

11**Rapid #: -711596****IP: 137.99.181.228**

-711596



137.99.181.228

CALL #: QL496 .J65
LOCATION: ORE :: Main Library :: Valley
TYPE: Article CC:CCL
USER JOURNAL TITLE:
OCLC JOURNAL TITLE: Journal of insect behavior.
ORE CATALOG TITLE: Journal of insect behavior.
ARTICLE TITLE: "Brood size regulation in a burying beetle"
ARTICLE AUTHOR:
VOLUME: 357
ISSUE: -
YEAR: 1990
PAGES: 491-500
ISSN: 0892-7553
OCLC #:
CROSS REFERENCE ID: 17037621
VERIFIED:

BORROWER: UCW :: Main Library
PATRON: Trumbo, Stephen
PATRON ID: stt02001
PATRON ADDRESS:
PATRON PHONE:
PATRON FAX:
PATRON E-MAIL: stephen.trumbo@uconn.edu
PATRON DEPT: EEB
PATRON STATUS: FAC
PATRON NOTES:

NOTICE: This material may be protected by copyright law (Title 17 U.S. Code)
System Date/Time: 2/10/2006 1:09:28 PM MST

The work from which this copy was made did not include a formal copyright notice.
This work may be protected by copyright law. Users may be allowed with permission
from the rights holder, or if the copyright on the work has expired, or if the use is "fair use"
or within another exemption. The user of this work is responsible for determining lawful use

Regulation of Brood Size in a Burying Beetle, *Nicrophorus tomentosus* (Silphidae)

Stephen T. Trumbo¹

Accepted July 20, 1988; revised December 13, 1989

Regulation of brood size in a biparental burying beetle, Nicrophorus tomentosus Weber, was studied by providing pairs with one of two sizes of mouse carcasses in the laboratory. For a given carcass size, there was an inverse relationship between number and mass offspring in a brood. The requirement for regulation was that brood size was adjusted such that mean mass of individual larvae was constant for carcasses of different size. Brood size was regulated if parents were present but regulation did not occur if parents were removed prior to hatching of larvae. Pairs bred in quick succession on two carcasses raised fewer than the regulated number of young in the second reproductive attempt. Reasons for regulation of brood size in this genus are discussed.

KEY WORDS: *Nicrophorus*; parental care; brood size; reproduction; Silphidae.

INTRODUCTION

Recent studies suggest that parents should allocate an optimal level of investment to offspring in spite of widely varying availability of resources (Smith and Fretwell, 1974; Hogstedt, 1980; Strickler, 1982; Morris, 1985; Winkler and Wallin, 1987). One way to achieve this goal is to adjust brood size. Such adjustments should not maximize the number of offspring that will survive to reproductive age or the size of offspring but should maximize total fitness of the parents' offspring (Smith and Fretwell, 1974). Raising fewer but larger offspring, for example, can be especially critical for species that experience interference competition and in which body size is an important component of reproductive success (Gill, 1974; Brockelman, 1975; Cowan, 1981).

¹Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599.

Burying beetles (Silphidae, *Nicrophorus* Fabricius) compete with rivals of the same sex for small vertebrate carcasses on which to reproduce. The dominant male and female bury the carcass, remove any hair or feathers, and round the carcass into a brood ball. Eggs are oviposited in the surrounding soil and newly hatched first instars crawl to a burial crypt that is formed by the parents. Both the male and the female parents construct a feeding pit in the carcass, regurgitate liquified carrion to offspring, and protect the brood from congeneric intruders (Pukowski, 1933; Milne and Milne, 1976). The male often deserts after larvae reach the third instar, while the female usually remains on the carcass until larvae are ready to disperse from the nest (Pukowski, 1933; Trumbo, 1987; Scott and Traniello, 1990). This is one of the most advanced forms of parental care described among the Coleoptera (Zeh and Smith, 1985).

Nicrophorus is known to regulate brood size by adjusting number of young to carcass size such that the mean mass of individual larvae at dispersal is similar on small and large carcasses (Wilson and Fudge, 1984; Kozol *et al.*, 1988; Scott and Traniello, 1990; Trumbo, 1989). Although females oviposit about the same number of eggs when they exploit small or large mouse carcasses, smaller carcasses eventually produce fewer offspring (Wilson and Fudge, 1984). Bartlett (1987) has shown that parents can reduce brood size by cannibalizing first-instar larvae.

Nicrophorus is an intriguing genus for a study of regulation of brood size and possible parental control of offspring size. Burying beetles use a wide range of carcass sizes (5–200 g), there is a 10-fold difference in body mass between the smallest and the largest species, body size is important in competitive interactions, and the mechanisms employed to assess resource size and brood size are poorly understood. The purpose of this study was (1) to determine if brood size is regulated in *N. tomentosus* Weber, (2) to determine the effect of reproduction on future reproductive ability, (3) to examine the relationship between number and size of offspring in a brood, and (4) to examine the ability of larvae to regulate brood size in the absence of parents.

MATERIALS AND METHODS

In early September, *N. tomentosus* was collected in pitfall traps baited with 200 g of carrion at the following sites in North Carolina: Mason Farm Biological Reserve, Orange Co.; Duke Forest, Durham Co.; and W. B. Umstead State Park, Wake Co. Although *N. tomentosus* appears as early as June in North Carolina, studies on mouse carcasses placed in the field demonstrated that this species was not present on carcasses of less than 50 g until early September (Trumbo, 1987). Presumably, this results because of interspecific competition with the larger *N. orbicollis* (Wilson *et al.*, 1984). Therefore, *N. tomentosus* used in laboratory trials were most likely first-time breeders.

Prior to experiments, beetles were housed in plastic containers, kept on the natural photoperiod, and fed chicken livers. The length of adult beetles was measured from the tip of the mandibles to the posterior edge of the elytra. Laboratory mice (*Mus musculus* L.) were killed with CO₂ and frozen until provided to beetles.

To examine the ability of *N. tomentosus* to regulate brood size, two experimental groups were established. Ten *N. tomentosus* pairs were each bred on a small mouse (10–15 g; Treatment 1) and 10 pairs were each bred on a large mouse (27–33 g; Treatment 2) in a container filled with soil. A full day after larvae dispersed from the nest, trials were dismantled, and the number of larvae and mass of the entire brood determined. To measure the effect of a single reproductive attempt on future reproductive ability, adult pairs from Treatments 1 and 2 were subsequently placed into a container with fresh soil and maintained on a quantity of chicken liver (2 g) which was too small for reproduction but was more than the beetles consume in a 3 day period. After 3 days, pairs from both Treatment 1 and Treatment 2 were provided with a large carcass (27–33 g). The number of larvae and mass of the entire brood were measured 1 day after larvae dispersed from the nest.

A subsequent experiment was conducted to determine whether larvae regulate brood size without the assistance of parents. Twenty-two adult pairs were each provided with a 24- to 28-g carcass and allowed to prepare a nest and oviposit normally. Before larvae hatched, adults were removed and carcasses were replaced with 5–7 g (Treatment 3) or 20–22 g (Treatment 4) of chicken liver. Chicken livers were substituted for carcasses because larvae sometimes have difficulty gaining access to the interior of a carcass in the absence of parents (Halffter *et al.*, 1983; Trumbo, unpublished results with *N. defodiens*). After larvae dispersed from the nest, the trials were dismantled, and the number of larvae and mass of the entire brood determined.

RESULTS

Regulation of Brood Size—Parents Present

For both Treatment 1 (small carcasses) and Treatment 2 (large carcasses), 9 of 10 pairs of *N. tomentosus* successfully produced a brood in their first reproductive attempt. The requirement for regulation was that brood size was adjusted to carcasses of different size such that mean mass of individual larvae was constant at dispersal. The number of offspring was strongly related to carcass size ($F = 49.43$, $P < 0.001$) but was not affected by the size of the female ($F = 1.64$, $P > 0.2$, analysis of covariance; Table I). Means mass of individual larvae, on the other hand, was not affected by carcass size ($F = 1.21$, $P > 0.2$) nor by female size ($F = 0.24$, $P > 0.2$). The mass of the entire brood

Table I. Production of Larvae by Pairs Initially Bred on a Small Carcass (Treatment 1) and Pairs Initially Bred on a Large Carcass (Treatment 2)

	Treatment 1		Treatment 2	
	First attempt	Second attempt	First attempt	Second attempt
Carcass mass (g)	10-15	27-33	27-33	27-33
Sample size	10	9	10	9
Number of pairs producing a brood	9	7	9	8
Mean (SD) number of larvae/brood	10.0 (6.8)	12.4 (6.4)	32.6 (8.6)	14.4 (6.3)
Mean (SD) mass of individual larvae (g)	0.24 (0.05)	0.31 (0.04)	0.26 (0.04)	0.32 (0.04)
Mean (SD) mass of entire brood (g)	2.3 (1.5)	3.7 (2.1)	8.4 (1.6)	4.5 (1.8)

was related to the carcass size ($F = 64.44$) but not to the size of the female ($F = 0.05$, $P > 0.2$).

Of the 18 pairs that produced a brood in their initial reproductive attempt, seven pairs from Treatment 1 and eight pairs from Treatment 2 were able to produce a second brood on a large carcass. All eight pairs in Treatment 2 raised fewer offspring per gram of carcass in their second reproductive attempt ($P < 0.01$, Wilcoxon's matched-pairs signed ranks test; Table I). In each case, the mean mass of individual larvae at dispersal was greater in the second reproduction ($P < 0.01$, Wilcoxon's MPSRT). Once differences in the number of larvae are taken into account, however, a prior reproductive attempt did not have an independent effect on the mean mass of individual larvae (prior reproduction, $F = 0.02$, $P > 0.20$; number of larvae, $F = 9.55$, $P < 0.01$; analysis of covariance).

For second reproductive attempts, there was no evidence that pairs in Treatment 1 were more successful than pairs in Treatment 2. There were no differences between treatments in the number of larvae per brood ($z = -1.04$, $P > 0.2$, Mann-Whitney U test; Table I), mean mass of individual larvae ($z = -0.58$, $P > 0.2$), or mass of the entire brood ($z = -1.33$, $P > 0.1$). When production from first and second reproductive attempts was combined, the effect of female size on total number of larvae ($t = 1.95$, $P = 0.08$; simple regression) and total brood mass ($t = 1.90$, $P = 0.09$) did not reach significance. Only one pair from each treatment was able to produce a third brood when provided with a third carcass.

There was an inverse relationship between the number and the size of individual larvae. These data are plotted for all 24 broods produced on a large carcass in Treatment 1 (second reproductive attempt only) and Treatment 2 ($r^2 = 0.51$, $t = -4.82$, $P < 0.001$, simple regression; Fig. 1). When the effect

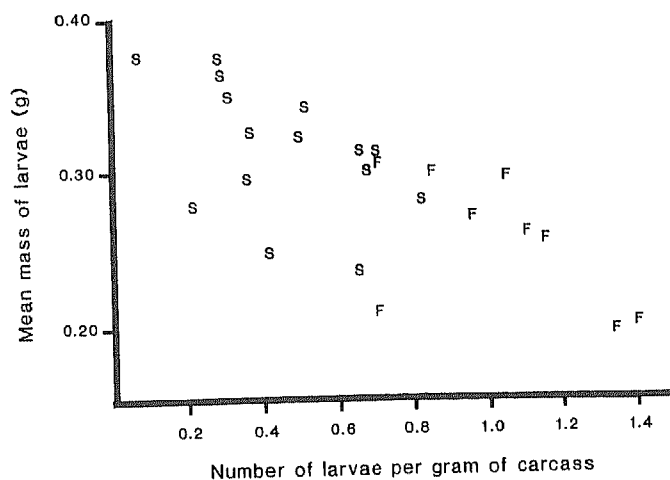


Fig. 1. Mean mass of individual larvae as a function of number of larvae per gram of carcass for first (F) and second (S) reproductive attempts (large carcasses only).

of total brood mass is removed, there is a strong partial correlation between number of larvae and mean mass of individual larvae on large carcasses ($r = -0.81$).

Regulation of Brood Size—Parents Removed

If parents are essential for regulation of brood size, larvae that develop on a limited resource without parental care are expected to be underweight. In the absence of parents, there was a trend for fewer larvae to mature on the small quantity of food (Treatment 3 versus Treatment 4, $z = -1.58$, $P = 0.11$, Mann-Whitney U test; Table II). This result would occur if starvation is more pronounced on smaller resources. Siblicide would produce a similar result although this behavior has not been observed in *Nicrophorus*. More impor-

Table II. Production of Larvae on a Small (Treatment 3) and a Large (Treatment 4) Quantity of Chicken Liver When Parents and Carcass Were Removed Prior to Hatching of Larvae

	Treatment 3	Treatment 4
Chicken liver substituted (g) (postoviposition)	5-7	20-22
Sample size	11	11
Number producing larvae	11	11
Mean (SD) number of larvae/brood	11.8 (4.1)	16.3 (8.6)
Mean (SD) mass of individual larvae (g)	0.10 (0.03)	0.24 (0.07)
Mean (SD) mass of entire brood (g)	1.2 (0.8)	4.0 (1.9)

tantly, individual larvae produced on a smaller resource were of significantly lower mass than larvae produced on a larger resource ($z = -2.18$, $P < 0.05$, Mann-Whitney U test). Furthermore, mass of dispersing larvae in Treatment 4 was not significantly different from mass of dispersing larvae when parents were not removed (Treatments 1 and 2, first reproductive attempts, $z = -1.05$, $P > 0.2$, Mann-Whitney U test). It is only when there is a limited resource and parents are removed (Treatment 3) that larvae disperse from the nest at well below normal mass.

DISCUSSION

When food is abundant and accessible, larvae of *N. tomentosus* can develop to the final instar and disperse at the normal size without posthatching parental care. Because larvae do not grow to a normal size when food is limited and parents are removed, larvae do not appear to be able to regulate brood size on their own. This suggests scramble competition for the resource in the absence of parents.

When parents were present with their brood, the requirement for regulation of brood size was met. The mean mass of individual larvae produced on small and large carcasses was the same. Apparently, maintaining a constant size of larvae is accomplished by regulating the number of larvae on the carcass. Although females are known to assess the suitability of a carcass prior to burial (Scott and Traniello, 1987), the mechanisms that parents use to determine carcass size and brood size are poorly understood. Burying beetles habitually dig beneath and lift the carcass with their legs while supine (Fabre, 1949; Pukowski, 1933; Milne and Milne, 1976), but there has been no experimental investigation to connect this behavior with assessment of carcass size. Parents' continuous movement around the brood ball also may permit assessment of carcass size but this has not been examined.

A female can produce two clutches in a short time in response to partial or total brood failure (Müller, 1987), an intruding male that destroys her initial brood (Trumbo, 1987; Scott and Traniello, 1990), or completing a reproductive attempt and locating a second carcass (Scott and Traniello, 1990). Since production of brood declined between reproductive attempts when carcass size was unchanged (Treatment 2), it appears that reproduction in *Nicrophorus* constrains future reproductive capacity in the short term. In a similar experiment with *N. orbicollis* which allowed 5 days between reproductive attempts, Scott and Traniello (1990) found that both the number and mean mass of larvae declined between the first and second reproductive attempt.

Wilson and Fudge (1984) found that females oviposit a nearly equivalent number of eggs around small and large carcasses in initial reproductive attempts. I have found that females of *N. orbicollis* oviposited a reduced clutch on smaller

carcasses in initial attempts, but only if a carcass weighed less than 10 g (also see Bartlett, 1987). Even then, differences in clutch size were small and could not account for marked differences in number of offspring produced on carcasses of varying sizes. These findings, as well as the high hatching rate of eggs (Easton, 1979; Wilson and Fudge, 1984; Bartlett, 1987), suggest that regulation of brood size begins with first instars reach the nest. Bartlett (1987) has shown clearly that parents of both sexes reduce brood size by cannibalizing larvae during their first 24 h on the carcass. Such intentional filial cannibalism is exceptional among invertebrates.

Bartlett (1987) also suggests that burying beetles oviposit excess eggs as insurance against poor recruitment of larvae. Recruitment may be poor because of fungal infection of the carcass or heavy predation on eggs and young larvae. According to Bartlett (1987), brood reduction under natural conditions might be employed only if larval survival is unusually high. Using both *N. defodiens* Mannerheim and *N. orbicollis* in field studies, I found that parents consistently produced many more larvae on large than on small carcasses (Trumbo, 1987; Trumbo, 1989). Burying beetles make little adjustment of clutch size over the range of carcass sizes (10–35 g) used in these experiments (Wilson and Fudge, 1984; Bartlett, 1987) and there is no reason to assume that recruitment should be lower on small rather than large carcasses. The production of excess eggs on small carcasses remains puzzling, therefore, since brood reduction appears to be very common on small carcasses in the field.

There are at least four as of yet unsubstantiated hypotheses for the large number of eggs oviposited around small carcasses. (1) If poor recruitment occurs but is rare, Bartlett's (1987) insurance hypothesis could explain overproduction of eggs if future reproductive opportunities are extremely limited and each reproductive attempt must be maximized. (2) Wilson and Fudge (1984) suggest that delaying regulation until after oviposition could be beneficial when a portion of the carcass might become unsuitable for larvae because of microbial decay. If this was the sole factor involved in overproduction of eggs, then *Nicrophorus* should produce a clutch that could be sustained under ideal conditions and then cannibalize young only if conditions deteriorate. This is not the case. There is substantial overproduction and cannibalism of larvae even when a small carcass is fully exploited under near-ideal reproductive conditions in the laboratory. (3) The costs of producing large numbers of eggs might not be severe for species which recover full reproductive potential quickly because of a high-protein diet. Although recovery of full reproductive potential may be rapid, it does not occur within 3 days for *N. tomemosus*. (4) Females that lose contests for carcasses sometimes oviposit before dispersing from the carcass in the laboratory (Müller *et al.*, 1989; Trumbo, unpublished results). Since parents of *Nicrophorus* do not have an absolute ability to discriminate between their own and conspecific offspring (Trumbo, 1987; Bartlett and Ashworth, 1988), a

resident female could increase her genetic representation in a mixed brood by producing excess eggs. It is not known if this scenario is important in the field.

On their own, hypotheses 2 and 3 cannot explain overproduction of eggs by *Nicrophorus* satisfactorily. However, these four hypotheses are not mutually exclusive and one would suspect that hypothesis 3 must be a partial explanation for a clutch size that is much larger than brood size on smaller carcasses.

This study demonstrates a trade-off between number of larvae in the brood and mean mass of individual larvae at dispersal. This effect is most clearly seen in two situations. When the number of offspring is too large for the resource in broods without parents, larvae are considerably underweight. When females have recently reproduced and subsequent brood sizes are low, resulting offspring are larger than offspring of first broods. Studies of other species of *Nicrophorus* also demonstrated an inverse relationship between number of larvae and mean mass of larvae at dispersal (Bartlett and Ashworth, 1988; Kozol *et al.*, 1988; Scott and Traniello, 1990). The much larger clutch size than brood size in first reproductive attempts, as well as the high survival rate of offspring that are below normal mass (Easton, 1979; Bartlett, 1987), suggests that *Nicrophorus* could raise a greater number of smaller larvae on small carcasses. A strategy which maximizes the number of young reaching the adult stage, however, could be disadvantageous for species in which small adult body size results in decreased reproductive success (Brockelman, 1975; Pianka, 1976). Smaller *Nicrophorus* often are forced off of carcasses during intra- and interspecific contests after the initial discovery of the resource (Pukowski 1933; Wilson and Fudge 1984; Wilson *et al.*, 1984; Bartlett and Ashworth, 1988), have less success holding onto carcasses they have incorporated into nests, and are more likely to sustain injuries (Trumbo, 1987; Scott and Traniello, 1990).

By regulating brood size, parents affect the body size of larvae and thus the eventual adult size and reproductive success that their young will achieve. This warrants the hypothesis that selection operates on body size of offspring (Lloyd, 1987) and adjustment of brood size is the mechanism employed to attain this goal. The optimal brood size is likely a compromise between producing a larger brood and producing larger larvae. When a female is physiologically unable to produce the number of eggs that is optimal for a particular carcass size, it is to the advantage of both parents and offspring that offspring use the additional resources to grow to a larger size.

Optimal brood size and offspring size at dispersal are expected to differ for parents and offspring (Trivers, 1974), but the roles that parents and offspring play in this interaction are difficult to separate (Brockelman, 1975). Since many species of *Nicrophorus* will raise larvae of congeners (Trumbo, 1987), this genus is suitable for studies of parent-offspring conflict. Cross-fostering experiments can be attempted, using species which differ both in body size and in number of larvae that are raised per gram of carcass. In this manipulation, the brood

size which is optimal for offspring in the natural context will be markedly different from the optimal brood size for their foster parents. Such experiments can place the interests of offspring and their foster parents in even greater conflict than under natural conditions and might be able to determine how the size and behavior of larvae affect brood size and which particular young the parents raise.

ACKNOWLEDGMENTS

I wish to thank Helmut Mueller, Haven Wiley, and three anonymous reviewers for suggested revisions of the manuscript. Nelson Hairston, Alan Feduccia, Alan Stiven, JoAnn White, and Sue Trumbo provided many helpful comments. Research at Mason Farm Biological Reserve was supported by Sigma Xi and the University of North Carolina. The Elizabeth Kennedy Foundation and The University of Michigan Biological Station also provided financial support.

REFERENCES

- Bartlett, J. (1987). Filial cannibalism in burying beetles. *Behav. Ecol. Sociobiol.* **21**: 179-183.
- Bartlett, J., and Ashworth, C. M. (1988). Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behav. Ecol. Sociobiol.* **22**: 429-434.
- Brockelman, W. Y. (1975). Competition, the fitness of offspring, and optimal clutch size. *Am. Nat.* **109**: 677-699.
- Cowan, D. P. (1981). Parental investment in two solitary wasps, *Ancistrocerus adiabatus* and *Euodynerus foraminatus* (Eumenidae: Hymenoptera). *Behav. Ecol. Sociobiol.* **9**: 95-102.
- Easton, C. (1979). *The Ecology of Burying Beetles (Nicrophorus, Coleoptera, Silphidae)*, Unpublished Ph.D. thesis, University of Glasgow, Glasgow.
- Fabre, J. H. (1949). The burying beetle. In de Mattos, A. T. (ed. and translator), *The Insect World of J. Henri Fabre*, Dodd, Mead, New York, pp. 232-258.
- Gill, D. E. (1974). Intrinsic rates of increase, saturation density, and competitive ability II. The evolution of competitive ability. *Am. Nat.* **108**: 103-116.
- Halffter, G., Anduaga, S., and Huerta, C. (1983). Nidification des *Nicrophorus*. *Bull. Soc. Entomol. F* **88**: 648-666.
- Hogstedt, G. (1980). Evolution of clutch size in birds: Adaptive variation in relation to territory quality. *Science* **210**: 1148-1150.
- Kozol, A. J., Scott, M. P., and Traniello, J. F. A. (1988). Natural history of a declining species, *Nicrophorus americanus*, the American burying beetle. *Psyche* **95**: 167-176.
- Lloyd, D. G. (1987). Selection of offspring size at independence and other size-versus-number strategies. *Am. Nat.* **129**: 800-817.
- Milne, L. J., and Milne, M. (1976). The social behavior of burying beetles. *Sci. Am.* **235**: 84-89.
- Morris, D. W. (1985). Natural selection for reproductive optima. *Oikos* **45**: 290-292.
- Müller, J. K. (1987). Replacement of a lost clutch: A strategy for optimal resource utilization in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Ethology* **76**: 74-80.
- Müller, J. K., Eggert, A. K., and Dressel, J. (1989). Intraspecific brood parasitism in the burying beetle, *Nicrophorus vespilloides*, (Coleoptera: Silphidae). *Anim. Behav.* (in press).
- Pianka, E. R. (1976). Natural selection of optimal reproductive tactics. *Am. Zool.* **16**: 755-784.
- Pukowski, E. (1933). Ökologische untersuchungen an *Nicrophorus* F. *Z. Morph. Ökol. Tiere.* **27**: 518-586.

- Scott, M. P. (1990). Brood guarding and the evolution of male parental care in burying beetles. *Behav. Ecol. Sociobiol.* 26: 31-39.
- Scott, M. P., and Traniello, J. F. A. (1987). Behavioural cues trigger ovarian development in the burying beetle, *Nicrophorus tomentosus*. *J. Insect Physiol.* 33: 693-696.
- Scott, M. P., and 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.
- Smith, C. C., and Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *Am. Nat.* 108: 499-506.
- Strickler, K. (1982). Parental investment per offspring by a specialist bee: Does it change seasonally? *Evolution* 36: 1098-1100.
- Trivers, R. L. (1974). Parent-offspring conflict. *Am. Zool.* 14: 249-264.
- Trumbo, S. T. (1987). *The Ecology of Parental Care in Burying Beetles (Silphidae: Nicrophorus)*. Unpublished Ph.D. thesis, University of North Carolina, Chapel Hill.
- Trumbo, S. T. (1989) Interference competition among burying beetles (Silphidae: *Nicrophorus*). *Ecol. Entomol.* (in press).
- Wilson, D. S., and Fudge, J. (1984). Burying beetles: Intraspecific interactions and reproductive success in the field. *Ecol. Entomol.* 9: 195-203.
- Wilson, D. S., Knollenberg, W. G., and Fudge, J. (1984). Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*). *Ecol. Entomol.* 9: 205-216.
- Winkler, D. W., and Wallin, K. (1987). Offspring size and number: A life history model linking effort per offspring and total effort. *Am. Nat.* 129: 708-720.
- Zeh, D. W., and Smith, R. L. (1985). Paternal investment by terrestrial arthropods. *Am. Zool.* 25: 785-805.