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Infanticide, sexual selection and task specialization in a biparental burying beetle

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Burying beetles (*Nicrophorus* spp.) compete for access to small vertebrate carrion, a highly valued resource. Intruders that take over a carcass will kill young of residents and use the carcass for a replacement brood. To examine whether sexual selection alters interactions with intruders, I staged encounters in which resource competition was the only important motivator for infanticide and then compared outcomes to those in which both sexual selection and resource competition might operate. On carcasses with first-instar larvae, a single resident male or female *N. orbicollis* was confronted with either a heterospecific or conspecific intruder of either sex (at this stage, a carcass retains 44−75% of its original value if used for a replacement brood). Single males defended their brood significantly better than did single females. Males appear to be efficient task specialists, having both a greater tendency and greater ability to guard the brood. When intruders were heterospecifics, there was no interaction between the two independent experimental variables of sex of defender and sex of intruder. When intruders were conspecifics, however, there was a significant interaction such that infanticide was more common when a defender confronted an intruder of the opposite sex. That is, when a defender had the opportunity to recoup some of its losses from infanticide by participating in a replacement brood with the intruder (opportunity for sexual selection), the probability of infanticide increased. A follow-up experiment staged at the second and early third instar indicated that infanticidal take-overs are quite common when single females defend second instars, but are infrequent when single females defend third instars, or when pairs defend second or third instars. Other measures of reproductive success (number and mass of broods in trials not including take-overs) were similar for single females and pairs. I hypothesize that the threat of infanticide and the inability of a parent to fully compensate for the absence of a partner that is a task specialist promote extended biparental care in burying beetles.

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There are few behaviours for which our perspective has changed so much as for infanticide. Once considered rare and pathologically maladaptive, most biologists today view infanticide as a product of natural selection. Although accepted as adaptive, there is disagreement in many systems over what particular factors select for infanticide. Hrdy (1979) proposed a number of hypotheses to explain infanticide by unrelated adults, including resource competition, cannibalism and sexual selection. These hypotheses are nonexclusive. Infanticide by males, for example, may increase access to both breeding females and to food resources for young (Hrdy 1979; Agoramoorthy & Rudran 1995). Sexually selected infanticide has been found in many vertebrate taxa and is usually committed by conspecific males that gain earlier access to breeding females (reviews in van Schaik & Janson 2000). The threat of infanticide is thought to select for female affiliation with friendly males (Palombit 1999; Prenschoft & van Schaik 2000), or monogamy (Freed 1986; van Schaik & Dunbar 1990). Experimental manipulation will help to separate the effects of multiple causes of infanticide but this is difficult with most of our model systems. Identification of the factors that promote infanticide will help to answer long-standing questions of how the threat of infanticide shapes social systems (Wrangham 1979; Packer 1986; van Schaik 2004).

Task efficiency (a subset of group or colony efficiency) is defined here as the linkage of a greater tendency to perform a task with a greater ability to perform the same task by an individual. All individuals are unique because

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of genetic and developmental differences, and would be expected to differ in both tendency and ability to perform tasks (idiosyncrasy). Unless a tendency to perform a task is linked to ability to perform the same task, however, no task efficiency will be achieved. Marked task specialization alone (without a test of ability) is often assumed to be associated with task efficiency. Three recent lines of evidence suggest that this assumption must be tested. First, when normally solitary ant foundresses are forced to nest together, task specialization is often pronounced even though there has been no selection for cooperation, complete flexibility is retained, and there is little to suggest that individuals differ in their ability to perform tasks (Wrangham 1979; Fewell & Page 1999; Cahan & Fewell 2004). Second, even in well-developed social groups, task specialists (especially nonforagers) do not necessarily perform with greater ability than nonspecialists (Biesmeijer & Toth 1998; Costa & Ross 2003; Julian & Fewell 2004). Third, manipulations of genetic diversity in social insect colonies have revealed that increased genetic diversity for tendency to perform tasks is not always associated with enhanced task or colony efficiency (Rosset et al. 2005). It is clear that even if two task specialists were to divide two tasks without overlap, no task efficiency is achieved unless individuals are superior in performing their particular task. Burying beetles (Nicrophorus spp.) have noted sex differences in the tendency to perform parental tasks; females spend more time feeding young and maintaining the nest and males spend more time guarding the nest and brood (Fetherston et al. 1994; Smiseth & Moore 2004). The relative ability of males and females to defend the brood is examined here. If care involves sex-related task efficiencies, then parental sex roles are hypothesized to promote stability of biparental care.

Biparental care is potentially unstable. Because parental investment reduces future reproduction (Trivers 1972; Zink 2003), there is the temptation to be the first to desert, saving the costs of parental effort. Partial compensation, when one parent responds to desertion by increasing its own effort at a fraction of the reduced effort of its partner, has been shown both theoretically (Chase 1980; Houston & Davies 1985; Houston et al. 2005) and empirically (Wright & Cuthill 1989; Hunt & Simmons 2002) to promote stability of biparental care. While additional behavioural mechanisms, including full compensation, may be associated with biparental care under particular ecological conditions (Jones et al. 2002), partial compensation appears to promote stability of biparental care in a wide variety of ecological circumstances. Partial compensation provides a disincentive for the first parent to desert if the resulting decreased success of the current brood outweighs the benefits obtained from enhanced future reproduction. By definition, when sex-related task efficiency operates, it will be difficult if not impossible for one parent to fully compensate for its partner. This should select for parents to stay until the need for their specialized parental task diminishes below the costs associated with additional care.

Specialization in parental tasks between males and females is known from many biparental invertebrates and may be the norm (reviews in Wilson 1971; Zeh & Smith 1985; Tallamy & Wood 1986; Trumbo 1996). In the most well-developed biparental systems in invertebrates, specialization and flexibility are compatible (e.g. Linsenmair 1987; Nalepa & Jones 1991; Valenzuela-González 1991; Fetherston et al. 1994). The ways in which task specialization increase efficiency when care is multidimensional, and alter decisions about whether to stay or desert have not been integrated into current models of biparental care (Houston et al. 2005).

Natural History of Burying Beetles

Burying beetles search for a small vertebrate carcass on which to breed. Competition for these protein-rich resources is intense, and beetles bury and prepare the resource quickly (Pukowski 1933). After oviposition, larvae hatch and crawl to the carcass on day 4 or 5 depending on temperature and species. The opening of the carcass and the arrival of first-instar larvae that feed from the carcass, begin the rapid deterioration of the resource (Eggert et al. 1998).

Burying beetles often breed as a male–female pair, the female doing more feeding and nest maintenance, and the male more guarding (Fetherston et al. 1990, 1994; Smiseth & Moore 2004). It is also common for a single female to go through the entire reproductive cycle on her own (using stored sperm), if a male does not discover the carcass. In laboratory studies, the removal of the male parent has little effect on female parenting behaviour (Fetherston et al. 1994; Jenkins et al. 2000; Rauter & Moore 2004; Smiseth et al. 2005) or on reproductive success (Scott 1989; Trumbo & Fernandez 1995; Sakaluk et al. 1998; Smiseth et al. 2005). In the field, the presence of a male reduces the probability of a take-over, in part, by reducing discovery of the buried carcass (Trumbo & Fiore 1994). The percentage of take-overs under natural conditions ranges from 0 to 55% and varies with species, study site, time of year and size of carcass (Scott 1990; Trumbo 1990a, 1991; Robertson 1993; Suzuki 2000). In field trials in which a take-over has not occurred, the presence of a male does not increase reproductive success significantly (Wilson & Fudge 1984; Robertson 1993; Trumbo & Fiore 1994; Müller et al. 1998).

The removal of the female parent, on the other hand, radically changes male parental behaviour. A lone male will increase his feeding rate substantially (Fetherston et al. 1994; Rauter & Moore 2004), and will stay several days longer until the brood disperses from the carcass (Trumbo 1991).

Infanticide in burying beetles is a regular occurrence in the field (Scott 1990; Koulianos & Schwarz 2000; Suzuki 2000) and produces direct genetic benefits (Trumbo 1990b). Both heterospecifics and conspecifics and both males and females show infanticide (Wilson et al. 1984; Trumbo 1990a; Koulianos & Schwarz 2000; Suzuki 2000). Robertson (1993), using N. orbicollis, suggested that a take-over will rarely occur after larvae reach the first-instar stage (also see Jenkins et al. 2000). In the present study, I exploit the high degree of experimental control made possible by varying the sex and species of the intruder. In encounters with heterospecifics and

same-sex conspecifics, resource competition is the only factor affecting infanticide. In encounters with conspecifics of the opposite sex, the intruder often pairs with the resident (Trumbo 1991; Robertson 1993), indicating that sexual selection might operate as well. In addition, varying the sex of the defending caregiver permitted an examination of parental task specialization.

METHODS

General Methods

Experimental subjects were laboratory-reared beetles maintained on a 15:9 h light:dark cycle at $21 \pm 1°C$ and fed scraps of chicken liver for 22−35 days before experimental trials. Beetles were measured (pronotal width), then isolated and provided with water the day before initiation of a trial. All trials were run in covered plastic containers ($30 \times 18 \times 11$ cm), two-thirds filled with soil, with a mouse carcass covered by a paper towel. Pronotal size of beetles was matched across treatments. The colony of *Nicrophorus pustulatus* Herschel was derived from beetles trapped in the research forest of Berea College, Kentucky, U.S.A. The *N. orbicollis* Say colony was started from beetles trapped on the property of the South Central Connecticut Regional Water Authority in Bethany, Connecticut, U.S.A. To minimize disturbance, subjects were not handled during experimental manipulations but were transferred directly from holding containers to experimental containers, covered with soil, and allowed to emerge naturally at the beginning of their active period. In experiments in which a manipulation was designed to occur after larvae arrived on the carcass, a replicate was excluded if the resident female failed to produce a brood.

Experiment 1: Value of Replacement Broods for *N. pustulatus* and *N. orbicollis*

Experiment 1 was structured to provide the necessary background to design experiment 2. To estimate the value of a deteriorating resource for producing a replacement brood following infanticide, residents were removed from carcasses and the undefended carcasses were presented to reproductively naïve females. *Nicrophorus pustulatus* females ('original' females, 10 per treatment) were placed on 27−30-g mouse carcasses and then removed after: 1 h, 30 h, 60 h, day 4 (first instars), day 5 (second instars), day 6 (small third instars), or day 7 (medium third instars). Each undefended carcass was then presented to an 'intruder' female that had no experience with a carcass. The 1-h treatment served as a control (the original female did not have time to produce eggs), giving an estimate of the value of a fresh carcass. Carcasses with the intruder were checked daily beginning on day 3 to determine whether the brood of the original female was killed before eclosion (30 h, 60 h), or after eclosion (days 4, 5, 6 and 7). If the intruder female killed the brood of the original female and produced her own brood, she was left with the carcass until her own brood matured and dispersed from the carcass. Number of dispersing larvae and mass of brood were determined.

The original female that was removed from the carcass was isolated for 3 days, fed one meal of 0.1 g of chicken liver, and presented a second 27−30-g carcass for reproduction to examine her ability to reproduce following termination of her initial reproductive attempt.

A similar design was used to examine the ability of *N. orbicollis* females (11 per treatment) to reuse a carcass (29−32 g) except that only three treatments were used. The original female was kept on a carcass for 1 h, until day 4 (first instars) or day 7 (third instars), and then removed. Subsequent procedures were as described above.

Experiment 2: Intrusions and Infanticide

Based on results from the previous experiment, I chose day 4 (first instar) as the stage to test single parents of *N. orbicollis* against heterospecific and conspecific intruders. This choice was made for three reasons. (1) By day 4, the value of the carcass for a replacement brood drops significantly so that the resident should be motivated to defend against an intruder. (2) On day 4, the value of a carcass for a replacement brood is still sufficient to attract the interest of an intruder. (3) If one *N. orbicollis* parent is removed from a carcass with first-instar larvae, the second parent will stay and provide care (Trumbo 1991; Fetherston et al. 1994). The relative size of the resident and intruder beetles for both heterospecific and conspecific intrusions was chosen to offset the asymmetry of resident advantage (in otherwise symmetric contests, *N. pustulatus* typically defeats a *N. orbicollis* of the same sex and pronotal width; Trumbo & Fiore 1994).

Experiment 2a: Heterospecific intrusions

Male−female pairs of *N. orbicollis* were established on 24−27-g carcasses as described above ($N = 30$ per treatment). On day 4, the set-up was checked to ensure that first-instar larvae were present on the carcass. If not, the set-up was checked again on day 5. Once larvae were on the carcass, either the male or female resident was removed from the carcass, and a male or female heterospecific intruder (*N. pustulatus*) with a pronotal width that was 0−5% smaller than the defending resident was introduced. Two days after the introduction of the intruder, a check was made to determine whether any brood of the resident had survived. Success for the resident was defined as producing one or more larvae.

Experiment 2b: Conspecific intrusions

Conspecific intrusions against a defending male or female *N. orbicollis* resident were performed similarly to heterospecific intrusions ($N = 30$ per treatment except female defender−male intruder, $N = 32$). For conspecific intrusions, the intruder was 5−10% larger in pronotal width than the defending resident.

Experiment 3: Intrusions against Single Females versus Male−Female Pairs

Experiment 3 was designed to determine at what point *N. orbicollis* is no longer susceptible to take-overs by

conspecific males. To compare the reproductive success of single females and male–female pairs when confronting a larger male intruder, beetles were established on 30–33-g mouse carcasses. On day 4, carcasses were checked to determine whether first-instar larvae were present. If first instars were present, the set-up was replaced and manipulated either the next day (day 5, second instars) or 2 days later (day 6, small third instars). The manipulation consisted of removing the male resident (for single female trials) and introducing a larger (+5–10% pronotal width) male conspecific intruder. If first instars were not present on day 4, containers were checked again for larvae on day 5, and the manipulation proceeded as above, one day behind schedule. Two days after the introduction of the intruder, the set-ups were again checked to determine whether a take-over and subsequent infanticide of the entire brood had occurred. If not, the resident male (in trials with pairs) and the intruder male were removed, and the number and mass of the brood were measured at the time larvae dispersed from the carcass.

Statistics

Statistical analysis followed SAS Institute (2000). Parametric measures (ANOVA, regression) were used to compare treatment means unless tests for homogeneity of variance indicated that a nonparametric test (Wilcoxon's) would be more appropriate. Tests of frequency used a 2×2 contingency table analysis unless small expected cell frequencies indicated Fisher's exact test. In each experiment, the two measures of reproductive success (number of larvae and total mass of brood) were highly correlated and suggested the same experimental effects. For this reason, only results for total brood mass are depicted graphically.

Frequency data relating outcome of an encounter (success versus complete infanticide of the brood) to two experimental variables, sex of defender and sex of intruder, were analysed using $2 \times 2 \times 2$ log-linear analysis of contingency tables. Values for the interaction between defender and intruder when outcome is removed, defender $\times$ intruder (outcome), are reported whether or not that interaction was significant, following Cox & Snell (1989).

RESULTS

Experiment 1: Value of Replacement Broods for *N. pustulatus* and *N. orbicollis*

The value of an undefended carcass for a female *N. pustulatus* intruder varied with the point during the reproductive cycle at which the 'intrusion' occurred (brood mass, Fig. 1; ANOVA: number of larvae: $F_{6,63} = 18.46$, $P < 0.001$). Carcasses that had been manipulated, but which did not yet have larvae (30 h, 60 h) retained much of the value (70–90%) of a fresh carcass (1 h). The value of a carcass declined rapidly once larvae of the original female were feeding from the resource. A carcass taken over on day 4 (first instars) had approximately one-half
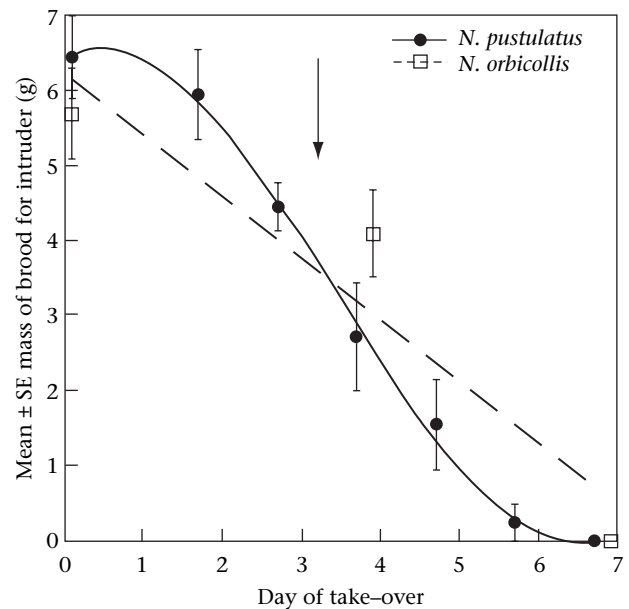

Figure 1. The mean brood mass produced by an 'intruder' female taking over an undefended carcass previously manipulated by another female for 1 h–7 days (ANOVA: *N. pustulatus*: $F_{6,63} = 23.80$, $P < 0.001$; *N. orbicollis*: $F_{2,29} = 18.31$, $P < 0.001$). The arrow indicates the approximate time when first-instar larvae hatch and move to the carcass to begin feeding. The curve fit for *N. pustulatus* ($N = 10$ per treatment) was a third-order polynomial and that for *N. orbicollis* ($N = 11$ per treatment) was linear.

the value of a fresh carcass (number of larvae: 55.1%; brood mass: 44.2%). By day 7, the carcass had no value for an intruder; in no trial was a replacement brood produced and in only one trial was the original brood completely killed. Larvae were always killed on days 1–5.

The period of time the original *N. pustulatus* female was with her first carcass had no significant effect on the reproductive success on a second fresh carcass initiated just 4 days later (brood mass, Fig. 2; regression analysis: number of larvae: $F_{1,68} = 0.19, P = 0.60$). Brood mass on a second carcass for females that were removed from their first carcass at the second-instar stage was 25% less than that for other treatments. The experiment was designed to detect a trend related to increasing duration of care on the first carcass and had limited power to isolate differences between two particular treatments. A sample of 25–30 per treatment would be required for an adequate test of a difference between two treatment means.

The value of a carcass for a replacement brood by an intruder also declined with time for *N. orbicollis* (brood mass, Fig. 1; ANOVA: number of larvae: $F_{2,29} = 14.30$, $P < 0.001$). A carcass on which first-instar larvae had recently arrived (day 4) retained considerable value as measured by both number of larvae (64.5%) and brood mass (74.4%), compared with a fresh carcass (1 h). By day 7, no carcass was used for a replacement brood and in no trial was the original brood completely killed. Larvae were always killed on days 1–5.

The length of time the first *N. orbicollis* female was with her original carcass did not affect her subsequent
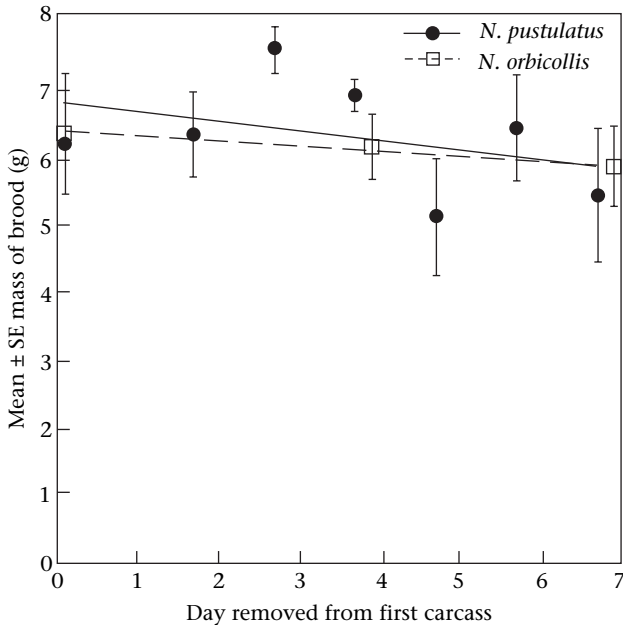
Figure 2. The mean brood mass produced by a female that was removed from one carcass and then provided a second carcass. The time period with the first carcass had no effect on a second reproductive attempt (regression analysis: *N. pustulatus*: $F_{1,68} = 0.79$, $P = 0.41$; *N. orbicollis*: $F_{1,30} = 0.14$, $P = 0.71$). Sample sizes as in Fig. 1.

reproductive performance on a fresh carcass 4 days later (brood mass, Fig. 2; regression: number of larvae: $F_{1,30} = 0.05$, $P = 0.84$).

Experiment 2a: Heterospecific Intrusions

Single male *N. orbicollis* defended their brood more successfully than did single females, and defence was more successful against heterospecific female intruders than heterospecific male intruders (Table 1; log-linear analysis: sex of defender: $G_1^2 = 5.57$, $P = 0.03$; sex of intruder: $G_1^2 = 3.90$, $P < 0.05$). The defender × intruder (outcome) interaction was not significant ($G_2^2 = 0.59$, $P = 0.74$), indicating that when the separate effects of defender and intruder were taken into account, the particular way in which the sex of the defender and sex of the intruder

were matched had no effect. In Table 1 the expected cell frequencies for success (a model based on the two significant effects only and no defender × intruder (outcome) interaction) are shown. The observed values are similar to the expected values, a result that was predicted for a heterospecific encounter in which there is no chance for the defender to pair with a successful intruder.

Experiment 2b: Conspecific Intrusions

Single male defenders were also more successful than single female defenders against conspecific intruders, and defenders were more successful against female intruders than male intruders (Table 2; log-linear analysis: sex of defender: $G_1^2 = 7.98$, $P < 0.01$; sex of intruder: $G_1^2 = 15.14$, $P < 0.001$). Expected cell frequencies based on the two significant effects on outcome, defender and intruder, without a defender × intruder (outcome) interaction, were generated as for heterospecific intrusions. Unlike the case with heterospecific intrusions, however, the observed cell frequencies involving conspecific intrusions were quite different, reflected by a significant defender × intruder (outcome) interaction ($G_2^2 = 16.94$, $P < 0.01$). In particular, when a resident male or female defended against a conspecific intruder of the opposite sex (possibility of re-pairing and producing a replacement brood on the carcass), the probability of successfully defending the brood was lower than predicted by a model not including the defender × intruder (outcome) interaction.

Experiment 3: Intrusions against Single Females versus Male−Female Pairs

Single females with second instars were less successful in defending their broods (4 of 12) than were single females with third instars (10/11), pairs with second instars (11/12), or pairs with third instars (12/12). In all eight trials in which the male intruder killed second instars that were defended by a single female, a replacement brood was produced (brood mass: $\overline{X} \pm SE = 2.80 \pm 0.38$ g).

At the second-instar stage, pairs produced a greater brood mass (Fig. 3) and more larvae than did single females when all trials (take-overs and no take-overs)

Table 1. Brood defence of *N. orbicollis* in heterospecific encounters (N = sample size, S = number of successful defences, I = number of cases of complete infanticide)

	Male intrudes			Female intrudes			Subtotals		
	N	S	I	N	S	I	N	S	I
Male defends	30	**12** (10.8)*	18	29	**16** (17.2)*	13	59	28	31
Female defends	30	**5** (6.2)*	25	30	**11** (9.8)*	19	60	16	44
Subtotals	60	17	43	59	27	32			

*The number in parentheses is the expected cell frequency (number of successes) based on two significant effects of defender and intruder, excluding the defender × intruder (outcome) interaction.

Table 2. Brood defence of *N. orbicollis* in conspecific encounters (*N* = sample size, *S* = number of successful defences, *I* = number of cases of complete infanticide)

	Male intrudes			Female intrudes			Subtotals		
	N	*S*	*I*	*N*	*S*	*I*	*N*	*S*	*I*
Male defends	30	**14** (9.2)*	16	30	**17** (21.8)*	13	60	31	29
Female defends	32	**0** (4.8)*	32	28	**16** (11.2)*	12	60	16	44
Subtotals	62	14	48	58	33	25			

*The number in parentheses is the expected cell frequency (number of successes) based on two significant effects of defender and intruder, excluding the defender × intruder (outcome) interaction.

were considered (Wilcoxon two-sample tests: number of larvae: $W = 236$, $N_1 = 16$, $N_2 = 12$, $P = 0.03$; brood mass $W = 236$, $P = 0.03$). There was no such difference, however, when the manipulation occurred at the third-instar stage (number of larvae: $W = 118$, $N_1 = 12$, $N_2 = 10$, $P = 0.87$; brood mass: $W = 115$, $P = 0.97$). By the time the brood reached the third instar, there was little chance of a take-over.

When trials with zero values (take-overs) for number of larvae and brood mass were excluded, the data satisfied the criteria of multiple tests of homogeneity of variance (SAS Institute 2000). In trials in which the original brood survived, neither the number of residents (two-way ANOVA: $F_{1,34} = 0.01$, $P = 0.98$) nor the stage at which the intruder was introduced ($F_{1,34} = 1.71$, $P = 0.16$) affected the number of larvae. Likewise, brood mass was unrelated to either the number of residents ($F_{1,34} = 0.01$, $P = 0.98$) or the stage of intrusion ($F_{1,34} = 2.00$, $P = 0.10$; Fig. 3). The absence of a male effect indicated that young did not benefit from paternal feeding or from other

paternal care, and that the male's presence had little effect on partial infanticide of the brood (some but not all larvae were killed by an intruder) in trials not involving a take-over. Partial infanticide was rare (4 of 50 trials). In summary, the presence of a male *N. orbicollis* had no significant effect on reproductive success except in cases involving the strong possibility of an infanticidal take-over and complete loss of the brood.

DISCUSSION

Infanticide by unrelated adults in burying beetles can be explained primarily by resource competition and sexual selection. Cannibalism seems to be of limited importance, as intruders sometimes did not consume larvae that they killed. Resource competition is the only explanation for infanticide by heterospecific burying beetles and also explains much of the motivation for intruding conspecifics, especially females. In conspecific encounters, infanticide was more common than expected when the
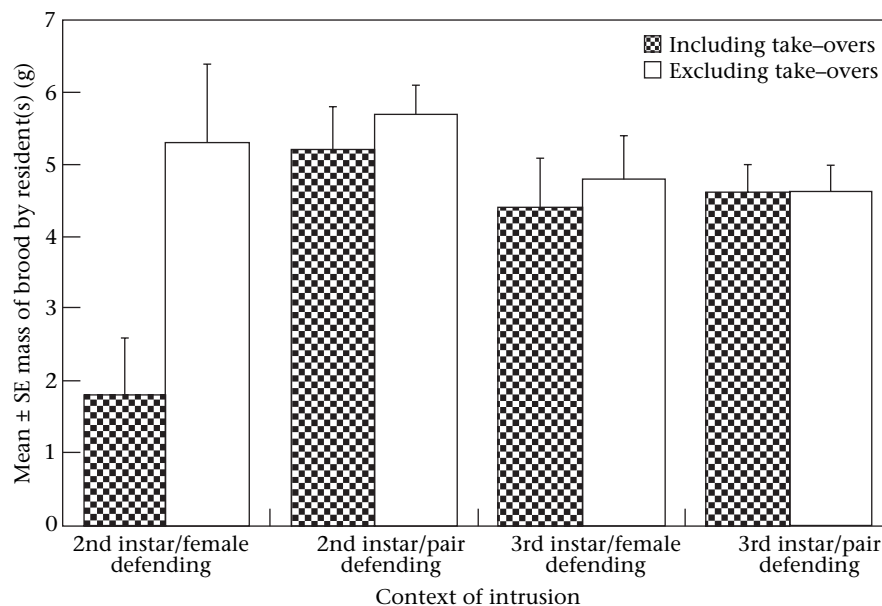

Figure 3. The brood mass produced by residents (female or male–female pair) when confronted by an intruder introduced at the second-instar or early third-instar stage. Statistical tests in text.

resident was matched with an intruder of the opposite sex. The deviation was in the direction expected if sexual selection affects the dynamics of the encounter, and is probably explained by the opportunity for the defending resident to renest, and for male intruders, the opportunity to secure a mate. Individuals providing parental care are expected to decrease current parental effort (including brood defence) when there is a higher probability of future reproduction (Williams 1966; Pflanz 2002). When a resident burying beetle loses a resource to a heterospecific or same-sex conspecific intruder, the probability of reproduction is the low background rate of finding a new carcass. If the intruder is a conspecific of the opposite sex, however, renesting quickly using the same resource is probable for the resident (Müller 1987; Trumbo 1990b; Robertson 1993; this study).

The reproductive performance of females removed from one carcass and given a second carcass suggests that renesting potential will depend on the quality of the resource being used and not on the duration of care prior to infanticide. At earlier stages of the parental cycle, a resource retains much of its original value (also see Suzuki 2004) and a victim of infanticide can recover much of its loss in a replacement brood. At the first-instar stage, a resource was found to retain 44–75% of its original value. By the third instar, the potential for renesting is low, so brood defence is expected to be high and intruder motivation low. Further insight could be gained by independently manipulating the perception of renesting of residents and intruders. The results support the hypothesis that both the strength and form of sexual selection can change rapidly with environmental conditions, and that sex roles are quite flexible, both for parents and intruders (see Gowaty 2004).

I hypothesize that the threat of infanticide is the primary explanation for extended biparental care in burying beetles. In biparental systems it is necessary to ask why one parent does not desert earlier, leaving the other parent to finish caregiving. One mechanism proposed here is efficient parental task specialization. The stability of biparental care is enhanced when one parent cannot or will not fully compensate for the absence of its partner (Chase 1980; Houston et al. 2005). Incomplete compensation can occur when one parent is already near its maximum rate of effort, or the costs of increasing care (measured as effects on future reproduction) are prohibitively high. Incomplete compensation may be inherent when one parent is an efficient task specialist, performing a parental task better and more often than its partner. A deserted parent that is less efficient for a task may not be able to complete a specific task. If it were possible to complete the task, the nonspecialist would require greater effort and incur the associated higher costs compared to a specialist. To avoid these potentially higher costs in the event of desertion, selection for no or incomplete compensation by the nonspecialist is expected.

A strong skew in task specialization, by itself, is not sufficient proof that task specialization results in efficiencies. Gordon (1996) noted that of the numerous studies of task specialization in social insects, only a handful have convincingly demonstrated efficiencies due to task specialization, per se, and not due to other aspects of division of labour such as mass action or divisibility of work (Wilson 1980; for more recent examples, Arnold et al. 2002; Julian & Fewell 2004; Johnson 2005). Differences in the propensity to perform a task can result from simple differences in response to task-related stimuli (Robinson & Page 1989; Cahan & Fewell 2004); these tendencies may or may not be related to superior ability to perform the task.

Male burying beetles are efficient task specialists, having both a greater tendency to guard (more time spent guarding: Fetherston et al. 1990, 1994; more injuries sustained in brood defence: S. T. Trumbo, unpublished data) as well as a greater ability to guard the brood. The superior ability of males to defend the brood was most clearly seen in heterospecific encounters, in which the potential for renesting with an intruder did not complicate residents' motivation. The magnitude of the difference between male and female fighting ability was surprising. The sexes are similar in body size (Trumbo 1990c), both are aggressive and both will perform all parental tasks if necessary. Male specialization for guarding and defence may be common in biparental insects. Among insects, male parental care may evolve from defence of a resource or mating site, as can be deduced from comparative study of closely related nonparental and parental species (Alcock 1975; Halffter 1977; Reid & Roitberg 1994; Rasa 1999). *Ptomascopus morio* Kraatz, a close relative of *Nicrophorus* that has resource defence polygyny and weakly developed parental care, has been found to have male but not female defence against predators and same-sex conspecifics (Trumbo et al. 2001; Suzuki et al. 2005).

The results of the present study suggest that in *N. orbicollis*, male defence is important up to the beginning of the third instar. Comparisons between studies are complicated by the different temperatures at which experiments were run, affecting developmental times of larvae. Scott & Gladstein (1993) found that infanticidal take-overs against single females of *N. orbicollis* were still common (47.1%) on day 8 in a field experiment. This corresponds to the second or early third instar based on my own field work (Trumbo 1991). At this stage, *N. orbicollis* males typically desert from a small carcass (10–15 g). The male typically stays on a large carcass (25–35 g) for about 8 days in laboratory experiments and for 9–10 days in field experiments (Scott & Traniello 1990; Trumbo 1991), roughly the middle third instar, when the threat of a take-over may have passed. Infanticidal take-overs are more common on larger carcasses (Trumbo 1991), and infanticide of some but not all larger third instars by an unsuccessful intruder occurred in the present study, but seems rare. The duration of male care on large carcasses is not completely understood. It is unlikely that duration of paternal care will be understood by an optimality approach as there are too many unknowns about burying beetle reproduction, especially the availability of high-quality resources (Eggert & Müller 1997). A more promising approach is to take advantage of the considerable variation in the duration of male care and to correlate this variation with variation in key environmental factors. Scott (1998) found that males kept at a higher density prior to breeding

provide longer care than males housed alone. I found that males stay longer on shallowly buried carcasses than on deeply buried carcasses (unpublished data). Both results are consistent with the hypothesis that variation in male care is correlated with vulnerability to a take-over. In the field, most infanticidal take-overs in *N. orbicollis* are committed by males intruding on female residents (Trumbo 1990b; Robertson 1993), suggesting that extended biparental care in this species is closely linked to sexual selection.

Acknowledgments

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