

Current brood size and residual reproductive value predict offspring desertion in the burying beetle *Nicrophorus vespilloides*

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Life-history theory suggests that offspring desertion can be an adaptive reproductive strategy, in which parents forgo the costly care of an unprofitable current brood to save resources for future reproduction. In the burying beetle, *Nicrophorus vespilloides*, parents commonly abandon their offspring to the care of others, resulting in female-only care, male-only care, brood parasitism, and the care of offspring sired by satellite males. Furthermore, when there is biparental care, males routinely desert the brood before larval development is complete, leaving females behind to tend their young. We attempted to understand these patterns of offspring desertion by using laboratory experiments to compare the fitness costs associated with parental care for each sex and the residual reproductive value of the 2 sexes. We also tested whether current brood size and residual reproductive value together predicted the incidence of brood desertion. We found that males and females each sustained fecundity costs as a consequence of caring for larvae and that these costs were of comparable magnitude. Nevertheless, males had greater residual reproductive value than females and were more likely than females to desert experimental broods. Our results can explain why males desert the brood earlier than females in nature and why female-only care is more common than male-only care. They also suggest that the tipping point from brood parasitism or satellite male behavior to communal breeding (and vice versa) depends on the value of the current brood relative to residual reproductive value. *Key words*: alternative reproductive tactics, biparental care, negotiation, reproductive skew, senescence, sexual conflict. [*Behav Ecol*]

The desertion of dependent young by parents seems, at first sight, to be pathologically maladaptive (Hrdy 1999). However, once the fitness costs associated with providing care are taken into account (Trivers 1972), offspring desertion can be viewed as an adaptive life-history decision (Williams 1966; Pianka and Parker 1975; Székely et al. 1996) in which current offspring are abandoned to defend residual reproductive value (Dawkins and Carlisle 1976; Boucher 1977; Maynard Smith 1977; Clutton-Brock 1991; Hrdy 1999). Just like total filial cannibalism (Rohwer 1978), brood desertion is a form of investment in future young (Székely et al. 1996). The factors that influence the decision to abandon offspring can therefore be partitioned into those that affect the fitness benefits of continued investment in the current brood and those that influence the parent's future fitness (for an excellent review, see Székely et al. 1996, also Balshine-Earn and Earn 1997; McNamara et al. 2000; Barta et al. 2002; Webb et al. 2002; Servedio and Hauber 2006; Broom et al. 2008; Steinhart et al. 2008). In general, those that yield a high residual reproductive value relative to low current fecundity will encourage brood desertion (Carlisle 1982; see Figure 2.5 in Lessells 1991; Székely et al. 1996).

One factor that is theoretically likely to influence this trade-off is the costliness of continued care for the current brood, but its importance in determining desertion has received relatively little experimental testing (e.g., see Table II in Székely et al. 1996). Two pioneering studies have shown that arthropods are ideal for investigating how the fitness costs of parental care affect residual reproductive value and consequently the deci-

sion to abandon the brood. Zink (2003) followed a marked population of treehoppers *Publilia concava* in the field for their entire life span. In this species, guarding eggs and nymphs increased offspring survival but carried an associated fecundity cost for mothers. Consistent with theoretical expectations, Zink (2003) discovered that females that quickly deserted their first clutch had greater future reproductive success than those that remained to guard their offspring. Similarly, Buzatto et al. (2007) showed that maternal egg guarding in the neotropical harvestman *Acutisoma proximum* prevented egg predation but reduced future fecundity. However, their calculations show that abandoning offspring can never yield greater fitness returns than continued care. Therefore, in this species, the life-history trade-off is always balanced in favor of care of the current brood (Buzatto et al. 2007).

Although these field studies show that a high residual reproductive value (relative to current brood size) is positively correlated with brood desertion, they do not demonstrate that the first is causally linked to the second. This is our aim here with experiments on the burying beetle *N. vespilloides*. Burying beetles differ from the harvestman and treehopper studied previously because care is supplied by both parents and is more complex than simply guarding offspring. To breed, burying beetles must first locate the carcass of a small vertebrate (Eggert and Müller 1997; Scott 1998). Together, the pair prepare the carcass by stripping the body of fur or feathers, rolling it into a ball and smearing it with antimicrobial anal exudates (Cotter and Kilner 2009), while interring it in a shallow grave. During this time, the female also lays her eggs in the soil near the carcass. Two to 3 days later, the larvae hatch and crawl to the carcass, where they take up residence in a crater specially prepared by their parents. There the offspring may be tended by both parents, whose duties of care include regurgitating partially digested carrion on demand to the brood, and defending the carcass from rival beetles (Eggert and Müller 1997; Scott 1998) and other organisms

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(Rozen et al. 2008; Cotter and Kilner 2009). Roughly 7 days after hatching, the larvae disperse to pupate in the soil. Their parents, meanwhile, depart in search of fresh carrion and further opportunities for breeding (Eggert and Müller 1997).

In nature, approximately 85% of *N. vespilloides* broods are tended by at least one male and one female (Müller et al. 2007), and uneasy breeding associations between 3 or more adults are common (Müller et al. 2007) due to the relative scarcity of carrion (Eggert and Müller 1997). When *N. vespilloides* males stay to assist with parental care, they always leave the brood 2–5 days earlier than females, which is well before the end of larval development, and the reason for their early departure is unclear (Eggert and Müller 1997). In addition, either sex might desert their offspring before the larvae have even hatched, and a diversity of social arrangements on the carcass can result from brood abandonment including male-only care, female-only care, brood parasitism, and the care of offspring sired by satellite males (Müller et al. 2007). Competition for carcasses does not cause brood desertion because communal breeding by multiple adults is also possible (Eggert and Müller 1997; Müller et al. 2007), especially on larger carcasses (Müller et al. 1990; Eggert and Müller 1992; Eggert et al. 2008). In these cases, all adults help care for offspring and they are incapable of identifying their own offspring for selective attention (Eggert and Müller 2000; Eggert et al. 2008). The patterns of offspring desertion seen in burying beetles thus raise 2 questions: 1) why do males leave the brood earlier than females (Eggert and Müller 1997)? and 2) when 2 or more members of the same sex share the carcass as a breeding resource, what determines whether parents will abandon their offspring to the care of others (Eggert et al. 2008)?

Answering these questions is less straightforward than the previous analyses of brood desertion, which were carried out on arthropod species with uniparental care (Zink 2003; Buzatto et al. 2007). Biparental care potentially introduces complexity into analyses of offspring desertion because the payoffs are then frequency dependent, being contingent on the behavior of the partner (e.g., Székely et al. 1996; Balshine-Earn and Earn 1997; Barta et al. 2002; McNamara et al. 2003; Trumbo 2007), and the behavior of the opposite sex in the wider population (e.g., Székely et al. 1996; Balshine-Earn and Earn 1997; Webb et al. 1999, 2002; Seno and Endo 2007). However, in burying beetles, there is probably always an excess of potential breeders available, due to the scarcity of carcasses (Eggert and Müller 1997; Scott 1998), and so desertion is less likely to be constrained by the frequency of available partners than it is in other species. Consequently, we ignore the possibility of frequency dependent payoffs for the moment and focus our experiments on the behavior of widowed parents in the laboratory. Previous work on this species has shown that widowhood does not change the quality of care on offer to offspring. Single mothers and fathers are equally effective at rearing larvae to independence in the laboratory (e.g., Smiseth et al. 2005), and each can take on the full range of parental duties in the absence of the other (Eggert and Müller 1997; Scott 1998). We ask 3 questions of our widowed beetles: 1) is there a fecundity cost associated with the provision of maternal or paternal care? 2) does it differ between the sexes? and 3) does residual reproductive value, relative to the current brood size, explain the varying patterns of brood desertion seen naturally in burying beetles?

MATERIALS AND METHODS

Nicrophorus vespilloides colony

The *N. vespilloides* colony was established in May 2005 from wild-caught beetles that had been trapped in Madingley

Woods, Cambridge, UK. Wild-caught beetles were added to the colony each subsequent year to maintain genetic diversity. Beetles were maintained individually in plastic containers (12 × 8 × 2 cm) at a temperature of 20 °C under a 16:8 h light:dark cycle. Nonbreeding adults were fed twice a week ad libitum with either thin strips of steak or minced beef. To breed the beetles, unrelated pairs of males and females were selected and each pair placed in their own breeding container (a plastic container, 17 × 12 × 6 cm) one-third filled with moist soil, furnished with a piece of steak (as a carcass substitute). We used steak for these experiments because it meant we could precisely control the resources available for reproduction, which is a key determinant of breeding success (Bartlett and Ashworth 1988) and desertion decisions (Müller et al. 1990; Eggert and Müller 1992, 1997), and this is less straightforward when beetles are allowed to breed on mice. Throughout the Methods and Results sections, we refer to the steak used for breeding as the “carcass.” For the duration of their breeding attempt, the pair was kept in the dark to simulate underground conditions. Larvae were removed from the breeding container after dispersal and placed individually in their own plastic container (12 × 8 × 2 cm) until eclosion, at which point they were kept under standard rearing conditions until they were required either for experiments or producing the next generation of stock beetles. The fate of the adult beetles after breeding depended on their experimental treatment (see below).

Experiment 1—fecundity costs associated with egg laying

When comparing the costs associated with larval care between the sexes, a potential confounding factor is that females produce and nourish eggs, so they have already invested more than males by the time the larvae hatch. We therefore began by investigating whether the fecundity costs of egg production alone could decrease a female's residual reproductive value.

Ten days after eclosion, virgin males were paired with unrelated virgin females of the same age and placed in breeding containers with a piece of steak. There were 2 treatment groups, and sisters were matched across treatments ($N = 20$ pairs of sisters). In the low-effort treatment, pairs were provided with a small piece of steak (4.98 ± 0.01 g) to encourage females to lay a small clutch, whereas in the high-effort treatment, pairs were provided with a large piece of steak as an inducement to lay a large clutch (29.91 ± 0.05 g). Pairs were left together for a total of 68 h to allow multiple matings to occur, at which point the male was removed. Females in each treatment were then transferred to a new container containing a small piece of steak (4.98 ± 0.01 g) that had been prepared by another set of parents. Eggs were collected from the original breeding containers and placed on moist filter paper. The new breeding container was additionally searched for eggs daily and if any were present, the female and the carcass were again transferred to a new container, and the latest eggs were placed with her previous ones. As the eggs hatched, larvae were placed on the carcass. To ensure that posthatching investment was similar between the treatment groups, all females were each given 5 cross-fostered larvae to rear. Larvae were weighed at dispersal from the carcass after which females were placed back into individual containers.

To measure any fecundity costs of egg laying, we compared the subsequent reproductive success of females in the 2 egg-laying treatments. Twelve days after they were paired for their first breeding attempt, females were again paired with an unrelated male and allowed to breed for a second time. In their second breeding attempt, females were given a 15 g (15.00 ± 0.1 g) steak carcass, 68 h after pairing, the male was removed, and the female and her carcass were transferred to a new breeding container. Her eggs were collected from the original

breeding container and placed on moist filter paper. Eggs were checked at regular intervals for hatching, and newly hatched larvae were transferred to the carcass to be reared by their mother. For this breeding attempt, we did not control brood size. Larvae were weighed at dispersal, and the numbers of survivors recorded. Twelve days after pairing for the second breeding attempt, and every 12 days thereafter until they died, females were allowed to breed again using exactly the same protocol as for the second breeding bout.

Experiment 2—fecundity costs of paternal and maternal larval care

This experiment created an “ideal world” for the beetles, in which there was an abundance of carcasses and virgin mates and therefore, no competition for either resource. The aim was to discover how many offspring a beetle could produce during its life in perfect breeding conditions, given an initial outlay on larval care that was varied experimentally.

We established pairs of unrelated virgin beetles, each with a medium sized piece of steak (14.98 ± 0.01 g), and allowed them to mate for 68 h. The subjects of the experimental treatments were either the male ($N = 40$) or the female ($N = 40$) in the mated pair but never both from the same pair. There were 2 treatment groups for each sex: a low-effort treatment which involved rearing 5 unrelated larvae and a high-effort treatment which involved rearing 20 unrelated larvae. Each of these brood sizes falls within the range naturally seen in *N. vespilloides* (Müller et al. 2007). Sixty-eight h after pairing, males and females were experimentally widowed, and the widowed beetle was transferred to a new container with their carcass. Eggs were collected from the original breeding containers and placed on moist filter paper (clutch size = 29.33 ± 0.40). For female subjects, the new breeding container was additionally searched for eggs daily and if any were present, the female and the carcass were again transferred to a new container, and the latest eggs were placed with her previous ones. As the eggs hatched, the larvae were placed on the carcass tended by one of the parents. Hatchlings were allocated to the widowed beetles according to their treatment. Larvae were weighed at dispersal, and the numbers of survivors recorded. After larval dispersal, adults were placed back into individual containers.

To measure the fecundity costs associated with larval care, we compared the subsequent reproductive success of individuals in the 2 parental effort treatments, within and between sexes. Twelve days after pairing for the first breeding attempt, all the experimental individuals were again paired with an unrelated partner and allowed to breed for a second time, using a 15 g (14.99 ± 0.01) steak carcass. They were then experimentally widowed 68 h after pairing. Beetles were transferred to a fresh breeding container at this point. Eggs were then collected as described above and placed on moist filter paper to hatch. Hatchlings were transferred to the carcass to be reared either by their mother or by their father. Larvae were weighed at dispersal, and the numbers of survivors recorded. Twelve days after pairing for the second breeding attempt, and every 12 days thereafter until they died, experimental subjects were allowed to breed again using exactly the same protocol as for the second breeding bout. Only those individuals that produced at least 3 broods were included in the analyses.

Experiment 3—current fecundity, residual reproductive value, and the probability of brood desertion

The aim of this experiment was to test how the incidence of brood desertion varied with the size of the current brood and residual reproductive value as measured in Experiment 2.

We established pairs of unrelated virgin beetles, with a medium sized piece of steak (14.98 ± 0.01 g), and allowed them to mate for 68 h at which point the nonexperimental subject was removed. The subjects of the experimental treatments were either the male ($N = 54$) or the female ($N = 50$) in the mated pair but never both from the same pair. There were 2 treatment groups for each sex: a low current fecundity treatment which involved rearing 5 unrelated larvae and a high current fecundity treatment which involved rearing 20 unrelated larvae. Note that in nature, abandoned broods of brood parasites and satellite males typically comprise approximately 5 larvae, whereas dominants of either sex stay to rear broods of roughly 20 young (see Tables 2 and 4 in Müller et al. 2007). The treatments were set up exactly as described for the first breeding attempt in Experiment 2. Larvae were weighed at dispersal, and the numbers of survivors recorded. Parents with zero surviving young were scored as “deserters.” A “deserting” parent almost certainly gave up on the current reproductive attempt, because when parents continue to care for larvae, it is very unlikely that none survive at all (Eggert and Müller 1997; Scott 1998). Parents either simply abandoned the larvae or additionally cannibalized the entire brood (Bartlett and Ashworth 1988). Total filial cannibalism is the more probable explanation because larvae can survive without parental care (Eggert et al. 1998), but we did not monitor the breeding boxes in sufficient detail to determine the cause of larval death.

Statistical analyses

All data were analyzed using linear mixed effects restricted estimate maximum likelihood models in Genstat with the family from which the focal beetle originated included as a random effect. We have previously shown that the amount of parental care received by the brood can be inferred by the number of larvae that survive to disperse and the mass of the brood at dispersal (Ward 2007). To control for any differences in parental effort between the sexes within each treatment, we initially included these measures in our models. However, because these 2 terms are highly correlated, 2 sets of models were run with each term including all possible interactions. For all analyses, there were no effects of number of survivors in the first brood nor of the total mass of the first brood at dispersal on any of the dependent variables nor any significant interactions with either of these variates (all $P > 0.10$). Consequently, these terms were dropped from the models. However, retention of these terms in the models did not qualitatively change the results in any case. Means \pm standard errors are reported throughout.

RESULTS

Experiment 1—fecundity costs associated with egg laying

Our experimental manipulation successfully induced different clutch sizes in the 2 treatments: females in the low-effort group laid 11.35 ± 0.82 eggs, whereas the females in the high-effort group laid 44.15 ± 0.92 eggs ($t_{38} = 26.62$, $P < 0.0001$). However, we could detect no evidence of fecundity costs associated with laying an increased clutch size for any of our measures of female fecundity: neither the mass of the second brood at dispersal (treatment effect: $F_{1,37} = 0.01$, $P = 0.943$), nor the total number of broods produced during the female’s lifetime (treatment effect: $F_{1,37} = 0.16$, $P = 0.693$), nor the total number of offspring produced during the females’ lifetime (treatment effect: $F_{1,37} = 0.03$, $P = 0.862$), nor the total mass of offspring produced during the females’ lifetime (treatment effect: $F_{1,37} = 0.05$, $P = 0.817$) changed as a result of the experimental treatment. We conclude that although there may be some fecundity costs associated with egg laying, they were too small for us to detect in this experiment.

Experiment 2—fecundity costs of paternal and maternal larval care

Fecundity costs associated with larval care

The experimental treatment successfully caused parents to put different levels of effort into larval care, and each sex responded similarly to the manipulation (parent sex \times treatment effect: mean larval weight, $F_{1,59} = 3.57$, $P = 0.064$; number of offspring, $F_{1,53} = 0.51$, $P = 0.476$; total mass of offspring, $F_{1,53} = 0.36$, $P = 0.55$; number of successful broods, $F_{1,53} = 0.62$, $P = 0.43$). Because the interaction between parent sex and treatment was not significant, it was dropped from the final model in each of the following analyses.

Females in the low-effort treatment reared 2.85 ± 0.35 offspring, whereas females in the high-effort treatment reared 13.75 ± 0.73 offspring ($t_{38} = 13.46$, $P < 0.001$). Similarly, males in the low-effort treatment reared 4.00 ± 0.16 offspring, whereas those in the high-effort treatment reared 16.00 ± 0.34 offspring ($t_{38} = 31.94$, $P < 0.001$).

There were future fecundity costs associated with the experimentally induced increase in larval care (Figure 1). Individuals of each sex that reared large broods in the first reproductive attempt subsequently produced offspring that were lighter at dispersal (treatment effect: $F_{1,60} = 9.107$, $P = 0.004$; Figure 1a) and fewer offspring in the rest of their life (treatment effect: $F_{1,54} = 22.81$, $P < 0.001$; Figure 1b), compared with those that had reared small broods the first time they bred. In addition, beetles that were experimentally forced to raise a large brood

in their first breeding attempt produced a smaller brood mass on each subsequent breeding attempt than those initially induced to rear a small brood (treatment effect: $F_{1,43} = 38.03$, $P < 0.001$; Figure 2a). As a result, the total mass of offspring from all broods was significantly greater in the low-effort group than the high-effort group (treatment effect: $F_{1,54} = 29.97$, $P < 0.001$; Figure 1c). The greater fecundity of adults in the low-effort treatment was not simply the result of them living longer, and therefore breeding more often, than their counterparts in the high-effort treatment. When we controlled for life span by including the number of lifetime breeding attempts as a variable in the model, adults in the high-effort treatment still produced fewer young than those in the low-effort treatment (treatment effect: $F_{1,53} = 20.89$, $P < 0.001$), independently of life span (number of broods effect: $F_{1,65} = 31.02$, $P < 0.001$). In addition, the total number of successful broods reared by adults did not differ significantly between the treatments (treatment effect: $F_{1,54} = 2.48$, $P = 0.115$; Figure 1d).

Sex differences in fecundity costs associated with larval care

In general, there was a pronounced difference between the sexes in subsequent fecundity after the first breeding attempt. Males reared more successful broods than females (parent sex effect: $F_{1,62} = 24.58$, $P < 0.001$; Figure 1d), although the total number of reproductive attempts did not differ between the sexes (parent sex effect: $F_{1,36} = 2.06$, $P = 0.16$). Males also

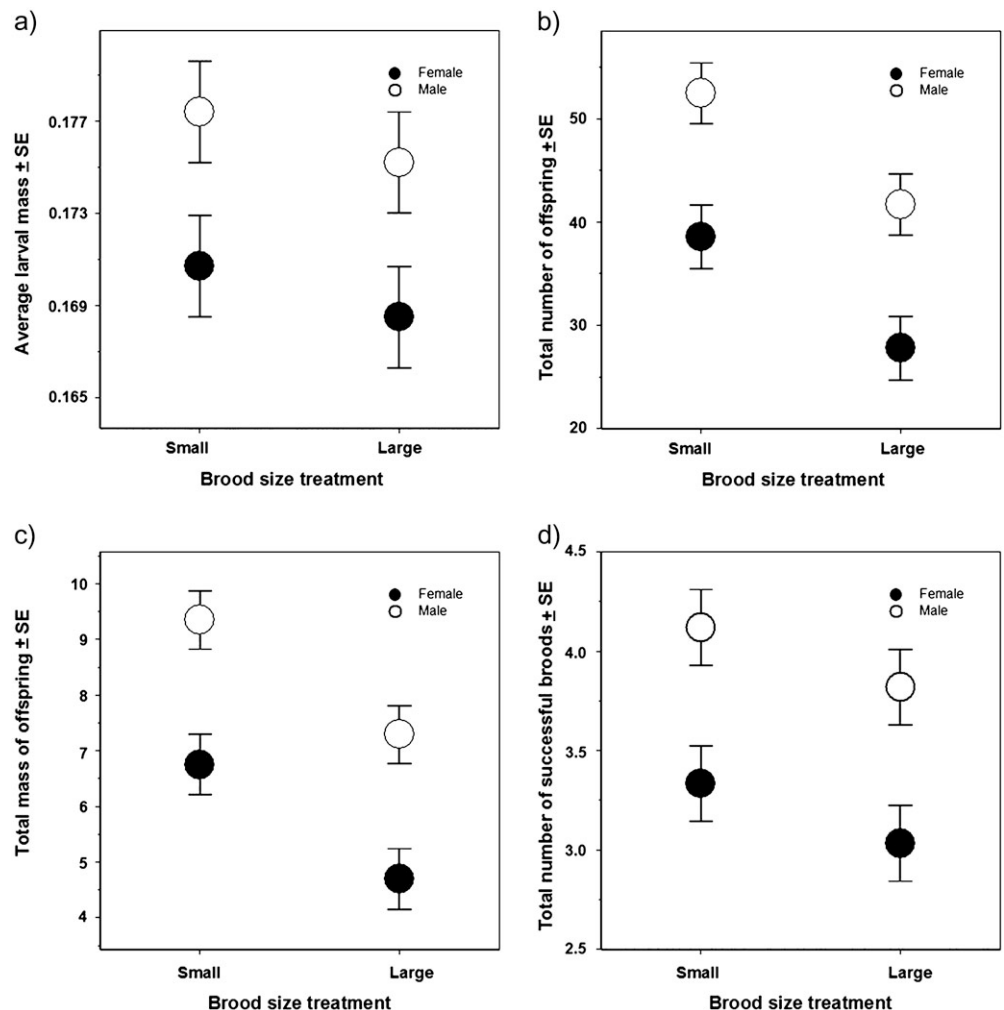


Figure 1

Mean (\pm standard error): (a) mean offspring mass, (b) total number of offspring, (c) total mass of offspring, and (d) total number of successful broods produced by males and females throughout their lives after they had been induced to rear small or large broods in their first breeding bout. All values displayed are estimates from the minimum adequate model.

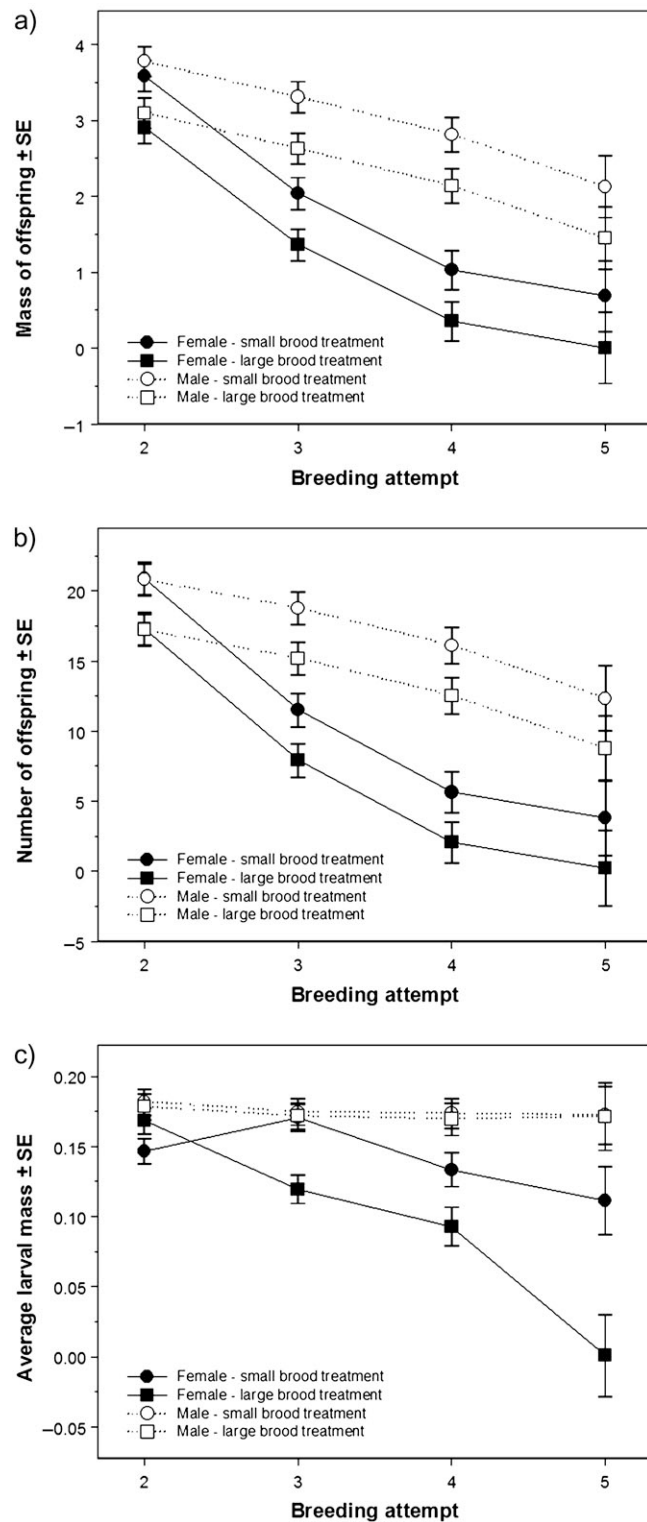


Figure 2
Mean (\pm standard error): (a) mean offspring mass, (b) number of offspring, and (c) mass of offspring produced by males and females for each subsequent breeding bout after they had been induced to rear small or large broods in their first breeding bout. All values displayed are estimates from the minimum adequate model.

produced more offspring during their life than females (parent sex effect: $F_{1,62} = 14.61$, $P < 0.001$; Figure 1b) that were heavier at dispersal (parent sex effect: $F_{1,66} = 17.19$, $P < 0.001$;

Figure 1a). Therefore, males had higher residual reproductive value than females after their first breeding attempt.

To examine these sex differences in more detail, we looked at the broods produced after the initial experimental brood and considered the effects of parent sex, treatment, and brood number on each of the offspring traits. Successive broods reared by females declined in mass more rapidly than those reared by males (parent sex \times brood number: $F_{3,167} = 6.95$, $P < 0.001$; Figure 2a) and contained fewer offspring (parent sex \times brood number: $F_{3,165} = 9.81$, $P < 0.001$; treatment effect: $F_{1,43} = 30.09$, $P < 0.001$; Figure 2b). For broods reared by females, average larval mass declined with each successive brood and fell much more steeply when females were induced to care for large broods in their first breeding attempt, whereas for those reared by males, average larval mass remained constant, regardless of the initial brood size treatment (parent sex \times treatment \times brood number effect: $F_{3,151} = 4.44$, $P = 0.005$; Figure 2c).

It might be argued that these differences between the sexes simply arise because females are underrepresented in later broods and so the quality of individuals sampled in each sex differed with each successive breeding attempt (Table 1). To compare the sexes using individuals of comparable quality, we restricted the analyses of each successive brood to include only those beetles that went on to produce at least 3 further broods after the initial experimental brood. The results were qualitatively unchanged (data not shown).

Experiment 3—current fecundity, residual reproductive value, and the probability of brood desertion

Individuals given small broods to rear were more likely to desert offspring than were individuals initially given large broods to look after (small brood desertion = 16/52, large brood desertion = 5/52; $G^2 = 7.52$, $P = 0.006$). It might be argued that these results are relatively meaningless. With fewer larvae on the carcass in the first place, perhaps chance events meant that we were more likely to mistakenly score small broods as deserted than large broods. The results of Experiment 2 allow us to reject this alternative interpretation of the results. Experiment 2 revealed that males have greater residual reproductive value than females: Therefore, males should be more inclined to desert offspring than females. This is exactly what we found (female desertion = 5/50, male desertion = 16/54; $G^2 = 6.50$, $P = 0.011$).

DISCUSSION

The first finding of our experiments is that caring for offspring carries an associated fitness cost for parents, which is of a similar magnitude in each sex. Mothers and fathers that were induced to care for 20 larvae in their first breeding attempt subsequently produced approximately 10 fewer larvae during their lives than those that cared for just 5 larvae the first time they bred (Figure 1). Our results are consistent with the results of previous research on *Nicrophorus* beetles, which has shown that fitness costs associated with parental care are only evident at the third breeding attempt or later (e.g., Trumbo 1991; Jenkins et al. 2000; Satou et al. 2001). They are also in accord with work on other arthropods, which has shown that offspring guarding (e.g., Tallamy and Denno 1982; Gilg and Kruse 2003; Zink 2003; Buzatto et al. 2007) or provisioning (e.g., Nalepa 1988; Hunt and Simmons 2004; Field et al. 2007; Kölliker 2007) imposes a fitness cost on parents.

The second finding from our experiments was that males had a markedly greater residual reproductive value than females after the first breeding attempt (Figure 1), which is curious given that each sex was unconstrained by reproductive

Table 1
The number of beetles that survived for each successive breeding attempt in Experiment 2

Brood number	Female	Male
2	40	40
3	36	38
4	21	28
5	3	7

competition, both sexes were made to care single-handedly for their broods throughout their lifetime, and the fecundity costs of care were similar for each sex. Because neither of the first 2 conditions is likely to hold in nature, it might be argued that the results are simply an artifact of the experimental design. We concede that our experiments are likely to have overestimated residual reproductive value, but we think it is unlikely that they introduced a sex bias in this estimate, for the following reasons. For *Nicrophorus* beetles, the majority of reproductive success accrued by either sex is contingent on securing a carcass for reproduction (Eggert and Müller 1997; Scott 1998; Müller et al. 2007), although males can sire a few offspring by mating with females elsewhere (Müller et al. 2007). There is no indication from field studies that competition for the carcass especially penalizes one sex: Males and females had roughly similar numbers of offspring whether they were dominants or subordinates (Müller et al. 2007). Removing competition from our laboratory experiments is therefore unlikely to have favored one sex in particular. Experimental widowing is also unlikely to have caused a sex bias in our estimates of residual reproductive value. Although males and females each specialize in certain parental duties under conditions of biparental care, each is capable of performing the full range of tasks when widowed (e.g., Smiseth et al. 2005). The widowed males in our experiments were certainly dutiful fathers because they produced as many or more surviving larvae than widowed females. Our experimental design relieved males of the more hazardous acts of brood defense (Trumbo 2007), but the same was true for females (Trumbo 2007; Trumbo and Valletta 2007), so again, it seems unlikely that widowing introduced a systematic sex bias into our measurements of residual reproductive value.

If our experimental design cannot account for the sex differences in residual reproductive value that we found, then what biological reasons might explain them? One possibility is that females put more effort than males into initial carcass preparation, including defense from microbial attack (Rozen et al. 2008). In previous work, we showed that females had higher levels of antibacterial activity in their anal exudates than males (Cotter and Kilner 2009) but whether this imposes additional fitness costs on females remains to be determined. In this study, we used lumps of steak as a breeding resource, rather than mouse corpses, which probably reduced the effort involved in carcass preparation and may mean that any sex differences at this stage were negligible. Alternatively, perhaps the costs of egg production were responsible for limiting female fecundity (e.g., Bateman 1948; Wigby and Chapman 2005; Field et al. 2007). The males in our experiments were not exposed to these costs because they were paired with virgins each time they bred). Although we found no evidence that laying additional eggs reduced future fecundity (Experiment 1; see also Satou et al. 2001; Nagano and Suzuki 2007), it may be that egg laying carries a fixed cost that is independent of the number of eggs actually produced. It is also possible that the effort of laying a large clutch may exacerbate any reproductive costs sustained later during larval care in the same breeding attempt. We did not test this possibility because

we presented our experimental subjects only with small broods of 5 larvae. There may also be cumulative costs associated with repeatedly laying large clutches, which we were unable to detect with our experimental manipulation because it was confined to the first brood. Alternatively, or as a consequence (Kirkwood and Austad 2000), the sex difference in residual reproductive value might be attributable to a faster rate of reproductive senescence in females than in males. Although females showed a marked reduction in fecundity after their third brood, males were able to sustain production of viable offspring well beyond this point, either because they could produce more viable gametes at a later age or because older males were better at tending their offspring. Previous work has shown that older females are less capable of caring for larvae (Lock et al. 2007, but see Trumbo 2009). Perhaps males are similarly affected but only at a later age. Sexual dimorphism in reproductive senescence such as this has now been characterized for a diversity of species (Packer et al. 1998) including insects (e.g., Zajitschek et al. 2009), humans (e.g., Hawkes et al. 1998), fish (Reznick et al. 2006) and birds (Reid et al. 2003; Reed et al. 2008), and evolutionary explanations for this phenomenon are equally diverse (e.g., Hawkes et al. 1998; Lee 2003; Reznick et al. 2006; Bourke 2007; Bonduriansky et al. 2008). Burying beetles offer a tractable experimental system for disentangling some of these hypotheses in future work.

The final key finding of our experiments is that residual reproductive value and current brood size together predict brood desertion in the burying beetle. Experiment 2 showed that males have greater residual reproductive value than females, whereas Experiment 3 revealed that when current fecundity was experimentally reduced during the first breeding attempt, males were more likely than females to desert their offspring. With a greater residual reproductive value to defend, presumably males were more inclined than females to forego the costs of continuing to care for a small, unprofitable brood.

These experimental data can also explain patterns of brood desertion seen in naturally breeding *N. vespilloides*, such as the greater incidence of female-only care than male-only care (Müller et al. 2007). In addition, they clarify why males typically desert the brood before larval development is complete. Previous work suggests that the duration of male care is determined by the benefits of his continued presence on the carcass. Males stay as long as the carrion is sufficiently valuable to elicit a takeover bid by a competitor, but they leave when this threat dissipates because females are then capable of caring for larvae single-handedly (Eggert and Müller 1997). Our measurements of residual reproductive value suggest that the earlier timing of the male's decision to desert might additionally be influenced by the greater future fitness that males stand to gain, relative to continued care of the current brood.

Finally, our experimental results help to explain the evolution of the inferior alternative reproductive tactics shown by burying beetles, namely brood parasitism and satellite male behavior. Each of these alternative tactics features low current fecundity coupled with offspring desertion. Low fecundity results from reproductive suppression by a dominant beetle of the same sex residing on the carcass (Eggert and Müller 1992). Dominant females fight subordinate females to keep them away from the carcass (Eggert and Müller 1992), and the ensuing starvation (Eggert et al. 2008) prevents the completion of ovarian development (Scott and Traniello 1987; Trumbo et al. 1995; Steiger et al. 2007) resulting in small clutch sizes (Müller et al. 2007). Similarly, the dominant male attacks any subordinate males that approach the carcass, and its resident female, thus curtailing a subordinate's opportunities to mate (Eggert and Müller 1997) and greatly reducing his chance of siring young (Müller et al. 2007). The results of Experiment 3 show that the low current fecundity, which follows as a result

of reproductive suppression, then causes offspring desertion by both males and females.

On larger carcasses, reproductive suppression by dominants of either sex is far less complete (Eggert and Müller 1992, 1997) and subordinate fecundity rises (Müller et al. 1990, 2007; Eggert and Müller 1992, 1997). Our experimental results suggest that this means subordinates now gain by staying to care for offspring, and the result is joint breeding (Eggert and Müller 1992, 1997) with indiscriminate communal care of larvae (Müller and Eggert 1990; Eggert and Müller 1992, 2000). From the subordinate's perspective, the tipping point from brood desertion to communal breeding (or vice versa) therefore depends, at least partly, on the value of the current brood relative to residual reproductive value. This might explain why carcass size alone cannot predict the incidence of joint breeding or brood parasitism (Müller et al. 1990; Eggert et al. 2008). From the dominant's perspective, it remains unclear whether communal breeding is an optimal strategy (e.g., Vehrencamp 1983, 2000) or a suboptimal compromise (e.g., Johnstone 2000).

Although we can potentially explain the evolution of burying beetle social mating systems by analyzing individual optimization of current and future reproductive effort, this approach is less likely to be successful in other taxa with biparental care. In other species, it is much more likely that the fitness consequences of offspring desertion are frequency dependent (Székely et al. 1996; Balshine-Earn and Earn 1997; McNamara et al. 2000; Barta et al. 2002; Webb et al. 2002; Servedio and Hauber 2006; Steinhart et al. 2008) and so the decision to abandon young will be determined primarily by the availability of new mates who have themselves deserted offspring. By contrast, the burying beetles' dependence on scarce carrion for reproduction probably means that there is a perpetual pool of potential new partners who are available for reproduction not because they have already abandoned young but because they have yet to find a suitable carcass. This means that a burying beetle's decision to abandon offspring will be primarily influenced by their current brood size and their intrinsic ability to produce offspring in the future.

To sum up, we have shown that male burying beetles have greater residual reproductive value than females and that this, together with current brood size, can explain the incidence of brood desertion both in laboratory experiments (Experiment 3) and in natural breeding associations (Müller et al. 2007). The challenge for future work is to explain how this sexual dimorphism in intrinsic residual reproductive value arises and why it has evolved.

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