Effect of larval body size on overwinter survival and emerging adult size in the burying beetle, *Nicrophorus investigator*

Rosemary J. Smith

Abstract: Body size may influence both adult fecundity and the probability of survival through each life stage. Previous studies of burying beetles (*Nicrophorus*, Coleoptera: Silphidae) have revealed reproductive advantages for larger adults and the role of parental care in determining larval size and number. In this study I measure the effect of size on survival over the winter period and the correlation between larval size and the size of emerging adults. I collected data from 24 groups of 20–25 larvae sorted by size and overwintered outside under natural conditions in Colorado, U.S.A. There was a significant positive correlation between larval size and adult size at emergence and a significant effect of size on overwinter survival. Data from 2 years yielded the following mean survival rates: small, 47.3 ± 1.0%; medium, 73.2 ± 0.7%; large, 85.7 ± 0.4%. These values were then used to accurately predict adult emergence from broods of larvae whose range of size was measured prior to the overwinter period. The results indicate that selection for large body size may result from an overwinter survival advantage and not just from reproductive success. This has implications for fitness models of parental care and models of population dynamics.

Résumé : La taille du corps peut influencer à la fois la fécondité des adultes et la probabilité de survie à tous les stades. Des études antérieures sur les nécrophores (*Nicrophorus*, Coleoptera : Silphidae) ont mis en évidence les avantages reproductifs des adultes de grande taille et l'influence des soins parentaux sur la taille et le nombre des larves. J'ai mesuré les effets de la taille sur la survie en hiver et la corrélation entre la taille des larves et celle des adultes à l'émergence. J'ai recueilli des données chez 24 groupes de 20 à 25 larves séparées d'après leur taille et soumises aux conditions climatiques naturelles en hiver au Colorado, É.-U. J'ai trouvé une corrélation positive significative entre la taille des larves et celle des adultes à l'émergence et constaté l'effet significatif de la taille des larves sur la survie en hiver. Des résultats sur 2 années ont donné les mesures de survie suivantes : 47,3 ± 1,0 % pour les petites larves, 73,2 ± 0,7 % pour celles de taille moyenne et 85,7 ± 0,4 % pour les grosses larves. Ces valeurs ont permis de faire des prédictions précises sur l'émergence des adultes issus de couvées de larves dans lesquelles l'étendue des tailles a été mesurée avant l'hiver. Ces résultats indiquent que la sélection qui favorise une grande taille peut résulter de l'avantage d'une meilleure survie à l'hiver et pas seulement du succès reproducteur. Cette constatation peut avoir une grande importance lors de la conception de modèles du fitness des soins parentaux et de modèles de dynamique des populations.

[Traduit par la Rédaction]

Introduction

Understanding the population biology of any species requires an understanding of both adult fecundity and the probability of survival through each of the life-history stages. Body size can be an important parameter to include in population models, because both fecundity (Roff 1992) and mortality (Calder 1983; Peters 1983) may be positively correlated with increasing body size (Fox and Czesak 2000). Considerable evidence suggests that adult body size influences insect reproductive success (Andersson 1994; Von Dongen et al. 1999; Sokolovska et al. 2000) but less attention has been paid to the effects of body size on mortality. Selection on body size prior to maturity has the potential to alter the body-size distribution of adults and, thus, constrain selection on adult competitive ability, reproductive behaviors, and fecundity (Arnholt 1991).

In the burying beetle (*Nicrophorus*, Coleoptera: Silphidae), adult body size does not appear to influence egg production in females (Scott 1998), but does limit the reproductive success of both males and females because smaller individuals are less likely to secure the small animal carcass that is required for reproduction (Scott 1998; Müller et al. 1990). The mechanisms by which *Nicrophorus* adult body size influences success in competitive interactions with conspecifics and congeners are well known. Larger individuals have the advantage in interference competition (direct combat) before burial, as well as in exploitative competition (removal of resource), by winning fights (Otronen 1988; Müller et al.

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R.J. Smith. Department of Biological Sciences, Idaho State University, Pocatello, Idaho, 83209-8007, U.S.A. (e-mail: smitrose@isu.edu).

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1990) and burying carcasses more quickly (Smith et al. 2000*b*) and more deeply (Eggert and Sakaluk 2000) than smaller adults.

Mortality and the duration of each stage of the life cycle in insects are typically measured at the egg, larva, pupa, and adult stages (Danks 2000). In all burying beetle species, adults breed and lay eggs and larvae develop during the spring, summer, or fall. However, the larvae of different species then follow one of two patterns of development. In one group, the larvae pupate and eclose within weeks, overwintering as adults. In the second group, the overwinter stage is a prepupae, with pupation and eclosion occurring the following summer (Pukowsi 1933; Scott 1998). In burying beetles, egg and larval survival in early instars has been studied extensively and is known to be primarily under the control of the attending parents (Bartlett 1987; Trumbo 1990; Eggert and Müller 1997). Parents influence larval size by manipulating the number of larvae consuming the fixed carcass resource (Smith and Heese 1995; Eggert and Müller 1997; Scott 1998). If body size is important for overwinter survival, then there is the potential for parental care decisions to be directly linked to the probability of overwinter mortality.

In *Nicrophorus investigator*, larvae enter underground overwintering chambers in July and August, immediately after completing consumption of the carcass resource (about 15–20 days after hatching from the egg). The overwintering period may extend as long as 11 months. The size of adults that emerge in late June is predicted to be correlated with the size of the larvae as they go into the winter dormancy period, paralleling the relationship between larval size and teneral adult size in *Nicrophorus* species that pupate immediately (Bartlett and Ashworth 1988; Rauter and Moore 2002). Nothing has been reported on overwinter survival and subsequent size at eclosion under natural conditions in *Nicrophorus* (Meierhofer et al. 1999), despite the fact that this could have a major influence on models of population dynamics and on interpreting the fitness consequences of parental care (Rauter and Moore 2002).

Efforts by the author to model the population dynamics of *Nicrophorus* and link these dynamics to the ecology and evolution of parental care of *Nicrophorus* are ongoing. The present work focuses on elucidating the reliability of the predicted positive relationship between larval and adult body size for a species with a long overwintering period spent in the prepupal stage. It directly tests the hypothesis that large body size enhances overwinter survival, and that size-specific survival probabilities can be used to predict the number of larvae that will emerge as adults from a given brood.

Materials and methods

The study was conducted as an enclosed field experiment at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado. The elevation at this site is 2900 m and the climate is typical of the southern Rocky Mountains. Two species of *Nicrophorus* (*N. investigator* and *N. defodiens*) occur at this location and their ecology and behavior have been extensively studied here since 1992 (Smith and Heese 1995; Smith et al. 2000*a*, 2000*b*; Smith and Merrick 2001).

Nicrophorus investigator is widely distributed in northern North America and has a Palearctic distribution (Anderson and Peck 1985). Studies in northern Europe (Pukowski 1933), northern Japan (Katakura and Fukuda 1975), and Colorado, U.S.A. (Smith et al. 2000*b*) indicate that adults emerge in late June through early July. Adults reproduce throughout July and August; the overwintering stage is a prepupa.

To measure overwintering success, I retained larval *N. investigator* from experiments on parental care conducted for other purposes. In each year, larvae were weighed and then sorted into size classes (small, <0.20 g; medium, 0.20–0.31 g; large, >0.31 g). Although it would be preferable to follow each individual larva, this is not practical. Thus, the data on overwintering refer to groups of larvae. In 1999–2000, larvae were placed in steel cans (15-cm diameter, 17-cm depth) with a wire-screen mesh placed on the bottom side and holes punched into the top side. Larvae were allowed to position themselves at any depth in the container. These cans were buried so that the bottom of the can was 20 cm under the soil surface. The larvae were sorted by size into groups of 15 each. Two cans of small larvae, three cans of medium-sized larvae, and four cans of large larvae were buried on 7 August 1999 and covered with 10 cm of native soil. The pupae were recovered and counted on 16 June 2000 and then reburied. This protocol and design led to low adult emergence, owing to the handling of pupae and the breaking of cells they formed around themselves.

In 2000–2001, the container was redesigned to allow for both drainage and undisturbed emergence of adults. The ultimate design was a steel can (15-cm diameter, 17-cm depth) with both ends covered with wire screening, the screening held in place with baling wire. The cans were placed in an array set into a pit 20 cm deep. The array of cans was covered with hardware cloth (1.2-cm mesh); soil was used to fill all the spaces between the cans and was added to a depth of 5 cm on top of them (slightly mounded up). About 15 days prior to expected emergence, the mounded surface soil was removed and 1 cm of soil at the top of each container was removed to allow space for emerging adults to be viewed and to move around. The top screens were replaced (held in place by large rubber bands). Adults were then collected as they naturally emerged. In 2000–2001, one can of 23 small larvae, five cans of 20 medium-sized larvae, one can of 13 medium-sized larvae, and eight cans of 20 large larvae were buried 9–12 August 2000; adults emerged naturally 3–20 July 2001.

To determine if I could predict the number of larvae from a given brood that would survive the overwinter period (based on their larval size), I also buried 20 broods (sibling groups) varying in number of larva (ranging from 4 to 21) and mass, using the same method as above. The adults were counted, sexed, and measured as they emerged each day.

The following data were calculated and analyzed for each cohort in each year: mean and standard error of larval mass (one can = the replicate of a cohort), count of pupae (in 2000), mean and standard error of cohort elytron length of emerging adults (in 2001), proportion of larvae in each co-

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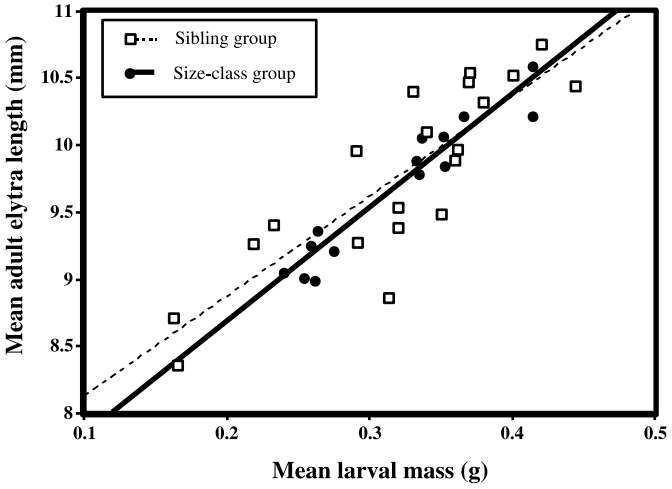
Fig. 1. Mean adult size at emergence (elytra length (mm)) is significantly positively correlated with mean mass (g) of larvae entering the overwinter period: for cohorts sorted by size, $F = 142.982$, $P < 0.0001$, $N = 14$, $Y = 6.975 + 8.479x$, $r^2 = 0.923$; for sibling groups, $F = 45.769$, $P < 0.001$, $N = 20$, $Y = 7.386 + 7.45x$, $r^2 = 0.718$.



hort that survived to pupation or adulthood, and emergence dates. Regression analysis of larval mass (g) versus adult elytra length (mm) and ANOVAs to detect body-size effects on survival were performed using StatView version 5.0 (SAS Institute Inc. 1999). In addition, using calculated mean probability of emergence of each size class from the combined 2000 and 2001 data, I calculated the expected emergence (based on larvae size) for each brood that was interred alone. I used a regression analysis of actual emergence number versus predicted emergence number to determine the fit of the model, paying particular attention to the slope. A slope of one would indicate that the predicted and actual numbers were similar.

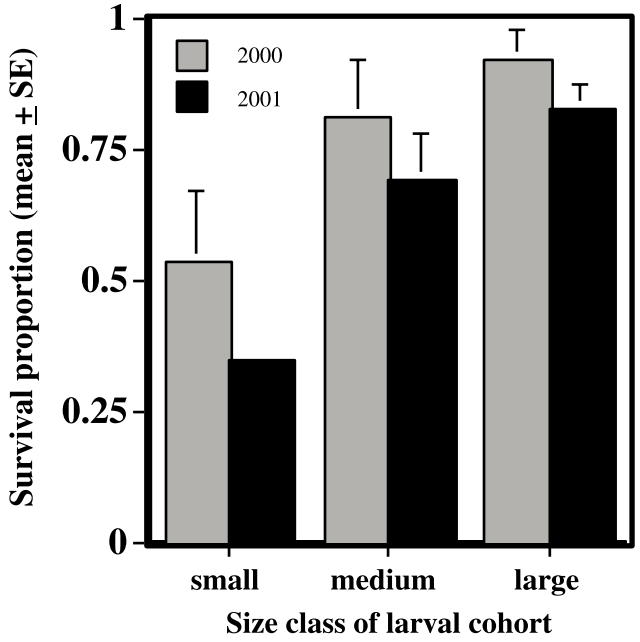
In each winter, two HOBO recording temperature loggers were buried for the duration of the overwinter period in two identical containers randomly positioned within the array of containers that held larvae. Temperature was recorded every 20 min throughout the winter period. Data on the first day of bare ground was collected from the RMBL weather station.

Results

Larger larvae metamorphose into larger adults (Fig. 1). For both larvae that overwintered in size cohorts and those that overwintered as sibling cohorts, there was a significant positive correlation between average larval mass and average adult elytra length. There was a stronger correlation coefficient (r^2) for larvae initially sorted by size ($r^2 = 0.923$) than for larval cohorts that comprised sibling groups ($r^2 = 0.718$). The initial variance around the mean in sibling-group larval mass was greater than the variance around the mean larval mass for size cohorts (ANOVA, $F = 17.331$, $P = 0.0002$).

Cohorts of large and medium-sized larvae had higher survival rates than cohorts of small larvae (Fig. 2), with survival approaching 90% in cohorts of larger larvae compared with only 50% for cohorts of smaller larvae. There was a significant effect of size class on survivorship in both years

Fig. 2. Large and medium-sized larvae have higher survival rates than small larvae (effect of size class on the probability of survival, combined data from both years; ANOVA, $F = 7.273$, $P = 0.005$; Fisher's PLSD (protected least significant difference) comparing proportion survival: large vs. medium-sized, $P = 0.093$; large vs. small, $P = 0.002$; medium-sized vs. small, $P = 0.029$). There is no significant effect of year ($P = 0.142$) or of the interaction between year and size class ($P = 0.912$).



($F = 7.273$, $P = 0.0048$, power = 0.899), with no significant effect of year ($P = 0.142$) or interaction of size × year ($P = 0.912$). Combined data from 2000 and 2001 yielded the following survival rates: small ($N = 3$), 47.3 ± 0.99%; medium-sized ($N = 9$), 73.2 ± 0.69%; large ($N = 12$), 85.7 ± 0.38%. Fisher's post-hoc tests indicate significant differences between large and small ($P = 0.0016$) and medium-sized and small size classes ($P = 0.0291$) but not between medium-sized and large size classes ($P = 0.093$). The sample size (N) refers to the combined number of cohorts of a given size. These values were used to make the predictions of brood survival.

There was a significant positive relationship between the actual number of adults that emerged from a brood and the number that was predicted to emerge based on applying mortality rates from the above analysis to the sizes of larvae that entered the winter period (Fig. 3; $N = 13$, $F = 875.41$, $P < 0.001$, $r^2 = 0.986$). The slope of the regression line was 1.029, with 95% confidence intervals of 0.953–1.105. Emergence data was incomplete for two of the broods.

Temperatures in the overwintering chambers cooled from 12 to nearly 2°C during the first 2 months of interment. The chambers remained at a steady temperature near 2°C for the duration of the winter months, never dropping below 0°C. The soil began to warm in late April, reaching 15°C by the beginning of May (Fig. 4). This pattern was similar across the 2 years.

In 2001, 85% of the *N. investigator* adults emerged from the overwintering containers between 4 and 14 July, parallel-

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Fig. 3. There is a significant positive relationship with a slope near one between the number of adults predicted to emerge from a particular brood and the actual number of adults that emerged (ANOVA, $F = 875.41$, $P < 0.001$, $N = 13$, $Y = 0 + 1.029x$, $r^2 = 0.986$; 95% confidence intervals around slope = 0.953–1.105). The number predicted was calculated by multiplying the number of larvae of a particular size class in a brood by the probability that larvae of that size would survive and then summing across all size classes.

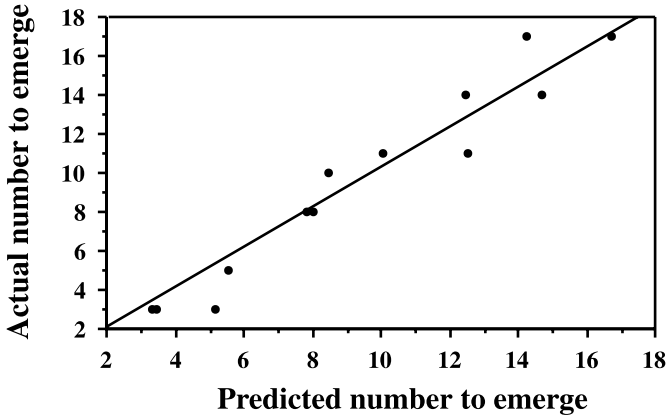
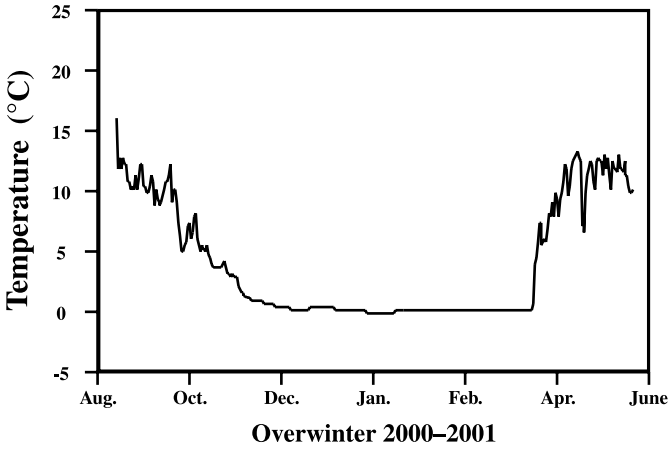


Fig. 4. Temperature log from a representative overwintering chamber. Note that the temperature did not fall below 0°C at any point during the winter period.



ing the cumulative emergence–captures at field trapping stations. There was a significant correlation between the date of first capture of *N. investigator* in field traps and the first day of bare ground at the RMBL ($F = 6.690$, $P = 0.049$); however, with the exclusion of one year (1995) in which snowmelt was very late, all the dates fall within a 10-day period (10–20 June).

Discussion

As expected, there was a positive correlation between the size at which larvae entered the overwintering period and the size of adults that emerged (Fig. 1). This is the typical result found for insects (Bartlett and Ashworth 1988; Tammaru 1998) and is directly related to the quantity of stored resources. The feature most relevant to modeling the evolution of *Nicrophorus* life history is the very high correlation coefficient ($r^2 = 0.923$), which indicates that parental investment and brood-manipulation decisions will have a highly reliable effect on the size of the offspring at maturity. A similar phenotypic correlation (0.92) between larval mass and mass at adult emergence was measured by Rauter and Moore (2002) for *Nicrophorus pustulatus*, a species that emerges as an adult within 40 days of hatching. Thus, although the overwinter period is extensive in *N. investigator*, it does not appear to increase phenotypic variation in mass.

Larval body size has a significant influence on overwinter survival, with lower survivorship for small larvae (Fig. 2). There was no significant difference in survival data between 2000 and 2001, indicating that survival to the pupal stage is similar to survival to the adult stage. The results of overwintering studies of other arthropods are variable; a few show increased survivorship with larger size (Rust 1995; Barron and Wilson 1998), some find no effect of size (Gunnarsson 1988; Kotiaho et al. 1999), and most do not include body size as a variable (Turnock 1993). However, all these studies were done on pupal or adult stages, and thus, are not directly comparable. The most relevant results are those of Rust (1995) showing local adaptations of bee populations, with larger individuals found in locations that experienced colder winter conditions and surviving better under variable conditions. This is also the case in *N. investigator*, with larger individuals found at higher elevations (Smith et al. 2000*b*). Emergence dates appear to be related to soil warming patterns, including date of snowmelt (first day of bare ground). Although the first individuals were captured in mid-June, the majority of *N. investigator* eclose in late June and over a short window of time (about 15 days). This corresponds to the emergence dates described in Anderson and Peck (1985) and Koulianos and Schwarz (2000) for *N. investigator*.

Generalizing trends in the effects of different environmental factors on population and species characteristics have recently received attention among the herbivorous insects (Cornell and Hawkins 1995) and carabid beetles (Sota 1996), with interesting results. Sota (1996) found that carabid beetles with larval overwintering had wider altitudinal ranges and colonized higher altitudes than did species without larval overwintering. It would be extremely valuable to have similar data for *Nicrophorus*. In particular, we need comparable survivorship data for species of *Nicrophorus* that overwinter as adults, more data on those that overwinter as larvae, and intraspecific trends in adult body size across either latitudinal or altitudinal gradients.

One application of the mortality information is to integrate progeny size into life-history models (Fox and Czesak 2000). The data presented in this paper indicate that it is possible to accurately predict the number of adults that will emerge from a given brood by applying size-specific survival probabilities (Fig. 3, note slope close to 1.0). This is of particular value, because it provides a better estimate of future population size. Although the specific size class survival probabilities will probably vary by region and species, this technique could be used to monitor and predict population sizes of any species of *Nicrophorus* when larval characteristics are known. This is perhaps of considerable interest in the conservation of the endangered American burying beetle (*Nicrophorus americanus*).

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These results provide important information for integrating different avenues of research. The first is to understand the consequences for selection on parental-care traits, in particular the trade-off between offspring size and number. If the reliability of the relationship between larval size and adult size is low, selection on parental care traits related to offspring size can be impeded and disadvantageous life-history pathways may not be eliminated from the population (Kirkpatrick and Lande 1989; Wiegmann et al. 1997). In contrast, the results of this study suggest that, although both parents and the environment influence the transmission of the life-history trait (body size), the direction of selection is similar. What remains is to include this size-dependent mortality in models measuring the fitness consequences of parental decisions regarding brood size and number. The data would also be applicable to modeling changes in the distributions of phenotypic traits.

Sequential improvements in design led to a useful overwintering chamber, which opens the door to further field studies of the behavioral ecology of *Nicrophorus* to complement those conducted in the laboratory (as suggested by Meierhofer et al. (1999) and Eggert and Sakaluk (2000)). The ideal overwintering chamber allowed for good drainage (especially during the period of spring snowmelt) and for observation of natural emergence without disrupting the pupal cells. It is possible that the containers protected the larvae from predation, thereby inflating survivorship. However, in nature, the depth of the overwintering cell would deter vertebrate predators such as shrews and no other predators or parasitoids of larvae have been described.

In conclusion, the size of larvae is clearly an important factor in overwinter survival and thus provides another factor that may influence parental decision-making. Clearly, mortality could be one of the strong selective forces acting on parents to reduce brood size and increase larval size, a factor that is rarely considered in treatments of the fitness consequences of parental investment (Fox and Czesak 2000). Application of a mortality factor in-between the termination of larval feeding and adult eclosion and reproduction provides a more accurate measure of parental fitness. Finally, adult body size is strongly correlated with larval mass, despite a delay of 10 or 11 months between the termination of larval growth and the emergence of the adult. This relationship is of critical importance to understanding the factors that influence selection on larval and adult phenotypes.

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