

Probability of Intra- and Interspecific Encounters, and the Duration of Parental Care in *Nicrophorus investigator* (Coleoptera: Silphidae)

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ABSTRACT In burying beetles (*Nicrophorus*), male and female pairs bury small carcasses to supply their larvae with food. Both parents care for their larvae for several days and defend them against other burying beetles that try to usurp the carcass. Male defense is very effective in preventing take-overs by conspecifics, but ineffective against attacks by larger congeners. From information on four species of *Nicrophorus*, Scott (1998) suggested that this asymmetry affects the duration of male care; males care longer when the major competitors are conspecifics, and leave early if they are larger congeners. We performed a field study examining the phenology of *N. investigator* Zetterstedt and its sympatric congeners in Bielefeld, Germany. Because of its relatively low abundance, an *N. investigator* arriving at a carcass had a much higher chance to meet an individual of another species of burying beetle than to meet a conspecific, suggesting that intraspecific competition is less important than competition by congeners. Breeding experiments showed that male care in *N. investigator* was shorter than in the numerically dominant species *N. vespilloides* Herbst and *N. vespillo* (L.), supporting Scott's hypothesis. However, we cannot exclude that the differences in male care were caused by other factors that vary between species, as for example the speed of larval development. Also, the probability of encounter used to estimate the relative importance of intra- and interspecific conflicts only gives a rough estimate of the competitive situation because of differences in fighting ability between species.

KEY WORDS *Nicrophorus*, burying beetles, carrion, competition, parental care, phenology

CARRION IS A short-lived, high-quality resource to many specialized insects (Hanski 1990, Kentner and Streit 1990). Competition for carrion is strong and has probably shaped many ecological, behavioral, and physiological traits of the associated insects (Hanski 1990). Burying beetles (Silphidae: *Nicrophorus* Fabricius), which exclusively rely on carrion as larval food, exclude most other competitors by burying small vertebrate carcasses underground (Pukowski 1933, Eggert and Müller 1997, Scott 1998). Fertilized females may reproduce singly or in groups, but usually a carcass is buried by a male and female beetle pair. During burial the pair remove the hair or feathers thereby probably destroying fly eggs and larvae. They form the carcass into a ball and store it in a small crypt, a brood chamber with stable walls of compressed soil. After burial is completed, which takes up to 1 d (Wilson et al. 1984, Otronen 1988, Scott 1990), the female lays its eggs in the surrounding soil. When the larvae hatch, they enter the crypt and congregate in a feeding hole that the parent beetles have prepared on top of the carcass ball. The parents remain in the crypt for several days; they maintain the crypt, preserve the carcass with anal fluids, defend the larvae against intruders, and feed them with predigested carrion. Both males

and females can reproduce more than once in a season (Bartlett and Ashworth 1988, Scott and Traniello 1990).

Burying beetles can discriminate between carcasses of different quality, probably by differences in scent (Wilson and Knollenberg 1984); teneral beetles preferably visit large carcasses to feed, but beetles with well-developed gonads specifically search for small carcasses suitable for reproduction. Most small carcasses are discovered by several beetles (Wilson and Fudge 1984, Wilson et al. 1984), resulting in violent fights between beetles of different species as well as between conspecifics of the same sex (Pukowski 1933). Because body size largely determines the outcome, it will usually be the largest male and female pair that secure the carcass and bury it (Pukowski 1933, Wilson and Fudge 1984, Wilson et al. 1984, Bartlett and Ashworth 1988, Otronen 1988, Müller et al. 1990, Trumbo 1990a). However, even after burial, the carcass can be discovered by other burying beetles, which try to usurp it and kill the residents' brood (Scott 1990; Trumbo 1990a, 1990b, 1994; Robertson 1993). Pairs are more successful than single females in retaining buried carcasses, which is thought to be the most important factor maintaining male participation in care (Trumbo 1991, Eggert and Müller 1997, Scott 1998). Males reduce take-overs because they contribute to carcass maintenance, which lowers the probability that it is located by other burying beetles

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(Trumbo 1994), and because they fight against intruding beetles (Scott 1990, Trumbo 1991). Male support helps to deter a conspecific intruder, even if it is larger than the same-sex resident (Scott 1990), but it seems ineffective if a larger congener invades a crypt (Scott 1994, 1998). From information on four species of *Nicrophorus*, Scott (1998) suggested that this asymmetry affects the duration of male care; males stay longer in the crypt if the major competitors are conspecific, and depart early if competitors are larger congeners. This hypothesis seems intriguing, however, because there are ≈ 70 species of *Nicrophorus*, data from more species are required before it can be generalized.

Here we present information on the competitive situation and the duration of parental care in *N. investigator* Zetterstedt, a moderately sized (12–22 mm) species that occurs in Europe, Asia, and North America (Pukowski 1933, Katakura and Fukuda 1975, Anderson and Peck 1985, Otronen 1988, Smith and Heese 1995). Its prepupae overwinter in the pupal cells and adults emerge and reproduce in summer (Pukowski 1933). We performed a field study to examine the spatial and seasonal activity patterns of *N. investigator* and its sympatric congeners on small carcasses in Bielefeld, Germany. From these data we calculated the probabilities of intra- and interspecific encounters and discuss the relative importance of intra- and interspecific competition. In laboratory experiments, we assessed the duration of parental care in *N. investigator*, and compared the results with published data on the duration of care in pairs of sympatric species bred under similar conditions (Schwarz and Müller 1992, Meierhofer et al. 1999).

Materials and Methods

Our study site was Gut Patthorst (Steinhagen) near Bielefeld, Germany, which included small clusters of forests (oak, beech, birch, and pine), meadows (mowed twice a year), and arable land. The predominant soil type is a sandy podsol-gley. We caught beetles at weekly intervals from 3 April until 30 October 1991, using 1-d-old mouse carcasses (15–25 g). Each carcass was enclosed in a tin covered by wire mesh and hung at a trestle above a pitfall trap. Thus, beetles attracted to the carcass were caught by the trap without getting into contact with the carcass. Each week, we placed four carcasses in woods and four on adjacent meadows. After 24 h, we removed the carcasses and took the trapped beetles to the laboratory for identification. As controls, we used one unbaited pitfall trap in woods and meadows, respectively. These never captured any burying beetles, indicating that beetles caught in the baited traps were attracted by the carcasses.

Burying beetles actively search for small carcasses, which they locate olfactorily (Anderson and Peck 1985). Therefore, our trapping did not measure absolute abundance or density, but rather the "availability" (Southwood 1978) of the beetles in the study area to mouse carcasses. This relative population estimate is

useful to assess the phenology of the potential of different species to colonize a resource (Southwood 1978). Here, we used it to calculate the probability of potential intra- and interspecific encounters (Hurlbert 1971) at small carcasses. Because we performed the trapping in two different habitats, we calculated this probability for each habitat separately.

It is assumed that all burying beetles that are active in the woods at a certain day i have the same chance of arriving at a carcass. Then, if a beetle of species A encounters another burying beetle on a carcass, the probability that this beetle is a conspecific is

$$E_i^{AA} = (a_i - 1) / (n_i - 1)$$

where a_i = the number of individuals of species A caught at carcasses in the woods on this day, and n_i = the total number of burying beetles caught in the woods on this day. Similarly, the probability for a beetle of species A that an encounter is with a beetle of another species B can be calculated as

$$E_i^{AB} = b_i / (n_i - 1),$$

where b_i is the number of individuals belonging to species B caught in the woods on this day. The mean probability for a beetle of species A to encounter a conspecific in the woods can be calculated as the average of the daily probabilities E_i^{AA} weighed by the daily abundances a_i

$$E^{AA} = \left(\sum_{i=1}^k E_i^{AA} a_i \right) / \sum_{i=1}^k a_i$$

similarly

$$E^{AB} = \left(\sum_{i=1}^k E_i^{AB} a_i \right) / \sum_{i=1}^k a_i$$

To study the duration of parental care and the reproductive success in *N. investigator*, we caught beetles in the study area in summer 1989. We took the beetles to the laboratory, sexed them, and put pairs into black box breeding containers (Müller et al. 1990) filled with moist peat. We supplied each pair with a freshly thawed mouse carcass weighing 14.5–15.5 g, and kept it at a temperature of $20 \pm 1^\circ\text{C}$ and a photoperiod of 18:6 (L:D) h. Each breeding container was equipped with a pitfall trap to catch beetles active on the surface of the soil. We opened the traps 1 d after the beetles buried the mouse and from then on checked them daily, recording the time from burial until the appearance of parent beetles or dispersing larvae. To establish the total number of offspring produced per beetle pair, we emptied the breeding containers and searched the peat for additional larvae 3 d after the second parent appeared on the soil surface. We compared the results to the published median values of beetle pairs from other species caught in Bielefeld and bred under similar conditions (Schwarz and Müller 1992, Meierhofer et al. 1999) by applying Wilcoxon one-sample median tests (Zar 1984). To correct for multiple testing, we used the Bonferroni method (Harris 1985).

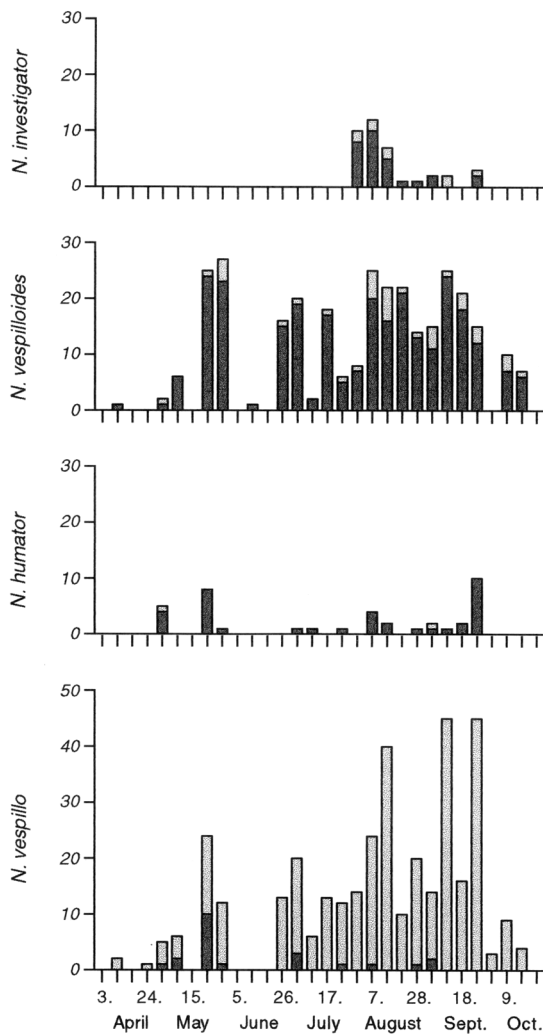


Fig. 1. Number of burying beetles caught at mouse carcasses in woods (dark bars) and in meadows (dotted bars) at weekly trappings in 1991. At each trapping day, four mouse carcasses per habitat were exposed for 24 h.

Results

The mouse carcasses on the study site were visited by four species of burying beetle (Fig. 1). Sex ratios were not significantly different from 0.5 (binomial tests, $P > 0.05$ for each species). Beetles were active from 10 April until 16 October 1991. From the 224 carcasses exposed during that period, 62.9% were discovered by burying beetles. The mean intensity was 5.25 (SD = 5.52, maximum = 31, $n = 141$) beetles per discovered carcass.

Nicrophorus investigator was active from 31 July until 25 September (Fig. 1). It occurred in both habitats, but most (75.7%) of the 37 individuals caught were at carcasses in woods ($\chi^2 = 9.757$, $P < 0.002$). It was the rarest species of burying beetle on our study site, comprising only 5% of the total catch ($n = 740$).

Because of its low relative abundance, encounters with other species of burying beetle were much more likely than intraspecific ones (Table 1). In woodland, the probability of an *N. investigator* encountering a conspecific was 2.2 times lower than the probability of encountering an individual of the most abundant wood species *N. vespilloides* Herbst. In meadows, the probability of meeting a conspecific was ≈ 30 times lower than the probability of meeting *N. vespillo* (L.).

In *N. investigator*, male care was shorter than female care (Fig. 2). There was only one case in which the female left before the male (after 3 and 6 d, respectively). Male care was significantly shorter than in pairs of *N. vespillo* and *N. vespilloides* bred under similar conditions (Fig. 2). Female care was shorter than in *N. vespillo*, but did not differ significantly from the median duration of care in female *N. vespilloides*. In all breeding containers ($n = 10$), larvae dispersing from the brood chambers came to the soil surface and were trapped. This happened 0–2 d (median = 1 d) after the last parent left the brood chamber. The median number of offspring produced per beetle pair was 11.5 (range, 6–15).

Discussion

Most of the carcasses that we placed on the study site were discovered by burying beetles, and on average >5 beetles arrived on a carcass. Because we introduced additional carcasses, the intensity of burying beetles on natural carcasses should be much higher, indicating that competition is intense. High competition for small carcasses was also demonstrated for other burying beetle communities (Wilson and Fudge 1984, Wilson et al. 1984).

Nicrophorus investigator was active from July until September, corresponding to the temporal activity pattern determined for other European and Japanese populations (Pukowski 1933, Springett 1968, Katakura and Fukuda 1975, Otronen 1988). It was the rarest of four species of burying beetle occurring on the study site, as in Schwarz et al. (1998). In meadows it was

Table 1. Average probabilities of potential inter- and intraspecific (in bold) encounters for the four species of burying beetles occurring on the study site in 1991

Species	Probability to encounter ^a			
	<i>N. investigator</i>	<i>N. vespilloides</i>	<i>N. humator</i>	<i>N. vespillo</i>
Woods				
<i>N. investigator</i>	0.28	0.62	0.08	0.02
<i>N. vespilloides</i>	0.07	0.78	0.09	0.06
<i>N. humator</i>	0.06	0.62	0.23	0.09
<i>N. vespillo</i>	0.03	0.69	0.15	0.13
Meadows				
<i>N. investigator</i>	0.03	0.09	0.00	0.88
<i>N. vespilloides</i>	0.02	0.10	0.01	0.87
<i>N. humator</i>	0.00	0.22	0.00	0.78
<i>N. vespillo</i>	0.02	0.10	0.01	0.87

^a Given are the average probabilities for the species in the first column that an encounter with another burying beetle will be with one of the species listed in columns 2–5.

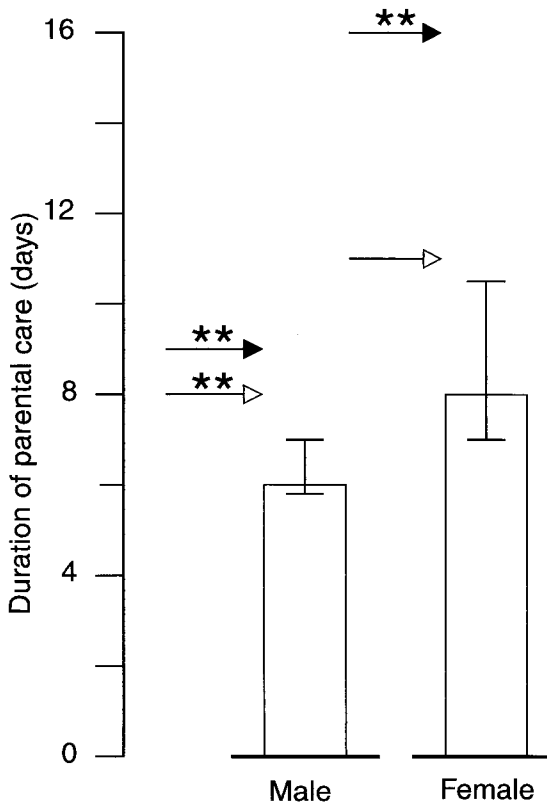


Fig. 2. Median duration (\pm quartiles) of parental care in *N. investigator* at 20°C ($n = 10$ pairs). Filled and open arrows indicate published median duration of care in *N. vespillo* (Meierhofer et al. 1999) and *N. vespilloides* (Schwarz and Müller 1992), respectively. To test for species differences, median values for *N. investigator* were compared with *N. vespillo* and *N. vespilloides* by Wilcoxon one-sample median tests (Zar 1984). **, $P < 0.01$ ($P < 0.05$ after Bonferroni correction for the $k =$ four tests performed).

outnumbered by *N. vespillo*, in woods the most abundant species was *N. vespilloides*. Both these species are multivoltine and in Germany can reproduce from May until September (Pukowski 1933, Schwarz and Koulianos 1998, Schwarz et al. 1998, Meierhofer et al. 1999). Less abundant was *N. humator* Olivier, which is a monovoltine woods specialist that reproduces in early spring (Pukowski 1933, Schwarz and Koulianos 1998).

Because of its relatively low abundance in Bielefeld, an *N. investigator* arriving at a carcass had a much higher chance to meet an individual of another species of burying beetle than to meet a conspecific. If we want to use the probabilities of potential encounters (Table 1) to estimate the relative importance of intra- and interspecific conflicts for *N. investigator* on unburied mouse carcasses, we have to consider that on average only half of the intraspecific encounters will be between individuals of the same sex and hence result in fights. Similarly, encounters with *N. humator* should not result in fights because this species does not

reproduce at the same time as *N. investigator* (Pukowski 1933, Springett 1968). Therefore, the ratio of potential intra- and interspecific conflicts for *N. investigator* can be estimated as the ratio of half the probability of intraspecific encounters and the sum of the probabilities of encounters with *N. vespillo* and *N. vespilloides*. Using the values from Table 1, this yields a ratio of 1:5 in woods and 1:67 in meadows. In woods, most conflicts will be with *N. vespilloides*, in meadows the most likely competitor is *N. vespillo*. These two species were numerically dominant in their respective habitats, therefore for them most conflicts will be with conspecifics.

The above calculations are only valid for the situation on unburied mouse carcasses. If we assume that the relative abundances of beetles arriving at unburied carcasses correspond to those of beetles invading crypts, then we can also estimate the ratio of intra- and interspecific conflicts at buried carcasses. Because beetles that possess a buried carcass fight a conspecific intruder regardless of its sex (Scott 1990, Trumbo 1990b), the ratio in this case is twice as high as on unburied carcasses. Still, the probabilities of encounter suggest that for *N. investigator* most conflicts will be with congeners, whereas for *N. vespillo* and *N. vespilloides* the most likely competitors are conspecifics.

In our breeding experiments, male care in *N. investigator* was significantly shorter than in *N. vespilloides* and *N. vespillo*. This seems to support the hypothesis of Scott (1998) that male care is shorter in species with relatively low intraspecific competition. However, we cannot exclude that the difference in male care could be caused by other factors that vary between species, for example differences in the rate of development, which was shown to influence the duration of male care in *N. orbicollis* Say (Trumbo 1991). The fact that *N. investigator* females care significantly shorter than *N. vespillo* females indicates that differences in offspring development between these two species exist because female burying beetles usually care until the prepupae disperse (Trumbo 1991, Scott 1998).

The probabilities of potential encounters only give a rough estimate of the competitive situation because in *Nicrophorus* the outcome of interspecific fights is mainly determined by body size (Pukowski 1933, Wilson et al. 1984, Otronen 1988, Trumbo 1990a). The size ranges of *N. investigator*, *N. vespillo*, and *N. vespilloides* broadly overlap with the minimum sizes being almost similar, but on average *N. vespilloides* is the smallest species and *N. investigator* is the largest (Otronen 1988). Therefore, *N. vespilloides*, despite its numerical superiority, may be a lesser threat to *N. investigator* than conspecifics. However, only the largest *N. investigator* individuals will manage to defend a carcass against *N. vespillo*, which is much more abundant and more similar in size. The presence of the relatively strong competitor *N. vespillo* on meadows may be the reason why *N. investigator* preferred carcasses in woods in Bielefeld and at another locality in Germany (Kentner and Streit 1990). In Finland, where the meadow specialist *N. vespillo* is rare and stops repro-

duction when *N. investigator* becomes active (Otronen 1988), and in Colorado, United States, where no competing burying beetles are present (Smith and Heese 1995), *N. investigator* prefers carcasses in meadows. It would be interesting to examine whether the duration of care varies between pairs of *N. investigator* from different populations. If beetles from Colorado, Finland, or other populations with low interspecific competition cared shorter than beetles from areas where strong interspecific competitors are present, this would further support Scott's (1998) hypothesis.

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