not been resolved satisfactorily. One hypothesis suggests that females remain on the carcass for extended periods of time because joint defence affords them improved probabilities of retaining the carcass successfully in the face of intense competition from intra-generic competitors.

2. In a field experiment designed to test this hypothesis in *N. defodiens* (Mannerheim), breeding associations of two females and a male were no more successful at retaining their carcass than were monogamous pairs, lending no support to the hypothesis.

3. Intra-generic intruders that usurped already-buried carcasses were typically much larger than the original residents.

4. The body size of original residents affected both the burial depth and the probability of a takeover. Larger beetles buried the carcass deeper and were more likely to retain possession of the carcass. Group composition also did not affect the depth at which carcasses were buried.

5. Severe and even fatal injuries incurred by some residents indicated the occurrence of violent and damaging fights between competitors over carcasses in the field.

Key words. Burying beetles, communal breeding, competition, co-operation, nest defence, *Nicrophorus defodiens*.

Introduction

Communal breeding occurs in a variety of vertebrate and insect species. In many such breeding associations, reproductive skew (Keller & Vargo, 1993; Reeve & Ratnieks, 1993) is high, involving reproductive suppression of some individuals or even acts of infanticide (e.g. see Hrdy & Hausfater, 1984). Benefits associated with communal breeding are frequently less obvious, at least for some of the individuals involved. Thus, relatedness to the dominant breeders or environmental constraints limiting singular breeding attempts of subordinate group members have been invoked as adaptive explanations for communal breeding (e.g. see Brown, 1987).

Burying beetles (Coleoptera: Silphidae: *Nicrophorus*) inter small vertebrate carcasses that serve as the sole food source for their developing young (Pukowski, 1933). Carcasses are frequently discovered by multiple individuals of both sexes but aggressive interactions typically lead to the monopolisation of the carcass by a single male–female pair. Communal breeding occurs, however, on carcasses that are large for the respective species. Communal breeding in these instances encompasses two distinct behavioural components: tolerant behaviour towards individuals of the same sex and species during carcass burial and preparation; and extended presence on the carcass by two or more females that may feed the brood jointly and even simultaneously (Eggert & Müller, 1997). When burying beetles reproduce in polygynous associations, reproductive output per female has been found to be consistently lower than in monogamous pairs in field and laboratory studies conducted by various researchers (*N. vespilloides* Herbst: Müller *et al.*, 1990; Eggert & Müller, 1992; *N. defodiens*: Trumbo & Fiore, 1994; *N. tomentosus* Weber: Scott, 1994a, 1997). This reduction in individual reproductive success even on large carcasses raises the obvious

Correspondence: A. Eggert, Behavior, Ecology, Evolution and Systematics Section, Department of Biological Sciences, Illinois State University, Normal, IL 61790-4120, U.S.A. E-mail: aegger@ilstu.edu

question of how selection has maintained communal breeding behaviour over evolutionary time. One possibility is that communal breeding reduces the probability of takeovers of the carcass by intra- and inter-specific competitors, a benefit that might ultimately render the expected reproductive output for co-breeders higher or equal to that of single or monogamous breeders (Eggert & Müller, 1992; Trumbo, 1992; Trumbo & Wilson, 1993; Scott, 1994a; Robertson *et al.*, 1998). This hypothesis was tested in a field experiment on *N. defodiens*, a species subject to intense competition for carrion by conspecifics and congeners.

Methods

The study was conducted in a tract of mixed forest (mostly deciduous with some conifers) on Wolfe Lake, a small lake in northern Ontario, Canada (46°02′N, 79°32′W). Beetles were collected in traps baited with 30–40 g carcasses of laboratory mice that had been obtained frozen from a commercial supplier and thawed as needed. Field-collected beetles were separated by sex and maintained on chicken liver for a minimum of 8 days before being used in experimental trials. Mouse carcasses used in the experiment weighed 30–35 g and were thawed in a refrigerator overnight before being placed in the field the following afternoon. A length of dental floss was tied to the hind leg of each carcass to facilitate its recovery once buried. Beetles were processed (measured, weighed, marked) between 09.00 and 11.00 hours on the day a trial was initiated and were assigned to either of two treatments: monogamous (a single female and a male) or polygynous (two females and a male) associations. Body size was measured as the width of the pronotum at its widest point at 12× magnification using a stereomicroscope (Wild, Heerbrugg, Switzerland) equipped with an ocular micrometer, and body mass was determined to the nearest milligram on an analytical balance. Individuals were assigned to treatments such that the body size of individuals in both treatments was similar. The body size of the largest female in polygynous groups (mean pronotum width ± SE $= 4.82 \pm 0.06$ mm, $n = 36$) was similar to that of monogamous females (4.82 ± 0.06 mm, $n = 34$; *t*-test, $t = 0.046$, $P > 0.5$), and the size of the males was also similar between treatments (monogamous: 4.61 ± 0.08 mm; polygynous: 4.57 ± 0.07 mm; $t = 0.418$, $P > 0.5$). The pronotum width of the largest beetle on a carcass varied between 4.19 and 5.71 mm. Beetles were marked individually by piercing the elytra with small insect pins (size 00) in specific number-encoding patterns. Holes in the orange-coloured areas of the elytra are readily visible under the stereomicroscope because their rims turn black, creating the appearance of distinct black spots.

Beetles were initially placed on the carcass in transparent 0.5-l plastic containers between 14.00 and 15.00 hours to acclimate them to the carcass; the beetles along with the carcass were placed in the field between 16.00 and 17.00 hours on the same day. Beetles were induced to bury carcasses inside open metal cylinders (coffee cans with the tops and bottoms removed: diameter 15.5 cm, height 17 cm) that had been hammered into the soil flush to the top of the surrounding forest litter. The carcass and the experimental beetles were placed gently on top of the soil and prevented from escaping by securing an inverted metal strainer (mesh size 2 mm) so that it fitted snugly around the upper rim of the metal cylinder. Carcasses were revisited the next morning between 09.00 and 10.00 hours to determine whether the carcass had been buried. The strainer covering a cylinder was removed 48 h after the carcass had been found buried, allowing experimental beetles to abandon the carcass and competitors to gain access to it. Possible earlier takeovers were of little interest because the objective of the experiment was to identify potential benefits of extended care by multiple females.

Cylinders were left open for 4 days before they were retrieved and transported to the field laboratory, where their contents were carefully unearthed and inspected. The retrieval time was selected on the basis of an earlier field study of takeovers in *N. orbicollis* Say, which had shown that >90% of takeovers occur during the first 6 days after carcass burial (Robertson, 1993). For each soil core recovered, the burial depth and condition of the carcass, the number and developmental stage of any larvae present, and the identity and species of beetles present on the carcass were recorded. When unmarked beetles of larger species were found near the carcass, it was scored as a successful takeover, unless some or all of the original residents and their brood were still present on the carcass. Unmarked conspecifics discovered on retrieval were considered successful intruders if the same-sex original resident had disappeared and the stage of the brood suggested that the original brood had been supplanted by a replacement brood.

Results

Seventy carcasses were placed in the field between 12 July and 20 August 1996. Of these, 11 were missing at the time of retrieval, probably due to the interference of larger mammalian scavengers, most likely racoons. Such failed broods occurred with similar frequencies in monogynous (6/34) and polygynous (5/36) trials, and were not included in subsequent analyses. One additional trial in which no burying beetles were found on the carcass at the time of retrieval was also excluded. Burying beetles were present on each of the remaining 58 carcasses. On 36 of these, at least one of the original *N. defodiens* residents was still present, while all the original residents on the other 22 carcasses were missing or found dead, and these carcasses were occupied by larger congeners. In 20 of these 22 takeovers, the carcass was well-maintained (rounded, solid) and would probably have supported another brood: *N. orbicollis* were present on 13 carcasses, *N. tomentosus* on another six, and both *N. orbicollis* and *N. tomentosus* were found on one carcass. In the remaining two takeovers, carcasses had many holes chewed into them, were stretched out, and did not appear fit for another reproductive attempt. All the beetles present on these carcasses were male (two *N. sayi* Laporte and one *N. defodiens* on one carcass, and one *N. tomentosus* and one *N. defodiens* on the other), and they were probably using the carrion as food for themselves rather than their broods.

In addition to these 22 unambiguous takeovers, there was one trial in which only one of the original residents disappeared and was replaced by a same-sex conspecific. When the carcass was retrieved, the original male was still present but the resident female (of a monogamous pair) had disappeared and another, significantly smaller female (18% smaller pronotum width, 38% smaller body mass) was present on the carcass. This may not have been a true takeover involving any agonistic encounters; the original female may not have been reproductively competent and left the carcass, and the new female may have been attracted by the resident male via pheromone emission. Even when this instance was counted as a successful takeover, there was no impact of group composition (monogamous vs. polygynous) on the probability of takeovers (monogamous: 16 carcasses retained, 13 lost; polygynous: 19 carcasses retained, 10 lost: log-likelihood ratio, $G=0.650$, $P>0.2$).

The body size of resident females appears to affect the risk that a carcass is lost to intruders. A logistic regression of takeover probabilities against the body size of residents (for polygynous groups, only the size of the largest female was included in the analysis) revealed that larger females were more likely to retain the carcass than were smaller females (log-likelihood ratio, $G=5.60$, $P=0.018$). Nearly all the newly arrived beetles (intruders) were larger and heavier than the original residents. The pronotum width of intruders was on average 34.4 ± 4.7% (± SE) greater than that of the residents (see Fig. 1a), and their body mass was on average 159.3 ± 22.4% greater (see Fig. 1b).

On five carcasses, original residents and their brood were present along with larger congeners. In one of these cases, the carcass had produced a large *N. defodiens* brood but was not suitable for another brood. The two individuals of larger species (*N. orbicollis*, *N. sayi*) that were present were probably feeding on the remaining carrion. In the remaining four cases, the intruders were *N. tomentosus* (three single individuals and a pair), all of which were similar in size to the largest original resident (between 8% smaller and 14% larger). These are best interpreted as unsuccessful takeover attempts in which residents defended their carcass successfully. Including these instances in the analysis as takeovers would not alter the conclusion because four of these five carcasses were originally controlled by polygynous groups.

Some of the original *N. defodiens* residents had attempted to defend the carcass to their death. Remains of one male and two female residents and another beetle's abdomen were found in the vicinity of three carcasses that had been taken over. On five carcasses that had been retained by their original owners, some or all beetles were found to be severely injured at the time of carcass retrieval. Most injuries involved the extremities, and each of these beetles had lost at least the tibia from one leg.

Body size also appeared to have an important effect on the depth at which the carcass was buried. Burial depth was measured as the distance of the bottom of the brood chamber or crypt to the soil surface. Any carcasses that had been taken over by intruders were excluded from the analysis because intruding beetles may relocate the carcass further into the soil to prevent another takeover. In contrast, when the carcass is removed by a scavenging mammal, the original location of the brood chamber is clearly visible, and such cases were included in the analysis. A multiple regression showed that burial depth depended on the size (pronotum width) of the largest resident beetle and on the time of season (days after the start of the study) at which the carcass was buried, but not on group composition ($F_{3,42}=4.32$, $P<0.01$, $R^2=0.24$). Larger residents buried carcasses deeper [partial r (± SE) = 1.43 ± 0.52, $t=2.75$, $P<0.01$], and the depth at which carcasses were buried decreased over the course of the season (partial $r=-0.036 \pm 0.016$, $t=2.25$, $P<0.05$), but the breeding association (the number of resident females) did not affect burial depth (partial $r=-0.08 \pm 0.41$, $t=0.20$, $P>0.5$).

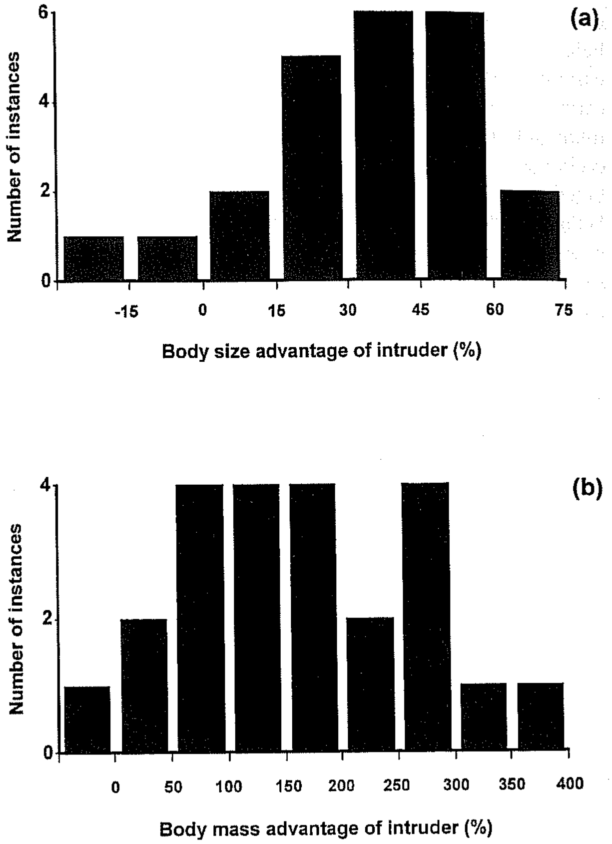

Fig. 1. Distribution of relative body size and body mass advantage for successful intruders ($n=23$ takeovers). (a) Pronotum width of largest intruder minus pronotum width of largest resident, as a percentage of the resident's pronotum width. (b) Body mass of heaviest intruder minus body mass of heaviest resident, as a percentage of the resident's body mass.

Discussion

The results of this study do not support the hypothesis that the presence of a second reproductive female *N. defodiens* on a large carcass reduces the risk that the carcass is lost to other burying beetles. Polygynous groups were as likely to lose their carcass to larger congeners as were monogamous pairs, and takeovers by conspecifics were extremely rare or absent. These results are consistent with those of a field study by Trumbo and Fiore (1994), who found that carcasses buried by polygynandrous groups of *N. defodiens* (two males, two females) attracted an equal number of competitors as those buried by monogamous pairs. Both results argue against improved carcass defence as a benefit to co-operative breeding in burying beetles. Scott (1994a) staged encounters with intruders by adding potential intraspecific or interspecific competitors to established broods of *N. tomentosus* that had either male–female pairs or foursomes (two males, two females) as original residents. She found no significant advantage for foursomes against any particular type of intruder, but a re-analysis of the overall takeover rates reported in her study suggests that such an advantage may still exist in *N. tomentosus* (pairs retained 33 carcasses, lost 14, foursomes retained 59 carcasses, lost 10; $G=3.92$, $P<0.05$).

Takeover rates appeared to be related to the body size of resident females, with larger residents experiencing a lower takeover risk than smaller residents. Two factors may contribute to this effect: larger residents may simply be superior competitors in actual aggressive interactions with other beetles, or they may be better able to conceal the carcass successfully from beetles searching actively for carrion, and thus to prevent aggressive encounters. The observation that burial depth was also related to the body size of resident beetles suggests that the latter effect may at least partially mediate the observed effect of body size on takeover rate, because burying the carcass deeper presumably affords better protection against discovery of the buried carcass by free-flying competitors. Interspecific differences may be due to a similar advantage conferred by larger body size: *N. orbicollis* buries carcasses deeper than does *N. defodiens* (Wilson & Fudge, 1984) and is less likely to lose them (Trumbo, 1995).

The effect of season on burial depth is probably mediated by soil properties that may have changed over the 2-month course of the study; later in the season, carcasses are buried less deeply, possibly because the soil is drier and harder for the beetles to manipulate. In addition, many of the individuals that are reproductively active late in the season are teneral adults whose exoskeleton may still be relatively soft, which could also hamper the efficient and deep burial of carcasses.

Takeovers by intraspecific competitors from established *N. defodiens* residents appear to be rare in general, especially on large carcasses. In the present study, this occurred at most in only one of 23 observed takeovers. Two other studies provide information on the frequency of intraspecific takeovers in *N. defodiens*; only five of 69 takeovers from male–female pairs and single females in Michigan (Trumbo, 1990a), and one of 14 takeovers from pairs in New Hampshire (Scott, 1994b), were by intraspecific competitors. It is possible but not likely that *N. defodiens* may not be as good at locating buried carcasses as its larger congeners. A better explanation is that large body size differences may be necessary for successful takeovers. The body size, and especially the body mass, of successful intruders was considerably larger than that of original residents in the study reported here, with few exceptions (Fig. 1). There is an important asymmetry between resident and intruder that probably contributes to the scarcity of intraspecific takeovers: the expected benefit of winning aggressive interactions, or the cost of surrendering, is not the same for both opponents. If the resident wins, its current brood can complete development on the carcass; the intruder, on the other hand, can only win the remaining amount of carrion, which is smaller and of lower quality than it was when the resident started her reproductive attempt. Some residents defended the carcass successfully against larger intruders, and some suffered severe or even fatal injuries in the process; such evidence of fatal fighting in the field previously existed for *N. orbicollis* (Trumbo, 1990b) but not for any other species.

The results of this study fail to resolve the adaptive significance of co-operative breeding in female burying beetles. The only progress they offer is that improved concealment or defence of the carcass is an unlikely explanation for the tolerant behaviour of females or their extended presence on large carcasses. One remaining possibility is that communal breeding reduces competition for carrion by fly maggots, as suggested by Scott (1994a) and Trumbo (1994). Large carrion flies cannot access carcasses once they are buried, however, which makes competition with flies an unlikely candidate for the explanation of the prolonged presence of multiple females on the carcass.

Trumbo (1995) suggested that for small species like *N. defodiens*, successful reproduction on large carcasses may be so rare that even in the absence of benefits to communal breeding, the cost of fighting is not offset by the benefits that accrue in the event of successful monopolisation of the carcass. In the present study, however, *N. defodiens* retained a much greater proportion of carcasses (50%) than reported by Trumbo (1995) in his summary of several earlier studies in the U.S.A. (on 16–35 g carcasses: 16% ± 8%). More northerly populations of this presumably cold-adapted species (Wilson *et al.*, 1984) may experience lower rates of nesting failure on larger carcasses, but females from these populations still exhibit tolerance towards conspecifics.

On small carcasses, where aggressive interactions are frequent and intense, the smaller of two competing females gets only limited access to the carcass, departs much sooner, and produces fewer offspring than does her larger rival (Müller *et al.*, 1990; Eggert & Müller, 1992; Scott & Williams, 1993). In communal associations on large carcasses, however, a female's genetic contribution to the joint brood need not be associated with her relative body size and the duration of her stay on the carcass (Eggert & Müller, 1992, in press; but see Scott & Williams, 1993). There are situations in which reproductive skew is largely shaped by acts of larval infanticide committed by co-breeding females; occasionally, entire broods are eradicated (Eggert & Müller, in press). Females will then produce replacement clutches if the carcass is still suitable for reproduction (Müller, 1987). The prolonged presence of two or more females on a large carcass may thus have less to do with benefits of joint care than with both females' selfish attempts to bias the composition of the brood in favour of their own offspring.

Acknowledgements

This study was supported by a research grant from the Deutsche Forschungsgemeinschaft to Dr Josef K. Müller (Mu 1175/2-1) and by grants from the National Science Foundation (IBN-9601042) and Illinois State University to S.K.S. We thank S. T. Trumbo and an anonymous reviewer for comments. Thanks also to the Toeppner family for allowing us to place dead rodents in their stretch of forest at our leisure, Donna Sr, Donna Jr, John and Marion Sakaluk for logistic support, and Wayne Riddle for an abundant supply of coffee cans.

References

Brown, J.L. (1987) *Helping and Communal Breeding in Birds: Ecology and Evolution.* Princeton University Press, Princeton, New Jersey.

Eggert, A.-K. & Müller, J.K. (1992) Joint breeding in female burying beetles. *Behavioral Ecology and Sociobiology*, **31**, 237–242.

Eggert, A.-K. & Müller, J.K. (1997) Biparental care and social evolution in burying beetles: lessons from the larder. *The Evolution of Social Behavior in Insects and Arachnids* (ed. by J. C. Choe and B. J. Crespi), pp. 216–236. Cambridge University Press, Cambridge.

Eggert, A.-K. & Müller, J.K. (in press) Timing of oviposition and reproductive skew in co-breeding female burying beetles (*Nicrophorus vespilloides*). *Behavioral Ecology.*

Hrdy, S.B. & Hausfater, G. (1984) *Infanticide: Comparative and Evolutionary Perspectives.* Aldine, New York.

Keller, L. & Vargo, E.L. (1993) Reproductive structure and reproductive roles in colonies of eusocial insects. *Queen Number and Sociality in Insects* (ed. by L. Keller), pp. 16–44. Oxford University Press, Oxford.

Müller, J.K. (1987) Replacement of a lost clutch: a strategy for optimal resource utilization in *Necrophorus vespilloides* (Coleoptera: Silphidae). *Ethology*, **76**, 74–80.

Müller, J.K., Eggert, A.-K. & Dressel, J. (1990) Intraspecific brood parasitism in the burying beetle, *Necrophorus vespilloides* (Coleoptera: Silphidae). *Animal Behaviour*, **40**, 491–499.

Pukowski, E. (1933) Ökologische Untersuchungen an *Necrophorus* F. *Zeitschrift für Morphologie und Ökologie der Tiere*, **27**, 518–586.

Reeve, H.K. & Ratnieks, F.L.W. (1993) Queen–queen conflicts in polygynous societies: mutual tolerance and reproductive skew. *Queen Number and Sociality in Insects* (ed. by L. Keller), pp. 45–85. Oxford University Press, Oxford.

Robertson, I.C. (1993) Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera: Silphidae). *Journal of Zoology (London)*, **231**, 583–593.

Robertson, I.C., Robertson, W.G. & Roitberg, B.D. (1998) A model of mutual tolerance and the origin of communal associations between unrelated females. *Journal of Insect Behavior*, **11**, 265–286.

Scott, M.P. (1994a) Competition with flies promotes communal breeding in the burying beetle, *Nicrophorus tomentosus. Behavioral Ecology and Sociobiology*, **34**, 367–373.

Scott, M.P. (1994b) The benefit of paternal assistance in intra- and interspecific competition for the burying beetle, *Nicrophorus defodiens. Ethology, Ecology and Evolution*, **6**, 537–543.

Scott, M.P. (1997) Reproductive dominance and differential ovicide in the communally breeding burying beetle *Nicrophorus tomentosus. Behavioral Ecology and Sociobiology*, **40**, 313–320.

Scott, M.P. & Williams, S.W. (1993) Comparative reproductive success of communally breeding burying beetles as assessed by PCR with randomly amplified polymorphic DNA. *Proceedings of the National Academy of Sciences of the United States of America*, **90**, 2242–2245.

Trumbo, S.T. (1990a) Interference competition among burying beetles (Silphidae, *Nicrophorus*). *Ecological Entomology*, **15**, 347–355.

Trumbo, S.T. (1990b) Reproductive benefits of infanticide in a biparental burying beetle *Nicrophorus orbicollis. Behavioral Ecology and Sociobiology*, **27**, 269–273.

Trumbo, S.T. (1992) Monogamy to communal breeding: exploitation of a broad resource base by burying beetles (*Nicrophorus*). *Ecological Entomology*, **17**, 289–298.

Trumbo, S.T. (1994) Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. *Oikos*, **69**, 241–249.

Trumbo, S.T. (1995) Nesting failure in burying beetles and the origin of communal associations. *Evolutionary Ecology*, **9**, 125–130.

Trumbo, S.T. & Fiore, A.T. (1994) Interspecific competition and the evolution of communal breeding in burying beetles. *American Midland Naturalist*, **131**, 169–174.

Trumbo, S.T. & Wilson, D.S. (1993) Brood discrimination, nest mate discrimination, and determinants of social behavior in facultatively quasisocial beetles (*Nicrophorus* spp.). *Behavioral Ecology*, **4**, 332–339.

Wilson, D.S. & Fudge, J. (1984) Burying beetles: intraspecific interactions and reproductive success in the field. *Ecological Entomology*, **9**, 195–203.

Wilson, D.S., Knollenberg, W.G. & Fudge, J. (1984) Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*). *Ecological Entomology*, **9**, 205–216.

Accepted 26 October 1999