Best regards,
Scott Sakaluk

Ethology **104,** 553—564 (1998)

ISSN 0179-1613

Institut für Biologie I (Zoologie), Albert-Ludwigs-Universität, Freiburg

The 'Widow Effect' and its Consequences for Reproduction in Burying Beetles, *Nicrophorus vespilloides* (Coleoptera: Silphidae)

Scott K. Sakaluk, Anne-Katrin Eggert & Josef K. Müller

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

Abstract

Burying beetles tend their young on small vertebrate carcasses, which serve as the sole source of food for the developing larvae. Single females are as proficient at rearing offspring as male–female pairs, yet males opt to remain with their broods throughout most of the larval development. One potential benefit of a male's extended residency is that it affords him the opportunity of additional copulations with the female, which could ensure his paternity in a replacement brood should the female's first egg clutch fail to hatch. We tested this hypothesis by manipulating males' access to their mates during the production of replacement clutches, using genetic colour markers to determine the paternity of offspring. Females were induced to produce a replacement brood by removing their first clutch of eggs. In one experimental treatment, we removed the female's mate upon the removal of her first egg clutch ('widowed' females); in a second treatment, the female was permitted to retain her mate up until she produced a replacement clutch. There was no significant difference in paternity between males removed from females before the initiation of replacement clutches and those permitted to remain with their mates. However, widowed females produced fewer offspring in replacement broods than did females permitted to retain their mates. This difference occurred primarily because a significantly greater proportion of widowed females opted not to produce a replacement clutch, a result we refer to as the 'widow effect'. This widow effect was further shown in those replicates in which females of both treatments produced replacement clutches: widowed females took significantly longer to produce a replacement clutch than did females permitted to retain their mates. The loss of her mate could be a signal to a female that a take-over of the carcass is imminent. Her reluctance to produce a replacement clutch under these circumstances might constitute a strategy by which she conserves carrion for a subsequent reproductive attempt with an intruding male successful at ousting her previous mate. Regardless of its functional significance, the widow effect favours the extended residency of males and therefore contributes to the selective maintenance of male parental care.

Corresponding author: Scott K. Sakaluk, Department of Biological Sciences, Illinois State University, Normal, IL 61790–4120, USA. E-mail: sksakal@rs6000.cmp.ilstu.edu

Introduction

Burying beetles (Coleoptera: Silphidae) derive their name from their habit of burying small vertebrate carcasses, which serve as the sole food source for their young (Pukowski 1933). They are one of only a handful of insect taxa exhibiting elaborate biparental care (Zeh & Smith 1985). A male and female cooperate in

U. S. Copyright Clearance Center Code Statement: 0179-1613/98/1047–0553$14.00/0

burying a carcass, stripping it of its fur or feathers, and gradually forming it into a tightly compacted carrion ball (Pukowski 1933). The pair remains with its brood throughout the period of larval development (1–4 wk), although the male typically abandons the brood a few days before the completion of larval development (Bartlett 1988; Scott & Traniello 1990; Trumbo 1991). Both parents feed the larvae by regurgitating partially digested food directly into their mouthparts. They assist the larvae in securing access to the interior of the carrion ball by excising a small opening in the integument of the carcass (Eggert et al. 1988). Both parents also continually smear the carrion ball with oral and anal secretions (Pukowski 1933) that appear to retard the rate of decomposition (Halffter et al. 1983; Wilson & Fudge 1984; Bartlett 1988), thereby extending the period over which food is available to the young. In addition to attending to the nutritional needs and health of their offspring, the parents actively defend the carcass from take-overs by conspecific rivals and congeneric competitors. Intruders pose a serious risk to offspring of the resident adults because they inevitably kill any larvae present on the carcass and subsequently utilize the carcass for their own reproduction (Scott 1990; Trumbo 1990a).

The rarity of paternal care in arthropods undoubtedly stems from the limited ability of parents of either sex to enhance offspring survival (Zeh & Smith 1985). However, even in those instances where care does occur, there is a distinct bias toward maternal care that occurs because of a difference between the sexes in the trade-off between enhanced offspring survival and future reproduction (Maynard Smith 1997; Zeh & Smith 1985). Nowhere have the conditions favouring the evolution of male parental care been examined more widely than in birds, where the production of highly altricial young often requires substantial investment by both parents (review in Ketterson & Nolan 1994). Although it is assumed that the male's parental contribution is vital to the success of the brood in those species that are socially monogamous, removal experiments pioneered by Gowaty (1983) have revealed that in some species, a male's removal has no discernible effect on the reproductive success of the female (but see Alatalo et al. 1988). These studies call into question the ubiquity of benefits attributed to male parental care and raise the question as to why males do not routinely desert their mates (Gowaty 1983).

Just as has been true for birds, there has been considerable discussion concerning the extent to which burying beetle offspring benefit from having two attending parents as opposed to one (see review in Eggert & Müller 1997). Much of this discussion has centred on the extended residency of males, since males, unlike females, forego additional mating opportunities by remaining with the brood (Müller & Eggert 1987; Eggert & Müller 1989a,b). Such behaviour could only be construed as adaptive if the increase in offspring survival resulting from a male's cohabitation with his brood more than offsets any decrease in the number of offspring he sired as a result of lost mating opportunities. A number of laboratory studies have shown, however, that broods receiving uniparental care survive and grow equally well as those receiving biparental care (Bartlett 1988; Scott 1989; Reinking & Müller 1990; Trumbo 1991). Even under field conditions, male parental care does not appreciably enhance offspring fitness in the absence of congeneric competitors and conspecific rivals (Müller et al. 1998). Although some field studies have shown that male–female pairs have a lower frequency of take-overs than do single females (Trumbo 1990b, 1991; Robertson 1993), in other populations, beetle densities appear to be so low that take-overs are extremely rare, if they occur at all (Scott 1990, 1994). Moreover, even if a male's presence enhances retention of the carcass, this alone might not be sufficient to account for the extended residency of males because as the carcass is consumed by the larvae, its attractiveness, and hence the probability of take-overs, diminishes (Robertson 1993).

We suggest that the traditional emphasis on the benefits to offspring of male parental care (paternal-care hypothesis) may be misplaced, and that males derive more important fitness benefits through their extended residency via an increase in fertilization success (mating-effort hypothesis). Specifically, we suggest that males may remain with their broods primarily to secure additional copulations with their mates, which may enhance their fertilization success in at least three contexts. First, if a female opts to produce a replacement brood upon the failure of her eggs to hatch or the loss of her larvae to predators (Müller 1987), a male may increase the probability that his sperm will have precedence over those of a female's previous mates in subsequent fertilizations (Bartlett 1988; Müller & Eggert 1989; Trumbo 1991; Scott & Williams 1993). Second, repeated copulations by the resident male may reduce sperm competition from satellite males (defeated rivals that remain in the vicinity of the carcass and attempt surreptitious copulations with the female; Dressel 1987; Bartlett 1988). Finally, copulations that occur even after the majority of brood development has been completed may increase a male's fertilization success in subsequent batches of eggs laid by females upon the location of other carcasses. This would be especially important in those cases in which the female locates a carcass on which no male is present, because females readily bury carcasses in the absence of a mate, using stored sperm from previous matings with which to fertilize their eggs (Pukowski 1933; Müller & Eggert 1989).

In the present study, we focused exclusively on the benefits of the extended residency of males as they pertain to the paternity of males in replacement broods. We manipulated males' access to their mates during the production of replacement clutches and used genetic colour markers to determine the paternity of offspring. The mating-effort hypothesis predicts that males allowed to remain with mates should exhibit greater paternity in replacement broods than males removed from their mates prior to the initiation of a replacement clutch.

Methods

The study was conducted using beetles from two laboratory strains of *Nicrophorus vespilloides* ('light' and 'dark', respectively) that differed only in the coloration of their elytra, providing us with a genetic marker with which to assess the paternity of offspring (see Müller & Eggert 1989; Eggert & Müller 1992; Eggert 1992). The posterior half of the elytra of light individuals is red-orange and lacks the black band characteristic of wild-type individuals, whereas the posterior half of the elytra of dark individuals is almost entirely black. When a female of one strain is mated to a dark and a light male, the paternity of offspring is readily ascertained. Within-strain matings yield offspring that exhibit their parents' colour, whereas between-strain matings produce offspring that resemble the wild type. The strains were developed through inbreeding of beetles originally trapped within 15 km of Bielefeld, Germany, and reared under standardized conditions in the laboratory (e.g. Müller 1987; Müller & Eggert 1990; Eggert 1992). The fertility of potential male subjects was assessed by pairing them initially with wild-type females on carcasses and determining the percentage of all eggs laid that hatched. Only males exhibiting a minimum fertility of 75% (range = 75–100%) were used in experimental treatments.

Experimental females of one or the other colour strain were mated to a male of one colour strain (non-parental male), before being paired on a 15-g mouse carcass with a male of the alternative colour strain (parental male). Initial insemination of females by non-parental males was accomplished by confining male–female pairs in small plastic chambers for 24 h prior to carcass presentation; under these conditions, the beetles copulate, on average, about 20 times (Müller & Eggert 1989). This protocol mimics the natural situation in which a female typically arrives at a carcass as a non-virgin, with viable sperm in her spermatheca (Müller & Eggert 1989). All females were induced to produce replacement broods by removing their first clutch of eggs. Broods derived from these initial egg clutches were reared by foster parents (see Müller & Eggert 1989). Two experimental treatments were established immediately upon the removal of the female's first egg clutch (Fig. 1). In one treatment, the parental male was removed upon removal of the female's first clutch and hence had no opportunity to copulate with the female prior to the production of the replacement clutch. Females in this treatment are henceforth referred to as widowed females. In a second treatment, the parental male was permitted to remain with the female until the replacement clutch was produced and hence was afforded the opportunity to mate with the female prior to the production of the replacement clutch. Previous observations have revealed that when production of a replacement clutch becomes necessary, males resume copulations with females at a rate comparable to that which occurs during carcass burial and preparation (Eggert & Müller 1997). If males remain with females to ensure their paternity in replacement broods, we would expect that males allowed to remain with their mates would have greater paternity than those males removed prior to the production of replacement clutches.

The experiment was a paired design in which the two males used in one treatment ('a' pairings) were subsequently used in the alternative treatment ('b' pairings); the male designated as the parental male remained the same across both treatments and the females used in a and b pairings were full siblings. The two males used in one set of pairings were subsequently used in another set of a and b pairings in which the roles of non-parental and parental males were reversed; hence, this protocol controls for any variation in paternity resulting from intrinsic differences between rival males. The order in which males experienced the two treatments was reversed for every other replicate. Light and dark males were employed as parental males in an equal number of replicates, and the colour strain

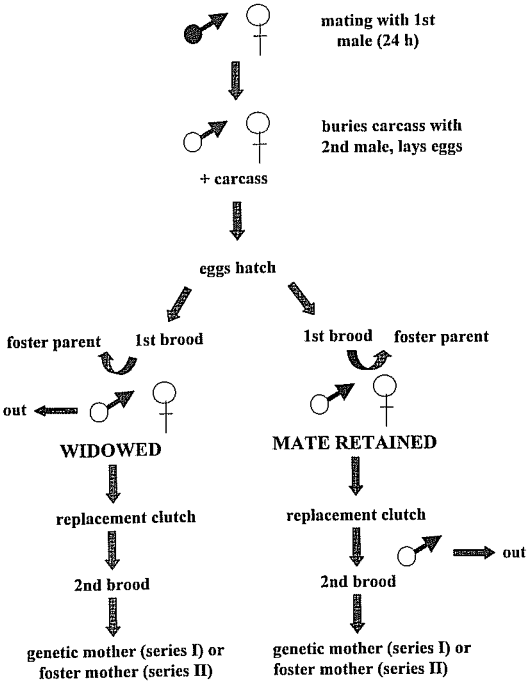

Fig. 1: Schematic of protocol used to establish experimental treatments. Females were inseminated first by a male of one colour strain (here, a dark male) before being paired on a carcass with a male of the other colour strain (here, a light male). Females were induced to produce a replacement clutch by removing their first clutch of eggs, at which time their mate was also removed (widowed females) or permitted to remain with the female (mate retained). The paternity of parental males in replacement clutches and number of offspring produced was compared across the two groups

of the female with which they were paired was reversed for every other replicate. These measures were taken to control for any variation in male reproductive success arising from differences across colour strains and to enhance our ability to detect any differences attributable to treatment should such exist.

Two experimental series, each using 20 replicates, were established that differed only in the manner in which offspring from the replacement brood were reared. In the first series (I), offspring were reared by their parents on the original carcass with which they had been provided, whereas in the second series (II), offspring were reared by foster parents on a new carcass that had previously been prepared for burial by non-experimental beetles. Carcasses tend to deteriorate over time (Müller 1987), and females in series I appeared to respond to this deterioration by killing a portion of their offspring; this does not constitute aberrant behaviour, as burying beetles typically adjust the size of their brood to match available resources by killing surplus larvae (Bartlett 1987; Trumbo 1990c). However, by using foster parents to rear offspring on freshly prepared carcasses in series II, we were able to ameliorate this brood adjustment and thereby maximize brood size, so that paternity determinations could be based on the largest possible sample sizes. This change in protocol does not confound comparisons involving paternity because these are determined on a percentage basis; however, in comparisons involving numbers of offspring produced by female siblings across treatments, 'series' was incorporated as a main effect in all statistical analyses.

In a number of instances, experimental females did not produce a replacement clutch or produced fewer than 10 offspring. In these instances, we repeated the treatment with a new female ('c' pairings), and used the offspring of replacement clutches derived from these supplementary pairings in calculating the percentage of offspring sired by each male. However, in comparisons involving the number of offspring produced by females of the two treatments, only data from primary pairings (a and b) were used, including those instances where reproductive failure occurred.

Experimental females and parental males were housed in clear plastic boxes (10 × 10 × 6 cm), half-filled with moistened peat. Experimental individuals were held in environmental chambers at 20°C, on a 16 h light/8 h dark photoperiod. After females had finished laying their replacement clutches, we searched the peat for eggs, which were subsequently hatched in Petri dishes on moistened tissue paper. Newly hatched larvae were placed back on the carcass with an attendant female (mother or foster mother) to complete their development. The end of larval development was marked by the departure of the larvae from the remains of the carcass (Eggert & Müller 1997). When this occurred, larvae were removed and placed in groups of 10 to undergo pupation in boxes filled with moistened peat. Boxes were held in complete darkness at 20°C. Under these conditions, the time to adult emergence was ≈ 20 d. Offspring emerging as adults from pupal cases were removed and scored with respect to the colour of their elytra to ascertain their paternity.

All statistical analyses were conducted using SYSTAT software for desktop computers (Wilkinson et al. 1996).

Results

The percentage of eggs fertilized by the parental male in the replacement clutch did not differ across treatments (paired t-test, $t = 1.20$, $df = 22$, $p > 0.05$). When the parental male was permitted to remain with the female until she produced a replacement clutch, his average paternity was 97.4% ± 0.02 (± SE, range = 55–100%), whereas when the parental male was removed upon removal of the female's first clutch, his average paternity in the replacement brood was 96.1% ± 0.02 (range = 57.7–100%).

A repeated-measures ANOVA was used to compare the number of offspring produced by females in replacement broods across treatments; in this analysis, series (I or II) was entered as a main effect and treatment (widowed or mate retained) was entered as the repeated measure. Three of the 40 replicates were not included in the analysis owing to the deaths of experimental individuals in one or the other treatment. As expected, series had a significant effect on the number of offspring produced in replacement broods, with females in series II producing more offspring than those in series I (F = 4.63, p = 0.038). More importantly, however, there was a significant effect of treatment on the number of offspring produced that was independent of the effect of series. Females that were permitted to retain their mates produced significantly more offspring in replacement broods than did widowed females (F = 4.87, p = 0.034, Fig. 2). There was no significant interaction between series and treatment (F = 0.57, p = 0.46). A similar repeated-measures ANOVA was used to compare treatments with respect to the number of offspring generated from the first clutches of females, which were removed to stimulate production of replacement clutches. There was no significant effect of series or treatment (offspring from first clutches were treated identically across series and treatments), nor was there any significant interaction between the two main effects (all $p > 0.05$). Hence, observed differences with respect to replacement clutches cannot be attributed to some intrinsic difference in the beetles assigned to the two different treatments.

The difference in the reproductive output of widowed females and those permitted to retain their mates can be explained by the proportion of females in each treatment that failed to produce a replacement clutch. Widowed females were significantly less likely to produce a replacement clutch than were females permitted to retain their mates (likelihood ratio χ^2, L = 7.56, p = 0.006; Fig. 3). This widow effect is also reflected in the time taken by females to produce a replacement brood, measured as the interval between the time at which the first larva in the replacement brood hatched and the time at which the first larva in the first brood hatched, minus 56 h – the time it takes an egg to hatch once it has been laid (Müller 1987).

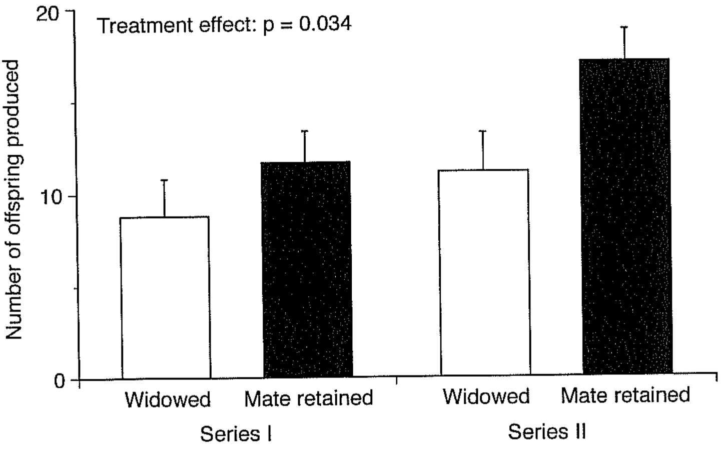

Fig. 2: Mean number of offspring produced in replacement broods by female burying beetles *Nicrophorus vespilloides* in two experimental series. Lines above bars represent one SE. Widowed females produced significantly fewer offspring than females permitted to retain their mates (repeated-measures ANOVA, F = 4.87, $p < 0.05$)

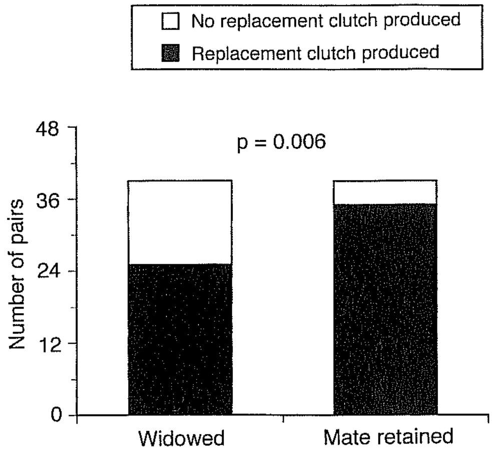

Fig. 3: The proportion of female burying beetles *Nicrophorus vespilloides* producing a replacement clutch upon experimental removal of the first egg clutch (solid portion of bar). A significantly lower proportion of widowed females produced a replacement clutch than did females permitted to retain their mates (likelihood ratio χ^2, L = 7.56, $p < 0.01$)

In those replicates in which females in both treatments produced a replacement clutch ($n = 21$), widowed females took significantly longer to produce a replacement clutch (55.0 ± 3.2 h, range = 29–78 h) than did females permitted to retain their mates (40.2 ± 4.3 h, range = 17–84 h; paired t-test, $t = 3.08$, $df = 20$, $p = 0.006$).

Discussion

Uniparental care in burying beetles occurs whenever a female locates a carcass that has not attracted any prospective mates, whereupon she buries it and uses sperm from previous matings to fertilize her eggs. Uniparental care in burying beetles occurs frequently under natural conditions (e.g. Scott & Traniello 1990; Trumbo 1991; Eggert 1992), and single females are as proficient at rearing offspring as two parents (e.g. Bartlett 1988; Scott 1989; Müller et al. 1998). Nevertheless, when a male and female jointly bury a carcass, the male remains with the brood throughout the majority of larval development (Bartlett 1988; Scott & Traniello 1990; Trumbo 1991). One potential benefit of a male's extended residency is that it affords him the opportunity of additional copulations with the female, which could ensure his paternity in a replacement brood should the female's first egg clutch fail to hatch. In the present study, however, males removed from females before the initiation of replacement clutches had the same paternity in replacement broods as males permitted continued mating opportunities. In both treatments the paternity of parental males in replacement broods exceeded 95%. We conclude, therefore, that the extended residency of males is not required to maintain the high level of sperm precedence in replacement broods that they have in initial broods (Bartlett 1988; Müller & Eggert 1989; Trumbo 1991; Scott & Williams 1993).

Although the paternity of males in replacement broods was uninfluenced by whether they were removed from, or retained with their mates following the removal of first clutches, this manipulation had a significant effect on the reproductive output of females. Specifically, widowed females produced fewer offspring in replacement broods than did females permitted to retain their mates. This difference occurred primarily because a significantly greater proportion of widowed females opted not to produce a replacement clutch. This widow effect was further shown by the time taken by females to produce a replacement clutch: in those replicates in which females in both treatments produced a replacement clutch, widowed females took significantly longer to produce one than did their siblings who were permitted to retain their mates. This latter feature of the widow effect has since been replicated in a follow-up study (Wussler et al. 1996).

The widow effect raises two important questions: 1. why are widowed females less willing to produce a replacement clutch than females whose mates have been retained? and 2. what consequences does the widow effect have for the reproductive tactics of males? We address each of the questions in turn.

Widowed females may opt not to produce a replacement clutch owing to energetic constraints: having helped to prepare and bury a carcass as well as produce an initial egg clutch, widowed females may lack the resources necessary to rear a replacement brood without the help of a male. If so, females' assessment of their own energy reserves may lead them to abandon a current reproductive attempt. Despite the intuitive appeal of this explanation, female burying beetles appear to be subject to remarkably few reproductive constraints once they have secured a carcass. Laboratory observations have revealed that single females presented with up to 12 carcasses in succession experience no diminution in reproductive output, provided that they have sufficient sperm with which to fertilize their eggs; such females survive as well and produce as many offspring as do females paired with males over a similar succession of reproductive opportunities (Müller, unpubl. data).The absence of reproductive constraints may stem from opportunities for females to feed on the carcass, thereby offsetting any energy expenditures on brood production or parental care. Hence, although a female's willingness to produce a replacement brood is influenced by the presence of her mate, it does not appear to be related to energetic considerations per se.

Alternatively, failure of the first egg clutch to hatch and the disappearance of the male might suggest a male partner of low vigour and/or genetic incompatibility (Zeh & Zeh 1996, 1997). If such were the case, a female could opt not to lay a replacement clutch if her eggs were likely to be fertilized by a male whose genetic attributes appeared to be less than desirable. However, the scarcity and ephemeral nature of carrion (see review in Eggert & Müller 1997) would appear to mitigate against the luxury of foregoing any reproductive opportunity, particularly since the production of a replacement brood does not appear to be especially costly in the first place.

Finally, failure of the first egg clutch to hatch, along with the disappearance of the male, might be a signal to the female that a take-over of the carcass was imminent. If the interloper were a conspecific male, his first act would be to consume any eggs or larvae present on the carcass before adopting the resident female as his mate (Scott 1990; Trumbo 1990a). Any subsequent egg clutch laid by the female would be fertilized principally by sperm of the usurper owing to the high level of last-male sperm precedence in burying beetles (Bartlett 1988; Müller & Eggert 1989; Trumbo 1991; Scott & Williams 1993). Under the uncertain circumstances surrounding the loss of a mate and failure of the first brood to hatch, a female might delay laying a replacement clutch because any larvae resulting from these eggs would invariably be killed by an intruding male. While the loss of a replacement brood would not constitute a serious energetic cost to the female (see above), the carrion she would need to consume to produce the doomed replacement clutch would leave fewer resources for a brood sired by the usurping male. Hence, the reluctance of females to produce a replacement clutch may constitute a strategy by which they conserve carrion for future reproductive attempts with males successful at ousting their current mates.

Regardless of why widowed females are reluctant to produce a replacement brood, such an effect might provide ample reason for males to remain with their mates even if their paternity in replacement broods was uninfluenced by their presence. If a male deserted his mate after she laid her eggs and a replacement brood became necessary later on, the male could conceivably suffer a decrease in fitness if the female opted not to produce a replacement clutch because of his absence. Deserting males can, however, secure additional mating opportunities, whereas males remaining resident with their broods cannot. Along with gaining increased time to locate a new carcass, deserting males also have the option of emitting pheromone in the absence of a carcass to attract females solely for copulation (Müller & Eggert 1987; Eggert & Müller 1989a,b). Whether these benefits are sufficient to offset the risk to a deserting male of foregoing a replacement brood depends on the availability of carcasses, the rate at which receptive females can be attracted via pheromone emission, and the frequency of replacement broods under natural conditions. There are few field data addressing any of these parameters (see review in Eggert & Müller 1997), but the rarity of brood desertion by males suggests that the benefits of desertion rarely, if ever, exceed the benefits of remaining with the brood. The present study suggests that, along with the improved defence of a carcass that a male's presence affords (Trumbo 1990b 1991; Robertson 1993), the widow effect may further contribute to the selective maintenance of male parental care.

Acknowledgements

We thank T. Ivy, C. Johnson, J. Schaus, S. Trumbo and an anonymous reviewer for helpful comments on the manuscript. This research was supported by grants from the Deutsche Forschungsgemeinschaft to J. K. Müller and A. K. Eggert, and grants from the National Science Foundation (DEB 91-07363 & INT-9224910) and Illinois State University, and a research fellowship from the Alexander von Humboldt Foundation to S. K. Sakaluk.

Literature Cited

Alatalo, R. V., Gottlander, K. & Lundberg, A. 1988: Conflict or cooperation between parents in feeding nestlings in the pied flycatcher *Ficedula hypoleuca*. Ornis Scand. **19,** 31—34.

Bartlett, J. 1987: Filial cannibalism in burying beetles. Behav. Ecol. Sociobiol. **21,** 179—183.

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

Dressel, J. 1987: The influence of body size and presence of females on intraspecific contests of males in the carrion beetle *Necrophorus vespilloides* (Coleoptera, Silphidae). Verh. Dtsch. Zool. Ges. **80,** 307.

Eggert, A.-K. 1992: Alternative male mate-finding tactics in burying beetles. Behav. Ecol. **3,** 243—254.

—— & Müller, J. K. 1989a: Pheromone-mediated attraction in burying beetles. Ecol. Entomol. **14,** 235—237.

—— & —— 1989b: Mating success of pheromone-emitting *Necrophorus* males: do attracted females discriminate against resource owners? Behaviour **110,** 248—257.

—— & —— 1992: Joint breeding in female burying beetles. Behav. Ecol. Sociobiol. **31,** 237—242.

—— & —— 1997: Biparental care and social evolution in burying beetles: lessons from the larder. In: The Evolution of Social Behavior in Insects and Arachnids (Choe, J. C. & Crespi, B. J., eds). Cambridge Univ. Press, Cambridge. pp. 216—236.

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

Gowaty, P. A. 1983: Male parental care and apparent monogamy among eastern bluebirds (*Sialia sialis*). Am. Nat. **121,** 149—157.

Halffter, G., Anduaga, S. & Huerta, C. 1983: Nidification des *Necrophorus*. Bull. Soc. Entomol. Fr. **88,** 648—666.

Ketterson, E. D. & Nolan, V., JR. 1984: Male parental behavior in birds. Annu. Rev. Ecol. Syst. **25,** 601—628.

Maynard Smith, J. 1977: Parental investment: a prospective analysis. Anim. Behav. **25,** 1—9.

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

—— & Eggert, A.-K. 1987: Effects of carrion-independent pheromone emission by male burying beetles (Silphidae, *Necrophorus*). Ethology **76,** 297—304.

—— & —— 1989: Paternity assurance by 'helpful' males: adaptations to sperm competition in burying beetles. Behav. Ecol. Sociobiol. **24,** 245—249.

—— & —— 1990: Time-dependent shifts between infanticidal and parental behavior in female burying beetles: a mechanism of indirect mother–offspring recognition. Behav. Ecol. Sociobiol. **27,** 11—16.

——, —— & Sakaluk, S. K. 1998: Carcass maintenance and biparental brood care in burying beetles: are males redundant? Ecol. Entomol. **23,** 195—200.

Pukowski, E. 1933: Ökologische Untersuchungen an *Necrophorus* F. Z. Morphol. Ökol. Tiere **27,** 518—586.

Reinking, M. & Müller, J. K. 1990: The benefit of parental care in the burying beetle, *Necrophorus vespilloides*. Verh. Dtsch. Zool. Ges. **83,** 655—656.

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

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

—— 1990: Brood guarding and the evolution of male parental care in burying beetles. Behav. Ecol. Sociobiol. **26,** 31—39.

—— 1994: Competition with flies promotes communal breeding in the burying beetle, *Nicrophorus tomentosus*. Behav. Ecol. Sociobiol. **34,** 367—373.

—— & Traniello, J. F. A. 1990: Behavioural and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). Anim. Behav. **39,** 274—283.

—— & Williams, S. M. 1993: Comparative reproductive success of communally breeding burying beetles as assessed by PCR with randomly amplified polymorphic DNA. Proc. Natl. Acad. Sci. USA **90,** 2242—2245.

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

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

—— 1990c: Reproductive success, phenology and biogeography of burying beetles (Silphidae, *Nicrophorus*). Am. Midl. Nat. **124,** 1—11.

—— 1991: Reproductive benefits and the duration of paternal care in a biparental burying beetle, *Necrophorus orbicollis*. Behaviour **117,** 82—105.

Wilkinson, L., Blank, G. & Gruber, C. 1996: Desktop data analysis with SYSTAT. Prentice Hall, Upper Saddle River.

Wilson, D. S. & Fudge, J. 1984: Burying beetles: intraspecific interactions and reproductive success in the field. Ecol. Entomol. **9,** 195—203.

Wussler, G. L., Müller, J. K., Eggert, A.-K. & Sakaluk, S. K. 1996: Do female burying beetles mourn the loss of their mates? Verh. Dtsch. Zool. Ges. **89,** 266.

Zeh, D. W. & Smith, R. L. 1985: Paternal investment by terrestrial arthropods. Am. Zool. **25,** 785—805.

Zeh, J. A. & Zeh, D. W. 1996: The evolution of polyandry I: intragenomic conflict and genetic incompatibility. Proc. Roy. Soc. Lond. B **263,** 1711—1717.

—— & —— 1997: The evolution of polyandry II: post-copulatory defences against genetic incompatibility. Proc. Roy. Soc. Lond. B **264,** 69—75.

Received: August 28, 1997

Accepted: December 15, 1997 (J. Brockmann)