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Seasonal variation in parental care, offspring development, and reproductive success in the burying beetle, *Nicrophorus vespillo*

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Abstract. 1. Beetles of the genus *Nicrophorus* reproduce on small vertebrate carcasses that they bury in the soil to provide the larvae with food. Usually, both parents cooperate in brood care by feeding and guarding their progeny.

2. In pairs of the common European species *N. vespillo,* the duration of care depended on the time of year when the beetles reproduced. Both in 1990 and in 1991, male and female parents stayed longer with their broods when reproduction started in spring than when reproduction started in early or late summer. This was probably due to the longer development time of the larvae caused by lower temperatures in spring, because laboratory experiments suggested a strong influence of temperature on both the duration of brood care and offspring development.

3. The number of adult offspring produced by a beetle pair did not vary among different times of the year.

4. The median time required for offspring development, measured as time from burial of the carcass to emergence of young adults, was between 62 and 84 days. When the beetles reproduced in late summer, only about three-quarters of the offspring left the soil and hibernated as adults. The remaining offspring stayed underground and adults appeared on the soil surface the following spring. They still showed the flexible cuticle typical of newly-hatched beetles, suggesting that they may have overwintered in a pre-adult stage.

Key words. Development time, hibernation, *Nicrophorus vespillo*, parental care, reproductive success.

Introduction

Burying beetles (*Nicrophorus* Fabricius; Coleoptera: Silphidae) are one of the few examples of elaborate parental care in insects outside the Hymenoptera and Isoptera (Clutton-Brock, 1991). They reproduce on small vertebrate carcasses that they bury as a food resource for their larvae. Communal breeding may occur, but in most cases a carcass is monopolized by a male and female pair that chases away competitors by combat (Trumbo, 1992; Eggert & Müller, 1997; Scott, 1998). When the pair of beetles buries the carcass, they remove the hair or feathers and gradually form it into a ball. The beetles' continual movement around the carcass ball results in the construction of a brood chamber with stable walls of compressed soil. The female lays her eggs singly in the surrounding soil. When the larvae hatch, they enter the brood chamber and congregate in a feeding hole that the parent beetles have prepared on top of the carcass ball. Excess larvae are killed by the parents to adjust larval number to carcass size (Bartlett, 1987; Trumbo, 1990). Both parents remain in the brood chamber for several days; they maintain the brood chamber, preserve the carcass, defend the larvae, and feed them by regurgitating pre-digested carrion onto their mouths. Larvae also feed directly from the prepared carrion, but parental regurgitation enhances development and in some species is required for survival (Pukowski, 1933; Eggert *et al.*, 1998; Scott, 1998). Usually, it is the male parent that stops brood care first and leaves the brood chamber, followed a few days later by the female. When the carcass ball is completely used up, the larvae leave the chamber and pupate singly in the

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surrounding soil. After eclosion, the adult beetles burrow their way out of their pupal cells and start to search for carcasses (Eggert & Müller, 1997; Scott, 1998).

Parents that care for their brood for an extended period forego time that could be used to seek additional breeding opportunities (Trivers, 1985). The duration of parental care therefore is thought to be determined by trade-offs between the increased survival of the offspring and the losses of additional reproductive opportunities incurred by the parents (Maynard-Smith, 1977; Grafen & Sibley, 1978). The parental decision whether to continue caring or to abandon the brood will vary with environmental factors that affect the costs and benefits of brood care (Scott & Traniello, 1990; Clutton-Brock, 1991). Although *Nicrophorus* has received much attention as a model organism to study the evolution of parental care, there is still a shortfall of experimental work under natural conditions, and published studies treat only a few of the approximately seventy described species (Eggert & Müller, 1997). Factors influencing the duration of parental care of monogamous pairs in the field have only been examined for the nearctic species *N. orbicollis* Say (Scott, 1990; Scott & Traniello, 1990; Trumbo, 1991; Robertson, 1993) and *N. tomentosus* Weber (Scott, 1994). In these studies, most factors examined, such as competition, burial depth, the timing of reproduction, the size and prior experience of the parents, and the degree of paternity, showed no significant influence on the duration of care. The main factors affecting the duration of parental care proved to be the size of the carcass (Scott & Traniello, 1990; Trumbo, 1991) and the stage of larval development (Trumbo, 1991). Carcass size is also a major determinant of reproductive success in *Nicrophorus* (Wilson & Fudge, 1984; Bartlett, 1987; Otronen, 1988; Scott & Traniello, 1990; Beninger & Peck, 1992; Robertson, 1992; Trumbo, 1992; Scott & Gladstein, 1993; Eggert & Müller, 1997), and is thought to influence the speed of larval development (Trumbo, 1991; Scott & Gladstein, 1993).

In this study, carcass size is kept constant in order to examine whether parental care, offspring development, and reproductive success vary within the reproductive season of the beetles. For this purpose, field experiments were performed with breeding pairs of *N. vespillo* (Linnaeus), a species of intermediate size (12–22 mm) common in fields and grassland areas of Europe and Asia (Hatch, 1928; Pukowski, 1933; Otronen, 1988; Rohner, 1990). Depending on the climatic conditions, *N. vespillo* can reproduce from mid-May until mid-September (Schwarz & Koulianos, 1998). During this period, reproducing beetles experience considerable temperature differences, so laboratory experiments were performed to determine how temperature alone influences beetle behaviour.

Materials and methods

Field study

The field study was performed in Gut Patthorst (Steinhagen) near Bielefeld, Germany, an area that is divided into 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 (Lienenbecker, 1971).

To study the duration of parental care, the development time, and the reproductive success in *N. vespillo*, beetles were caught in pitfall traps (Müller & Eggert, 1987) baited with dead mice (15–25 g). Beetles had no direct access to the bait because it was enclosed in a tin covered by wire mesh that hung from a trestle above the pitfall trap. Trapped beetles were kept in cages in the field until enough individuals for a breeding experiment were collected. They were then paired and put into breeding containers placed 50 cm apart along a transect in a meadow. These containers consisted of a piece of metal tube (length 31 cm, diameter 23 cm) buried vertically to a depth of ≈ 24 cm. The round enclosure formed by the 7 cm of the tube protruding from the soil was covered by a removable lid made of wire mesh to prevent beetles from escaping. A small pitfall trap (diameter 4.5 cm) was placed inside the enclosure, in contact with the inner wall of the tube, to catch beetles that were active on the soil surface.

The tubes and pitfall traps were buried at least 1 month before the start of an experiment. Care was taken to preserve and return the original soil and grass patch, which was removed to facilitate burial of the tube, to the inside of the tube. Thus, a natural layer of grass level with the surrounding meadow was growing inside the protruding part of each tube. The meadow was not mowed during the study. Temperature 3 cm above soil level was recorded by a mechanical thermograph (Typ T 81027, Ketterer, Sölden, Germany), which was protected by a roof and situated in the middle of the row of breeding containers. The mean daily temperature was calculated using the formula given in Hempel (1974). The average temperature during the first 10 days of an experiment was used to estimate temperature conditions during biparental care, because it was known from laboratory experiments that most parent beetles stay with their brood for at least 10 days.

In 1990, four breeding experiments were performed (starting on 18 May, 22 June, 19 August, and 17 September). Each time, ten pairs of beetles that had been caught up to 3 days before the experiment were used. At the start of an experiment the pitfall traps in the breeding containers were closed. Each pair was then put on the grass in one of the containers, supplied with a dead mouse (14.5–15.5 g, frozen immediately after killing and thawed 8–12 h before the experiment), and the container was closed with the lid. One day after a pair of beetles buried the mouse, the pitfall trap was opened and from then on checked daily in order to collect trapped beetles. The traps of all ten containers were checked until 1 week after the emergence of the last beetle offspring. The duration of parental care was measured as time between the burial of the mouse and the day the parent beetles were caught in the trap. Development time was estimated as the time between burial and the day the adult offspring appeared in the trap. The reproductive success of a beetle was measured as the number of adult offspring. Only replicates in which both parents survived were included in the analysis, because the death of one parent influences the duration of brood care of the remaining parent (Trumbo, 1991).

Table 1. Duration of parental care, time until offspring emergence, and number of offspring in *N. vespillo*, measured at three different times in 1990. Start = start of the experiment, *n* = number of beetle pairs, T-dev = average daily temperature (°C) between start and the emergence of 50% of the offspring, T-care = average daily temperature (°C) during the first 10 days of the experiment, Med = median, 25%, 75% = quartiles.

				Duration of parental care (days)						Emergence of offspring (days)			Number of offspring		
				Male			Female								
Start	*n*	T-dev	T-care	Med	25%	75%	Med	25%	75%	Med†	25%	75%	Med	25%	75%
18 May	9	14.5	12.3	19	15	21	30	28	31	69	68	70	13	13	15
22 June	8	17.2	20.2	12	7	15	24	23	24	62	61	62	13	10	13
19 August	9	12.8	19.5	8	6	14	22	20	24	68	65	71	11	11	12
Kruskal–Wallis ANOVA				$H = 8.08829$ $P = 0.0175$*			$H = 11.9400$ $P = 0.0026$*			$H = 14.369$ $P = 0.0008$*			$H = 2.2724$ $P = 0.3211$		

†Calculated as the *grand* median of the median values of the *n* beetle families.
*Significant at the 5% level after Bonferroni correction.

In 1991, two breeding experiments were conducted (starting on 2 June and 2 September) using twenty pairs of beetles in each. Again, pairs in which one parent died were excluded from the analysis. In the experiment starting on 2 September, the last offspring appeared in the trap very late in the year (12 December), after the first snowfall. Therefore, the containers were left in the field with the traps open and checked again on 1 April 1992.

Laboratory experiment

A laboratory experiment was performed to examine whether duration of parental care, development time, and reproductive success vary at two different temperatures. For this purpose, beetles from laboratory stocks that had not reproduced previously were used. Pairs of beetles were put into black-box breeding containers (Müller *et al.*, 1990) in which they could reproduce without disturbance. Each pair was supplied with a freshly thawed mouse carcass weighing 14.5–15.5 g. Fifteen containers were kept in climate chambers at a temperature of 15 ± 1 °C and a LD 18:6 h regime, and thirty containers at a temperature of 20 ± 1 °C and a LD 18:6 h regime. Each breeding container was equipped with a trap to catch beetles leaving the brood chamber or the pupal cells. These traps were checked daily, and the duration of male and female care, the time from burial until offspring emergence, and the number of offspring were recorded.

Statistics

The experiments were designed to test for differences between pairs of beetles at different times of the year or at different temperatures by comparing four variables: time until male dispersal, time until female dispersal, time until offspring emergence, and number of offspring. This is a multivariate design that could be analysed, for example, by a MANOVA. The variables were not distributed normally, however, so each variable was tested separately by a non-parametric test (Kruskal–Wallis ANOVA or Mann–Whitney *U*-test). The experiment-wise probability of Type I error was controlled by the sequential Bonferroni method (Harris, 1985; Rice, 1989).

Results

Field study

In the field experiment starting on 17 September 1990, the beetles did not reproduce, suggesting that they were in reproductive diapause. This experiment was therefore excluded from further analysis. In the remaining experiments performed in 1990 and 1991, most pairs reproduced (Tables 1 and 2). The pairs buried the carcasses within a median duration of 1 day after the start of the experiment (quartiles: 1 day, 2 days). The males stayed with their broods for several days (Tables 1 and 2), but almost always left before the females; there was only one case in which the female left before the male, and in one case both parents left on the same day. In both years, there was a significant seasonal variation in the duration of parental care. In 1990, both male and female parents stayed with their brood longer when reproducing in May than when reproducing in June or August (Table 1). This difference in brood care was associated with a marked temperature difference. The average temperature during the first 10 days after burial of the mouse for beetles reproducing in May was more than 7 °C lower than the temperature for beetles reproducing later in the season (Table 1). Similarly, beetles reproducing in June 1991, when it was very cold, cared longer than beetles reproducing in September 1991, when the temperature during the first days of brood care was 2.7 °C higher (Table 2).

Despite the marked differences in parental care and temperature, the mean reproductive success of the beetles

Table 2. Duration of parental care, time until offspring emergence, and number of offspring in *N. vespillo*, measured at two different times in 1991. Start = start of the experiment, *n* = number of beetle pairs, T-dev = average daily temperature (°C) between start and the emergence of 50% of the offspring‡, T-care = average daily temperature (°C) during the first 10 days of the experiment, Med = median, 25%, 75% = quartiles.

				Duration of parental care (days)						Emergence of offspring (days)			Number of offspring		
				Male			Female								
Start	*n*	T-dev	T-care	Med	25%	75%	Med	25%	75%	Med†	25%	75%	Med	25%	75%
2 June	16	15.4	11.7	13	12	14	31	29	31	68	66	70	10	9	11
2 September	18	8.4	14.4	7	3	10	22	10	25	84‡	80‡	86‡	10	0	12
Mann–Whitney *U*-test				*U* = 52.000 *P* = 0.0014*			*U* = 19.000 *P* = 0.0001*			*U* = 0.000 *P* = 0.00001*			*U* = 133.5 *P* = 0.511		

‡Only the beetle offspring that emerged in 1991 are considered.
†Calculated as the *grand* median of the median values of the *n* beetle families.
*Significant at the 5% level after Bonferroni correction.

showed no significant variation in either 1990 or 1991 (Tables 1 and 2). There were, however, significant differences in development time. In both years, the time from burial until offspring emergence was shortest when the mean daily temperature during offspring development (T-dev) was highest.

In the breeding experiment starting on 2 September 1991, only 71% (*n* = 151) of the offspring left the soil within the same year. Of those, the first adult beetle appeared on 13 November and the last on 12 December, when the soil was already covered with snow. The remaining 29% of the offspring stayed underground until the following spring, with the first adult appearing on the soil surface on 8 April, and the last on 2 May 1992. All beetles that left the soil in 1992 had the soft and lightly stained cuticle typical of newly-hatched adults.

Laboratory experiment

In the breeding experiment performed in the laboratory, parental care and time until offspring emergence was longer at 15 than at 20 °C. There was no significant difference in the number of adult offspring between beetles raised at the two temperatures (Table 3).

Discussion

In *N. vespillo*, both the male and the female parent cared longer when reproducing early in the season than when reproducing later. Many ecological and physiological factors vary during a reproductive season, but temperature seemed to be a major factor influencing the duration of parental care, because average temperatures during the first 10 days of brood care were markedly lower for beetles reproducing earlier in the year. This is supported by the laboratory experiment, in which parental care was longer at 15 than at 20 °C. There is evidence that the duration of parental care is linked to larval development (Trumbo, 1991; Eggert & Müller, 1997), so a functional explanation for the influence of temperature would be that larval development takes longer at lower temperatures and therefore parent beetles care for longer (cf. Trumbo, 1991). An effect of temperature or of another factor that varies with season could also explain the unusually short duration of parental care in *N. tomentosus* at the end of the reproductive season (Scott, 1994).

The males of *N. vespillo* abandoned their broods several days before the females, as in all species of *Nicrophorus* examined to date (Bartlett, 1988; Scott & Traniello, 1990; Brown & Wilson, 1992; Robertson, 1992; Sikes, 1996; Schwarz *et al.*, 1998). This was also observed by Pukowski (1933), who reported that females of *N. vespillo* actively chase away their males. The results of the field experiments show that this does not happen when the female finishes egg laying about 2 days after burial of the carcass, as suggested by Pukowski, but instead 7–19 days after burial, depending on the season.

The time a burying beetle spends with its brood is usually considered a cost because the beetle forgoes searching for new breeding or mating opportunities (e.g. Trumbo, 1991; Robertson, 1993; Scott & Gladstein, 1993; Eggert & Müller, 1997). If the probability of finding such opportunities were constant within a reproductive season, it could be concluded from the results of the field study that the costs of parental care are higher for beetles reproducing early in the year. Unfortunately, this probability cannot be estimated because there seems no way to measure important variables like the chance of finding a carcass or the number of broods a beetle may rear in its lifetime (Scott & Gladstein, 1993). Nevertheless, the results suggest strongly that studies assessing the costs and benefits of parental care in *Nicrophorus* should include replicate experiments performed during the whole breeding season of the species examined.

The results presented here are in contrast to those of Scott & Traniello (1990), who found no effect of time of reproduction on the duration of parental care in *N. orbicollis*. This may

Table 3. Duration of parental care, time until offspring emergence, and number of offspring in *N. vespillo*, measured in the laboratory at 15 and 20 °C, respectively. *n* = number of beetle pairs, Med = median, 25%, 75% = quartiles.

Temperature (°C)	*n*	Duration of parental care (days)						Emergence of offspring (days)			Number of offspring		
		Male			Female								
		Med	25%	75%	Med	25%	75%	Med†	25%	75%	Med	25%	75%
15	13	14	12	15	20	19	21	56	54	58	13	11	19
20	23	9	8	10	16	15	17	45	41	47	12	6	14
Mann–Whitney *U*-test		*U* = 76.000 *P* = 0.0147*			*U* = 55.000 *P* = 0.0017*			*U* = 0.000 *P* = 0.00001*			*U* = 95.500 *P* = 0.0744		

†Calculated as the *grand* median of the median values of the *n* beetle families.
*Significant at the 5% level after Bonferroni correction.

indicate differences in the behaviour or ecology of the two species. *Nicrophorus orbicollis*, for example, reproduces between June and August (Scott, 1998), whereas *N. vespillo* has a much longer reproductive season (Schwarz & Koulianos, 1998) and may thus encounter more heterogeneous conditions during brood care. Differences in experimental design, however, may also be responsible; Scott & Traniello (1990) excavated the carcasses after burial and kept them at ambient temperature, whereas in this study the beetles were left undisturbed during brood care.

In *N. vespillo*, the number of adult offspring produced by a beetle pair did not vary significantly, either between beetles bred at different times of the season or between beetles reproducing in the laboratory at different temperatures. There also was considerable overlap in the offspring numbers measured for laboratory- and field-bred *N. vespillo*, and the numbers reported in another field study (Schwarz *et al*., 1998). *Nicrophorus* spp. are known to adjust the number of larvae to carcass size at an early stage of brood care (Bartlett, 1987; Trumbo, 1990; Eggert & Müller, 1997). Results from the present study suggest that in *N. vespillo* offspring mortality after culling is fairly constant within a wide range of environmental conditions. This may be different in other species of burying beetle for which seasonal variation in offspring number has been reported (Wilson & Fudge, 1984; Scott & Traniello, 1990). Offspring numbers established for *N. vespilloides* Herbst (Otronen, 1988; Schwarz & Müller, 1992; Schwarz *et al*., 1998) and *N. defodiens* Mannerheim (Trumbo & Eggert, 1994) indicate that these species have many more offspring than *N. vespillo* on carcasses of comparable size. Offspring numbers given for other species (Wilson & Fudge, 1984; Scott & Traniello, 1990; Trumbo, 1991, 1992; Beninger, 1994; Sikes, 1996) cannot be compared directly to *N. vespillo* because different-sized carcasses were used in these studies.

Like the duration of parental care, the time between burial and offspring emergence was affected strongly by the timing of reproduction, with median values between 62 and 84 days. Again, temperature seemed to be the main factor causing this variation because lower temperatures were associated with longer offspring development in both field and laboratory experiments. A comparison between laboratory and field experiments suggests that in the laboratory development is faster at similar temperatures. In carabid beetles, it was shown that the fluctuating temperature in the field can affect development in a different way than a constant laboratory temperature of the same magnitude (Thiele, 1977). The development times measured for *N. vespillo* in the present study are considerably longer than those established for *N. vespilloides* (Schwarz & Müller, 1992; Schwarz *et al*., 1998). Development times for other species of *Nicrophorus* are only available from laboratory studies in which the exact temperature conditions are not given (Halffter *et al*., 1983; Scott & Traniello, 1990; Robertson, 1992; Sikes, 1996).

Nicrophorus vespillo is known to hibernate in the adult stage (Pukowski, 1933; Roussel, 1963). In September 1991, when beetles reproduced at the end of the reproductive season, only about three-quarters of their offspring left the soil as adults in the same year. The remaining offspring stayed underground and adults appeared on the soil surface the following spring, all showing the weakly-sclerotized cuticle typical of newly-moulted imagoes. It is possible that these beetles, like their siblings, had moulted into adults late in 1991 but stayed underground until spring 1992. If this was the case, the sclerotization process of their cuticles had slowed down, possibly because of the cold temperatures during winter. This is thought to happen in some carabid species, where adults may stay callow at low temperatures for several weeks (den Boer & den Boer-Daanje, 1990). Alternatively, the beetles appearing in spring may have overwintered in a juvenile stage and moulted into adults shortly before leaving the soil. It seems possible that *N. vespillo* is able to hibernate both in the adult and in a juvenile stage, because other Coleoptera have the ability to overwinter in many if not all life-cycle stages (Kaufmann, 1986; den Boer & den Boer-Daanje, 1990; Guppy & Harcourt, 1990; Convey, 1996). Also, there are species of *Nicrophorus* that overwinter regularly as prepupae (Pukowski, 1933; Peck & Kaulbars, 1987), indicating the potential of this genus to overwinter in a juvenile stage.

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