The Costs of Confronting Infanticidal Intruders in a Burying Beetle

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Abstract

Infanticide by unrelated adults is a complex behavior in burying beetles (*Nicrophorus* spp.) serving multiple functions (resource competition, access to mates, cannibalism). The costs of confronting an infanticidal intruder are likely to vary with context. To assess these costs for a single female parent (*Nicrophorus pustulatus*), we systematically manipulated the sex of a conspecific intruder and the timing of the intrusion. Male intruders were a greater takeover threat than female intruders, and infanticidal takeovers were more common earlier in the breeding cycle. Even though a male intruder posed a greater threat to the brood, a female intruder was a greater threat to the reproductive success of the resident female. Female intruders that took over a carcass excluded the resident female from the resource. When a male intruder took over a carcass, the resident female was able to recover much of her loss by producing a replacement brood. Even when females successfully defended their broods, they suffered decreased reproductive output relative to control females that never had to confront an intruder (expt 1), but the mechanisms underlying this cost were unclear. To test the hypothesis that defeated female intruders attempt to parasitize late-stage broods, female intruders whose eggs could be identified by a fat-soluble dye were introduced to resident females caring for larvae (expt 2). Fifteen of 20 intruders oviposited eggs and the number of eggs were related to intrusion pressure. Because resident females rarely produced eggs while caring for larvae, it is uncertain whether the behavior of the defeated female should be characterized as brood parasitism, a failed takeover attempt, or an attempt to use the remains of the depleted resource. This study provides the most complete picture of the changing costs of confronting an infanticidal threat throughout the vulnerable period of offspring development.

Introduction

Infanticide by unrelated adults represents an extreme conflict of interest. A number of adaptive explanations have been proposed for infanticide including sexual selection, resource competition, cannibalism, and avoiding paternal care directed toward non-kin (Hrdy 1979; Ebensperger 1998). Models of infanticide related to sexual selection and resource competition are becoming increasingly quantitative (van Schaik & Janson 2000; Broom et al. 2004) and are being applied not only to primates and rodents, but also to ungulates (Pluhacek & Bartos 2005), reptiles (O'Connor & Shine 2004),

birds (Hansson et al. 1997; Veiga 2004), and insects (Hager & Johnstone 2004; Trumbo 2006). To successfully model decisions made in these complex systems, data are required on the comparative reproductive performance of females that do not encounter infanticidal intruders, females that fail to prevent infanticide, and females that successfully defend against infanticide but whose reproduction might be disrupted. It is possible that females who successfully defend at least some of their offspring will experience egg destruction by rivals, partial infanticide of the brood, or a decreased ability to provide care (Hansson et al. 1997; Scott 1997; Digby 2000; Eggert & Sakaluk 2000; van Schaik 2004; Veiga 2004). Data are also required on how the costs of potentially infanticidal intrusions change for females throughout the vulnerable period of offspring development.

Here, we present information on a complex but manipulable system in which both resource competition and sexual selection can be important and in which both males and females commit infanticide (Trumbo 1990b; Robertson 1993; Trumbo 2006). We quantify the costs for female *Nicrophorus pustulatus* Herschel confronting a potentially infanticidal male or female intruder throughout the vulnerable period of offspring development. We also test the hypothesis that females who successfully prevent infanticide experience diminished reproductive output compared with females that do not confront an intruder. In a second experiment we test the hypothesis that defeated female intruders attempt to parasitize late-stage broods of residents.

Burying beetles compete for a small vertebrate carcass on which to breed (*N. pustulatus* will breed readily on carcasses or snake eggs (Trumbo 1994; Blouin-Demers & Weatherhead 2000). A male–female pair or single female prepare the resource for their young (Pukowski 1933). Oviposition typically occurs within 12–24 h of discovery in *N. pustulatus*, and on a small resource, many more eggs are oviposited than will be reared (Trumbo 1992; Rauter & Moore 2002). Larvae hatch and crawl to the carcass on day 4 or 5, depending on temperature. The opening of the carcass and the arrival of first instar larvae lead to the rapid depletion of the resource (Eggert et al. 1998). Infanticidal takeovers in *Nicrophorus* spp. are a regular occurrence in the field and produce direct genetic benefits for the intruder (Trumbo 1990b). Infanticide can occur with both hetero- or conspecifics, and by both male and female intruders (Trumbo 1990a; Scott 1994; Koulianos & Schwarz 2000). Infanticidal takeovers are more common

earlier in the parental cycle and by male rather than female intruders (Trumbo 2006).

Methods

General Methods

A colony of *N. pustulatus* was established from wild-caught beetles trapped at Berea College, Kentucky. Experimental subjects were maintained in mixed-sex groups of 8–10 on a 15L:9D cycle at $21 \pm 1°C$ and fed chicken liver for 25–35 d before experimental trials. Subjects were measured (pronotal width) with digital calipers and isolated in a small container (9-cm diameter) with water the day before a trial. All subjects were uninjured at the start of the trial. Trials were conducted in covered plastic containers ($30 \times 18 \times 11$ height, cm), three-fifths filled with soil, and containing a mouse carcass partially covered by a paper towel. All carcasses were *Mus musculus* L., frozen shortly after death, and thawed 20 h prior to experimental trials. Mean carcass mass was equivalent (± 0.2 g) across treatments.

Experiment 1 – Intrusions on Days 2–7 of the Parental Cycle

To examine how the resident-intruder interaction changes throughout the parental cycle, single females were established on 22–25 g mouse carcasses and an intruder was introduced at different stages. Mean pronotal size of residents was equivalent (± 0.1 mm) across treatments. Pronotal size of an intruder was 5–10% greater than the resident for each trial. On day 2, breeding chambers were checked to determine whether eggs had been oviposited. Three of the 158 replicates did not yield any eggs and were excluded from further analysis. Three additional females were taken from the colony to restore the original sample size. There were 12 experimental treatments (n = 12 per treatment): a male or female intruder introduced on day 2, 3, 4, 5, 6, or 7. A control treatment consisted of single females breeding without an intruder (n = 14). Intruders were introduced on the carcass without handling, by direct transfer from an isolating container to the breeding container. Two days after the intruder introduction, the breeding chamber was checked to determine whether any larvae were present. The absence of larvae and the presence of the intruder on the carcass was scored as an infanticidal takeover. If a takeover was determined to have occurred, the resident female was removed in trials involving a female intruder but not in trials with a

male intruder. Trials continued until the replacement brood dispersed from the carcass.

If larvae from the resident female were still present 2 d after intruder introduction, the intruder was removed and the female was kept with her original brood until larvae dispersed from the carcass. The removal of a defeated intruder (or defeated resident above) occurred because under natural conditions defeated individuals will typically disperse from the nest within 48 h. In all trials, the larvae (whether from the original or a replacement brood) were counted and weighed within 24 h of dispersing from the carcass.

Experiment 2 – Brood Parasitism by Defeated Female Intruders

To examine possible brood parasitism by defeated female intruders late in the breeding cycle, 37 single females were established on 24–25 g mouse carcasses. On day 4, carcasses were checked for larvae (two trials did not have larvae and were excluded). Females were either allowed to breed without an intruder (n = 15) or bred in the presence of a larger female intruder (4–6% greater in pronotal width) introduced in the soil away from the carcass on day 4 (n = 20). The difference in pronotal width between the intruder and resident was less than in expt 1 to decrease the number of takeovers and increase the number of defeated intruders that could be examined for possible brood parasitism. After 2 d (day 6), the breeding chamber was checked to determine whether an infanticidal takeover had occurred, and the soil was sifted for eggs. Eggs could be assigned to individual females by color because all females (residents, intruders, and controls) had been fed a diet of ground beef suffused with either Solvent Blue 35 (400 mg per 20 g of meat) or Red Sudan Red 7B dye (200 mg per 20 g of meat) (Sigma, St. Louis, Missouri, USA) for 4-wk prior to experiments (Eggert & Müller 2000). After counting all eggs, the carcass, eggs, larvae, and the female in possession of the carcass were returned to the breeding chamber. Within 24 h of dispersing from the depleted carcass, the larvae were counted and weighed.

Statistical Analysis

Statistical analysis followed SAS (2000). Frequency data organized into 2 × 2 tables were analyzed using Fisher's exact tests (two-tailed) if the expected value of one or more cells was <5. Frequency data relating a takeover outcome to day of intrusion and sex of

intruder were analyzed using $2 \times 2 \times n$ log-linear analysis. Values for the interaction between experimental variables are reported for frequency tests whether or not the interaction was significant, following Cox & Snell (1989). The day of intrusion and the sex of intruder were also examined for their effect on reproductive output of females confronting an intruder (expt 1). The initial analysis (two-way ANOVA) included all trials, whether or not a takeover had occurred. A follow-up analysis (two-way ANOVA) examined output of only the replacement broods subsequent to a takeover. Because the two measures of brood production (number of larvae and mass of the brood) were highly correlated, only number of larvae in the brood is reported in tables and figures. The statistical analysis of brood mass is reported only if the level of significance differed from the results of the analysis of number of larvae.

Results

Experiment 1 – Intrusions on Days 2–7 of the Parental Cycle

Takeovers and complete infanticide of the brood were common. Broods were defended more successfully later in the parental cycle, and more often when the intruder was female rather than male (Fig. 1; $2 \times 2 \times 6$ log-linear analysis, $G_{day}^2 = 69.42$, 5
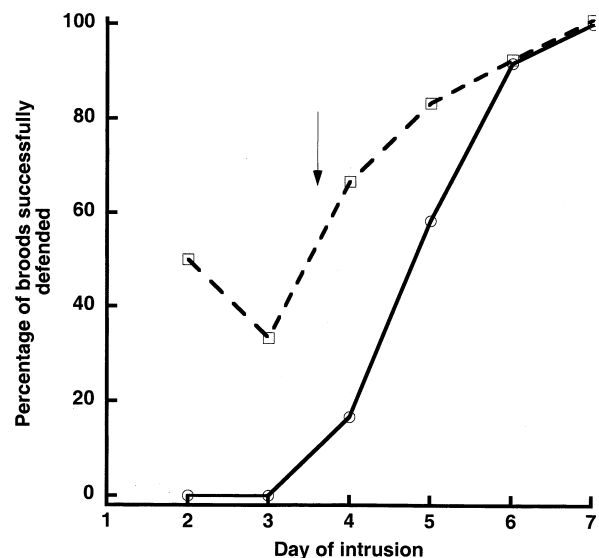

Fig. 1: Percentage of broods successfully defended when single females were confronted by male and female intruders on days 2–7 of the parental cycle. Trials with male intruders indicated by a solid line, trials with female intruders by a dashed line. The arrow indicates the approximate time at which larvae from the original brood typically appeared on the carcass

Table 1: Mean $\pm$ SE number of larvae produced by control females, by resident females who successfully defended their original brood, by females (resident or intruder) producing a replacement brood, and by resident females over all trials

Day – intrusion	Controls	Original broods		Replacement broods		Output of female resident	
		Female intruder defeated	Male intruder defeated	Takeover by female intruder	Takeover by male intruder	Confronting a female intruder	Confronting a male intruder
No intruder	28.7 $\pm$ 2.2 (14)	–	–	–	–	–	–
Day 2	–	15.7 $\pm$ 1.6 (6)	– (0)	13.2 $\pm$ 3.3 (6)	16.7 $\pm$ 2.8 (12)	7.8 $\pm$ 2.5 (12)	16.7 $\pm$ 2.8 (12)
Day 3	–	16.8 $\pm$ 1.3 (4)	– (0)	15.1 $\pm$ 3.5 (8)	16.6 $\pm$ 1.6 (12)	5.6 $\pm$ 2.4 (12)	16.6 $\pm$ 1.6 (12)
Day 4	–	20.5 $\pm$ 1.5 (8)	22.5 $\pm$ 1.5 (2)	7.3 $\pm$ 1.9 (4)	14.1 $\pm$ 2.1 (10)	13.7 $\pm$ 3.1 (12)	15.4 $\pm$ 2.0 (12)
Day 5	–	20.1 $\pm$ 2.3 (10)	28.3 $\pm$ 2.5 (7)	0.5 $\pm$ 0.5 (2)	6.4 $\pm$ 3.9 (5)	16.8 $\pm$ 2.9 (12)	19.2 $\pm$ 3.9 (12)
Day 6	–	20.7 $\pm$ 3.2 (11)	24.6 $\pm$ 2.5 (11)	0.0 $\pm$ 0.0 (1)	1.0 $\pm$ 0.0 (1)	18.8 $\pm$ 3.5 (12)	22.7 $\pm$ 3.0 (12)
Day 7	–	24.2 $\pm$ 1.7 (12)	22.6 $\pm$ 2.0 (12)	– (0)	– (0)	24.2 $\pm$ 1.7 (12)	22.6 $\pm$ 2.0 (12)
Grand mean	28.7 $\pm$ 2.2 (14)	20.5 $\pm$ 1.0 (51)	24.5 $\pm$ 1.2 (32)	11.0 $\pm$ 2.0 (21)	14.3 $\pm$ 1.3 (40)	14.4 $\pm$ 1.3 (72)	18.8 $\pm$ 1.1 (72)

Sample sizes in parentheses.

df, $p < 0.001$, $G^2_{\text{sex of intruder}} = 10.40$, 1 df, $p = 0.001$, $G^2_{\text{day} \times \text{sex of intruder}} = 14.68$, 10 df, $p = 0.09$).

The reproductive output of the resident female was estimated by combining her output in trials in which infanticide did not occur (original broods) with trials in which she produced a replacement brood with a male intruder (Table 1). Although male intruders were more likely to commit infanticide and take over the carcass, female intruders caused a greater overall decline in reproductive output of the resident female (Table 1; two-way ANOVA, $F_{5,132(\text{day})} = 6.55$, $p < 0.0001$, $F_{1,132(\text{sex of intruder})} = 7.94$, $p < 0.01$, $F_{5,132(\text{day} \times \text{sex of intruder})} = 1.53$, $p = 0.18$). This occurred primarily because resident females produced a replacement brood with an infanticidal male in every trial involving a takeover. Infanticidal females, on the other hand, excluded resident females from the nest. The mean mass of larvae produced by resident females in all trials was not affected by the day of intrusion or the sex of the intruder (two-way ANOVA, $F_{5,132(\text{day})} = 1.59$, $p = 0.17$, $F_{1,132(\text{sex of intruder})} = 1.02$, $p > 0.20$, $F_{5,132(\text{day} \times \text{sex of intruder})} = 0.93$, $p > 0.20$).

Even when the brood was successfully defended by the resident female there was disruption caused by the presence of the potentially infanticidal intruder in expt 1. Control females produced more larvae (Table 1; t-test, $t = 3.10$, $p = 0.002$) than resident females that successfully defended against intruders. A post hoc test of only trials involving a defeated female intruder suggests that the earlier in the breeding cycle the intrusion occurred, the greater the effect on depressing reproductive output of the resident female (Regression analysis; number in brood – $F_{1,49} = 7.39$, $p < 0.01$, $r = 0.35$).

The value of a carcass for producing a replacement brood clearly decreased for intrusions occurring later in the breeding cycle (Table 1). There also was evidence that replacement broods were more valuable when the intruder was male rather than female (Table 1, two-way ANOVA with data for days 5 and 6 combined because of small sample sizes; number in brood – $F_{3,53(\text{day})} = 6.08$, $p = 0.001$, $F_{1,53(\text{intruder sex})} = 3.72$, $p = 0.06$, $F_{1,53(\text{day} \times \text{sex of intruder})} = 0.32$, $p > 0.20$; brood mass – $F_{3,53(\text{day})} = 10.80$, $p < 0.001$, $F_{1,53(\text{intruder sex})} = 5.06$, $p = 0.03$, $F_{1,53(\text{day} \times \text{sex of intruder})} = 0.26$, $p > 0.20$).

Experiment 2 – Brood Parasitism by Defeated Female Intruders

In 20 trials with a female intruder, there were 18 trials in which the intruder did not take over the carcass. In 13 of these 18 trials there were eggs in the soil on day 6, significantly more often than in control trials (one of 15, Fisher's exact test $p < 0.001$). It was also more likely that a dead third instar would be found in trials with an intruder (seven of 18) than in trials without (one of 15, Fisher's exact test, $p = 0.046$). Of the 188 eggs produced in trials with a defeated female intruder, 187 were assigned to the intruder. The number of eggs assigned to the intruder was related to the level of intrusion. The greatest numbers of eggs produced by intruders were in the two trials in which a takeover occurred (Fig. 2). In trials with a defeated intruder, there were more intruder eggs when at least one-third instar had been killed than when no third instars had been killed (Fig. 2; t-test, $t = -2.87$, $p = 0.01$).

In contrast to expt 1, females confronting an intruder in expt 2 did not produce fewer young than females not confronting an intruder (Fig. 3, t-test, $t = 0.91$, $p > 0.20$).
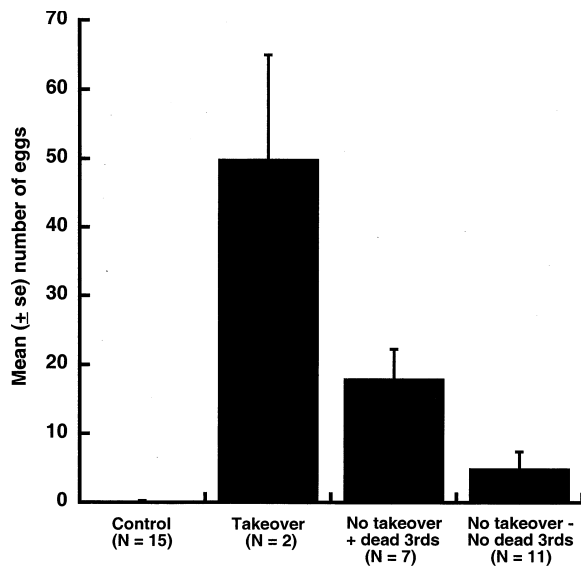
Fig. 2: The number of eggs discovered in the soil on day 6 for controls (no intruder), for intruders that took over a carcass, for intruders that failed to take over a carcass but one or more dead third instars were found, and for intruders that failed to take over a carcass and no dead third instars were found
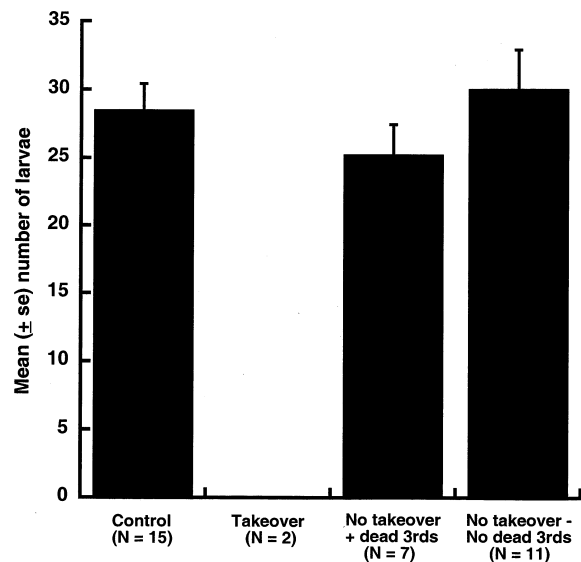

Fig. 3: The number of larvae produced by the resident female for controls (no intruder), for a resident that lost her brood to an infanticidal takeover, for residents that retained their carcass but in which one or more dead third instars were found, and for residents that retained their carcass and no dead third instars were found

Discussion

The success rate for single females defending against infanticide increased throughout the breeding cycle. This is related to the decreasing value of a replacement brood, decreasing intruder motivation. Very late in the breeding cycle when the carcass has no potential to support a replacement brood, even undefended offspring are often not attacked (Trumbo 2006). Male intruders were more likely to take over carcasses than female intruders. This was also found for *Nicrophorus orbicollis* Say and is related, in part, to the greater competitive ability of males. Relative competitive ability of male and female defenders is best judged in interspecific encounters where sexual selection does not play a role (Trumbo 2006).

The present study makes it clear that takeovers by male intruders early in the parental cycle may also be common because female motivation to prevent infanticide will be low. Male intruders were a lesser threat to the reproductive output of a resident female than female intruders. While female intruders that took over a carcass excluded resident females, male intruders produced a replacement brood with the resident in every trial involving a takeover. Early in the parental cycle, the cost of attempting to prevent infanticide by a male intruder may be too high given the robust replacement broods that were produced. Attempts to prevent a male from committing infanticide may result in a critical delay in producing a replacement brood on a resource that is rapidly deteriorating.

Even when an infanticidal takeover was prevented, there were costs for the defending female in expt 1. These costs are manifest both in the possibility of injury (Trumbo 1990b) and in decreased reproductive output compared with control females that did not experience an infanticidal threat. Brood production for female residents confronting a female intruder may have been slightly overestimated, and costs slightly underestimated, because of the possibility of late-stage brood parasitism. An excluded female may be responsible for up to 20% of a brood if she is present from day 0 in *Nicrophorus vespilloides* Herbst and *N. orbicollis* (Müller et al. 1990; Scott 1997). In the present study, however, intrusions did not begin until day 2. Even if an excluded intruder laid eggs within 12 h, the late arrival of her larvae would almost guarantee that there would be insufficient resource to complete development unless there was elevated mortality of the resident's offspring. Costs of avoiding infanticide, in addition to the possibility of injury (van Schaik & Janson 2000), have been suggested for a number of species but have not been tested by experimental manipulation. Potential costs include decisions about mate choice (Agrell et al. 1998), foraging patterns (Ben-David et al. 2004), active periods (Odden & Wegge 2005) and

group size (Steenbeek & van Schaik 2001) that might not otherwise be optimal except for the threat of infanticide. Such costs are difficult to quantify but need to be assessed and incorporated into models of parental and reproductive behavior.

In expt 2, resident females did not suffer a decrease in reproductive output when confronting a potentially infanticidal intruder. The failure to find a significant effect on reproductive output may have been caused by a smaller difference in body size between intruder and resident, and a smaller overall sample size compared with expt 1. If the intruder pressure is not great (few extended takeover attempts, few injuries), costs to the resident female may be minimal.

We can think of three non-exclusive hypotheses for the decreased reproductive output of females successfully repelling an intruder in expt 1: (1) cannibalism of a portion of the brood by the intruder, (2) the time required, or injuries incurred, when repelling an intruder might result in a decline in the quality of parental care, and (3) ovicide and larvicide related to a reproductive attempt by the intruder. Hypotheses 1 and 2 cannot explain the lower reproductive output when female intruders were repelled on days 2 and 3 because larvae were not yet present to be cannibalized by an intruder or to be cared for by a parent. Hypothesis 2 is also unlikely to explain the lower reproductive output for intrusions on day 4 or after: preliminary evidence indicates that injury to a single leg does not impact the ability of a female to feed young (Trumbo and Rothberger, own data), and the importance of care for offspring growth is minimal in *N. pustulatus* (Rauter & Moore 2002). Lower reproductive output for resident females when female intruders discover a carcass earlier in the parental cycle may be related to a greater opportunity for ovicide (hypothesis 3). Because eggs are oviposited away from the carcass and are difficult to defend, ovicide during days 2 and 3 may have been more common than larvicide on days 4–7 (expt 1), and may have caused a greater decrement to reproductive output of the resident female. Competing female *N. orbicollis* and *N. vespilloides* are known to eat each other's eggs and larvae (Scott 1997; Eggert & Müller 2000), and attempt brood parasitism, behaviors that are common when two females discover a resource on day 0 (Müller et al. 1990; Trumbo et al. 2001). In the present study, larvicide and oviposition by defeated intruders (expt 2) were occurring for intrusions beginning after the start of larval care.

The correlation between intruder oviposition and larvicide of resident young after day 4 suggests that larvicide is related to a reproductive attempt by the intruder. It is not clear whether this behavior is best characterized as brood parasitism (as hypothesized), as part of a failed takeover attempt, or an attempt to allow intruder young to use the remains of a partially depleted resource. For each of these scenarios, the ability of a female intruder to kill some resident young might increase her reproductive success. If brood parasitism were the primary explanation we would have expected to see greater numbers of late-stage eggs by resident females indicating that the resident would produce a replacement brood (see Müller 1987). Because the resource is deteriorating, it may be beneficial for an intruding female to start ovipositing as quickly as possible, before it is clear whether she will be able to kill all offspring of the resident and take over the resource. When the intruder fails to take over a resource, it may still be possible to gain a limited reproductive benefit from brood parasitism or her offspring's use of the remains of the resource.

Conflicts with male intruders were settled more quickly and more generally in the intruder's favor than conflicts with female intruders. This may explain, in part, the greater brood mass in replacement broods when the intruder was male rather than female. The larger brood mass by male–female pairs is unlikely to be due to male care because male care does not enhance reproduction in the absence of a takeover threat in *N. pustulatus* (Trumbo, own data) or for other species of *Nicrophorus* (Bartlett 1988; Scott 1989; Sakaluk et al. 1998; Jenkins et al. 2000; Smiseth & Moore 2004; Smiseth et al. 2005). Once infanticide by a male intruder is complete, there is little conflict of interest between the male and female. If a female intruder takes over a carcass following infanticide, however, there may be ongoing conflict with the defeated resident female.

The findings reported here suggest that to understand the reproductive decisions of parents that face a potentially infanticidal individual it is necessary to know the comparative reproductive success of parents that do not confront an infanticidal threat and of parents that prevent or fail to prevent infanticide. Although male intruders were by far the greater takeover threat for *N. pustulatus*, the overall costs were greater when confronting a potentially infanticidal female intruder. Substantial costs may be incurred even when an intruder is prevented from committing infanticide.

Acknowledgements

Literature Cited

Agrell, J., Wolff, J. O. & Ylonen, H. 1998: Counter-strategies to infanticide in mammals: costs and consequences. Oikos **83**, 507—517.

Bartlett, J. 1988: Male mating success and paternal care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). Behav. Ecol. Sociobiol. **23**, 297—303.

Ben-David, M., Titus, K. & Beier, L. R. 2004: Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? Oecologia **138**, 465—474.

Blouin-Demers, G. & Weatherhead, P. J. 2000: A novel association between a beetle and a snake: parasitism of *Elaphe obsoleta* by *Nicrophorus pustulatus*. Ecoscience **7**, 395—397.

Broom, M., Borries, C. & Koenig, A. 2004: Infanticide and infant defence by males – modeling the conditions in primate multi-male groups. J. Theor. Biol. **231**, 261—270.

Cox, D. R. & Snell, E. J. 1989: The Analysis of Binary Data. Chapman & Hall, New York.

Digby, L. 2000: Infanticide by female mammals: implications for the evolution of social systems. In: Infanticide by Males and its Implications (van Schaik, C. P. & Janson, C. H., eds). Cambridge Univ. Press, Cambridge, pp. 423—446.

Ebensperger, L. A. 1998: Strategies and counterstrategies to infanticide in mammals. Biol. Rev. **73**, 321—346.

Eggert, A.-K. & Müller, J. K. 2000: Timing of oviposition and reproductive skew in cobreeding female burying beetles (*Nicrophorus vespilloides*). Behav. Ecol. **11**, 357—366.

Eggert, A.-K. & Sakaluk, S. K. 2000: Benefits of communal breeding in burying beetles: a field experiment. Ecol. Entomol. **25**, 262—266.

Eggert, A.-K., Reinking, M. & Müller, J. K. 1998: Parental care improves offspring survival and growth in burying beetles. Anim. Behav. **55**, 97—107.

Hager, R. & Johnstone, R. A. 2004: Infanticide and control of reproduction in cooperative and communal breeders. Anim. Behav. **67**, 941—949.

Hansson, B., Bensch, S. & Hasselquist, D. 1997: Infanticide in great reed warblers: secondary females destroy eggs of primary females. Anim. Behav. **54**, 297—304.

Hrdy, S. B. 1979: Infanticide among animals: a review, classification and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology **1**, 13—40.

Jenkins, E. V., Morris, C. & Blackman, S. 2000: Delayed benefits of paternal care in the burying beetle *Nicrophorus vespilloides*. Anim. Behav. **60**, 443—451.

Koulianos, S. & Schwarz, H. H. 2000: Probability of intra- and interspecific encounters, and the duration of parental care in *Nicrophorus investigator* (Coleoptera: Silphidae). Ann. Entomol. Soc. Amer. **93**, 836—840.

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). Anim. Behav. **40**, 491—499.

O'Connor, D. E. & Shine, R. 2004: Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). Anim. Behav. **68**, 1361—1369.

Odden, M. & Wegge, P. 2005: Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. Wildlife Biology **11**, 145—152.

Pluhacek, J. & Bartos, L. 2005: Further evidence for male infanticide and feticide in captive plains zebra, *Equus burchelli*. Folia Zoologia **54**, 258—262.

Pukowski, E. 1933: Ökologische untersuchungen an *Necrophorus* F. Zeitschr. Morph. Ökol. Tiere **27**, 518—586.

Rauter, C. M. & Moore, A. J. 2002: Quantitative genetics of growth and development time in the burying beetle *Nicrophorus pustulatus* in the presence and absence of post-hatching parental care. Evolution **56**, 96—110.

Robertson, I. C. 1993: Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera: Silphidae). J. Zool. (Lond.) **231**, 583—593.

Sakaluk, S. K., Eggert, A.-K. & Müller, J. K. 1998: The 'widow effect' and its consequences for reproduction in burying beetles. Ethology **104**, 553—564.

SAS. 2000: JMP Statistics and Graphics Guide v. 4. SAS Institute, Inc., Cary, North Carolina.

van Schaik, C. P. 2004: Sexual Selection in Primates. Cambridge Univ. Press, Cambridge.

van Schaik, C. P. & Janson, C. H. 2000: Infanticide by Males and Its Implications. Cambridge Univ. Press, Cambridge.

Scott, M. P. 1989: Male parental care and reproductive success in the burying beetle, *Nicrophorus orbicollis*. J. Ins. Behav. **2**, 133—137.

Scott, M. P. 1994: The benefit of paternal assistance in intra- and interspecific competition for the burying

beetle, *Nicrophorus defodiens*. Ethol. Ecol. Evol. **6**, 537—543.

Scott, M. P. 1997: Reproductive dominance and differential ovicide in the communally breeding burying beetle *Nicrophorus tomentosus*. Behav. Ecol. Sociobiol. **40**, 313—320.

Smiseth, P. T. & Moore, A. J. 2004: Behavioral dynamics between caring males and females in a beetle with facultative biparental care. Behav. Ecol. **15**, 621—628.

Smiseth, P. T., Dawson, C., Varley, E. & Moore, A. J. 2005: How do caring parents respond to mate loss? Differential response by males and females. Anim. Behav. **69**, 551—559.

Steenbeek, R. & van Schaik, C. P. 2001: Competition and group size in Thomas's langurs (*Presbytis thomasi*): the foliovore paradox revisited. Behav. Ecol. Sociobiol. **49**, 100—110.

Trumbo, S. T. 1990a: Interference competition among burying beetles (Silphidae, *Nicrophorus*). Ecol. Entomol. **15**, 347—355.

Trumbo, S. T. 1990b: Reproductive benefits of infanticide in a biparental burying beetle *Nicrophorus orbicollis*. Behav. Ecol. Sociobiol. **27**, 269—273.

Trumbo, S. T. 1992: Monogamy to communal breeding: exploitation of a broad resource base by burying beetles (*Nicrophorus*). Ecol. Entomol. **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. 2006: Infanticide, sexual selection and task specialization in biparental burying beetles. Anim. Behav. **72**, 1159—1167.

Trumbo, S. T., Kon, M. & Sikes, D. S. 2001: The reproductive biology of *Ptomascopus morio*, a brood parasite of *Nicrophorus*. J. Zool. (Lond.) **255**, 543—560.

Veiga, J. P. 2004: Replacement female house sparrows regularly commit infanticide: gaining time or signaling status? Behav. Ecol. **15**, 219—222.