Regulation of brood size by male parents and cues employed to assess resource size by burying beetles

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Burying beetles prepare small vertebrate carcasses as a resource for their young and adjust the size of their brood to match the size of the resource. We tested whether single males of *N. orbicollis* can regulate brood size in the absence of clutch or brood size adjustments by females, and whether parents use mass- or volume-related cues to estimate resource potential. When provided with 25 first instar larvae, single males reared significantly more young on larger carcasses than on smaller carcasses (18.5 versus 11.4). Mortality of young occurred almost exclusively during the early stages of parental care, and therefore was unrelated to depletion of the resource. The mean mass of individual larvae at dispersal did not vary with resource size, and was consistent with 15 previous experiments utilizing *N. orbicollis*, suggesting that regulation of brood size had occurred. Examination of previous experiments also suggested that the number and mean mass of young was not affected by whether one or two parents provide care. Mass and volume of carcasses were manipulated to examine possible cues that burying beetles might employ to assess resource size. The addition of lead weights into the body cavity of a mouse corpse (mean increase in mass of 64%) did not alter the number of young produced by male-female pairs. When volume of a corpse was experimentally increased using hollow plastic tubes (mean increase of 21%), however, pairs reared 17% more offspring than on control carcasses. Mean mass of individual offspring on volume-enhanced carcasses was significantly less (– 18%) than on control carcasses. This suggests that burying beetles use a volume- but not a mass-related cue to assess resource potential. We also present evidence that increased handling time of a carcass during nest preparation may lead to deterioration in resource quality.

KEY WORDS: brood size, brood reduction, burying beetles, *Nicrophorus*, infanticide, carrion, parental care, paternal care.

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INTRODUCTION

In many organisms, the number of young that parents attempt to rear reflects environmental conditions. In both invertebrates and vertebrates, the primary mechanism that is employed to vary offspring number is regulation of clutch size (LACK 1947, SKINNER 1985, GODFRAY 1987). The female parent, therefore, is normally responsible for variation in numbers of young. Brood reduction that occurs after hatching, on the other hand, is most often carried out by siblings. Direct post-hatching regulation of brood size by parents is rare (BARTLETT 1987). There are no clear examples of the male parent adjusting brood size to match resource availability.

The mechanisms that translate environmental differences into differences in brood production are poorly understood. For example, variation in clutch size may reflect variation in female body condition which is an indirect measure of breeding conditions (STEARNS 1980, JONES et al. 1987). Alternatively, organisms that utilize an exclusive territory or that exploit a discrete resource, may directly assess environmental capacity prior to a decision regarding the number of young that will be produced (KLOMP & TEERINK 1962, HOGSTEDT 1980, WILSON & FUDGE 1984, SCHMIDT & SMITH 1987, PILSON & RAUSHER 1988). In such cases, effective adjustment of offspring production depends on the parent's accurate assessment of the environmental capacity to support young. This may not always be possible. Parents may not adjust brood number appropriately if the range in cue intensity that they are able to perceive does not match the range of environmental quality, or if reliance on one or a few cues does not fully account for the multiple factors which can affect environmental potential. The parasitoid, *Colpoclypeus florus*, for instance, uses a cue related to host width to vary clutch size, and may over- or understimate host size in species which have a variable width/length ratio (DIJKSTRA 1986). Until the cues that organisms use to assess environmental potential are understood, it will be impossible to determine whether constraints on optimal responses exist (KING & SKINNER 1991).

In this study we: (1) examined the ability of male *N. orbicollis* to regulate brood size; and (2) manipulated mass and volume of carcasses to determine whether correlates of these factors were important as cues in the assessment of resource potential. Burying beetles locate and bury a small vertebrate carcass and prepare it as a food resource for their brood. Competition for carcasses is often intense (WILSON & FUDGE 1984, TRUMBO 1992), and smaller beetles are excluded from carcasses by larger conspecifics and congeners (OTRONEN 1988, BARTLETT & ASHWORTH 1988, MÜLLER et al. 1990a, TRUMBO 1994). The dominant male and female remove hair or feathers from the carcass, which is then rounded into a brood ball (PUKOWSKI 1933). Male and female parents perform a similar repertoire of nesting and caregiving behaviors (PUKOWSKI 1933, FETHERSTON et al. 1994). Larger carcasses support

lárger broods such that variation in mean size of individual larvae at dispersal is far less than variation in size of the carcass (WILSON & FUDGE 1984, BARTLETT & ASHWORTH 1988, KOZOL et al. 1988, OTRONEN 1988, TRUMBO 1990a, SCOTT & TRANIEL-LO 1990). For a given carcass size, there is an inverse relationship between number of larvae reared and mass of individual larvae dispersing from the nest. This indicates a clear compromise between brood number and size of offspring (BARTLETT & ASHWORTH 1988, TRUMBO 1990a, SCOTT & TRANIELLO 1990). Adjustment in numbers of offspring occurs in two ways. First, females oviposit fewer eggs in the soil near the smallest carcasses. Variation of clutch size is limited, however, and a much finer adjustment occurs once larvae eclose and crawl to the carcass (BARTLETT & ASHWORTH 1988, MÜLLER et al. 1990b). On smaller carcasses, parents cannibalize a subset of their brood during the first 24 hr larvae are in the nest such that adequate resources remain for surviving young (BARTLETT 1987).

METHODS

Burying beetles were trapped in pitfall traps baited with ripe carrion during June, 1993 at The University of Michigan Biological Station (UMBS) in northern Michigan. Subjects for the experiment investigating paternal regulation of brood size were held for at least 1 week in the laboratory prior to experimental trials at 15L:9D and 20-23 °C. Subjects for other experiments were taken from the F_1 and F_2 generation laboratory stocks maintained at the University of Illinois. Mouse carcasses were obtained from breeding facilities, frozen shortly after death, and thawed 6-8 hr before trials.

Regulation of brood size by males

To determine whether the male parent can regulate brood size irrespective of the actions of the female, male-female pairs were established on small (17-19 g) or large (28-30 g) carcasses in plastic containers 3/4 filled with topsoil. Mean size of male was equivalent for the two treatments. Shortly after larvae eclosed (checks were made twice daily), the female was removed and the carcass and male were transferred to a new container. Twenty-five first instar larvae were then placed on the carcass. The number of larvae remaining in the nest was checked after 48 hr and then again shortly after larvae dispersed from the nest. Total mass of the brood also was determined at dispersal.

Manipulations of mass and volume

To examine the effect of carcass mass on offspring production, 17-19 g carcasses were opened up transversely along the abdomen, and 11.3 g of lead weights or an equivalent volume of hollow plastic beads were inserted and distributed along either side of the body cavity (the volume increase was approximately 3%). The opening was stitched closed and carcasses were then presented to male-female pairs. The male parent was removed 3 days after the larvae arrived on the carcass because a paired male normally deserts before larvae disperse from the nest (TRUMBO 1991). Reproductive measures were taken as described above.

Attempts to experimentally alter volume by insertion of plastic tubes generally led to loss of the tubes during prepararion of the carcass. Volume, therefore, was manipulated as follows: 15-17 g carcasses were presented to pairs which were allowed to prepare the resource for 48 hr (rounding of the carcass is complete by this time). The carcass was then removed, unfolded, and a hollow plastic tube was placed lengthwise along the midline of the abdomen. The carcass was re-folded over the plastic tube such that the tube did not protrude

from the brood ball. This manipulation resulted in an approximate increase in volume of 21% (determined by water displacement with 15-17 g carcasses not utilized in the experiment). Control carcasses were handled similarly but no tubes were inserted. Carcasses were given back to the original male and female for 24 hr to allow the repair of brood balls. The carcass was then removed again and presented to a new (experimental) pair of beetles in new soil-filled containers. In this way, the experimental pair of beetles handled the volume-enhanced or control carcasses for their entire nesting period. The male was removed 3 days after the appearance of larvae and reproductive measures of the brood produced by the experimental pair were taken as described above.

RESULTS

Regulation of brood size by males

When single males were presented with 25 young larvae, the number of larvae at 48 hr and at dispersal was significantly greater on larger carcasses (Table 1). The size of the male had no effect on reproductive output. Larval mortality occurred primarily within the first 48 hr on the carcass, well before the carrion resource was substantially reduced. More than 96% of young alive at 48 hr survived to disperse from the nest. The result of greater brood reduction on smaller carcasses was that larvae dispersed from small and large carcasses at an equivalent mass (Table 1). The high quality of the protein-rich resource was indicated by a high conversion of carcass mass to larval mass (> 27%).

The considerable number of studies measuring number and size of young in burying beetles allow for additional analyses. The mean number of larvae reared by single parents and male-female pairs of *N. orbicollis* from 17 experiments (nine different studies) is shown as a function of carcass mass in Fig. 1A. Data from male-female pairs were excluded if the male parent was not allowed to disperse or was not removed within the first 3 days of parental care. If the male is not removed he may commit pathological infanticide during the latter stages of parental care [this

Table 1.

Reproductive measures (mean ± SE) of broods cared for by single males on small and large carcasses.

Carcass size (g)	n	Number of larvae (at 48 hr)	Number of larvae (at dispersal)	Survival after 48 hr (%)	Total brood mass (g)	Mean mass of larvae (g)	Resource conversion (%)
18.3 (0.1)	15	11.4 (0.7)	11.1 (0.8)	97.2 (2.2)	4.98 (0.19)	0.46 (0.02)	27.2 (1.0)
29.2 (0.2)	15	18.5 (0.7)	17.9 (0.7)	96.8 (2.4)	8.32 (0.37)	0.47 (0.02)	28.5 (1.2)
P		$F^*_{1,27}=42.50$ < 0.001	$F_{1,27}=39.41$ < 0.001	$U^{**}=78.5$ > 0.20	$F_{1,27}=59.08$ < 0.001	$F_{1,27}=0.12$ > 0.20	$F_{1,27}=1.51$ > 0.20

*One-way ANOVAs, F values represent effects of carcass size. Male size did not affect any measure of reproductive output (P's > 0.20). **Mann-Whitney U test.

would rarely occur in the field since males normally disperse prior to this stage (SCOTT & GLADSTEIN 1993)]. Number of larvae was positively related to carcass size ($F_{1,14}$ = 48.05, P < 0.001) but not to whether 1 or 2 parents provided care ($F_{1,14}$ = 0.63, P > 0.20; ANCOVA). The size of the carcass explained a large proportion of the variance among studies in mean number of young despite the use of different methodologies by experimenters. [Simple regression: number of young = – 0.63 + (0.58) (carcass mass); r^2 = 0.78]. The mean mass of larvae was not affected by the size of the carcass ($F_{1,14}$ = 0.32, P > 0.20) nor by the presence of 1 vs 2 parents ($F_{1,14}$ = 0.91, P > 0.20) (Fig. 1B). The slope of the regression of mean larval mass against carcass size (0.002) was not significantly different from zero (P > 0.20). It is clear from Fig. 1A and B that single males of *N. orbicollis* raised broods of similar number and mass as those raised by single females and pairs in previous studies.
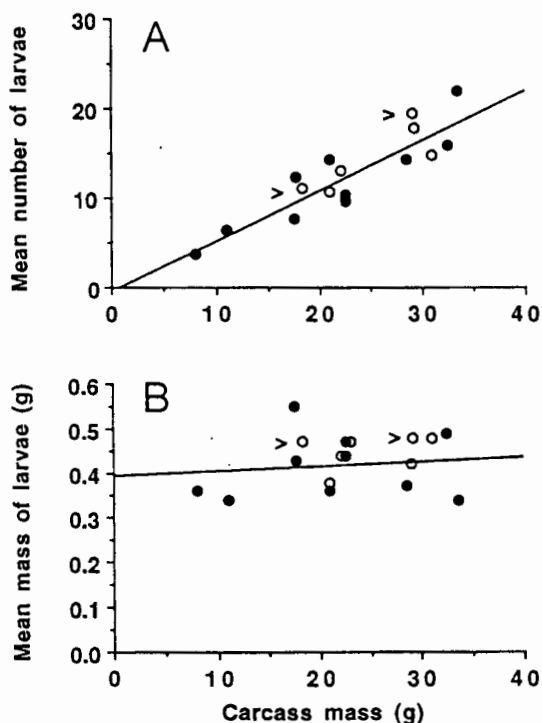

Fig. 1. — The mean number (A) and mass (B) of individual larvae as a function of carcass mass. Each point represents a mean value from a separate experiment utilizing *Nicrophorus orbicollis* and is based on a minimum sample of eight. Data were obtained from WILSON & FUDGE (1984), SCOTT (1989), SCOTT & TRANIELLO (1990), TRUMBO (1990c, 1991), TRUMBO & FIORE (1991), TRUMBO & WILSON (1993), ROBERTSON (1993), and SCOTT & GLADSTEIN (1993). Open symbols represent means of broods reared by single parents and darkened symbols represent broods reared by male-female pairs. Since no differences were found between broods reared by single parents and pairs (see statistical tests in text), regression lines were determined using all data points, equally-weighted. In some cases, means were estimated from graphical values. All values from broods reared by single males in the present study (indicated by arrows) fall within 95% confidence limits of the regression lines.

Manipulations of mass and volume

The addition of lead weights into the body cavity of mouse carcasses had no effect on the number of young, total brood mass, mean larval mass or conversion efficiency in reproductive attempts by pairs of *N. orbicollis* (Table 2). The addition of volume, however, had a significant effect on reproductive decisions by parents. Carcasses which had their volume enhanced (mean increase of 21%) produced broods that were 17% larger than control carcasses (Table 3). Again, almost all larval mortality occurred within the first 48 hr, well before carrion became limiting. Even though a greater number of offspring were produced on volume-enhanced carcasses as compared to controls, the total mass of the brood was not significantly different. This occurred because mean mass of individual larvae was smaller (– 18%) on volume-enhanced as compared to control carcasses (Table 3).

Table 2.

Reproductive measures (mean ± SE) of broods on mass-enhanced and control carcasses.

Carcass size (g)	n	Number of larvae (at 48 hr)	Number of larvae (at dispersal)	Survival after 48 hr (%)	Total brood mass (g)	Mean mass of larvae (g)	Resource conversion (%)
17.8 (0.2) + plastic beads	19	12.6 (0.6)	12.3 (0.6)	97.6 (1.0)	5.21 (0.11)	0.43 (0.03)	29.2 (1.0)
17.7 (0.2) + 11.3 weights	17	12.1 (0.7)	11.9 (0.8)	97.8 (1.4)	5.12 (0.16)	0.43 (0.03)	28.9 (1.2)
P		$F^{*}_{1,34}=0.26$ > 0.20	$F_{1,34}=1.65$ > 0.20	$U^{**}=149$ > 0.20	$F_{1,34}=1.32$ > 0.20	$F_{1,34}=0.00$ > 0.20	$F_{1,34}=1.55$ > 0.20

*F values are from one-way ANOVAs. **Mann-Whitney U test.

Table 3.

Reproductive measures (mean ± SE) of broods on volume-enhanced and control carcasses.

Carcass size (g)	n	Number of larvae (at 48 hr)	Number of larvae (at dispersal)	Survival after 48 hr (%)	Total brood mass (g)	Mean mass of larvae (g)	Resource conversion (%)
16.1 (0.1)	24	7.30 (0.3)	7.00 (0.3)	96.1 (1.3)	3.06 (0.09)	0.44 (0.01)	19.0 (2.1)
16.1 (0.2) + plastic tube	24	8.70 (0.4)	8.22 (0.4)	94.2 (1.4)	2.91 (0.07)	0.36 (0.01)	18.1 (2.4)
P		$F^{*}_{1,46}=7.75$ < 0.01	$F_{1,46}=5.61$ $= 0.02$	$U^{**}=326$ > 0.20	$F_{1,46}=2.20$ $=0.15$	$F_{1,46}=18.97$ < 0.001	$F_{1,46}=1.32$ > 0.20

*F values are from one-way ANOVAs. **Mann-Whitney U test.

The number of larvae reared and total brood mass per gram of carrion (resource conversion) were considerably lower for control carcasses in the volume-enhancement experiment compared to controls in the mass-enhancement experiment, and compared to either carcass size when single males provided care (Mann-Whitney U tests, P's < 0.01). This suggests that the experimental design (allowing two sets of parents to prepare carcasses, and having an 8 day rather than a 5 day period of carcass preparation), may have caused a deterioration in the quality of the resource (also see MÜLLER 1987). Further comparisons between experiments, therefore, are not possible.

DISCUSSION

One fundamental life history compromise is the tradeoff between number and size of offspring (SMITH & FRETWELL 1974, WINKLER & WALLIN 1987). The ability to adjust the production of young to match available resources can be especially critical for organisms in which body size is an important determinant of competitive success (BROCKELMAN 1975, HARDY et al. 1992). In burying beetles, the ability to regulate brood size is redundant. Females make clutch size adjustments (MÜLLER et al. 1990b) and both male and female parents regulate brood number by filial cannibalism, whether alone or in concert. The presence of one or two parents does not seem to affect brood size regulation. An examination of all studies of brood size regulation employing *N. orbicollis* (in which males were removed after 3 days of care or were allowed to disperse after providing care) demonstrates that pairs produce the same number of young as single parents. This was consistent with SCOTT & GLADSTEIN's (1993) finding that pairs and single females produce an equivalent number of young when the male is removed after 3 days.

In both vertebrates and invertebrates, it is extremely rare for the male parent to be involved in regulating number of offspring. Male burying beetles adjust brood size such that mean mass of individual larvae at dispersal was equivalent over the size range of 18-30 g carcasses. Why should males participate in brood size reduction, especially when it is somewhat rare to find a brood in the field that is being cared for by a single male (TRUMBO 1990c, 1991, 1992; SCOTT & TRANIELLO 1990)? In the absence of either parent to regulate brood size, a greater number of underweight larvae will disperse from the nest (TRUMBO 1990b). The redundancy in brood size regulation of burying beetles may have been selected because of severe penalties for the failure to adjust brood number. Smaller burying beetles are routinely excluded from carcasses by larger conspecifics and congeners (WILSON & FUDGE 1984; BARTLETT & ASHWORTH 1988; OTRONEN 1988; TRUMBO 1990b, 1994, 1995). If a females leaves the carcass or is injured during competition for the resource, male care becomes much more essential. Males are known to compensate for females by feeding the larvae at greater rates, maintaining the nest, and staying longer with the brood (TRUMBO 1991, FETHERSTON et al. 1994). The present study demonstrates that in the absence of the female, males perform the additional task of brood size regulation. Thus, the male will perform the full repertoire of parental behaviors, if necessary.

We feel that intense competition among burying beetles has selected for elaborate regulation of brood size in the following manner. Because of the scarcity of suitable resources, burying beetles cannot reject any carcass which has the potential to produce even a few larvae. This would select for a wide range of carcasses to

be accepted [*Nicrophorus orbicollis* utilizes carcasses from 7-200 g (TRUMBO 1990c, TRUMBO & WILSON 1993), and *N. vespilloides*, carcasses from 2-75 g (BARTLETT & ASHWORTH 1988, MÜLLER et al. 1990b)]. The broad size range of carcasses that is accepted, in conjunction with the selective disadvantage of producig undersized off-spring, would strongly favor parents that make appropriate adjustments of brood number to the available resource.

The evolution of brood size regulation in burying beetles was likely facilitated by exploiting a compact, discrete resource such as carrion. Brood size adjustments require that individuals obtain reliable information about environmental quality. We have demonstrated that burying beetles use a volume-related cue rather than a mass-related cue to determine resource capacity. Recently, C. CREIGHTON (pers. comm.) also has found that volume but not mass-related cues are important in reg-ulation of brood size in burying beetles. The particular assessment behaviors are unknown. The parasitoid wasp *Trichogramma* likewise varies offspring number rela-tive to host volume, and apparently estimates volume by measuring the time inter-val it takes to walk around the host (SCHMIDT & SMITH 1987). Burying beetles also spend considerable time walking around the resource during nest preparation (PUKOWSKI 1933), and this behavior might be related to assessment of carcass size.

The assessment of carcass size is separated temporally from the act of brood reduction. BARTLETT & ASHWORTH (1988) found that if they allowed *N. vespilloides* to prepare a 30 g carcass, and then removed it and presented a prepared 10 g carcass shortly before larvae eclosed, parents reared the number of young appropriate for the larger resource. The number that will be raised, then, is determined sometime during nest preparation (before larvae are present) when the brood ball is normally well-rounded. A temporal separation between assessment of resource quality and brood size regulation also occurs in *Trichogramma* (KLOMP & TEERINK 1962). When resource quality can change during this time interval, as can occur when a carrion resource deteriorates, individuals may be constrained in their ability to make appropriate decisions.

If shaping carrion into a sphere facilitates estimation of volume, then adjust-ments in clutch size may be rather imprecise because oviposition begins before car-casses are completely rounded and prepared. At the time of oviposition, the female may not have highly reliable behavioral mechanisms for estimating resource size. The finer adjustment in brood size that occurs within the first 24 hr larvae are on the carcass, may then depend on the estimation of the volume of a rounded carcass during the post-oviposition nesting period.

This study has demonstrated that volume of the brood ball is one important factor affecting brood size in burying beetles. It would be of interest to know how other factors such as condition of the resource, the presence of dipteran larvae, the competitive environment, and the type of carcass (mammal, bird, reptile) affect reproductive decisions. Unfortunately, studies of regulation of brood size in burying beetles have generally employed rodent carcasses from laboratory stocks that were frozen shortly after death. In the field, burying beetles exploit carcasses in a variety of states of decomposition, and from many taxa. Variation in the kinds of available carcasses may pose a challenge. Bird carcasses, for example, have different re-source/volume ratios than do rodent carcasses, and the stiffness of adult avian skele-tons and wings would make it difficult for beetles to form the corpse into a brood ball which could be accurately estimated for size. An examination of responses to the full spectrum of resources available in the field, and knowledge of the behavioral mechanisms employed to assess resource size, may reveal constraints on the ability

to make brood size adjustments which are optimal (DHONDT et al. 1990). Alternatively, further investigation might reveal that only a portion of burying beetle reproductive plasticity has been uncovered to date.

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