Original article

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Biparental investment and reproductive success in a subsocial desert beetle: the role of maternal effort

Abstract *Parastizopus armaticeps* is a nocturnal subsocial detritivorous desert tenebrionid that produces very few offspring per brood. The two environmental factors that constrain reproduction, rapid sand desiccation rate and food scarcity, are countered by biparental effort. Males dig and extend breeding burrows, maintaining their moisture level; females forage on the surface at night for high-quality detritus, the larval food. This was shown to be a scarce and unpredictable resource for which there is high competition. When food was supplemented in a field experiment, offspring number and survivorship doubled and burrow failure due to desiccation dropped from approximately half, the typical failure rate for unsupplemented burrows, to zero. Food supplementation did not, however, increase larval foodstore size and there was no difference in the size of the offspring produced. Supplemented females reallocated their time, foraging less and digging more with the male. This change in maternal behaviour patterns resulted in deeper burrows which remained moist longer, thus extending the larval production period. Female foraging efficiency, particularly food retrieval speed, determined how much time females could allocate to digging, consequently increasing the reproductive success of the pair. Burrow depth and sand moisture level at the burrow base were the major correlates of reproductive success, but the scarcity and unpredictability of high-quality food on the surface and the competition for this resource influenced the number of offspring indirectly through their effect on female behaviour.

Key words Coleoptera · Subsociality · Maternal effort · Tradeoff · Reproductive success

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Introduction

Reproduction in detritivourous insects living in arid regions, such as the subsocial nocturnal tenebrionid *Parastizopus armaticeps* (Peringuey) in the southern Kalahari, is constrained by two major environmental factors. The first is water, which is only available as sporadic rainfall; *Parastizopus* can only breed after heavy rain when the sand is saturated. Rapid sand desiccation after such rainfall then sets a sharp limit to the time available for reproduction and thus the number of young that can be reared. The second constraint is food and the effort necessary to obtain it. Although detritus is commonly considered a non-limiting factor for desert detritivores (Wise 1981), detritus quantity and quality may be very different variables. Although detritus may be abundant, high-quality detritus necessary for feeding larvae and the competition for this could be crucial to reproductive success. Food abundance increases offspring number in several bird species, especially raptors (Dijkstra et al. 1982; Newton and Marquiss 1981; see Arcese and Smith 1988 for a review) while, for insects, restricted larval food is correlated with small adult size (Beaver 1973; Haupt and Busvine 1968; Miller 1964).

Since male and female cooperate in raising the brood and show division of labour (Rasa 1990), *Parastizopus* provides an ideal model to test how parental effort influences reproductive success. Most other coleopterans with cooperative brood care, such as scarabaeids (Halffter 1977; Halffter and Edmonds 1982) burying beetles (*Nicrophorus*) (Pukowski 1933; Scott 1990; Scott and Traniello 1990; Trumbo 1991), scotylids (Ashraf and Berryman 1969; Reid and Roitberg 1994) and passalids (Schuster and Schuster 1985), do not show division of labour. The exceptions are *Nicrophorus orbicollis* (Fetherston et al. 1990) and the scarabaeid genus *Cephalodesmius* (Monteith and Storey 1981). In *Parastizopus*, as in *Cephalodesmius*, male and female roles differ qualitatively as well as quantitatively (Rasa 1990). The male parent digs, guards and extends a special

breeding burrow, maintaining the moisture level as the surface sand dries out after the rainfall that initiated breeding. This maintenance of burrow moisture is essential since larvae are unable to burrow and require 100% relative humidity (RH) to survive. The female parent forages on the surface at night, searching up to 8 m from the burrow for food items, mainly fallen twigs of the major foodplant, *Lebeckia linearifolia* (Papillionaceae), a broom-like bush. Food items are carried, usually vertically in the mandibles, to the burrow entrance, dropped and then pulled down to the larval foodstore by the male (Rasa 1990). Females emerge to forage just after sunset, when surface temperatures are 29–30 °C and RH 5–10%, approximately 30–40 min before non-breeding individuals and other common detritivores in the habitat emerge to feed (Rasa 1994). By this time, surface temperature has decreased to 21–24 °C and RH increased to 20%. Females thus expose themselves to harsh surface conditions to forage for larval food, which suggests that competition for this resource is high.

Parastizopus, unlike most insects, produces very few offspring for each successful breeding attempt (1.6 ± 1.8 teneral adults; Rasa 1996). Free-living adult beetles live for at least 2 years and, owing to their highly effective chemical defensive secretion (Brits 1981; Hein et al. 1996), have no predators. They either die of various types of accident, which result in their desiccation after the next sunrise (Rasa 1995), or old age. Young beetles that eclose successfully can therefore be considered effective units of reproductive success.

To test the hypothesis that food and the effort necessary to obtain it limit reproductive success, a sample of breeding burrows was provided daily with a small food supplement in a field experiment. If food is a constraint, provisioned burrows should produce more or larger young than control burrows and/or females should compensate by decreasing foraging effort and investing more time in other parental activities.

Methods

The study was conducted in the southern Kalahari, on a dune at Twee Rivieren, Kalahari Gemsbok National Park, South Africa (26°27′S, 20°36′E) in March 1996, 14 days after heavy rainfall (total 64.5 mm). Typically, the southern Kalahari has heavy summer thunderstorms separated by weeks of drought. At the start of the study, the beetles had already dug breeding burrows and these contained larvae. Usually 1–2 eggs/day are laid between the 1st and 3rd days following courtship and the start of breeding burrow construction. Eggs hatch within 1–2 days, larval development takes approximately 11–13 days and pupation 11–12 days.

Breeding burrows were identified by the characteristic digging spoor at their entrances and by observing females provisioning burrows in the early evening. Each burrow was marked with a numbered plastic flag. Experimental (E) burrows ($n = 32$) were provisioned each evening at 1800 hours, before activity started, with four thin, freshly dried *Lebeckia* twigs 3 cm long (total mass 0.04 g) which were laid directly at the burrow entrance. This food supplement represents only a small proportion (approximately 15%) of the total food a female is capable of retrieving per night (Rasa 1990). Control (C) burrows ($n = 32$), which were not provisioned, were located on the same dune face.

Breeding burrows occurred either in groups around a *Lebeckia* bush, or isolated on the flat, bare sand areas between bushes, a mean distance of 8.0 ± 2.8 m away from other burrows or a foodsource. Since location could influence both food availability and foraging efficiency, 14 randomly selected, isolated burrows were included in each E and C burrow sample. The remaining 36 burrows (18 in each sample) were located in 11 groups of 2–6, with groups being selected at widely separated locations on the dune (>15 m apart) to reduce interference. Burrows in a group were 1.5 ± 0.8 m apart. An entire group was randomly assigned either E or C status. Female beetles steal food they find at the entrance of neighbouring burrows. Since all burrows in an experimental (E) group were provisioned simultaneously stealing did not occur. Provisioned females, however, started to forage later than unprovisioned ones since they first pulled the food at the entrance down into the burrow. Because E burrows were grouped, this delay did not result in these females being disadvantaged when they began foraging since they were not competing for surface food with non-provisioned ones in the same locality.

Each burrow was checked in the same sequence at 1900, 2000 and 2100 hours for 16 days, after which all except nine burrows had ceased activity with the entrances closed from within, indicating larval pupation. Each burrow was observed for approximately 1 min during each of the three checks, using a dim red light to avoid disturbing the animals. Beetle activity was recorded either as digging (scraping away sand at the burrow entrance) or foraging (either searching for food or carrying a food item to the burrow). Surface digging and foraging only occur at night, the beetles remaining underground during the day to avoid desiccation as a result of the high daytime surface temperatures (40–70 °C) and low surface RH (2–8%) (Rasa 1997). Individuals were not marked, since preliminary studies showed that capture and marking of breeding females resulted in severe disturbance, even burrow abandonment. A foraging female's burrow was determined by presenting her with a tiny piece of food (approximately 0.001 g, one-third of a *Lebeckia* leaf) and recording which burrow she took it to.

Each individual received a score of 1 for each check during which it performed one of the two activities, digging or foraging. If a female was observed foraging during all three checks, her score was therefore 3. Males were rarely observed on the surface, confining their activity to the burrow interior. Male surface activity was therefore excluded from these analyses. Mean daily activity scores for burrow classes were the sum of all scores per class per night divided by the number of active burrows. E burrows were considered inactive when provisioned food was not pulled in for 3 successive nights and C burrows when neither foraging nor digging was observed for 3 successive nights. Since the number of inactive burrows increased with time, calculating the mean activity per active burrow allowed data comparison over the entire observation period. These activity data were used to estimate maternal investment for C and E burrow females, the mean nightly digging and foraging scores being calculated for each day of the 16-day observation period. Since only 9 of 38 E burrows were still active on day 16 and no C burrows had been active since day 13, this comparison was restricted to the period from days 1 to 15, 14 E burrows still being active at this time.

Burrows were excavated after 17–20 days and their contents recorded. Foodstore size was classed as small (10 or fewer food items), medium (11–20 food items) or large (>20 food items). This estimate of foodstore size was used rather than foodstore weight since foodstores are not compact, as is typical for dung beetles and burying beetles. They also contain various amounts of items not eaten by larvae (e.g. julid millipede droppings and *Lebeckia* seeds) as well as inedible frass, sand and faecal material. Sand moisture level was estimated and classed as moist (dark with a crumb-like texture) or dry, and the borderline between dry and moist sand was always clearly visible. Burrow length and depth were measured to the nearest centimeter. The number of larvae and pupae per burrow

were recorded. Larvae were all late-stage (IV–V instar) and fed in the laboratory until pupation, 1–6 days later. These larvae were included in the measurement of reproductive success since all originated from moist, active burrows and would have completed metamorphosis under natural conditions. Pupae from different burrows were kept in separate boxes at 30 °C and 100% RH until the teneral adults eclosed. Their body lengths from the front angle of the pronotum to the tip of the elytra were then measured to the nearest mm. Cocoons that did not eclose were considered dead after 20 days and were opened to confirm this.

Rainfall data were obtained from a government weather station situated 250 m from the study dune. The rate of subsand desiccation was measured using a Vaisala HMP 35A humidity and temperature probe implanted in a burrow 45 cm long and 30 cm deep, the mean dimensions of a breeding burrow. This was constructed in the sand at the base of a *Lebeckia* bush on the same dune. Recordings were made at 30-min intervals and logged on a Grant 12-bit Squirrel data logger.

Lebeckia detritus falling into traps enclosing four separate average-sized bushes (bush area 7.8–9.2 m^2) on the same study dune was collected monthly over 2 years (October 1993–November 1995). Traps consisted of a loose bag of strong, porous material, approximately 1.5 m high (just below bush height), fastened around the bush base but held open at the top by a thick wire rim attached to posts. They were large enough to avoid friction with the branches and allowed normal bush growth through the open top. Detritus was removed through a flap at the base. The number of leaves, small twigs (up to 4 cm) medium twigs (4–10 cm) and large twigs (> 10 cm) were determined for each month. Large twigs were not included in this analysis because beetles cannot carry them, small and medium twigs forming the largest proportion of the larval food. Only data for high-quality twigs, which are green to yellow in colour and not abraded, were analysed, these being the preferred food items (Rasa 1997). Since dry *Lebeckia* leaves are small and extremely fragile, a representative sample of 20 entire leaves was selected from each monthly sample, weighed, and the number of leaves per month extrapolated from the total leaf mass. The number of leaves collected in traps is an overrepresentation of their availability on the surface by nightfall. Because they are very light, they are easily scattered by the typical strong afternoon winds and blown off the dune into the dune streets where foraging beetles do not go. The estimated number of the different detrital units produced/bush/day over the summer breeding season was the mean daily value for all four bushes.

Statistical tests used are two-tailed and given at the appropriate points in the text. Since normality of the scores and frequency data could not be assumed, non-parametric tests were used. In cases of parametric measurements, data were checked for normality using the Kolmogorov-Smirnov one-sample test before analysis with the parametric *t*-test. The level of significance was set at $\alpha = 0.05$ in all cases.

Results

Rainfall, sand desiccation rate and food availability

Rainfall in the southern Kalahari is restricted to the summer months and its onset varies annually and is temporally unpredictable (Table 1). Observations over 5 years have shown that a minimum of 10 mm in one shower is necessary to initiate breeding attempts in *P. armaticeps*. After rainfall events of 10 mm or more, independent of the amount of precipitation, dune sand desiccates at a constant rate, as a series of microclimatic measurements of desiccation rate have shown (see Fig. 1 as an example for this study). Sand remains at 100% RH at the mean depth of breeding burrows (30 cm) for 23 days but desiccates rapidly afterwards.

Most detritus falls in October and November (early summer), as shown for summer 1994–1995 (Table 2). The amount of preferred food, especially twigs, falling on any average day was low and highly variable, particularly between bushes and months, and times of food abundance might or might not coincide with the timing of rainfall events and thus reproduction.

From March onwards the mean number of transportable twigs (< 10 cm length) decreased compared to previous months. During the late summer (March–May), only an average of one to two twigs of transportable size were available/bush/night. The amount of food supplemented at E burrows (the equivalent of one average-sized medium twig) was thus equal to an average bush's nightly twig production at this time. This scarcity of twigs emphasises the degree of competition that must exist between females for larval food.
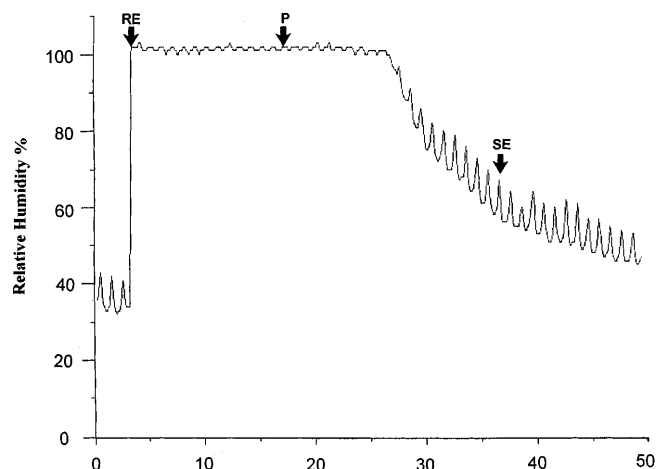
Table 1 Annual summer rainfall pattern in mm per month at Twee Rivieren, Kalahari Gemsbok National Park from 1990 to 1996. Months with at least one rainfall heavy enough to initiate *Parastizopus* reproduction are shown in **boldface** with an asterisk (*)

Year	Nov	Dec	Jan	Feb	March	Apr
1990–91		**25.5***			**32.0***	
[a]	–	–	–	–	–	
1992–93		**162.5***	5.6	**77.5***		
1993–94		**16.5***	49.5*	**115.5***	**35.0***	
1994–95	5.5	**21.3***	3.0		**23.1***	
1995–96	**61.5***	26.0	5.0	**64.5***	3.5	

[a] Data for 1991–1992 not available

Fig. 1 The relative humidity at the mean depth of breeding burrows (30 cm) before and after a rainfall event (*RE*) which initiated beetle reproduction. *P* indicates the start of provisioning for experimental burrows, *SE* the first day of burrow excavation for both experimental and control burrows

Table 2 The mean number of high quality *Lebeckia* detritus units falling daily from four sample bushes for different months of the summer 1994–1995 with standard deviations of the mean. Months in which a rainfall event (> 10 mm rain in one shower) occurred, allowing reproduction by beetles, are indicated by asterisks

Rainfall event	Leaves	Small twigs < 4 cm	Medium twigs 4–10 cm
Oct	55.4 ± 26.6	2.2 ± 0.8	1.6 ± 1.0
Nov	55.8 ± 48.2	4.4 ± 3.2	1.8 ± 0.7
Dec *	11.4 ± 6.1	1.9 ± 1.8	1.3 ± 1.2
Jan	12.2 ± 10.6	2.1 ± 1.7	0.9 ± 0.5
Feb	3.9 ± 2.7	1.4 ± 0.3	3.7 ± 5.3
Mar *	35.5 ± 11.2	0.5 ± 0.4	0.5 ± 0.3
April	27.5 ± 18.4	0.5 ± 0.6	0.1 ± 0.2
May	27.8 ± 31.1	0.5 ± 0.4	0.2 ± 0.2

The tradeoff between foraging and digging for females

Since high-quality larval food is scarce and competition for this resource is high, food supplementation at E burrows should decrease female foraging effort. As predicted, E burrow females foraged less often (mean score 11.4 ± 3.9) than C burrow females (mean score 14.5 ± 4.2; Mann-Whitney U-test, $z = -2$, 16, $n_1 = 25$, $n_2 = 26$, $P = 0.015$) but dug more frequently (mean score 15.8 ± 7.1) than those from C burrows (mean score 11.0 ± 6.2; Mann-Whitney U-test, $z = -1$, 75, $n_1 = 25$, $n_2 = 26$, $P = 0.040$). At the time of experimental excavation, 11 C burrows contained no offspring and were considered unsuccessful. To determine whether failure depended on maternal effort, the data for these two C burrow categories were compared. Successful and unsuccessful females foraged equally frequently (successful: 16.9 ± 7.9; unsuccessful 14.4 ± 6.2; $U = 59$, 5, $n_1 = 14$, $n_2 = 11$, $P = 0.34$) but successful females had higher digging scores (successful: 14.3 ± 5.8, unsuccessful 6.7 ± 3.6; $U = 33$, 5, $n_1 = 14$, $n_2 = 11$, $P = 0.025$), indicating a higher maternal investment.

The mean scores per day for digging and foraging are shown in Fig. 2A for C and Fig. 2B for E burrows. Since these sample points were not independent, regression slopes for digging versus foraging were calculated for each beetle and these compared for C and E burrows. Digging and foraging relationships differed significantly between the two (Mann-Whitney U-test, $z = -4.97$, $n_1 = 25$, $n_2 = 26$, $P < 0.001$). The slopes were negative for 20 of the C burrow beetles but only 3 of those from E burrows (binomial test, $x_1 = 3$, $n = 23$, $P < 0.001$), showing that for C burrows there is a time-allocation tradeoff between digging and foraging. The negative relationship between the two maternal activities is reversed when food is supplemented, supporting the prediction that females would decrease foraging effort and invest more time in other parental activities.

The stage of development of the offspring would be expected to influence maternal activity, since younger offspring require more food to support their rapid growth, which would result in increased foraging activity by females. Because all C burrows were inactive after 14 days, to allow comparison between E and C burrows the data were divided into the first 7 days, when young larvae were present, and the next 7 days, when burrows contained late-instar larvae and/or pupae. As predicted, during the first 7 days females from C burrows foraged more frequently than those from E burrows (Kolmogorov Smirnov two-sample test, $K_D = 6$, $P < 0.01$);
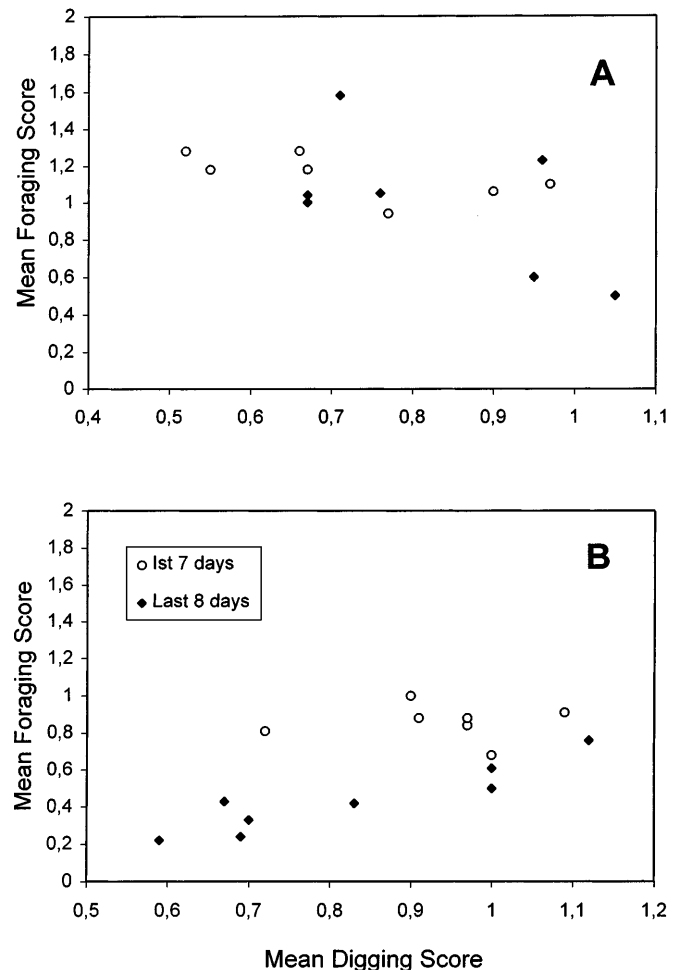

Fig. 2 The relationship between the mean nightly digging and foraging scores for females during the observation period for **A** control burrows ($n = 25$), and **B** experimental burrows ($n = 26$). *Open circles* are data for the first 7 days of observation, *filled diamonds* those for the following 7 days

foraging decreased during the last 7 days for both burrow categories but remained higher for C burrows (Kolmogorov-Smirnov two-sample test, $K_D = 6$, $P = 0.05$). Digging scores for E burrows were significantly higher than those for C burrows during the first period (Kolmogorov-Smirnov two-sample test, $K_D = 5$, $n = 7$, $P = 0.05$) but almost equal for the subsequent 7 days (Kolmogorov Smirnov two-sample test, $K_D = 2$, $P = 0.61$). Females therefore show higher maternal investment when younger offspring are present, this being especially evident for C burrows.

Causes of reproductive failure

A major cause of failure for both burrow classes was entrance collapse due to damage by mammals such as Cape fox (*Vulpes chacma*), ground squirrels (*Xerus inaurus*) and springhare (*Pedetes capensis*). Although beetles attempted to dig the entrance clear, six C burrows and five E burrows were abandoned within 48 h after disturbance. Burrow failure was independent of location, (C burrows: $n = 3$ isolated, 3 grouped, E burrows: $n = 3$ isolated, 2 grouped; Fisher exact probability test, $P = 0.72$). These burrows were dropped from the analysis.

If successful C burrow females spend more time digging, their burrows should be deeper and a higher percentage of them should be moist than for unsuccessful ones. There was no significant difference in the length of successful (56.7 ± 11.8 cm, $n = 14$) and unsuccessful (50.1 ± 8.7 cm, $n = 11$) burrows ($t = 1.615$, $df = 23$, $P = 0.12$) but successful ones were significantly deeper (32.8 ± 3.6 cm) than unsuccessful ones (29.3 ± 2.5 cm; $t = 2.90$, $df = 23$, $P = 0.008$), indicating a steeper digging angle in the former. As predicted, the sand was dry at the base of all unsuccessful burrows, whereas 5 of 14 successful ones were still moist (Fisher exact probability test, $P = 0.05$).

Only 1 of 26 E burrows had no offspring compared with 14 of 26 C burrows. The former had therefore a higher success rate (χ^2 test, $\chi^2 = 19.01$, $df = 1$, $P < 0.001$). The one unsuccessful E burrow contained a scorpion (*Parabuthus raudis*) in the foodstore area, and the adult beetles had retreated to the upper burrow. Failure was almost certainly due to predation. Since E burrows have a high success rate and E burrow females dig more than females from successful C burrows, E burrows should be longer and deeper than the latter. E burrows were both significantly longer (61.2 ± 9.2 cm, $n = 26$) and deeper (33.8 ± 4.8 cm) than C burrows (length: $t = 2.632$, $df = 47$, $P = 0.011$; depth, $t = -2.177$, $df = 46$, $P = 0.034$) and 16 of them were still moist, significantly more than C burrows (χ^2 test, $\chi^2 = 7.03$, $df = 1$, $P < 0.01$). These data support the prediction that increased female digging effort correlates with deeper burrows and thus with moisture level and that it is premature sand desiccation that is the cause of lower reproductive success for C burrows.

The effect of food supplementation on foodstore size and on reproductive success

Experimental supplementation did not affect total larval food quantity. Foodstore size did not differ between successful (2 small, 9 medium and 8 large stores) and unsuccessful (2 small, 5 medium and 4 large) C burrows ($\chi^2 = 1.33$, $df = 2$, $P = 0.52$) or between C burrows and E burrows (9 small, 9 medium and 8 large stores; $\chi^2 = 3.12$, $df = 2$, $P = 0.38$).

The frequency distributions of broods of different sizes for C and E burrows are shown in Fig. 3. These differed significantly ($\chi^2 = 17.36$, $df = 1$, $P < 0.001$), more C than E burrows failing and E burrows containing larger broods. As predicted, food supplementation increased reproductive success. In C burrows, foodstore size did not correlate with offspring number ($r = 0.107$, $n = 25$, $P > 0.05$), although a positive correlation was found for E burrows ($r = 0.470$, $n = 26$, $P < 0.01$). This, however, reflects a positive relationship between offspring number, foodstore size and burrow moisture. Of 9 dry burrows 5 had small foodstores compared with only 3 of 17 moist ones (Fisher exact probability test, $P = 0.025$) and moist burrows contained twice as many offspring as dry ones, 2.4 ± 1.09 vs. 1.2 ± 0.4 (Mann Whitney U-test, $U = 13.5$, $n_1 = 9$, $n_2 = 16$, $P < 0.002$).

C burrows contained only pupae while a late-instar larva was present in addition to these in 9 of the E burrows, suggesting that these females had oviposited subsequent to food supplementation. To test this hy-
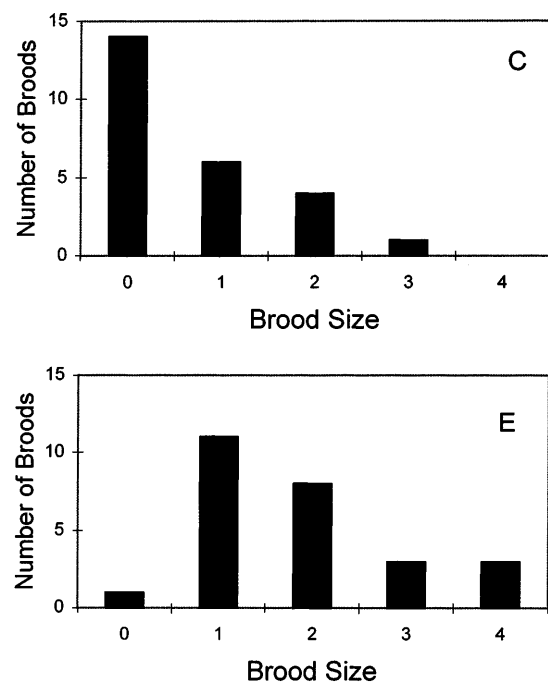

Fig. 3 The frequency distributions of broods of different sizes (*n*) in control (*C*) burrows and experimental (*E*) burrows receiving a food supplement

pothesis, the number of days a burrow was actually provisioned (number of days provisioned food was taken in) was correlated with brood size. Figure 4 shows the positive relationship ($r = 0.577$, $n = 25$, $P < 0.002$) between these two variables. All burrows which were provisioned for 13 days or more contained a larva, while those where forage was retrieved for 8 days or less only contained pupal cocoons. Since the timespan from oviposition to larval development to the late instar stage is 13–14 days, this finding confirms that oviposition had occurred within a few days of the start of provisioning. This raises the question as to why not all E burrow females oviposited once extra food was provided. In those burrows where no larva was present, the teneral adults all emerged from the cocoons within 10 days, while in burrows with a larva, emergence dates all exceeded 10 days. Because pupation lasts 11–12 days, the offspring in burrows with no larva were therefore already mature and shortly about to pupate by the time food was first supplemented. In burrows containing a larva, food supplementation coincided with the presence of early instar larvae, as indicated by pupal emergence times. Whether females oviposit or not therefore depends on the age of the brood already present.

Pupal mortality was higher for successful C burrows than for E burrows, 8 of the 14 broods containing at least one dead pupa compared with 5 of the 25 E broods ($\chi^2 = 5.45$, $df = 1$, $P < 0.025$). There was no support for the hypothesis that supplementary feeding increased offspring body size as there was no significant difference in the body lengths of C and E burrow progeny (C burrow offspring, $n = 13$, 1.29 ± 0.05 cm; E burrow offspring, $n = 34$, 1.30 ± 0.08 cm; $t = -0.794$, $df = 36$, $P = 0.433$).

Burrow location and reproductive success

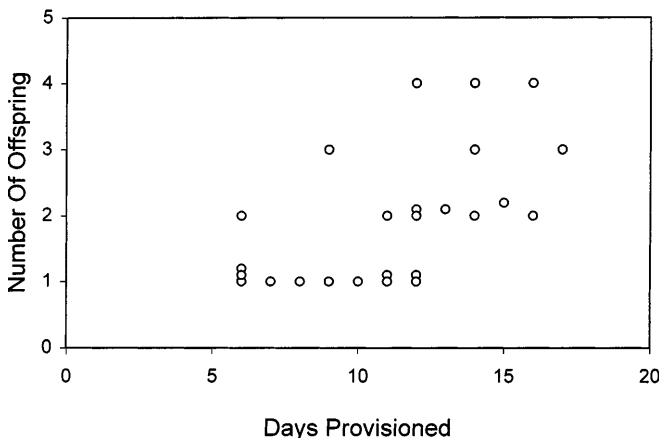Females from isolated burrows must travel long distances to the nearest food source. Because there is no

Fig. 4 The number of offspring present in experimentally provisioned burrows at excavation in relation to the number of days in which the food supplement was taken in

food on the flat, bare sand areas where these burrows are located, such burrows would be expected to have smaller foodstores and a lower reproductive success. Since foodstore size distribution for E and C burrows did not differ, these data were pooled and analysed for location. There was no significant difference in foodstore size distribution between burrows grouped near bushes (8 small, 14 medium and 7 large stores) and isolated burrows on open sand (5 small, 9 medium and 8 large stores; $\chi^2 = 0.89$, $df = 2$, $P = 0.66$).

Females, however, could have compensated for burrow isolation by increasing their foraging effort. Surprisingly, comparison of the total foraging scores for isolated and grouped C burrow females showed the opposite; females from isolated burrows foraged less frequently (mean 10.5 ± 4.7) than those from grouped ones (mean 19.9 ± 6.1, Mann Whitney U-test, $U = 1$, $n_1 = 11$, $n_2 = 14$, $P < 0.02$) and their digging scores were also higher (mean 14.1 ± 4.6 for isolated, 10.6 ± 5.6 for grouped burrows, Mann-Whitney U-test $U = 29.5$, $n_1 = 11$, $n_2 = 14$, $P < 0.02$). The difference in average depth between isolated (32.6 ± 5.3 cm) and grouped burrows (31.9 ± 4.3 cm) was not significant ($t = 0.519$, $df = 51$, $P = 0.62$).

Isolated and grouped E burrows showed no significant difference in the number of offspring per burrow (Mann-Whitney U-test, $U = 87.5$, $n_1 = 11$, $n_2 = 15$, $P = 0.8$), the same being true for successful C burrows (Mann-Whitney U-test, $U = 9$, $n_1 = 4$, $n_2 = 7$, $P = 0.28$). C burrow failure was equal for both locations ($n = 7$). Thus burrow location did not influence reproductive success.

Discussion

Ecological variables and maternal effort

Breeding in *Parastizopus* is dependent on infrequent and unpredictable biannual rainfall events which may or may not coincide with peaks in food abundance. High-quality *Lebeckia* detritus is a scarce resource and also very variable in both distribution (individual bush production) and timing. The primary constraints on reproduction are therefore the scarcity and unpredictability of these two environmental factors.

Male and female roles in *Parastizopus* appear adapted to counter these two constraints, males maintaining burrow moisture level by digging and females searching on the surface at night for the scarce high-quality larval food. Females invested the majority of their time in foraging and there was a tradeoff between foraging and digging at the burrow. When the amount of food available per night was increased experimentally (E burrows), this tradeoff became more pronounced; female foraging rate decreased and digging rate increased significantly. The major increase in digging effort occurred during the first week after provisioning

started. These breeding burrows were deeper and remained moist longer.

Almost half the non-supplemented, control (C) burrows were unsuccessful and contained no offspring. Unsuccessful and successful C burrows did not differ in larval foodstore size or in female foraging effort, but females from unsuccessful burrows dug less often. Unsuccessful burrows were shallower than successful ones and all had dried out. There was no indication that females were capable of assessing the situation (insufficient burrow depth) and reducing their foraging rate accordingly, to allocate more time to burrow excavation. In the maternal behaviour pattern hierarchy, foraging thus appears to have first priority. Females may be able to estimate how many items or how much food has been carried in per night since they spent more time digging when food supply was increased experimentally. The mechanisms involved and whether females adjust for larval number are unknown. Estimation of the amount of food provided for offspring has been described for sphecid wasps (Hymenoptera: Sphecidae). Here, offspring sex allocation depends on female estimates of prey size or number (Dow 1942; Klostermeyer et al. 1973; Lin 1979; Strohm 1994).

Females only select high-quality *Lebeckia* detritus as larval food and they compete for this scarce resource. *Lebeckia* is the major nitrogen-fixing plant in the environment and fresh detritus has a high protein content (Bocock 1963). Nitrogen is a scarce and limiting nutrient for many herbivores, especially in deserts with their low plant abundance and species diversity (Mattson 1980). In *Parastizopus*, food with a high nitrogen content would be necessary to support both the rapid larval growth rate, more typical for a carnivore such as *Nicrophorus* (Pukowski 1933) than a detritivore, as well as protein synthesis for the pupal cocoon, which consists almost entirely of glycine (Brown 1975). Ultimately it may be the low availability of nitrogen in the environment which necessitates an extended foraging effort at the expense of maternal digging.

Burrow characteristics and causes of failure

On average, unsuccessful C burrows were 2.5 cm shallower and E burrows were 1 cm deeper than successful C burrows. Digging effort, however, increases with burrow depth. Sand at the base of E burrows must be moved over a mean distance of 60 cm (approximately 45 beetle lengths), 5 cm and 11 cm further than successful and unsuccessful C burrows, respectively. With this increase in depth, more E than C burrows were still moist at the base and thus capable of sustaining reproduction.

Sand desiccation rate at mean breeding burrow depth (successful C burrows) indicated that, if pairs started breeding directly after a rainfall event, they had approximately 23 days in which to complete reproduction to the pupal stage before the burrow sand started to dry out. As previously stated, this equals the average time-span from courtship to pupation for the first eggs laid (about 23 days). Only larvae which are able to pupate before the burrow desiccates survive. Almost half the C burrows contained no offspring. At the mean depth of these unsuccessful burrows, according to Fig. 1, the sand had dried out just prior to 23 days, before the larvae could pupate, which resulted in reproductive failure. A major effect of provisioning was to reduce this burrow failure rate, the only failure being probably due to predation. If E burrows were still moist when excavated at the end of the experiment (days 33–34 after rain) then, extrapolating from Fig. 1, the period during which offspring could be produced had been extended by approximately 10 days. The high failure rate of C burrows was unlikely to be due to pairs not all starting to breed immediately after rain, since burrow allocation to E or C status was random. If male digging effort was equal between burrow classes, then it was the additional female digging effort at E burrows, and the effect this had on maintaining burrow moisture, that determined their success.

Foodstore size and the effect of food supplementation on reproduction

The absolute amount of food available on the surface was unlikely to influence reproductive success since foraging rate did not differ between successful and unsuccessful C burrows, nor did foodstore size distribution differ between any of the burrow classes or correlate with success, failure or the number of offspring produced. The amount of food available for larvae thus did not limit reproductive success directly. Offspring size also showed no difference between C and E burrows, which would be expected if food amount was a limiting factor, as typical for other insects (Beaver 1973, Maupt and Busvine 1968). Food supplementation, however, more than doubled the number of young produced as well as increasing pupal survival rate. This increase in reproductive success was attributable to the effect of food supplements on female behaviour. Supplemented females foraged less and dug more frequently with the male, which resulted in deeper burrows that remained moist longer. Females in burrows with young larvae oviposited again within a few days after supplementation started, producing further offspring. In burrows where older larvae were present, the increased digging resulted in significantly lower pupal losses due to desiccation. Together, these two factors accounted for the higher reproductive success recorded for supplemented burrows.

Burrow location, forage retrieval time and reproductive success

Isolated burrows had equal-sized foodstores and equal reproductive success to burrows grouped around bushes.

Despite their increased distance from a food source, females from isolated C and E burrows foraged less frequently than those from grouped ones, the opposite to what would be expected. During foraging, however, a female must first locate and then retrieve a food item.

Since food is located by chance, the time spent in location would be expected to be equal for E and C females. Food tends to occur in patches, wind action blowing detritus into hollows in the sand to which a female returns until the patch is depleted (Rasa 1990). How rapidly such a patch can be exploited before competitors find it, however, depends on forage retrieval time. Females usually carry food vertically in the mandibles during retrieval and grouped burrows near *Lebeckia* bushes are surrounded by vegetation in which food items, especially larger twigs, often become entangled, thus delaying the onset of subsequent foraging (author, personal observations). No such obstacles exist around isolated burrows and these females spend less time in foraging, dig more frequently and have slightly deeper burrows than grouped females. It is therefore forage retrieval time that determines a female's foraging efficiency.

One explanation for the finding that females from grouped burrows foraged twice as often as those from isolated ones is that, although food patches are more common near food sources, beetle population density is also higher near bushes (Rasa 1994, 1995). A delay in food retrieval would result in rapid foodpatch depletion by competitors, necessitating a time-consuming search for another patch. However, although female foraging efficiency is lower, locations around bushes afford advantages with regard to digging effort and shade (Rasa 1995). This may explain why, despite the difference in female foraging effort between grouped and isolated burrows, they show no difference in reproductive success.

This study has shown that food itself, although it is scarce and unpredictable, is not the major constraint on reproductive success in *Parastizopus*. It is the temporal costs of foraging, especially the time required to retrieve the food, that determines how many offspring can be produced. Burrow depth and sand moisture level at the burrow base are the major correlates of reproductive success and females that can provision their young rapidly can then reallocate their time budget in a tradeoff against digging, increasing the burrow depth and thus the timespan over which offspring can be produced. This results both in low brood failure rate and larger broods. Increased food therefore increases reproductive success indirectly through its effect on female behaviour.

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