REPRODUCTIVE BENEFITS AND THE DURATION OF PATERNAL CARE IN A BIPARENTAL BURYING BEETLE, NECROPHORUS ORBICOLLIS

by

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Introduction

Iteroparous breeders either must invest in an ongoing reproductive attempt or seek additional breeding opportunities. Such life history tradeoffs are the basis of current notions of parental investment (TRIVERS, 1972; MAYNARD SMITH, 1977; GRAFEN & SIBLEY, 1978; LOW, 1978) and suggest that patterns of parental care depend on the parent's ability to enhance the survival of current offspring relative to its ability to achieve reproductive success elsewhere (ROBERTSON & BIERMAN, 1979; PRESSLY, 1981).

Experimental work under natural conditions on reproductive benefits and the duration of parental care in insects is rare (reviews in WILSON, 1971; HINTON, 1977; ZEH & SMITH, 1985; TALLAMY & WOOD, 1986). Removal experiments demonstrate that parental care can reduce predation or parasitism (EBERHARD, 1975; PECKHAM, 1977; WOOD, 1978; MELBER *et al.*, 1980; TALLAMY & DENNO, 1981; WYATT & FOSTER, 1990) and can protect larvae in a physiologically difficult environment (SMITH, 1980; WYATT, 1986). Little effort has been made, however, to

systematically vary the context of care-giving and thereby alter the benefits of care or to examine variation in the duration of care.

To understand the evolution and variation of paternal care it is necessary to estimate benefits a male receives by providing care in the field and to examine plasticity of male behavior. In this study we examine the reproductive benefits and duration of paternal care in *Necrophorus orbicollis* Say. Similar studies of *N. orbicollis* have shown that the presence of a male parent reduced the number of larvae raised on a carcass but decreased the probability of a takeover by an intruder introduced near the carcass. No environmental or social variables affected male residence time as determined by multiple regression analysis (Scott, 1989; Scott, 1990; Scott & Traniello, 1990).

In this study I: estimate the reproductive benefits of paternal care on small and large carcasses in the field; extend the finding that males reduce takeovers by demonstrating that this occurs when competitors are free-flying beetles; find that males decrease the time that a large carcass is vulnerable to a takeover; find no evidence that males decrease other components of reproductive success; and determine that three variables (carcass size, the developmental stage of the larvae and the presence of the female) affect the duration of male care. I relate a longer duration of care on larger carcasses to estimates of reproductive benefits from the field and rule out two alternative hypotheses for more care on larger carcasses. In addition, the effect of prior reproduction on a male's reproductive success and residence time in a subsequent reproductive attempt is examined.

The study animal.

Parental care in *Necrophorus* is one of the most highly developed among the Coleoptera (Wilson, 1971; Zeh & Smith, 1985). Male and female burying beetles independently arrive at small vertebrate carcasses and compete with conspecifics of the same sex and heterospecifics until a single dominant pair remains (Pukowski, 1933; Milne & Milne, 1976). If a male fails to locate the carcass a lone female uses stored sperm to produce a clutch (Bartlett, 1988; Müller & Egbert, 1987). The single female or pair then inters the carcass, removes hair or feathers, rounds the carcass into a brood ball, deposits anal secretions, regurgitates to larvae and makes repairs in the crypt (Pukowski, 1933; Halftter *et al.*, 1983; Bartlett, 1988). A male that cooperates with a female in burying a carcass fathers over 90% of the brood (Müller & Eggert, 1989). At

the time of dispersal, mean mass of larvae is equivalent over a wide range of carcass sizes because parents adjust brood size to match carcass size (OTRONEN, 1988; TRUMBO, 1990b; TRUMBO, 1990c) by killing excess young on smaller carcasses (BARTLETT, 1987). Although either parent alone is competent to produce a normal brood (SCOTT, 1989), the male parent generally deserts first (PUKOWSKI, 1933; WILSON & FUDGE, 1984; BARTLETT, 1988; SCOTT & TRANIELLO, 1990). Both males and females can breed more than once in a season (BARTLETT & ASHWORTH, 1988; SCOTT & TRANIELLO, 1990a).

After a pair has initiated reproduction, residents become aggressive toward intruders of both sexes (SCOTT, 1990). Intruders that successfully take over a carcass tend to be larger than the same-sex resident they replace. Successful intruders kill any larvae on the carcass and appropriate the resource for their own reproductive benefit (SCOTT, 1990; TRUMBO, 1990a).

Methods

Reproductive benefits and the duration of paternal care in the field.

The initial study was conducted at the University of Michigan Biological Station (UMBS) near Pellston, Michigan (described in WILSON & KNOLLENBERG, 1984). During June and July of 1985 and 1986, *N. orbicollis* was collected in pitfall traps baited with approximately 200 g of carrion. Traps were located at least 2 km from experimental sites. Mixed sex groups of 10-20 beetles were housed in plastic containers for 10-20 days and fed small pieces of chicken livers (<2 g) before being used in field trials. All females tested in the laboratory under these conditions were able to produce a brood without male assistance (N = 12). Body length was measured as the distance from the tip of the mandibles to the edge of the elytra. Beetles were marked by clipping off a small part of the posterior edge of one elytron. All carcasses used in field experiments were laboratory *Mus musculus* L. that were killed with CO_2, frozen until needed, and thawed overnight in a refrigerator prior to trials.

Ten transects, separated by a minimum of 100 m, were established in a birch-beech-aspen secondary woodland (12 points/transect with 15 m intervals between points). To measure the effect of a male's presence on reproductive success, I placed either a single female or a pair of beetles on either a small or large mouse carcass during the periods of 29 June to 3 August, 1985 and 24 June to 13 July, 1986. Opposite ends of a 1 m length of dental floss were tied to a stake and to the hind leg of the mouse to help locate the carcass after burial. The carcass was placed adjacent to the stake and beetles were deposited into a small depression in the ground and covered loosely with soil. Leaf litter which had been removed from the site during the procedure was then replaced. The setup was covered with an inverted plastic pot (23 cm diameter) for 1 day to prevent rivals from contesting the resource during interment. The pot was pressed 2 cm into the sand and banked with soil. Carcasses moved away from the stake by the next morning were categorized as accepted and were subsequently left uncovered for the remainder of the trial (also see TRUMBO, 1990a).

Small carcasses were exhumed on day 10 or 11 and large carcasses on day 11 or 12 (see Table 1). Trials were staggered so that broods that had reached a similar stage of

larval development on small and large carcasses could be compared. In order that the number of larvae could be determined accurately and that a profile of the duration of paternal care relative to larval development could be ascertained, carcasses were exhumed before larvae had completed feeding and dispersed. Therefore, mean mass of individual larvae at exhumation is an estimate of larval development rather than size at dispersal.

Nests were exhumed by removing leaf litter in the vicinity of the nest, carefully digging down to the crypts and searching the surrounding soil within a 30 cm radius. Tunnels leading away from the crypt were followed up to 50 cm. Upon exhumation, the presence of marked and unmarked adults, number of larvae and mass of the entire brood were determined. In 1986 only, the size of the depleted carcass and the depth of the burial chamber were also measured. A nest containing only marked adults and larvae was classified as a success, a nest with any unmarked adult as a takeover, a nest with marked adults and no larvae a brood failure, and a carcass that was removed from the site as scavenged.

The methodology was designed to avoid two potential problems. I sealed the enclosure with sand to prevent beetles from leaving without discovering the carcass. This prevented intruders from 'replacing' the resident without confrontation. The low frequency of intrusion on small carcasses established with pairs (6.1%, $N = 98$) confirms that beetles were not readily leaving the enclosure since some level of intrusion is expected in all treatments. Careful exhumations were done to catch all beetles in and around the nest that were actually present. Previous work (PUKOWSKI, 1933; SCOTT & TRANIELLO, 1990) suggests that nearly all females should be present with broods that have not yet reached their dispersal size. I found 93.1% ($N = 101$) of females present with broods whose mean mass of individual larvae ≤ 0.32 g. A desertion rate of 7% is comparable to the frequency of females departing before their mates from a study in which all individuals were trapped as they left the nest (SCOTT & TRANIELLO, 1990) and confirms that overlooking beetles at exhumation was not a problem.

Since all beetles were protected from competitors for 24 h, the reproductive success of a single female was an estimate of a male's reproductive success had he mated with a female and deserted after the first day. I calculated the reproductive benefits (B) a male gains from parental care on small and large carcasses as follows:

$$B = S \left\{ (P_{MF})(L_{MF}) - (P_F)(L_F) \right\}$$

where S is the resident male's paternity in the brood, P is the probability of a success, equal to 1 − (probability of takeover + probability of brood failure + probability of scavenge). L is the mean number of larvae produced in successful reproductive attempts. The subscript MF denotes that a pair was established on a carcass and F denotes that a single female was established. Benefits of paternal care are determined by subtracting the overall reproductive success of single females $S(P_F \times L_F)$ from the overall reproductive success of pairs $S(P_{MF} \times L_{MF})$. Thus, B is an estimate of the number of additional larvae that are produced as a consequence of male care.

Stepwise discriminant procedures and discriminant analysis (SAS, 1985) were used to examine male desertion. Ten variables selected a priori were examined for their ability to predict whether or not the male had deserted prior to exhumation. These were: year, day of exhumation, mean mass of individual larvae (MMSL), original carcass mass (CMAS), carcas mass remaining at exhumation (1986 only), number of larvae, male length, female length, the difference between male and female length, and burial depth (1986 only).

The incorporation of variables into models using stepwise procedures can be sensitive to the order in which variables are considered, the method of selection and particular combination of variables considered, and the significance criteria to enter and remove variables in the model (STEVENS, 1986). Therefore, these parameters were varied

systematically to pinpoint variables that were consistently related to male desertion (across models and across years) in a highly significant manner. Only two variables (MMSL and CMAS) met these criteria. The particular analyses reported are stepwise selection models calculated separately for each year with the significance criteria for entry into and elimination from the model = 0.30. The variable year was investigated by analysing data from both years in a single model before employing stepwise discriminant procedures.

Discriminant analysis then was used to calculate standardized coefficients for each variable selected by the stepwise procedures. The ability of models based only on MMSL and CMAS to predict desertion also was examined. Separate models were generated from 1985 and 1986 data and then tested with results from both years to determine their ability to classify correctly whether males had deserted from the carcass by the time of exhumation. The known (or prior) probability of desertion was not incorporated into these models (see SAS, 1985). Each of the other 8 variables was then incorporated separately into models based on MMSL, CMAS and a third variable to determine whether the models' ability to predict male desertion could be improved.

Effect of prior reproduction.

A first attempt to examine the effect of prior reproduction on subsequent reproductive success and paternal behavior was undertaken at Duke Forest (DF), Durham Co., North Carolina and at UMBS in 1986. At DF, males were trapped as before from May 11-16, and at UMBS from June 17-21. Males were fed for 5-10 days and then divided into two groups. Treatment 1 males were each paired with a female and provided with a 21-24 g mouse on which to breed in the laboratory. After 9 days, males were removed and maintained for 1-2 days on a quantity of chicken liver (2 g) which was too small for a breeding resource but which was adequate for feeding requirements. Treatment 2 males were maintained during the entire period on chicken livers but were not given an opportunity to reproduce or provide parental care. Males from both treatments were then paired with a female and isolated for 2 days before being placed in the field. Females had been trapped 10-14 days prior to isolation.

At DF, 3 transects (16 points/transect, 15 m intervals between points) were established in an oak-pine woodland. From 2-4 June, a burying beetle pair along with a mouse carcass (33-36 g) was placed on each transect point for a total of 48 experimental placements. The order of placement on transect points was determined randomly. Subsequent procedures were similar to the previously described field experiment except that the cover was left over the carcass for 48 h, all carcasses were exhumed on Day 10, and injuries to legs and antennae of marked adults were noted.

At UMBS, 4 transects (10 points/transect) were established. Over a 4 day period (11-14 July), a beetle pair provided with a mouse carcass (18-21 g) was placed at each transect point. Nearly every transect point was used twice and a total of 73 experimental placements were made. Set-ups established near the same transect point were initiated 3 days apart and placed at least 4 m apart. Subsequent procedures were similar to the trials conducted at DF except that carcasses were exhumed on Day 9. The large majority of males in these trials probably had not completed a reproductive attempt prior to trapping. To do so would have required males to initiate reproduction by the first week of May at DF and by the first week of June at UMBS. This is when *N. orbicollis* begins to appear at single mice at these two sites (WILSON *et al.*, 1984; TRUMBO, unpubl. results).

Laboratory experiments.

The effect of the presence of a mate on the duration of parental care, and the comparative reproductive success of pairs, single females and single males was examined in two

laboratory experiments in 1990. F_2 beetles bred from wild stock were reared at 23°C and 15L:9D. In the first experiment, males and females were paired 1 day before being provided a 21-24 g carcass. Beetles were then placed into plastic containers (8 × 15 × 30 cm) filled with soil, and a carcass was presented beneath a paper towel. Male pronotal width, female pronotal width and carcass mass were controlled variables; means varied less than 2% across treatments. Four treatments were established: In Treatment 1, only the female was placed in the container with the carcass; in Treatment 2 both the male and female were placed in the container with the carcass but the male was removed on day 4; in Treatment 3 the female was removed on day 4; and in Treatment 4 the nest was disturbed on day 4 but no beetles were removed.

On day 4 the containers were covered with a plywood sheet which had a 9 cm hole in the center. An inverted cone of window screen was inserted into the hole, allowing beetles to disperse from the nest area through a narrow opening. A paper towel was crumpled in the cone to facilitate beetles' access. Fluon-covered tape was placed in a belt around the outside of the cone to prevent beetles from re-entering the container after exiting through the cone. The inverted cone was covered with a plastic cup which was removed 3 times daily {23 h A.Z.T. (Arbitrary Zeitgeber Time, PITTENDRIGH, 1965), 5 h A.Z.T. and 15 h A.Z.T.} to determne whether beetles had left the container. Larvae dispersed from the carcass and pupated in the soil. At emergence, the adult offspring were weighed and counted. Beetles apparently did not wander out of the container when desertion was not "intended". Beetles remained with larvae until approximately the same developmental stage as in field trials (see Treatment 3 for a possible exception) and all individuals except one emerged from the container during the natural flight period for this species (between 23 h and 5 h A.Z.T., see WILSON & KNOLLENBERG, 1984). In addition, for males caring alone and for females, only one individual emerged between days 5 and 9.

In the second experiment, two treatments were established. In Treatment 5, the female was removed on the first day that larvae appeared and in Treatment 6 the nest was disturbed on the first day that larvae appeared but both sexes were allowed to remain on the carcass. On the night the male deserted the cover was removed and larvae were counted. If larvae had not dispersed they were returned to the carcass and the number of days until dispersal was determined. In Treatment 6 the female was not returned to the carcass with larvae on the day the male deserted.

Results

Reproductive benefits in the field.

Of the 339 carcasses placed in the field, 316 were both accepted by beetles and not scavenged during the trial. For each treatment shown in Table 1, there were no significant differences between years in the proportions of carcasses with intruders (all $P > 0.10$, G tests). Therefore, results for the two years were combined for analysis. The probability that the intruder would be found on the carcass at exhumation was related significantly to both carcass size and number of parents established as residents. There was no carcass size-number of parents interaction (Fig. 1a). The percentage of takeovers from pairs was approximately half that of single females on both large and small carcasses. However, when small and large carcasses are considered separately, pairs suffered significantly

TABLE 1. The placement of beetles in the field according to carcass size, number of parents and eventual day of exhumation

	Day of exhumation	
Small carcasses (10-18 g)	Day 10 single females (20)[a] pairs (52)	Day 11 single females (37) pairs (52)
Large carcasses (30-33 g)	Day 11 single females (48) pairs (50)	Day 12 single females (31)[a] pairs (49)

On each day (N = 17) that the experiment was run in 1985, placements were: a pair on each of 4 large mice; a pair on each of 4 small mice; a single female on a large mouse; and a single female on a large mouse. On each day in 1986, placements were: a pair on each of two large mice; a pair on each of two small mice; a single female on each of three large mice; and, a single female on each of two small mice. Some transect points were used a second time after the original carcass had been removed. Sample sizes are shown in parentheses (total, 339). [a] = 1986 only.

fewer takeovers on large carcasses (G = 10.49, P < 0.001) while there was no difference on small carcasses (G = 0.77, ns; G tests of 2×2 contingency tables using William's correction). A sample size of over 400 would be required to demonstrate a significant difference at the low rate of takeovers on small caracasses (11.5% for single females, 6.1% for pairs).

The number of young in successful broods (at least 1 larva and no intruder present) was related significantly to carcass size but not the number of parents established at the beginning of the trial (Fig. 1b).

Carcass size had a weak effect on mass of individual larvae at exhumation (Fig. 2a, b). While the number of parents had no effect on larval size, there was a significant interaction between carcass size and number of parents. When large carcasses are considered alone, pairs had significantly larger larvae at exhumation than single females when the variables year, day of exhumation and date are controlled statistically (F = 8.90, P < 0.001, N = 117).

On large carcasses with larvae, the mean (± SE) body length of males (21.0 ± 0.2, N = 76) was greater than the body length of males which did not produce a brood because of a takeover or nest failure (19.4 ± 0.5, N = 17, z = 2.75, P < 0.01, Mann-Whitney U test). On small carcasses, there was no effect of male size (P > 0.2).

For small carcasses, B (estimate of the number of additional larvae produced as a consequence of male care; see Methods)

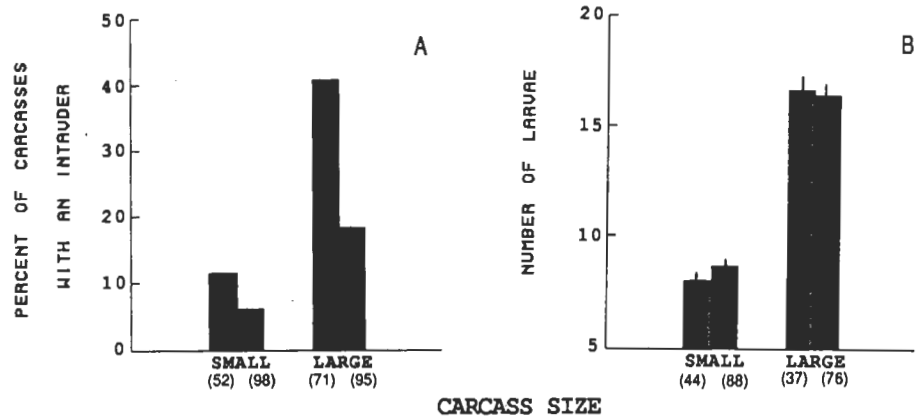$$= 0.92 \{(0.87) (8.7) - (0.85) (7.9)\} = 0.78$$

Fig. 1. (A) Percent of carcasses with an intruder (unmarked adult) at the time of exhumation for carcasses established with single females (gray bars) and pairs (black bars). Sample sizes are shown in parentheses. Hierarchical log-linear analysis of $2 \times 2 \times 2$ contingency table (SOKAL & ROHLF, 1981): Carcass size × Intrusion, $G = 20.03$, $P < 0.001$; Number of parents × Intrusion, $G = 11.00$, $P < 0.001$; Carcass size × Number of parents × Intrusion, $G = 0.40$, ns. (B) Mean ($\pm$ SE) number of larvae produced, threeway ANOVA: carcass size, $F = 321.46$, $P < 0.001$; year, $F = 0.08$, ns; number of parents, $F = 0.17$, ns. No two-way interactions were significant.
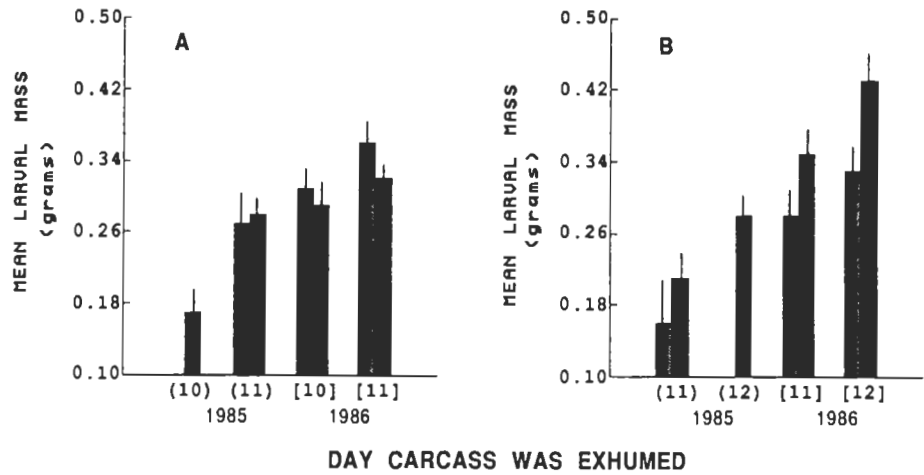

DAY CARCASS WAS EXHUMED

Fig. 2. Mean ($\pm$ SE) mass of individual larvae at exhumation on small (A) and large (B) carcasses established with single females (gray bars) and pairs (black bars). $N \geq 13$ for each sample except single females, large carcass, Day 11, 1985 ($N = 6$). Multiway ANOVA, $N = 245$, Carcass size (1) $F = 5.96$, $P < 0.02$; Number of parents (1) $F = 1.83$, ns; Year (1) $F = 91.26$, $P < 0.001$; Day of exhumation (2) $F = 9.70$, $P < 0.001$; Date (3) $F = 14.13$, $P < 0.001$; Carcass size × Number of parents interaction (1) $F = 8.15$, $P < 0.01$. The reproductive season was divided into 4 equal periods to examine the effect of 'Date' on larval size at exhumation.

For large carcasses:

$$B = 0.92 \; (\{(0.78) \; (16.2) - (0.51) \; (16.8)\} = 3.74$$

The estimate of paternity was determined using a genetic marker (TRUMBO & FIORE, unpubl. results) and is the same paternity estimate for *N. vespilloides* Herbst (MÜLLER & EGBERT, 1989). Only data from carcasses accepted by beetles were used in calculations. Paternal care produced more than four times the reproductive benefits on large as compared to small carcasses.

Duration of care in the field.

The proportion of males and females that deserted during trials on carcasses of different sizes is shown in Table 2. My measure of paternal care was the length of time a male stayed on the carcass relative to the developmental stage of the larvae. Mean mass of individual larvae was used as an estimate of larval development.

Only two variables had a consistent and significant effect on desertion. Mean mass of larvae (MMSL) was related positively to desertion (1985, $F = 22.23$, $r^2 = 0.20$, $P < 0.001$; 1986, $F = 6.98$, $r^2 = 0.10$, $P = 0.01$) and carcass mass (CMAS) was related negatively to desertion (1985,

TABLE 2. The proportion of males and females that were present or absent on the carcass at exhumation

Established as pairs Carcass size	Small	Large
N	87	73
Female present, male present	0.10	0.63
Female present, male absent	0.77	0.28
Female absent, male present	0.03	0.05
Female absent, male absent	0.09	0.03
Established as single females Carcass size	Small	Large
N	44	37
Female present	0.86	0.86
Female absent	0.14	0.14

Only nests containing larvae and without adult intruders included. Four additional cases were excluded because of known mortality of a resident or unidentified individual during the trial.
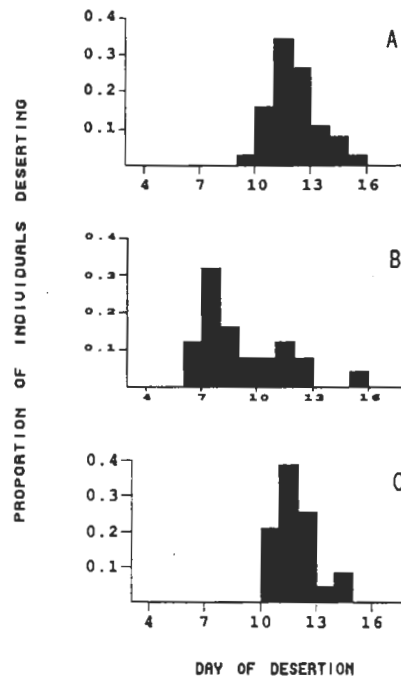
Fig. 3. Percent of resident males that were established on small (open bars) and large (hatched bars) carcasses that were found at exhumation as a function of mean mass of individual larvae within the brood. Sample sizes are shown at the base of the bar graphs. * = P < 0.10, ** = P < 0.01, Fisher's Exact tests.

$F = 38.00$, $r^2 = 0.30$, $P < 0.001$; 1986, $F = 42.90$, $r^2 = 0.40$; $P < 0.001$, Stepwise discriminant analysis, see Methods). It is clear that at all stages of larval development, males were more likely to have deserted from small rather than large carcasses (Fig. 3).

Four variables were correlated with either MMSL (year and day of exhumation) or CMAS (remaining carcass mass and number of larvae) and therefore were also correlated with desertion. None of these variables, however, had a consistent and independent effect on the probability of desertion (all $P > 0.15$ for each year investigated, stepwise discriminant analysis). The remaining 4 variables {male length, female length, the difference between male and female length, (all $P > 0.15$) and burial depth ($P = 0.11$, 1986 only)} did not affect nor were they correlated with male desertion. Table 3 gives the standardized discriminant coefficients for all variables that were selected by the stepwise procedure for either year.

TABLE 3. Standardized discriminant coefficients for variables selected by stepwise discriminant procedures

	1985	1986
Carcass size	−1.647	−3.254
Mean mass of larvae	1.094	1.186
Number of larvae	−0.545	−0.845
Burial depth	−	0.767
Day of exhumation	−	0.661
Male size	−	0.608

Using discriminant analysis, models incorporating only MMSL and CMAS were developed to predict whether a male would be on the carcass at exhumation (see Methods). The model generated from 1985 data correctly predicted 80.2% of 1985 cases (N = 91) and 82.6% of 1986 cases (N = 69). The 1986 model correctly predicted 79.1% of 1985 and 81.2% of 1986 cases. In both 1985 and 1986, the addition of a third variable only increased the number of accurately predicted cases by one at most.

Effect of prior reproduction.

All Treatment 1 males survived the reproductive attempt in the laboratory and were placed in the field. Treatment 2 males (no reproductive attempt in the laboratory) were not more likely to produce a brood at either Duke Forest (DF) or at The University of Michigan Biological Station (UMBS; Table 4). There was no evidence that Treatment 2 males produced more young or had larger young at the end of the trial than Treatment 1 males in successful reproductive attempts at either site. In addition, there was no treatment effect on the duration of parental care on nests with young at DF or UMBS. The higher rate of desertion at DF compared to UMBS likely can be explained by faster larval development at warmer temperatures. Of beetles that were established on a carcass and still present at exhumation, 18% at UMBS and 29% at DF received a leg or antennal injury during the trial. Injury rates did not differ for males and females (UMBS, $N_M = 39$, $N_F = 61$, $G = 0.29$, $P > 0.2$; DF, $N_M = 6$, $N_F = 18$, Fisher's Exact Probability = 0.41, $P > 0.2$).

TABLE 4. Reproductive success of males in Duke Forest and the University of Michigan Biological Station

	Duke Forest		UMBS	
	Treatment 1	Treatment 2	Treatment 1	Treatment 2
Number of carcasses	22	26	37	36
Mean (± SE) body length of males	19.5 (0.50)	20.7 (0.46)	20.2 (0.38)	20.1 (0.30)
Mean (± SE) body length of females	20.4 (0.41)	20.0 (0.24)	20.2 (0.43)	20.2 (0.34)
Number that produced larvae	15	13[a]	31	28[b]
Mean (± SE) number of larvae per brood	13.1 (1.44)	15.3[c] (1.53)	11.5 (0.53)	10.1[d] (0.64)
Mean (± SE) mass of larvae (g) at exhumation	0.39 (0.3)	0.33[e] (0.3)	0.25 (0.2)	0.27[f] (0.2)
Percent of carcasses containing larvae and resident male at exhumation	20	15[g]	61	68[h]

All tests of significance are within site. [a] $G = 0.86$, $P > 0.2$, G test; [b] $G = 0.21$, $P > 0.2$; [c] $U = 72$, $P > 0.2$, Mann-Whitney U test; [d] $U = 347$, $P > 0.1$; [e] $U = 63.3$, $P > 0.1$; [f] $U = 375.5$, $P > 0.2$; [g] $P = 0.57$, Fisher's Exact test; [h] $G = 0.14$, $P > 0.2$.

Laboratory experiment.

In the first laboratory experiment, there were no significant differences among Treatments 1-4 in the number of adult offspring produced or the mean mass of offspring at adult emergence (Table 5). There was no treatment effect on female residence time but a highly significant effect on male residence time on those carcasses that produced broods. Male residence time in Treatment 3 (female removed on day 4) was not significantly different than female residence times in Treatments 1, 2 and 4 (combined data set for females, $U = 241$, $P = 0.18$, Mann-Whitney U test). Four males in Treatment 3 left the container shortly after female removal and produced no offspring. Two males left prior to larvae appearing on the carcass, one male left after larvae arrived and in one case, no larvae appeared on the carcass.

The second experiment was designed to avoid premature desertion and only one male deserted without producing a brood. Again, there was a significant treatment effect on male residence time (Table 5). Males did not provide longer care when alone because of slower larval development. At the time of male desertion, larvae were more likely to have dispersed in Treatment 5 than in Treatment 6. In Treatments utilizing

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TABLE 5. Reproductive success and duration of parental care in the laboratory

	Treatments					
	1	2	3	4	5	6
N	14	14	14	14	14	13
Number that produced a brood	13	14	10	13	13	13
Mean (±SE) number of larvae[a]	–	–	–	–	10.2 (1.4)	10.2 (0.9)
Mean (±SE) days until larval dispersal after male deserted[b]	–	–	–	–	0.0 (–)	1.7 (0.3)
Mean (±SE) number of adult offspring[c]	9.9 (1.5)	10.4 (0.8)	11.0 (0.7)	10.4 (1.1)	–	–
Mean (±SE) mass of adult offspring[d]	0.36 (0.02)	0.37 (0.01)	0.38 (0.02)	0.38 (0.02)	–	–
Mean (±SE) day of female desertion[e]	11.7 (0.32)	11.4 (0.33)	–	11.8 (0.49)	–	–
Mean (±SE) day of male desertion	–	–	11.0 (0.23)	8.3 (0.49)[f]	11.7 (0.40)	8.9 (0.81)[g]

[a] U = 83, ns, Mann-Whitney U test; [b] U = 19, P < 0.001; [c] F = 1.12, ns, Kruskal Wallis 1-way ANOVA; [d] F = 0.54, ns, Kruskal Wallis 1-way ANOVA; [e] F = 0.24, ns, Kruskal Wallis 1-way ANOVA; [f] Treatment 3 vs 4; U = 109, P = 0.001; [g] Treatment 5 vs 6, U = 134, P = 0.01.
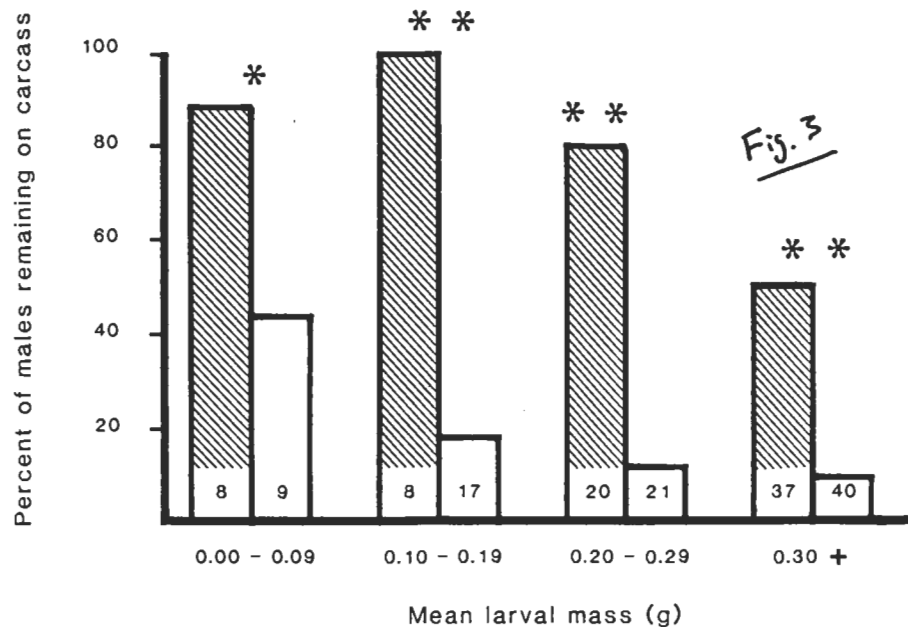
Fig. 4. Proportion of individuals deserting on each day of the trial: (A) females from all treatments; (B) paired males; and (C) males caring alone.

pairs (4 and 6), females never deserted before the male although in 3 of 26 cases, both parents left on the same day.

Discussion

Prior to the end of the breeding season, *N. orbicollis* males that invest time in their brood must forfeit time spent searching for new breeding opportunities. Such costs imply that benefits must be derived from paternal care.

The presence of a male on a carcass reduced the probability that free-flying beetles would usurp the resource from one or both residents. Beetles also were less susceptible to takeovers when placed on small rather than large carcasses. The result of a takeover is infanticide of the brood and reproductive benefits for the usurper (SCOTT, 1990; TRUMBO, 1990a). Working in southern New Hampshire, SCOTT (1990) did not find that a *N. orbicollis* male reduced the probability of takeovers by free-flying individuals. Nor was it found that large carcasses were more susceptible to takeovers than small carcasses. However, the study was conducted

during a low density year and used a smaller sample size than the present study. SCOTT (1990) recorded no takeovers at unaugmented density and 7 takeovers when beetles were released 3-15 m from established nests.

A male could reduce takeovers by lowering the probability that the nest will be discovered by competitors or by lowering the probability that an intruder will be successful once a nest is discovered. SCOTT (1990) demonstrated that the presence of a male is important once intruders locate the nest. I found support for this finding. Larger males were more successful in preventing takeovers than smaller males, which suggests that fighting ability was important. In addition, a successful intruder, whether male or female, is usually larger than the same-sex beetle it replaces (SCOTT, 1990; TRUMBO, 1990a).

A male also might reduce takeovers by lowering the probability that an intruder will discover the carcass. This might be especially important on large carcasses where it may be more difficult to control decomposition and olfactory cues escaping from the nest. Males as well as females contribute oral and anal secretions to the carcass which affect decomposition and push soil over exposed carcasses (PUKOWSKI, 1933; HALFFTER *et al.*, 1983). The presence of a male in a smaller species, *N. defodiens* Mannerheim, greatly reduced takeovers by larger congeners (TRUMBO, 1990b). Because there is a 2-4 fold difference in body size for the species involved, the decreased rate of takeovers is likely due to lowering the discovery rate rather than repelling intruders that find the nest.

Slower larval development on large rather than small carcasses also points to the greater difficulty in utilizing a large carcass (also see SCOTT & TRANIELLO, 1990; TRUMBO, 1990b). Large carcasses are not rounded as perfectly as small carcasses and the removal of hair from the carcass is sometimes incomplete (BARTLETT & ASHWORTH, 1988; TRUMBO, 1990b). On large carcasses, broods raised by pairs were further along in development than broods raised by single females. No difference was found on small carcasses. On large carcasses, therefore, the carcass is vulnerable for a shorter period of time when the male is present; this is the only report of a benefit of paternal care in *Necrophorus* other than reducing takeovers.

SCOTT (1989) found that the presence of a second parent reduced the number of larvae raised on a carcass. I found no evidence that a male decreased production of larvae in the field and no evidence that a second parent decreased larval production in the laboratory. The methodology of the two laboratory studies was somewhat different although both studies used carcasses of approximately the same size. In the present

study males were allowed to disperse from the nest area and were then removed. In Scott's study, "males were retained by design until larvae mature". The behavior of males that attempt to disperse but are confined to the nest area is not documented but the interaction between a resident female and a male that periodically disperses and returns to the carcass might be abnormal. At the time of dispersal males are undergoing rapid physiological changes as evidenced by increasing JH esterase activity and protein titres in the hemolymph (Trumbo, unpubl. results). It is interesting that in Scott's study, a male that cared alone had no detrimental effect on brood success even when he was retained until larvae matured. The laboratory experiment discussed here suggests that this might have occurred because males delay desertion until larval maturation when the female parent is removed. In two other species of *Necrophorus*, the presence of a male did not decrease the number (Trumbo, 1990b) or size of larvae (Bartlett, 1988; Trumbo, 1990b). As in Scott's study, there was no effect of a second parent on mass of larvae at dispersal in laboratory experiments.

Scott (1990) demonstrated that two parents were no better than one in protecting the brood from staphylinid predators introduced near the nest. Our studies suggest that this holds for nests in the field exposed to the full spectrum of potential predators. Males of both *N. defodiens* (Trumbo, 1990b) and *N. orbicollis* do not appear to reduce predation of the brood. If this had been the case, we would have seen a difference in the production of larvae by pairs and single females.

At two field sites, we found no effect of prior reproduction on the ability of a male to produce a brood, the number of larvae in a brood, or mean mass of larvae. This occurred despite the fact that the second reproductive attempt was initiated within two days of the first reproductive attempt. The experiment was designed to isolate possible physiological costs of paternal care by not allowing competition for the carcass, eliminating costs of fighting or 'ethological' component (*sensu* Calow, 1979). Physiological costs can be significant in many species (Coleman *et al.*, 1985; DeMartini, 1987) and can decrease future reproductive ability (Slavsvold, 1984; Linden, 1988; Nalepa, 1988). Laboratory studies of *N. vespilloides* found no difference in the life span of males that provided care and males that initiated reproduction but were removed before they could provide care. Further, males of *N. vespilloides* that completed a breeding attempt were the same mass as males that never initiated breeding (Bartlett, 1988). Besides lost time, paternal care might accrue significant costs only when a congener or

predator discovers the carcass. An absence of physiological costs has been found in other organisms for which the primary component of care is guarding the brood (TALLAMY & DENNO, 1982; TOWNSEND, 1986).

SCOTT & TRANIELLO (1990) found that *N. orbicollis* females showed a 23-35% decrease in both number of offspring and total weight of offspring between successive reproductive attempts. Pairs of *N. tomentosus* Weber showed a 46-56% decline in measures of reproductive success in two successive attempts on 27-33 g carcasses. Most of the decline is likely attributed to lower female fecundity since broods were smaller in the second reproductive attempt at the first instar stage (TRUMBO, 1990c). Females feed larvae more often than males and males spend more time guarding (PUKOWSKI, 1933; HALFTTER *et al.*, 1983; FETHERSTON, pers. comm.; but see BARTLETT, 1988). Parental care costs which differ for the two sexes also has been noted by BRYANT (1979) and NUR (1984).

Duration of care.

Paternal care produced greater reproductive benefits for a male on larger carcasses primarily because a single female has little difficulty retaining a small carcass and because a large carcass supports nearly twice the offspring as a small carcass. If paternal care evolved to reduce takeovers then we should expect the duration of male care to be related to vulnerability of the brood and the carcass.

In field experiments, the probability of finding the resident male on the carcass at exhumation was strongly related to only two variables, mean mass of larvae at exhumation and original carcass mass. Mean mass of individual larvae was a useful estimate of larval development because larvae were growing throughout the trial period (see Fig. 2). The relationship between larval development and desertion appears straightforward. As the brood nears independence, the carcass is depleted, the resource becomes less attractive to competitors, and male care becomes less essential. Although it was not determined whether males assess larval size or some correlated unmeasured variable, it is clear from the multivariate analysis that males do not use length of time on the carcass as a proximate cue for desertion.

The mechanism by which *Necrophorus* assesses carcass size or a highly correlated variable is not known. BARTLETT (1988) found a positive correlation between carcass size and male residence time. SCOTT & TRANIELLO (1990) found a weak association of a shorter duration of care on the smallest carcasses used in their study although carcass size had no

effect on male residence time (P = 0.82) in their multivariate analysis. Neither study, however, controlled for slower development of larvae on larger carcasses nor related the duration of care to expected benefits. In the present study, carcass size was the most important determinant of male residence time and clearly had an effect independent of the developmental stage of larvae.

An alternate explanation for longer care on larger carcasses is the possible greater costs of paternal care on a large resource. If males are receiving high reproductive benefits on large carcasses (*e.g.*, greater benefits than they could expect over their lifetime following desertion), then males might provide care beyond the point at which they rapidly accumulate physiological costs that could lower their residual reproductive value (*sensu* WILLIAMS, 1966) upon desertion. Males in poor condition might then do better to continue with their present brood (SARGENT & GROSS, 1985). This does not appear to occur in *Necrophorus*. An entire additional reproductive attempt did not affect subsequent reproductive success or the duration of care at either field site.

The number of larvae, although a function of carcass mass, did not have an independent effect on male desertion. There are several reasons why the benefits a male receives by providing parental care are not related in a simple way to brood size. First, for a given carcass size there is a tradeoff between the number and size of offspring (BARTLETT & ASHWORTH, 1988; TRUMBO, 1990c; SCOTT & TRANIELLO, 1990). Because body size is an important component of reproductive success (WILSON & FUDGE, 1984; BARTLETT & ASHWORTH, 1988; OTRONEN, 1988; SCOTT, 1990), there likely is an optimal brood size for a particular carcass that is less than the maximum number of young that could be raised (SMITH & FRETWELL, 1974). In addition, carcasses supporting very small broods in relation to carcass size should not be deserted because under-utilized carcasses are sometimes used for a second breeding (MÜLLER, 1987). Males that desert small broods prematurely will miss such breeding opportunities. Further, the number of larvae is likely to be a poorer predictor of vulnerability than carcass size. Since paternal care reduces vulnerability to takeovers, carcass size should be a better indicator of high parental payoffs for males.

There was no evidence that male or female body size affected male desertion. Similar results were reported by BARTLETT (1988) and SCOTT & TRANIELLO (1990).

Burial depth might be related to vulnerability and consequently to the probability of desertion. This prediction was not confirmed. The amount

of light which enters the crypt might also be correlated with carcass vulnerability and therefore might be a proximate cue for male behavior. Light should be investigated for its effect on desertion since beetles respond to light by pushing loose soil over the nest (PUKOWSKI, 1933).

The absence of the female parent markedly increased male residence time. At least one parent is needed throughout larval development to defend against predators, control microbial activity, and open new portions of the carcass to larval feeding. The male's facultative response to early female departure raises the question of why a female does not desert and force the male into a bind (TRIVERS, 1972). If the female deserts soon after larvae arrive on the carcass, the male would almost always stay until larvae disperse. The brood would receive approximately the same amount of parental care since the male will depart shortly if the female does not leave. What is more, reproductive success is equivalent whether the single parent is male or female (also see SCOTT, 1989), apparently because a male facultatively increases his rate of regurgitation to larvae if the female is removed (FETHERSTON, pers. comm.). Removal or hindrace of one parent also increase care-giving by the deserted parent in birds (WOLF et al., 1988; WRIGHT & CUTHILL, 1989; WHILLANS & FALLS, 1990) but has not been investigated in insects, undoubtedly because of the few species which exhibit both biparental care and overlapping parental tasks.

Why is *Necrophorus* not like snail kites in which both parents can be the first to desert at high frequencies (BEISSENGER & SNYDER, 1987)? SCOTT & TRANIELLO (1990) suggest that males desert first because a deserting female receives no representation in a replacement brood produced by a same-sexed intruder while a deserting male might receive a benefit if the intruder is a male. This occurs because of incomplete sperm displacement in the resident female. However, a deserting male receives no benefit if the resident female does not remain on the carcass following a takeover (68% of all successful intrusions, 57% of intrusions against single females; TRUMBO, 1990a). Even when the resident female does remain, use of a genetic marker demonstrates that the departed male will father only 15% of a replacement brood. Replacement broods do not always survive and are smaller in number (TRUMBO, 1990a) and weight (MÜLLER, 1987; TRUMBO, 1990a) than first broods because the carcass is depleted and the resident female must produce a second clutch quickly.

SCOTT & TRANIELLO's (1990) hypothesis may provide only a partial explanation for male behavior. Males also might desert first because they have greater expected benefits upon desertion. While female reproduc-

tive ability declines with successive breeding attempts even when the carcass is protected from competitors experimentally, there is no evidence of a decline in male ability in the same situation. Although further studies might point out a small physiological cost of paternal care not related to competitors, these costs are not ecologically appreciable. The effect of such costs on male reproductive success is likely obscured by variation in resource size, female reproductive ability and the competitive environment. Since injury rates for the two sexes are similar (also see TRUMBO, 1990d; and SCOTT & TRANIELLO, 1990), costs of defending the carcass against competitors are unlikely to differ for the two sexes.

A female that deserts will carry her costs of reproduction to the next attempt. The success of a male in a reproductive attempt following desertion will depend on the proportion of first, second and third time breeders in the population with which he might mate. Since competition among females in intense, deserting males have a significant probability of pairing with a female that is breeding for the first time.

Evolutionary history might be important as well. Females that desert early depend on a facultative increase in parental care from males. If the percent of early desertion by females and female mortality are initially low then males are under weak selection to make the appropriate facultative response. In the present study, 2 of 25 males that cared alone failed to produce a brood because they abandoned the carcass prematurely after larvae appeared.

In every species of *Necrophorus* which has been observed, males provide some degree of parental care (PUKOWSKI, 1933; MILNE & MILNE, 1976; HALFTTER *et al.*, 1983; BARTLETT, 1988). No other genera within the Silphidae exhibits paternal care. TRUMBO (1987) and SCOTT & TRANIELLO (1990) hypothesize that extended paternal care in *Necrophorus* evolved to protect the brood from infanticidal takeovers. When infanticide is common, it can select for increased parental care in a manner similar to predation (DOMINEY & BLUMER, 1984; CRESPI, 1990). The present study demonstrates that protecting against takeovers is ecologically important in the field for nests exposed to free-flying competitors, especially when a large carcass is being exploited. In addition, males adjust their behavior in three important ways depending on the vulnerability of the brood. They provide a longer duration of care on a large carcass, when brood development is slow, and when the female is absent. Hypotheses related to parental care in *Necrophorus* are refined as follows: the duration of female care is less variable, generally persists until larvae are ready to disperse from the carcass, and therefore depends primarily on the rate of

larval development (*e.g.*, maternal care will last longer at lower temperatures and on larger carcasses because of slower development of larvae). Male care, on the other hand, is more variable both within and between species, and depends on the vulnerability of the brood. Vulnerability will be related to infanticide and other factors and likely will be affected by carcass size, rate of larval development, presence of a female, the competitive environment and quality of the burial. I suggest that the duration of care relative to some measure of larval development be used to test parental care hypotheses in order to standardize for differences in the rate of larval development across species, carcass size and temperature.

Infanticide related to resource competition and sexual selection can have important effects on shaping the social system of vertebrates (FREED, 1986; MØLLER, 1988; WATTS, 1989; reviewed in SHERMAN, 1981; HAUSFATER & HRDY, 1984) but is not well documented in noneusocial insects. To better understand the effects of biotic and abiotic variables on patterns of parental care in *Necrophorus*, more information on variation in maternity and paternity of broods in the field will be required (see BARTLETT, 1988; DRESSEL & MÜLLER, 1988; MÜLLER *et al.*, 1990; TRUMBO, 1990a for laboratory studies of maternity and paternity). In addition, different components of reproductive costs for both sexes, reproductive prospects following desertion and the benefits of care at different stages of larval development need further investigation.

Summary

A monogamous pair of burying beetles (*Necrophorus* spp.) prepares a vertebrate carcass as a food source for their young and then protects the carcass and young from aggressive congeners. It was estimated that *N. orbicollis* males received four times the reproductive benefit on large (27-33 g) as opposed to small carcasses (10-18 g) in the field. Large carcasses were more likely to be taken over by free-flying intruders than small carcasses and the presence of a male parent reduced the probability of such takeovers. A male also decreased the time that a large carcass was vulnerable to a takeover. The presence of a male did not affect the number of larvae produced in field or laboratory experiments or the size of larvae reared in the laboratory. Males provided a longer duration of care when on a large carcass, when larval development was slow, or when the female was removed experimentally. The number of larvae, the number of days spent on the carcass, the mass of the carcass remaining at the end of the trial, female size, male size, burial depth and prior reproduction were not found to have independent effects on the probability of finding the male on the carcass. In addition, males that were allowed to provide care prior to being placed in the field did not show a subsequent decline in reproductive success as compared to males that did not provide prior care.

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