

Effects of parental body condition and size on reproductive success in a tenebrionid beetle with biparental care

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Abstract. 1. The beetle *Parastizopus armaticeps* (Coleoptera: Tenebrionidae) inhabits the Kalahari desert of southern Africa, constructs breeding burrows after rainfall, and shows extensive biparental care. Previous work has shown that it is predominantly male size, not female size, that determines breeding success; however, in the field these beetles show size assortative mating. This might obscure or override effects of female size on reproduction. Moreover, the inaccessibility of the breeding burrows makes it impossible to test effects of female and male size on offspring development and survival before adulthood.

2. To disentangle the effects of male and female length, body mass, and body condition on reproductive success, males and females were paired randomly in small breeding cages in the laboratory ($n = 887$ breeding pairs). The construction of the breeding cages allowed a clear view of the brood chamber contents at each stage in offspring development. Larva, pupa, and imago numbers and development were monitored daily, and imago mass at hatching from the pupa (*hatchlings*), offspring mass, and offspring body length at complete exoskeleton melanisation (*juveniles*) were determined.

3. There was a weak positive correlation between body condition and body length for females only. Breeding chronology was related to male body condition: males in better condition were fast to start and finish a breeding bout. Males in better condition produced heavier hatchlings and juveniles, and larger-sized males produced larger-sized juveniles. In contrast, numbers of larvae and juveniles produced were determined mainly by female length and body condition: larger females in better condition hatched more larvae and produced more offspring.

4. The results suggest that male size and condition will be the most important determinant of reproductive success under relatively dry conditions, when burrow length is critical for reproductive success. Female size might be more important for the pair's reproductive success under wet breeding conditions, when burrow length is less critical for successful reproduction.

Key words. Biparental care, body condition, body size, offspring development time, offspring size, *Parastizopus armaticeps*, reproductive success, Tenebrionidae.

Introduction

Biparental care is a rare phenomenon in insect societies (Clutton-Brock, 1991; Trumbo, 1996; Choe & Crespi, 1997). Male and female caring for offspring is restricted to some cockroach species (Nalepa & Bell, 1997), beetles of the families Passalidae, Platypodidae, Scarabaeidae, Scolytidae, Silphidae (Trumbo, 1996; Eggert & Müller, 1997; Halfpeter, 1997; Kirkendall *et al.*, 1997; Schuster & Schuster, 1997; Scott, 1998), and some spider mites (Acari; Saito, 1997).

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In addition, Rasa (1990, 1998, 1999) has studied biparental care in the burying Kalahari desert beetle *Parastizopus armaticeps* (Peringuey), of the family Tenebrionidae (Coleoptera). *Parastizopus armaticeps* pairs mate shortly after rainfall, form stable monogamous associations, and excavate breeding burrows in the sand. Breeding burrows are extended and maintained continuously by both the male and the female. They are stuffed with detritus twigs and leaves of the bush *Lebeckia linearifolia* (E. Meyer, Papilionaceae), collected on the surface (Rasa, 1998, 1999). During the largest part of a breeding episode, which lasts 38 or 39 days in the field (from start of burrow excavation to offspring emerging on the surface), the burrow must maintain a humidity of nearly 100%, otherwise larvae and pupae will desiccate and die (Rasa, 1997, 1999). Males stay in the breeding burrow for 85–94% of the breeding time and are the main diggers, while females do most of the food collection outside, particularly after the larvae have emerged (Rasa, 1999). Food supplementation experiments in the field did not increase the food store of a breeding pair. Instead, females spent more time digging, resulting in deeper breeding burrows and higher reproductive success compared with control pairs (Rasa, 1998).

In many insect species, female attributes determine egg laying potential (e.g. female size, female condition) and hence reproductive success of the males (Clutton-Brock, 1991); however, *P. armaticeps* breeding males have a considerable influence on the reproductive output of a pair via their digging capacity. Rasa *et al.* (1998) were able to show experimentally that females prefer to mate with heavy males. Field data showed that male size, but not female size, is correlated with burrow depth, and that burrow depth is correlated with brood size (Rasa *et al.*, 1998; because body length and body mass are highly correlated, and their potential independent effects often indistinguishable, *body size* is used here to refer to their combined effect). The important effect of paternal care on reproductive success has been found in some other vertebrate and invertebrate systems with predominant male care, for instance in birds (e.g. Szekely, 1996), frogs (Clutton-Brock, 1991), fish (Clutton-Brock, 1991; Sabat, 1994), some anurans (Beck, 1998), some Hemipteras (Tallamy & Schaefer, 1997), and giant waterbugs (Heteroptera: Belostomatidae; Smith, 1997), or where mate removal experiments indicate that biparental care is essential for successful reproduction (e.g. in oystercatchers *Haematopus ostralegus* Linnaeus; Heg *et al.*, 2000). *Parastizopus armaticeps* tends to mate size assortatively in the field (Rasa *et al.*, 1998) however. Without forcing pairs to randomly mate based on size, it is impossible to estimate independently the effects of male and female size on reproductive success. Moreover, the inaccessibility of the breeding burrows makes it impossible to determine the number of larvae, pupae, or imagines without destroying the burrows, parameters which might be more affected by the females, but which might go unnoticed due to the overriding effect of male size on offspring survival via burrow depth.

To disentangle the effects of male and female size on both reproductive success and offspring size, breeding experiments were designed in the laboratory. Males and females were mated at random by creating different combinations of large and small sized males and females. The reproductive behaviour of the breeding pairs was followed daily. It was tested whether male or female body mass, body size, or body condition influences breeding chronology, the number of larvae and pupae, offspring mass, and reproductive success.

Methods

Laboratory population

The laboratory breeding stock originated from Twee Rivieren, Kalahari Gemsbok Park, South Africa (26°27'S, 20°36'E). Non-breeding individuals were housed in terraria of 50 × 50 × 20 cm (with a layer of Kalahari sand, water, and wheat flocks provided), in same sex groups of up to 200 individuals. From these colonies, males and females were transferred to small breeding terraria (20 × 30 × 20 cm glass containers) with a plastic inset box (19 × 29 × 20 cm), one pair per terrarium, randomly with respect to male and female size. This inset created a 1-cm gap on one long and one short side of the glass container, which was filled with moist Kalahari sand. The roof of the inset was covered with a thin layer of Kalahari sand, which allowed the animals to walk freely throughout the cage. Rainfall was simulated by spraying water over the sand once or twice daily, until beetles started digging a breeding hole. The inset forced the beetles to dig breeding burrows within 1 cm of the glass, allowing an open view of the breeding hole. Pairs received a Petri dish containing fine gravel and drinking water, and a stone at the long glass-side to hide under. Most pairs started a breeding burrow from this hiding place. Trials were aborted when pairs showed no signs of breeding behaviour (digging, storing food); or when one of the adults had died, and no breeding behaviour was observed; or when all the offspring had died. In all these cases, reproductive success was set to zero. The minimum duration of a trial was 14 days, otherwise the pair was omitted from the analyses, leaving a total sample size of 887 pairs. Fresh food was provided *ad libitum* with the natural food source *Lebeckia linearifolia* ($n = 774$ pairs) or as an alternative, *Trifolium pratense* (Linnaeus, $n = 113$ pairs). Waste material from these plants is used by the larvae to line their pupae (fibres glued together) and thus is essential for reproduction. As an extra protein source, 345 pairs were supplemented with wheat flocks. Breeding terraria were placed in a darkened room at 32–36 °C (warmer during the light period) with LD 13:11 h photoperiod, which was adjusted to LD 14:10 h during the summer. Temperature, sand moisture (water-soaked sand in the breeding terraria to simulate heavy rainfall), and light

regimes were approximately equivalent to the regimes experienced by the beetles in the Kalahari (natural light period: 1 January, 13 h 46 min light; 1 June, 10 h 35 min). Data were gathered from 1994 to 2000; the majority of data were collected in 1999 and 2000.

Body measurements and breeding parameters

Before the start of a breeding trial, male mass (± 0.02 mg), male length (0.1 mm), female mass (± 0.02 mg), and female length (± 0.1 mm) were determined (accuracy of the measurement equipment in parentheses). Body length was measured from the caudal tip of the abdomen to the lateral-rostral tip of the thorax, using a magnifying binocular. Body condition was determined as follows: (1) the bodies of 94 previously measured and marked individuals that had died during the years 1999 or 2000 were stored for several months, until most of their flesh had decomposed. (2) Dry mass of these individuals was determined then related to their body length using the equation: dry mass = $0.34238 \times \text{body length}^{2.21508}$ ($r^2 = 0.372$, $P < 0.01$). (3) This formula was used to estimate the dry mass of all individuals. (4) Body condition was defined as (body mass – dry mass)/body mass, the proportion of body mass beyond the expected structural mass. This measure was preferred above the residual mass measure (based on the expected body mass from the body length vs. mass regression, see review by Jakob *et al.* (1996)), since a residual mass of +20 mg for two individuals with either a small or a large body length would have us conclude they have the same body condition using the residual mass measure, whereas with our measure we would justly infer the smaller individual has a relatively larger body condition than the larger individual. The body condition index used in this study was unrelated to body length for males and only weakly related to body length for females (see Results), which might be explained by larger individuals having on average larger fat stores (Rasa *et al.*, 2000).

All breeders were marked permanently with numbered plastic discs with numbers glued to their abdomen (width ± 2.6 mm; used in bees *Apis* spp., Melzer's Bienenfarm, Bonn, Germany). Parameters of breeding chronology were determined: start of digging the breeding burrow, first larvae hatched (both in days since start of trial), days between first larvae hatched and first pupa constructed, and days between first pupa constructed and first pupa eclosed. The number of larvae in the burrow was counted by daily inspection of the breeding burrows. Because larvae were very small when newly hatched, the number of larvae was underestimated in most cases. If several batches of larvae hatched within 3–5 days, rarely up to 20 days, the maximum number of larvae detected in each batch was summed to give the total number of larvae. Similarly, the summed number of pupae and the number of offspring emerging from the pupae (referred here to as *hatchlings*) were counted. Additional measurements in the 1999–2000 trials included hatchling mass (± 0.02 mg) and sex, determined

within 1 day of hatching. Hatchlings were marked individually using white paint.

Offspring mass, body length, and sex were again determined when the largest part of the exoskeleton has melanised and when they resemble adults in appearance and body mass (i.e. imagines reaching ≈ 10 days of age, Rasa, 1998, 1999; henceforth called *juveniles*). *Parastizopus armaticeps* females can be distinguished readily from males: females have small bristles on the femur of the middle legs, which are absent in males and the hind-leg femur of the male is more bent than that of the female. It carries three spines, which are small in the female, whereas the middle spine is enlarged in the male (Koch, 1963). To arrive at one data point per pair, body measurements of hatchlings and juveniles were averaged per family, the small sexual dimorphism in size between juvenile males and females was neglected (2–4%, D. Heg, unpubl. data). Juveniles were marked permanently with small numbered plastic discs glued to their abdomen. Juveniles and their parents were then transferred to the colonies.

Due to their defensive secretion, predation of adults and offspring in the field is negligible (Rasa, 1990). Collapse of the breeding burrow due to vertebrate activity on the surface or heavy rainfall might be two reasons for total brood failure in the field. Because loss of offspring due to predation or burrow collapse is absent in the laboratory, reproductive success in the trials was defined as the total number of hatchlings produced.

Total burrow length (cm) was measured in 1999 and 2000 only. Because the cages have a fixed height, it would not make sense to measure burrow depth in the laboratory. Instead, the total burrow length was determined (including branches), since beetles made burrows of highly variable length in the laboratory (0–60 cm), sometimes digging in several directions and often producing burrow branches presumably in search of the best moisture level within the cage. It was assumed that burrow length correlates with the digging effort of the breeding pair.

Statistical analyses

Analyses were performed using SPSS10.0 (SPSS Inc., Chicago, Illinois). All *P*-values are two-tailed. Multiple regressions with backward elimination of terms, using dummy variables for categorical variables, were constructed (Hardy, 1993). Interaction terms were also fitted, and incorporated in the model if they gave a significantly better fit than more parsimonious models including only main effects. Additional quadratic terms of the linear parameters were fitted to evaluate whether some of the parameters might have non-linear effects. Nested ANOVAS of offspring body measurements nested within broods were constructed, but because they gave essentially the same results, they are not presented here. In some cases, data were missing for one or several of the individual or breeding parameters, particularly since additional parameters were measured in 1999 and 2000, which accounts for the variation in sample sizes.

Results

Body size and condition

Average length of a breeding trial was 46.0 ± 16.6 days (mean \pm SD, range 14–104 days, $n = 887$). Mean male body mass, body condition, and body length were (\pm SD, range, n): 267.1 mg (± 39.7 , 156–368, 887), 0.624 (± 0.032 , 0.45–0.72, 853), and 12.9 mm (± 0.77 , 10.3–15.2, 853), and for females: 257.9 mg (± 44.0 , 122–394, 887), 0.608 (± 0.043 , 0.31–0.69, 851), and 12.9 mm (± 0.77 , 9.8–15.1, 851).

Male and female body mass correlated highly with male and female body length respectively (Pearson's $r = 0.84$, $n = 853$; $r = 0.82$, $n = 851$, both $P < 0.001$) and also with male and female body condition, although only weakly for females (Pearson's $r = 0.50$, $n = 853$; $r = 0.15$, $n = 851$, both $P < 0.001$). Male length was not related to male body condition ($r = -0.03$, $n = 853$, $P = 0.34$), whereas female length was related significantly, but weakly, to female body condition ($r = 0.08$, $n = 851$, $P = 0.014$).

Breeding chronology and burrow length

Although most pairs started with digging activities on the surface of the cage floor on the first or second day of the trial, the actual start of a burrow was on average 5.8 ± 6.3 days from the start of the trial (\pm SD, range 1–40, $n = 712$; 85% of all pairs produced a burrow). Only 4.2% of the pairs with larvae ($n = 475$) did not dig a burrow at all, but dug a furrow instead. Average burrow length, measured only in 1999 and 2000, was 21.2 ± 11.0 cm (\pm SD, range 1–64, $n = 537$). The first larvae emerged in 14.5 ± 6.8 days from the start of the trial (\pm SD, range 7–66, $n = 472$), and larvae took on average 17.7 ± 4.8 days to grow and pupate (\pm SD, range 9–51, $n = 427$). Hatchlings emerged from the pupa within 10.8 ± 1.3 days (\pm SD, range 7–24, $n = 420$).

Pairs that started burrow construction quickly produced longer burrows ($r = -0.22$, $n = 515$, $P < 0.001$), hatched larvae more quickly ($r = 0.56$, $n = 456$, $P < 0.001$), hatched more larvae ($r = -0.15$, $n = 712$, $P < 0.01$), and their larvae took less time to pupate ($r = 0.14$, $n = 415$, $P < 0.01$). Pupae from pairs with longer burrows took less time to hatch than pairs with shorter burrows, but this effect was only marginally significant ($r = -0.12$, $n = 265$, $P < 0.05$). No other significant correlations were detected between burrow length and the timing variables, or between pairs of timing variables ($-0.10 < r < 0.10$, days to burrow construction, days to first larvae, larval development time, pupal development time). Pairs going quickly through the breeding process produced more larvae and offspring (Table 1, results on number of pupae and hatchlings were similar and not shown, because they correlated highly with the number of larvae, $r = 0.88$, $n = 480$, $P < 0.001$; $r = 0.78$, $n = 444$, $P < 0.001$ respectively).

To disentangle the partial effects of male and female attributes, multiple regressions on the timing variables and burrow length with three dummy variables for food (because one or two food types could be present in different combinations: wheat, *Lebeckia*, or *Trifolium*) were constructed (Table 2). Food type had a considerable influence on many of the variables, pairs supplemented with wheat and/or *Trifolium* performing better. When corrected for the other factors, male and female mass had no effect on the breeding chronology variables, or on burrow length. Instead, male body condition had a significant effect on the onset of burrow construction (negative, Fig. 1a), burrow length (positive, Fig. 1c), days to first larvae (negative, Fig. 1e), and days between pupation and hatching (negative, Fig. 1g). Hence, males in good condition went quickly through the breeding process. Female length was related to the onset of burrow construction (positive, Fig. 1b), burrow length (negative, Fig. 1d), and days between pupation and hatching (negative, Fig. 1h). Females in good body condition

Table 1. Linear correlations between the breeding parameters. Sample sizes are indicated in parentheses.

Parameter	Development time (days)						
	Larva hatched†	Larva to pupa	Pupa to eclosure	Juvenile production	Hatchling body mass	Juvenile body mass	Juvenile body length
Number of larvae	-0.38*** (472)	-0.16*** (427)	-0.14** (420)	0.88*** (887)	-0.004 (261)	0.08 (421)	0.001 (409)
Juvenile production	-0.24*** (472)	-0.22*** (427)	-0.19*** (420)		0.029 (261)	0.14** (421)	0.08 (409)
Hatchling mass	-0.02 (243)	-0.47*** (243)	0.07 (292)			0.97*** (305)	0.90*** (303)
Juvenile body mass	-0.08 (403)	-0.49*** (403)	0.06 (306)				0.86*** (527)
Juvenile body length	-0.05 (391)	-0.47*** (391)	0.08 (303)				

** $P < 0.01$, *** $P < 0.001$ (two-tailed probabilities).

†Measured in days since start of trial.

Table 2. Results of multiple regressions between parental body measurements (continuous independent variables, including squared effects), food types (dummy independent variables, wheat, *Lebeckia*, or *Trifolium*), and the variables of breeding chronology, reproductive success, and offspring body measurements (dependent variables, separate models for each variable). Indicated are the sample size n , the overall variation explained by the final model r^2 , with the partial regression coefficients (\pm SE) of the constant and the significant variables. Abbreviations: mm, male body mass; ml, male length; mb, male body condition; fm, female mass; fl, female length; fb, female body condition; mm2, ml2, mb2, fm2, fl2, and fb2 = squared effects; W , wheat; L , *Lebeckia*; T , *Trifolium*.

Dependent variable	n	r^2	Final model
Days to first burrow†	679	0.02	$6.60 (\pm 6.48) - 19.23 (\pm 8.01) \times mb^* + 0.87 (\pm 0.31) \times fl^{**}$
Total burrow length (cm)	652	0.06	$-190.20 (\pm 90.53) + 691.01 (\pm 297.25) \times mb^* - 554.80 (\pm 244.18) \times mb2^* - 0.06 (\pm 0.03) \times fl2^* + 3.96 (\pm 1.09) \times W^{***} + 3.98 (\pm 1.46) \times T^{**}$
Days to first larva hatched†	442	0.06	$33.71 (\pm 4.61) - 18.38 (\pm 8.75) \times mb2^* - 30.99 (\pm 8.94) \times fb2^{***} - 2.36 (\pm 0.89) \times T^{**}$
Days from first larva hatched to first pupa	427	0.20	$19.69 (\pm 0.28) - 4.31 (\pm 0.42) \times W^{***}$
Days from first pupa to first hatchling	395	0.06	$12.84 (\pm 1.75) - 8.46 (\pm 2.18) \times mb^{***} + 0.25 (\pm 0.08) \times fl^{**}$
Number of larvae	851	0.11	$39.67 (\pm 19.24) - 7.17 (\pm 2.98) \times fl^* + 0.28 (\pm 0.12) \times fl2^* + 14.47 (\pm 2.86) \times fb^{***} + 1.97 (\pm 0.25) \times W^{***}$
Number of pupae	480	0.13	$3.82 (\pm 0.18) + 1.74 (\pm 0.30) \times W^{***} + 1.13 (\pm 0.42) \times T^{**}$
Number of hatchlings	444	0.08	$3.74 (\pm 0.17) + 1.08 (\pm 0.29) \times W^{***} + 1.03 (\pm 0.39) \times T^{**}$
Juvenile production	851	0.08	$-2.87 (\pm 1.46) + 8.62 (\pm 2.29) \times fb^{***} + 1.11 (\pm 0.23) \times W^{***} - 0.75 (\pm 0.33) \times L^*$
Hatchling mass (mg)	261	0.21	$52.32 (\pm 43.36) + 167.65 (\pm 69.27) \times mb^* + 35.33 (\pm 4.60) \times W^{***}$
Juvenile body mass (mg)	396	0.25	$30.45 (\pm 37.99) + 242.92 (\pm 61.58) \times mb^{***} + 36.78 (\pm 3.85) \times W^{***}$
Juvenile body length (mm)	394	0.13	$11.04 (\pm 0.34) + 0.006 (\pm 0.002) \times ml2^{***} + 0.63 (\pm 0.082) \times W^{***}$

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

†Measured in days since start of trial.

were faster to produce larvae than females in poor condition (Fig. 1f).

Reproductive success

Overall, 54.9% of the breeding pairs produced larvae, 54.1% produced pupae, and 50.1% produced hatchlings ($n = 887$). Average brood sizes were as follows: 3.2 ± 3.7 larvae (\pm SD, range 0–20, $n = 887$); or 5.8 ± 3.2 larvae of pairs producing at least one larva, range 1–20, $n = 487$). Pairs with larvae produced 4.8 ± 3.1 pupae (\pm SD, range 0–18, $n = 480$); or 2.6 ± 3.3 pupae of all pairs, $n = 887$); and pairs with pupae produced 4.4 ± 2.8 hatchlings (\pm SD, range 0–18, $n = 444$); or 2.2 ± 2.9 including all pairs, range 0–18, $n = 887$); or 4.5 ± 2.7 of the pairs producing at least one hatchling, range 1–18, $n = 431$). The overall reproductive success, including all breeding failures, was 2.20 ± 2.94 offspring per breeding pair (\pm SD, range 0–18, $n = 887$). The number of larvae emerging was a good predictor of overall reproductive success (Table 1).

Multiple regressions were calculated to estimate the partial effects of male and female body measurements on the reproductive parameters (Table 2, with three dummy variables for the food types, see above). Significant effects were found between the number of larvae and female length (plus length squared; Fig. 2a), and female body condition (Fig. 2b). The number of pupae and hatchlings were affected significantly by food type only (more pupae and hatchlings when the beetles were fed with wheat or *Trifolium*). Also, juvenile production was related significantly to food type and was related positively to female body condition (Fig. 2c).

Hatchling mass, juvenile mass, and length

Hatchling and juvenile body measurements were averaged per family, so each case represents one family. The mean hatchling mass was 179.1 ± 38.5 mg (\pm SD, range 84–336, $n = 305$), juvenile mass was 194.5 ± 42.3 mg (\pm SD, range 78–337, $n = 527$), and juvenile body length was 12.3 ± 0.9 mm (\pm SD, range 9.7–14.6, $n = 500$). Not surprisingly, hatchling mass, juvenile mass, and juvenile length all correlated highly with each other (Table 1). Pairs producing more juveniles also produced significantly heavier juveniles (Table 1). Larvae pupating swiftly produced significantly larger offspring (Table 1).

Multiple regressions were used to estimate the partial effects of parental body size, parental body condition, and food type on hatchling mass, juvenile mass, and juvenile length (Table 2, three dummy variables for food type, see above). Hatchling and juvenile mass increased significantly with wheat as food and male body condition (Fig. 3a,b). Juvenile length was related significantly to wheat as food and male body length (male body length squared gave a significant fit, whereas male body length fitted linearly approached significance, Fig. 3c).

Discussion

Male body condition and size were the most important determinants of burrow length and parameters of breeding chronology in the laboratory: larger males in better condition produced longer burrows and were faster to breed than small males or males in bad body condition. Because body

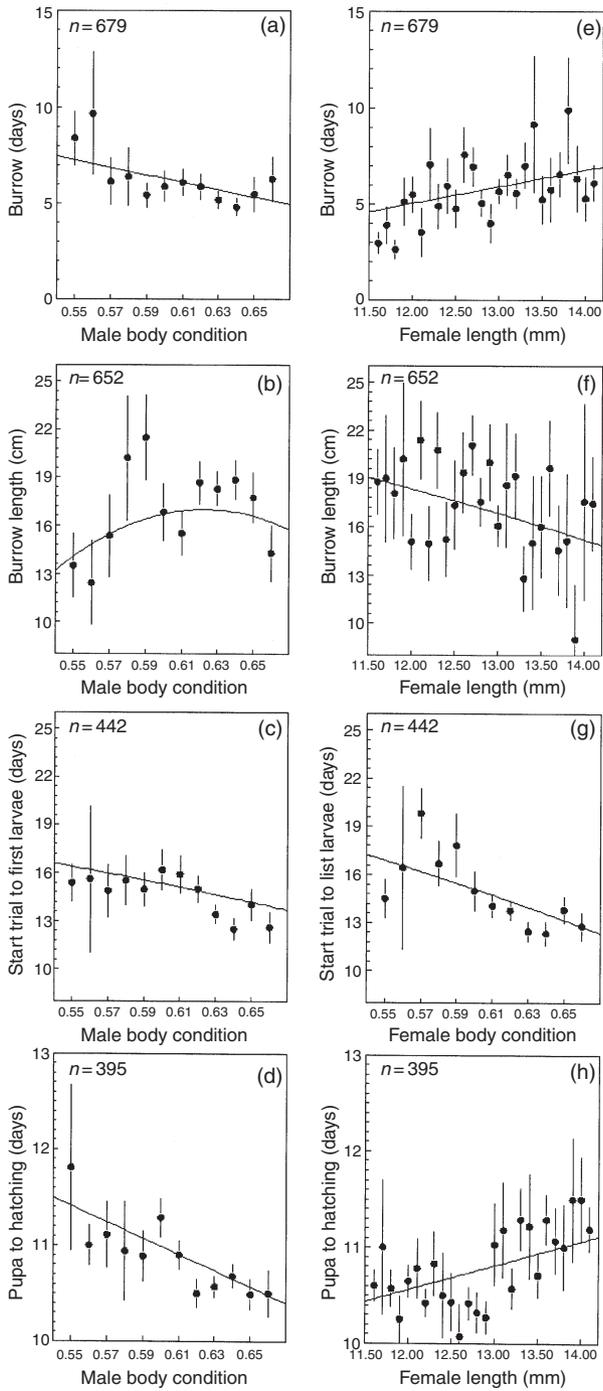


Fig. 1. The effects of male body condition, female body condition, and female length on the breeding chronology and total burrow length (data were grouped, and means \pm SE per group presented for clarity). Depicted are the significant relationships from the multiple regressions (see Table 2). The effects of other significant variables were set to the population average.

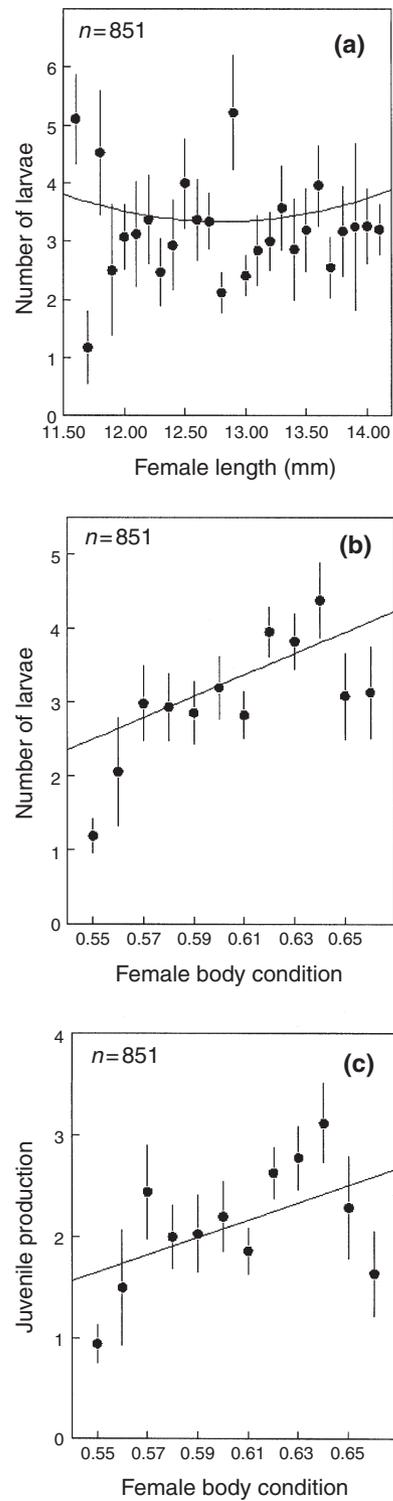


Fig. 2. The effects of female length and body condition on (a, b), the number of larvae, and (c) reproductive success (data were grouped and means \pm SE per group presented for clarity). Depicted are the significant relationships from the multiple regressions (see Table 2). The effects of other significant variables were set to the population average.

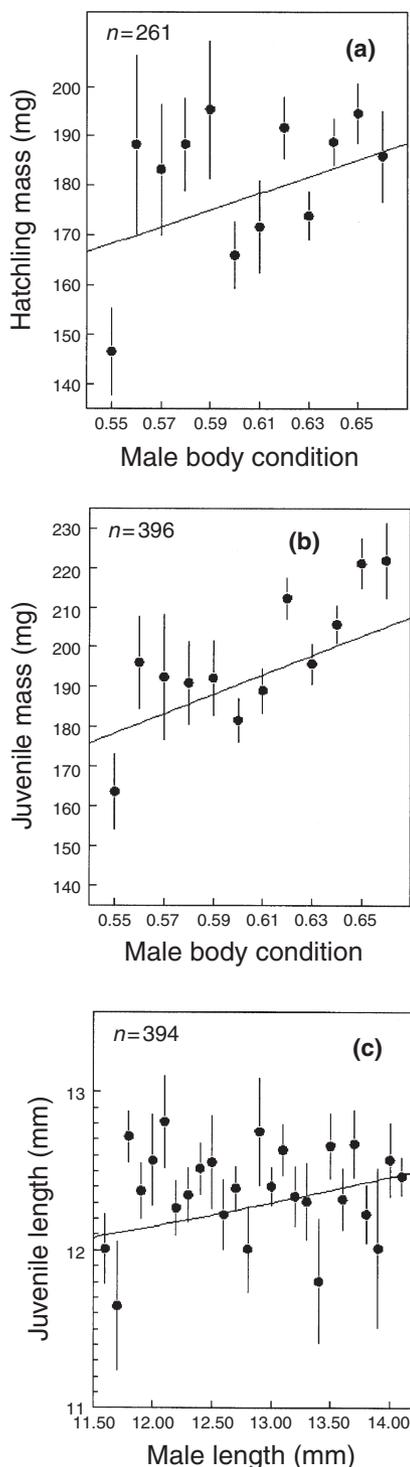


Fig. 3. The effects of male body condition and length on (a) hatchling mass, (b) juvenile mass, and (c) juvenile length (data were grouped and means \pm SE per group presented for clarity). Depicted are the significant relationships from the multiple regressions (see Table 2). The effects of other significant variables were set to the population average (because hatchling mass was only measured in 1999 and 2000, the 2-year population average was used instead).

mass, body length, and body condition were all correlated (except body condition with body length in males), in many respects these factors might be used interchangeably, although body condition explained the largest part of the variance in the multiple regressions. Female body condition was the most significant factor determining the reproductive success. When controlled for other factors, males had comparatively little effect on reproductive success in the laboratory situation. Male body condition was related positively to hatchling mass and juvenile mass, and male length squared was related positively to juvenile length. Experimental manipulations of male and female body condition are needed to establish whether these relationships are causal. Wheat flocks could be used, because they had a significant positive effect on reproductive success and offspring mass.

In the field situation, only male length was related to burrow depth and mainly determined reproductive success (Rasa *et al.*, 1998) although male mass was not determined in the field. Rasa *et al.* (2000) demonstrated in a 10-day starvation experiment with *P. armaticeps* that large individuals were slower to lose their body reserves (measured as percentage fat content) than small individuals. This might explain why body condition (which is correlated with body mass but less to length) is the predominant determinant of reproductive success in the study species. It also suggests that females *weighing* potential breeding partners during nocturnal courtship (the *push-up* display, Rasa *et al.*, 1998) might actually measure male body condition, assuming that they also measure male body length using tactile information. The effects of male and female body condition on reproductive success and offspring size leaves ample scope for mutual condition-dependent sexual selection in this species (e.g. Rowe & Houle, 1996; David *et al.*, 1998). These ideas need further experimental testing.

Although at first sight some of the field and laboratory data on body size and reproductive success in *P. armaticeps* contradict each other (field: male size, laboratory: female size more important), there are some important differences between the laboratory and field situation (note that body mass and condition were not measured in the field). First, in the laboratory environment, moisture levels were optimal for breeding, and breeding burrows reaching the bottom of the cages retained optimal moisture levels throughout larval and pupal development. In the field, desiccation of sand is continuous, rainfall following breeding being rare and usually destructive to the breeding burrow and its contents. Consequently, in the field breeding pairs are always busy extending the burrow, and male digging capacity will be much more important for reproductive success in the Kalahari desert than in the laboratory. Nevertheless, male size influenced burrow length in the laboratory significantly, as it does in the field (Rasa *et al.*, 1998). Second, in the field breeding failures due to eggs not hatching or larvae not pupating will go largely unnoticed. Hence, important components of natural variation in breeding success, e.g. female egg laying potential, remain untested, and may

explain the differences found between the field and laboratory results.

As can be expected, male size having a strong effect on reproductive success has been found in several other beetle species with male parental care. In the bark beetle *Ips pini* (Say, Scolytidae; Reid & Roitberg, 1995; Kirkendall *et al.*, 1997; Robertson, 1998; Robertson & Roitberg, 1998), male size was related to offspring production and offspring size, but the effect of female size was not tested. Male removal experiments resulted in lower reproductive success and lower female survival (Robertson, 1998; but see Lissemore, 1997). Male size also influences reproductive success in some dung beetles (Scarabaeidae, *Onthophagus vacca* Linnaeus: Sowig, 1996; *O. taurus* Schreber: Hunt & Simmons, 1998, 2000; Moczek, 1999; and *O. binodis* Thunberg: Cook, 1988; but not related to male and female size in *Kheper platynotus* Bates: Sato & Imamori, 1987). In the burying beetles of the genus *Nicrophorus* (Silphidae), carcass size is the prime determinant of reproductive success, irrespective of whether the female alone, the male alone, or both parents attend the carcass. Parents raise more offspring on large carcasses, irrespective of male size, and mean larva size is unrelated to carcass or male size (Trumbo & Fernandez, 1995; Eggert & Müller, 1997; Eggert *et al.*, 1998; Müller *et al.*, 1998; Sakaluk *et al.*, 1998); however, large-sized individuals are better able to monopolise and defend the carcass against competitors (see review by Eggert & Müller, 1997). Reid and Roitberg (1995) found that male body size in male pine engravers was related to offspring size and number. In burying beetles *Nicrophorus* spp. (Silphidae), males defend the brood and food source against competitors (Scott, 1998), but in the absence of competitors, male assistance is not necessary for successful reproduction (Eggert & Müller, 1997; Jenkins *et al.*, 2000). Consequently, reproductive success and offspring size are in general more related to female size, than to male size (Wilson & Fudge, 1984; Bartlett, 1988; Bartlett & Ashworth, 1988; Scott, 1990; Trumbo, 1990, 1994; Trumbo & Fernandez, 1995; Eggert & Müller, 1997). In the curculionid beetle *Diaprepes abbreviatus* (Linnaeus), larger females are more fecund than smaller females, and males prefer to mate with large females (Harari *et al.*, 1999); however, in all these studies male and female body condition were not determined and might be more important determinants of fecundity than body size itself. Experimental manipulation of body condition independent of body size and measuring its effects on reproductive success should resolve this point.

The results show that larvae of large females took more time to hatch, pupate, and eclose. This (genetic) correlation between development time and final size is a very general finding in insects (e.g. Blanckenhorn, 1998; see reviews by Roff, 1992; Stearns, 1992). Moreover, female size influenced burrow length negatively and burrow construction was delayed, compared with small females. This might be due to smaller females being more likely to engage in burrow construction, rather than searching for food on the surface and bringing it to the burrow. As argued above, on the surface smaller females lose water more quickly than large females, hence they might be forced to

stay on the surface for shorter periods, and instead spend more time digging.

The principal difference between *P. armaticeps* and the other beetle species with biparental care is that in the other species males, and often also females, might compete for additional breeding opportunities within the same breeding season, whereas *P. armaticeps* has to wait for the next rainfall to dig a new breeding burrow and breed again. This selective difference compared with other beetle species may have contributed to the fact that both male and female *P. armaticeps* show high levels of co-operative parental care, accompanied by a division of labour between the sexes (Rasa, 1998, 1999). This obligate division of labour in *P. armaticeps* might be the key to its success under the adverse conditions of the Kalahari desert, allowing continuous burrow maintenance and guarding, and sufficient food delivery to the offspring within the short breeding time frame of the wet season. It would be interesting to identify the environmental conditions under which conflicts of interests might occur between the male and the female over the amount of parental care to spend.

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