



Reproductive skew and communal breeding in the subsocial beetle *Parastizopus armaticeps*

DIK HEG*†, STEPHANIE HEYL‡, O. ANNE E. RASA* & KLAUS PESCHKE‡

*Abteilung Ethologie, Zoologisches Institut, Universität Bonn, Germany

†Department of Behavioural Ecology, Zoological Institute, University of Bern

‡Institut für Biologie (Zoologie), Universität Freiburg

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The monogamous beetle *Parastizopus armaticeps* (Tenebrionidae) constructs breeding burrows in the Kalahari Desert after rainfall, and shows extensive biparental care. However, occasional communal breeding has been reported, where the male shares the burrow with more than one female (ca. 5% of breeding burrows). We induced communal breeding in the laboratory by confining one male with two females in a small breeding cage. In 33% of these trios females stopped being aggressive towards each other and reared offspring communally. Larger females dominate smaller females, so we expected the incidence of communal breeding to be higher, and the reproductive skew to be lower, for equally sized females than for unequally sized females competing for the male. These predictions were not borne out: the incidence of communal breeding was similar in both situations and reproductive skew was independent of the (difference in) body measurements of the two females. The calculated binomial reproductive skew was in close agreement with the distribution expected from random sharing of maternity among the two females. Time spent in parental care per individual and (group) reproductive success of trios were not different from those of monogamous breeding pairs.

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Cooperative breeding is a widespread phenomenon in the animal kingdom, particularly in insects (Bourke 1997; Choe & Crespi 1997; Emlen 1997). Evolutionary theory predicts that individuals should stay in the group when the net fitness benefits of group living outweigh the net fitness benefits of dispersal and independent breeding. If individuals share in the group's reproductive success, this might be a strong incentive for them to stay and help rear offspring. Much effort has been put into modelling the factors influencing shared and nonshared reproduction (the amount of 'reproductive skew'), and its effects on group living (reviewed in Johnstone 2000). Theory suggests three important factors influence group structure and reproductive skew: (1) relatedness among group members; (2) ability to acquire or monopolize reproductive success within the group (i.e. because of differences

in fighting abilities and possibilities to suppress reproduction of same-sexed individuals in the group, Beekman et al. 2003); (3) costs and benefits of group living versus dispersal and independent breeding (Cant 1998; Clutton-Brock 1998; Emlen et al. 1998; Cant & Johnstone 1999, 2000; Johnstone & Cant 1999a, b; Kokko & Johnstone 1999; Johnstone 2000; Reeve & Emlen 2000; Cant & Field 2001; Ridley et al. 2003).

Despite the recent theoretical advances and intensive modelling effort, the number of experimental studies has been limited (e.g. Trumbo & Wilson 1993; Scott 1997). When and why do groups show high levels of reproductive skew? Who controls the amount of reproductive skew, and how is control effected? Insect species offer an excellent opportunity to study the ecology and evolution of sociality and the effects on reproductive skew; for example they show considerable variation in sociality, between closely related species and sometimes between populations (Choe & Crespi 1997). Subsocial insect species, that is, those species with some level of postovipositional parental care but not advanced levels of sociality (Tallamy & Wood 1986), are particularly interesting, since many species show the most basic forms of sociality beyond mere biparental care (Zeh & Smith 1985), such as

Correspondence: D. Heg, Department of Behavioural Ecology, Zoological Institute, University of Bern, Wohlenschtrasse 50a, CH-3032, Hinterkappelen, Switzerland (email: dik.heg@esh.unibe.ch). S. Heyl and K. Peschke are at the Institut für Biologie (Zoologie), Universität Freiburg, Hauptstrasse 1, D-79104 Freiburg, Germany. O. A. E. Rasa is at the Department of Zoology, University of Pretoria, 0001 Pretoria, South Africa.

communal breeding (e.g. Sakagami & Maeta 1977; Abrams & Eickwort 1981; Yamane et al. 1983; McCorquodale 1988; Trumbo & Wilson 1993) and hence have only a few within-group competitors for reproduction. They are thus more amenable to experimental analyses. Communal breeding systems in primitively social insects are often, but not always, associated with low relatedness (reviewed in Kukuk & Sage 1994). Our aim in this study was to address the likelihood of communal breeding, reproductive skew and participation in cooperative activities in relation to experimentally varied differences in the ability to dominate (by varying size differences) in a subsocial tenebrionid beetle (*Parastizopus armaticeps*, Peringuey), which occasionally breeds communally. We varied the females' possibilities of dominating reproduction in a controlled laboratory breeding experiment, using unrelated individuals only, which allowed us to control many confounding factors potentially affecting reproductive skew.

Parastizopus armaticeps is a beetle species from the Kalahari Desert (Rasa 1990). Males and females mate monogamously shortly after rainfall, and together dig a breeding burrow in the sand (Rasa 1995). Eggs are deposited within a few days of mating, and the burrow is filled with food for the offspring (sticks and leaves from the shrub *Lebeckia linearifolia*). The male and female show division of labour: males do most of the digging and burrow maintenance and turn and clean the pupae, whereas females do most of the food gathering on the surface (but also guard when not feeding, Rasa 1999). The burrow entrance is guarded against intra- and interspecific intruders (predators and kleptoparasites, Rasa & Endrody-Younga 1997; Rasa & Heg 2004) and a highly effective defensive abdominal secretion is used to deter most predators (Rasa 1998, 1999; Rasa et al. 2000). Male size, but not female size, affects the reproductive success of the pair, and females compete for the males (Rasa et al. 1998). This is the result of variation in male digging effort: large males dig deeper burrows, and deeper burrows stay moist during egg, larval and pupal development. Eggs, larvae and pupae need approximately 100% humidity to develop and hatch, and suboptimal moisture levels reduce their development rate (Rasa 1999). Supplementary feeding experiments in the field did not increase the size of the food store, but instead females spent less time collecting food and more time digging (Rasa 1998), suggesting that burrow size is the most important factor determining the pair's reproductive output. Although *P. armaticeps* is usually monogamous, occasional communal breeding appears to occur in the field, as sometimes two females and a male with offspring are found in the same burrow after excavation (O. A. E. Rasa, personal observations). However, the true frequency of communal breeding is difficult to assess in the field, since mature offspring cannot always be distinguished from adults, and it is unknown whether secondary females may join or desert broods. The most conservative estimate from excavated burrows, and from adults seen to leave the burrow with offspring, is 5% of all the occupied breeding burrows (O. A. E. Rasa, personal observations).

Larger individuals are able to dominate smaller individuals in competition for resources (Rasa et al. 2000), which

is commonly found in beetle species (e.g. Otronen 1988; Trumbo 1990; Sato 1998). Furthermore, females and males mate assortatively in the field and larger females are able to monopolize males to breed monogamously (Rasa et al. 1998). These two facts suggest that larger females should be able to monopolize reproduction in a same-sex competitive situation, that is (1) the incidence of communal breeding should be lower for two dissimilar-sized females competing for access to a male, and/or (2) in communal breeding, the larger female should obtain the larger share in reproduction, and the smaller female the smaller share. We tested these hypotheses in breeding trials in the laboratory, where two similar-sized or two dissimilar-sized females were mated to a male in small breeding cages. This experiment allowed us to test the likelihood of communal breeding depending on the size of the females, the size inequality of the females, and the size of the male. We also tested whether differences in female body condition, which correlate positively with reproductive success in the laboratory (Heg & Rasa 2004), might have affected reproductive skew. Furthermore, we measured the reproductive output and parental effort of communally and monogamously breeding females and males, and tested the hypothesis (3) that communal breeding might enhance the reproductive success per female, as has been found in some other communally breeding insect species (e.g. Mappes et al. 1995).

METHODS

Laboratory Population

The laboratory breeding stock originated from Twee Rivieren, Kalahari Gemsbok Park, South Africa (26°27'S, 20°36'E). All individuals were permanently marked with plastic numbered discs glued on their abdomen (width ca. 2.6 mm; used in bee *Apis* spp. agriculture, Melzer's Bienenfarm, Bonn, Germany). Nonbreeding individuals were housed in terraria (50 × 50 cm and 20 cm high, with a layer of Kalahari sand, water and shredded wheat), in same-sex groups of up to 200 individuals (sexing was conducted according to Koch 1963). We used unrelated individuals in the breeding trials (based on the pedigrees established in the marked laboratory population). During a breeding trial, one male and one or two females from the nonbreeder groups were transferred to small breeding terraria (glass containers, 20 × 30 cm and 20 cm high) with a plastic inset box (19 × 29 cm and 10 cm high). This inset created a 1-cm gap on one of the long and one of the short sides of the glass container, which was filled with moist Kalahari sand (see Heg & Rasa 2004 for more details). Fresh food was provided ad libitum (the natural food source *L. linearifolia*, with *Trifolium pratense* as an alternative, supplemented with wheat). Breeding terraria were placed in a darkened room at 32–36°C (warmer during the light period) with a light cycle of 13:11 h light:dark. Temperature, moisture and light regimes were approximately equivalent to those in the breeding season in the Kalahari. Data were gathered in May–August 2000.

Experimental Set-up

Before the start of a breeding experiment, we determined male mass (± 0.02 mg), male length (± 0.1 mm), female mass (± 0.02 mg) and female length (± 0.1 mm) for a sample of individuals from the nonbreeding colonies. Body length was measured with a magnifying binocular from the caudal tip of the abdomen to the lateral-rostal tip of the thorax.

Three treatments were made. In the first treatment, two females of unequal body mass and one male were introduced into one breeding terrarium, and allowed to pair and breed ($N = 69$; see Table 1 for body measurements). The larger females weighed 160–384 mg and measured 11.8–14.7 mm in length; the smaller females weighed 124–304 mg and measured 10.5–13.9 mm. On average, the body mass and body length of the smaller female were 72.9% and 82.0% of the larger female, respectively. In two trials males failed to pair with either female, and these trials were discarded from all analyses, giving a total sample size of 67. To determine whether female–female competition was more severe for large males, we used males weighing 198–328 mg and measuring 11.9–13.7 mm. In the second treatment, two females of equal body mass and one male were placed in a breeding terrarium, and allowed to pair and breed ($N = 22$). Females weighed 204–338 mg and measured 11.0–13.6 mm. The two rival females were of approximately similar body mass (average difference 0%) and body length (average difference 1.6%). Males weighed 224–330 mg and measured 11.8–14.1 mm. Body condition was determined following Heg & Rasa (2004), as the proportion of body mass beyond the expected structural mass. Unpaired females remained in the terraria for the total duration of all trials involving two competing females. The third treatment was the control group, where one female and one male were introduced into one breeding terrarium and allowed to breed. Pairing and burrow construction usually starts within a few days after the start of a trial, and in this respect there were no differences between the treatments (see below).

Breeding Parameters

We monitored all terraria on a daily basis, to determine the pairing result and reproductive success. Standard

parameters of breeding chronology (in days since the start of the experiment) were determined on a daily basis: start of digging the breeding burrow, first larvae hatched, days between first larvae hatched and first pupa constructed, days between first pupa constructed and first pupa eclosed (Heg & Rasa 2004). We also counted the larvae, pupae and hatchlings in each terrarium. Since the larvae are very small when newly hatched, the number of larvae will be underestimated in most cases. If several batches of larvae hatched within 3–5, rarely up to 20 days, we summed the maximum number of larvae detected in each batch to give the total number of larvae.

Total burrow length (cm) was measured as follows. Since the terraria had fixed height, it would not have made sense to measure burrow depth in the laboratory. Instead, we determined total burrow length (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 to ‘find’ the corner with the best moisture level within the terrarium.

Experiments were aborted when pairs showed no signs of breeding behaviour (digging, storing food); when one of the adults had died and no breeding behaviour was observed (minimum duration of the experiment 30 days); or when all the offspring had died. In all these cases reproductive success was set to zero. Collapse of the breeding burrow from vertebrate activity on the surface or heavy rainfall might cause total brood failure in the field. Since in the laboratory these losses of offspring were absent, we defined reproductive success as the total number of hatchlings produced.

Behavioural Observations

Behavioural observations were made during the dark period of the day, when the beetles are most active. Observations were done in two time periods: during burrow construction and during food provisioning for the larvae. Three to six terraria were observed simultaneously for 1–2 h, including one or two terraria with one male and one female, and two to four with one male and two females. We used the software program ‘the Observer 3.0’ (Noldus, Wageningen, The Netherlands) to record the location and behaviour of each individual separately. We analysed the percentage of the total observation time

Table 1. Average body length (mm) and body mass (mg) of the male and the one or two females in the three treatments \pm SD together with the mean difference (with range) between the two females in a terrarium

	Control (one female)			Treatment 1 (two unequal females)			Treatment 2 (two equal females)		
	N	Body length	Body mass	N	Body length	Body mass	N	Body length	Body mass
Male	22	12.6 \pm 0.6	268.8 \pm 29.4	69	12.6 \pm 0.5	254.7 \pm 27.5	22	12.9 \pm 0.7	273.7 \pm 28.2
1st Female	22	13.0 \pm 0.5	257.8 \pm 29.0	69	13.2 \pm 0.7	283.8 \pm 44.7	22	12.9 \pm 0.5	260.4 \pm 29.1
2nd Female				69	12.1 \pm 0.7	206.8 \pm 32.1	22	12.7 \pm 0.6	260.4 \pm 30.2
Difference (range)				69	1.1 \pm 0.9 (–0.8–3.3)	76.9 \pm 39.9 (12–188)	22	0.2 \pm 0.4 (–0.4–1)	0.0 \pm 4.4 (–12–10)

spent in the breeding burrow and the following major parental behaviours: digging, guarding burrow entrance, transporting food (from surface to burrow entrance), storing food (moving food from burrow entrance to burrow end). Females need access for copulation and egg laying, so if two females compete for the burrow, the time spent inside the burrow indicates whether these females have access to it and might participate in reproduction.

DNA Analysis

Fourteen communally breeding trios with their brood were sampled, killed by cooling, then decapitated and stored at -20°C . Offspring sampled included hatchlings, dead embryos (failed to hatch from their pupa) and dead full-grown larvae (failed to pupate). Multilocus DNA fingerprints were obtained following the procedure adapted from Benken et al. (1998). Each sample was homogenized and proteins were degraded for 60–90 min at 55°C with Proteinase K. Proteins were denatured in sodium chloride solution and separated from the DNA after centrifugation in a chloroform/isoamylalcohol solution. DNA was denatured in 100% ethanol, centrifuged and twice washed in 70% ethanol solution. Subsequently, the sample was dried in a Speed-Vac, dissolved in TE buffer and stored at 4°C for at least 24 h. Per individual, 24 μl of chromosomal DNA was digested with *HinfI* and hybridized with probe (GTG)₅. DNA fingerprint electrophoresis was carried out on 0.7% agarose gels in $1\times$ TBE buffer at 55°C at 40 V for 70 h. A λ -DNA *HindIII* digest deoxygenated size marker was added to each gel to determine the fragment size of the DNA fingerprint bands. DNA fragments were purinized with HCl (15 min) and denatured with NaOH (30 min), and transferred to an immobilizing nylon membrane (2 h, type Hypobond N+, Amersham, Little Chalfont, Buckinghamshire, U.K.). Afterwards, the membranes were washed in SSC (10 min), air dried and subsequently incubated with blocking solution (at least 1 h). Hybridization was conducted overnight (at least 3 h) at 40°C in a hybridizing incubator (Bachofer), and afterwards washed in SSC for three times during 10 min and stored in blocking solution. For signal detection we used a chemoluminescent marker with a nonspecific antibody (Boehringer, see Benken et al. 1998). On average, 3.6 bands per individual were detected. Band profiles were consistent with Mendelian inheritance. Owing to the simple experimental design (one known father, two potential mothers) maternity could be unambiguously assigned, but assignment failed for the majority of dead larvae and unhatched pupae, owing to DNA decay and the resulting failure to amplify the DNA or the appearance of mismatching bands with all putative parents.

Statistical Analyses

For analyses we used SPSS 11.0 (SPSS Inc., Chicago, IL, U.S.A.) and GLIM (Crawley 1993). The likelihood of both females breeding communally with the male was analysed with a logistic regression. The proportion of offspring attributable to the two communally breeding females was

analysed with weighted logistic regressions in GLIM. Both full models with backward elimination of terms and null models with forward selection of terms were constructed. By these methods, and by constructing slightly deviant final models, we checked the final models for overall robustness (significance of terms and magnitude of the coefficients). Interactions were fitted as well, but since they gave no significantly better fit than more parsimonious models including only main effects, they are not presented here. Reproductive skew was determined with the binomial skew index (*B*) of Nonacs (2000), with the larger female set as individual 1 and the smaller female as individual 2. Sample sizes varied because some pairs or communal trios lost their offspring before sampling or before behavioural observations during a certain period could be conducted. All *P* values are two tailed.

RESULTS

The combination of treatments (single male with single female, or single male with two females) and eventually monogamous or communal breeding gave five 'pairing results': control monogamous breeding; monogamous breeding, unequal-females treatment; monogamous breeding, equal-females treatment; communal breeding, equal-females treatment; communal breeding, unequal-females treatment.

Incidence of Communal Breeding

In 33% of all trials involving competing females, the male and the two females bred communally ($N = 89$). All trios cooperatively constructed one breeding burrow and delivered food, which was stored at the end of the burrow where moisture is highest. The burrow was indiscriminately used by both females and the male, and no signs of partitioning of the burrow (e.g. into tunnel branches) were observed. Virtually no overt aggressive behaviour was observed between the two females, or between one of the females and the male during any period. Contrary to expectation, the likelihood of communal breeding was similar for males pairing with unequal females (36%, 24 of 67 trials) and equal females (23%, 5 of 22 trials; $\chi^2_1 = 1.1$, $P = 0.29$; Table 2). We constructed a logistic regression model to predict the likelihood of communal breeding, depending on male and female body mass, body length and body condition, and the difference in these measurements between the two females (both

Table 2. Pairing result depending on the treatment

	Monogamous breeding	Communal breeding
Control	22	—
Treatment 1 (unequal females)	43*	24
Treatment 2 (equal females)	17	5

*With larger female: $N = 37$; with smaller female: $N = 6$ (binomial test: $P < 0.001$).

expressed in absolute and relative values). However, no single factor or interaction of factors predicted the incidence of communal breeding (Table 3).

Reproductive Success

Of 111 trials, 95% of the breeders dug a burrow and 65% produced at least one larva. In both these respects, there were no differences between the pairing results (digging burrow: $\chi^2_4 = 1.6$, $P = 0.81$; producing larva: $\chi^2_4 = 6.8$, $P = 0.14$). Most breeders started burrow construction within 5 days of the start of the trial (83 of 106, median 2 days, range 1–40 days). There were no differences in the onset of burrow construction depending on the pairing result (Kruskal–Wallis: $\chi^2_4 = 1.9$, $P = 0.76$). Average burrow length \pm SD was 22.3 ± 11.8 cm ($N = 89$), and did not depend on the pairing result (ANOVA: $F_{3,85} = 0.22$, $P = 0.89$). Monogamous breeding pairs ($N = 60$) and communal breeding trios ($N = 29$) constructed burrows of similar length (pairs: $\bar{X} \pm SE = 22.9 \pm 11.2$; trios: 20.9 ± 13.0 cm; ANOVA: $F_{1,87} = 0.55$, $P = 0.46$).

We predicted a higher reproductive success for communal breeding trios than for monogamous breeding pairs, but this was not substantiated by the data (Fig. 1). There was a significant effect of pairing results on the number of larvae and pupae and total number of offspring (Kruskal–Wallis tests: larvae: $\chi^2_4 = 17.2$, $P = 0.002$; pupae: $\chi^2_4 = 17.2$, $P = 0.002$; offspring: $\chi^2_4 = 12.1$, $P = 0.017$), but this was entirely due to a significant difference between the control monogamous pairs and the monogamous breeding pairs where two unequally sized females had been competing for the male (Mann–Whitney U tests: all three tests with $Z = -3.46$, $N_1 = 11$, $N_2 = 33$ (larvae and pupae), $N_1 = 22$, $N_2 = 43$ (total offspring), $P = 0.01$ after Bonferroni correction, all other pairwise tests $P > 0.10$).

Table 3. The probability of communal behaviour in relation to male and female body measurements

Variable	Wald χ^2_1	P
Male length	0.632	0.43
Male mass	1.700	0.19
Male condition	1.631	0.20
Larger female length	0.836	0.36
Larger female mass	0.023	0.88
Larger female condition	0.922	0.34
Smaller female length	0.051	0.82
Smaller female mass	0.323	0.57
Smaller female condition	0.328	0.57
Δ Female length	0.987	0.32
Δ Female mass	0.083	0.77
Δ Female condition	0.036	0.85
$\Delta\%$ Female length	1.149	0.28
$\Delta\%$ Female mass	0.263	0.61
$\Delta\%$ Female condition	0.001	0.97

A logistic regression ($N = 89$) was used with the independent variables body mass, length and condition of the male and both females, and the difference (Δ) in mass, length and condition between the two females (larger – smaller, both in absolute and percentage from smaller female value). The significance of each variable when included in the null model is indicated.

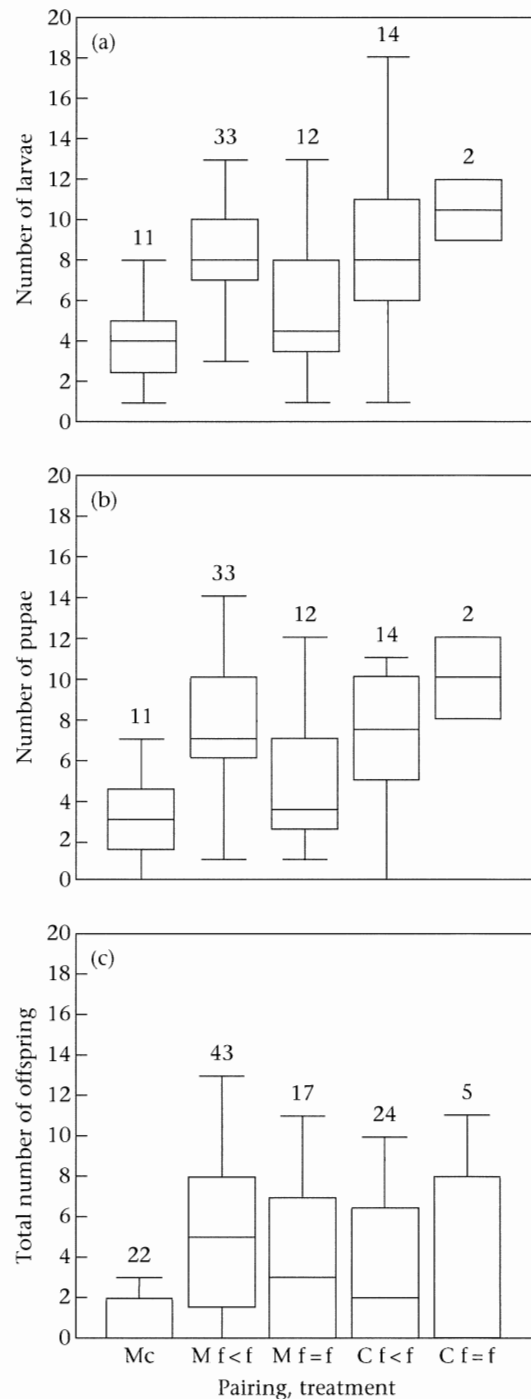


Figure 1. Reproductive success of monogamous pairs versus communally breeding trios: (a) number of larvae, (b) number of pupae (both measures of pairs producing at least one larva) and (c) total number of offspring (includes total breeding failures). Depicted are medians, quartiles and range with sample sizes. M: monogamous pair; C: communal trio; c: control breeding pair; f < f: two unequally sized females in terrarium; f = f: two equally sized females in terrarium.

Reproductive Skew

Maternity could be assigned to 93 offspring of 14 broods reared by communal trios (Table 4). Offspring maternity could not be determined in 16 cases because of unclear or missing DNA bands and in eight cases because of insecure assignment of offspring DNA profiles to either of the two female DNA profiles, probably owing to DNA degradation. In total, 44 offspring were attributed to the larger female and 49 to the smaller female (binomial test: $P = 0.68$; excluding the two broods of the equal-females treatment: 39 versus 40, $P = 1.0$). Of 14 broods 11 were of mixed maternity, but in the other three broods no offspring of the larger female were detected (Table 4).

Figure 2 shows the observed and the expected skews under the three scenarios of partitioning of reproduction for the 14 broods (observed: $\bar{X} \pm SE = -0.004 \pm 0.058$; equal: -0.096 ± 0.015 ; random: all 0; monopolization: 0.404 ± 0.015). The observed skew was significantly different from the complete monopolization scenario (paired t tests: $t_{13} = -7.6$, $P < 0.001$), tended to be different from the equal share scenario ($t_{13} = 1.7$, $P = 0.11$) and was in close agreement with the random distribution scenario ($t_{13} = -0.06$, $P = 0.95$). Although the sample size is arguably small, the skew data suggest that females shared reproduction randomly.

If females lay sequentially, offspring of each female should be closely clustered according to the timing of pupation, that is, hatch from adjacent pupa orders. Instead, offspring of the two females seemed to be fairly mixed, suggesting synchronized egg laying (Table 4). Unfortunately, only three mixed broods (from cages 388, 441 and 530) allowed a statistical test. Nevertheless, all three tests were nonsignificant, supporting synchronized egg laying (change-point test: $mn^*D_{mn} = 28, 12$ and 7 , $P > 0.05, 0.1$ and 0.05 , respectively; Siegel & Castellan 1988, page 64).

We predicted that the reproductive skew would increase in the unequal-females treatment compared to the equal-females treatment, with the larger female taking the higher share. Twelve broods of the unequal-females treatment and two broods of the equal-females treatment were sampled (Table 4) and the low sample size allowed no direct statistical comparison. Hence, we had to use the variation in body measurements between the two females of both treatments combined for the statistical analyses. Contrary to expectation, there was a nonsignificant, negative correlation between the difference in body mass and body length and the proportion of offspring attributed to the heavier and larger female, respectively (weighted logistic regressions: difference in body mass, null model: $\chi^2_{13} = 37.7$, change in χ^2_1 due to difference in body mass = 3.5 , $P < 0.075$; difference in body length, null model: $\chi^2_{13} = 34.8$, change in χ^2_1 due to difference in body length = 1.0 , $P > 0.30$; Fig. 3a, b). In contrast, the correlation between the difference in females' body condition and the proportion of offspring attributed to the female in better condition was positive but also nonsignificant (null model: $\chi^2_{13} = 35.5$, change in χ^2_1 due to difference in body condition = 3.3 , $P < 0.075$; Fig. 3c).

Table 4. Maternity of 14 broods of communal trios

Cage	Treatment	Male		Female 1		Female 2		Number of			Maternity of offspring*																	
		Length	Mass	Length	Mass	Length	Mass	Larvae	Pupae	Offspring	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
379	Unequal	12.3	228	12.7	274	12.0	232	7	6	6	2	2	?	2	?	2	?	1	?	?	2	?	?	?	?	?	?	?
380	Unequal	12.7	270	12.3	204	10.7	164	11	10	8	2	2	2	2	2	2	1	?	1	?	?	?	?	?	?	?	?	?
382	Unequal	12.2	248	13.9	330	13.2	262	8	7	5	1	2	2	2	1	?	2	?	?	?	?	?	?	?	?	?	?	?
386	Unequal	13.6	310	12.8	290	13.0	218	8	8	7	1	1	1	1	1	1	1	2	?	?	?	?	?	?	?	?	?	?
388	Unequal	12.3	226	13.0	282	11.6	206	18	18	18	1	1	1	1	2	2	1	2	2	2	?	1	2	1	2	1	1	—
389	Unequal	12.0	234	12.9	272	12.7	214	11	10	10	1	1	1	1	1	1	2	1	1	1	?	?	?	?	?	?	?	?
390	Unequal	12.4	264	12.8	268	12.8	224	3	3	3	1	2	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
392	Unequal	12.5	248	13.7	258	12.0	224	5	5	5	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
394	Unequal	12.5	270	13.1	288	12.2	208	8	8	7	?	2	2	1	2	1	2	?	?	?	?	?	?	?	?	?	?	?
437	Unequal	12.8	268	13.7	308	11.6	192	6	3	3	2	2	2	2	2	2	2	2	2	2	?	?	?	?	?	?	?	?
440	Unequal	12.7	198	13.0	260	11.5	206	11	11	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
441	Unequal	12.1	236	12.5	240	11.8	212	16	9	8	1	1	?	1	—	2	2	2	2	2	—	—	—	—	—	—	—	—
497	Equal	12.6	295	13.4	240	12.8	244	9	8	8	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
530	Equal	12.6	256	12.0	208	11.0	204	12	12	11	?	1	2	2	2	2	2	2	2	2	?	?	?	?	?	?	?	?

Body length (mm) and mass (g) of the male and the two females, the total number of larvae, pupae and offspring hatched, and the maternity of each offspring (1 = offspring from female 1; 2 = offspring from female 2) are shown. Offspring are ranked according to pupa order: 1 = offspring from first pupated larva; 2 = offspring from second pupated larva, etc). Treatments were females unequal or equal in size.
 *: DNA analysis or maternity assignment failed; —: offspring dead before sampling or no DNA sampled.

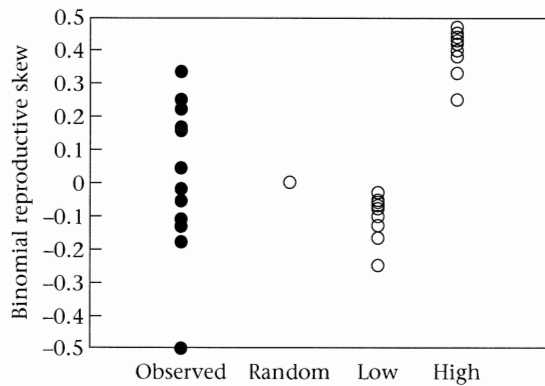


Figure 2. Observed binomial reproductive skew (Observed), compared with three expectations of reproductive sharing among the two females (all $N = 14$ broods): random distribution of maternity (Random, all 0), equal sharing (Low skew) and complete monopolization by one female (High skew).

Parental Effort

No significant differences were found in parental behaviours between the two females in the communal breeding trials in the two periods, burrow construction and larval feeding (% time spent in burrowing, digging, guarding, transporting food, storing food; Wilcoxon tests: $T = 68.5-85.0$, $N = 9$, all $P > 0.10$). Hence, in subsequent analyses only the data of the first female were used. We also detected no significant differences in female or male behaviours between monogamously breeding pairs from the control treatment, the equally sized and unequally sized female treatments, for the two periods (Kruskal-Wallis tests: burrow phase: $N = 15, 12, 11$; larval phase: $N = 17, 17, 20$, respectively, all $P > 0.10$), so the results of all the monogamously breeding pairs were pooled in the analyses.

Contrary to expectation, males and females of communally breeding groups spent similar amounts of time in parental duties compared with males and females from monogamous breeding pairs (Fig. 4). Males spent more time in the burrow and digging, whereas females spent more time in collecting food on the surface.

DISCUSSION

The results did not support our hypotheses that: (1) equally sized females show more communal breeding than unequally sized females; (2) within communal trios, larger females gain the larger share of reproduction; (3) in communal trios, single females produce more offspring than monogamously breeding females; and (4) communal trios spend less time in parental behaviours than monogamous pairs. These results compare well to joint nesting in *Nicrophorus* beetles, which show a similar breeding system, and where also no evidence of relative size-dependent communal breeding was detected, and reproduction per female was not enhanced compared to that of monogamously breeding females (Trumbo & Wilson 1993). Furthermore, in *Nicrophorus tomentosus* the degree of reproductive skew was not related to the body size ratio

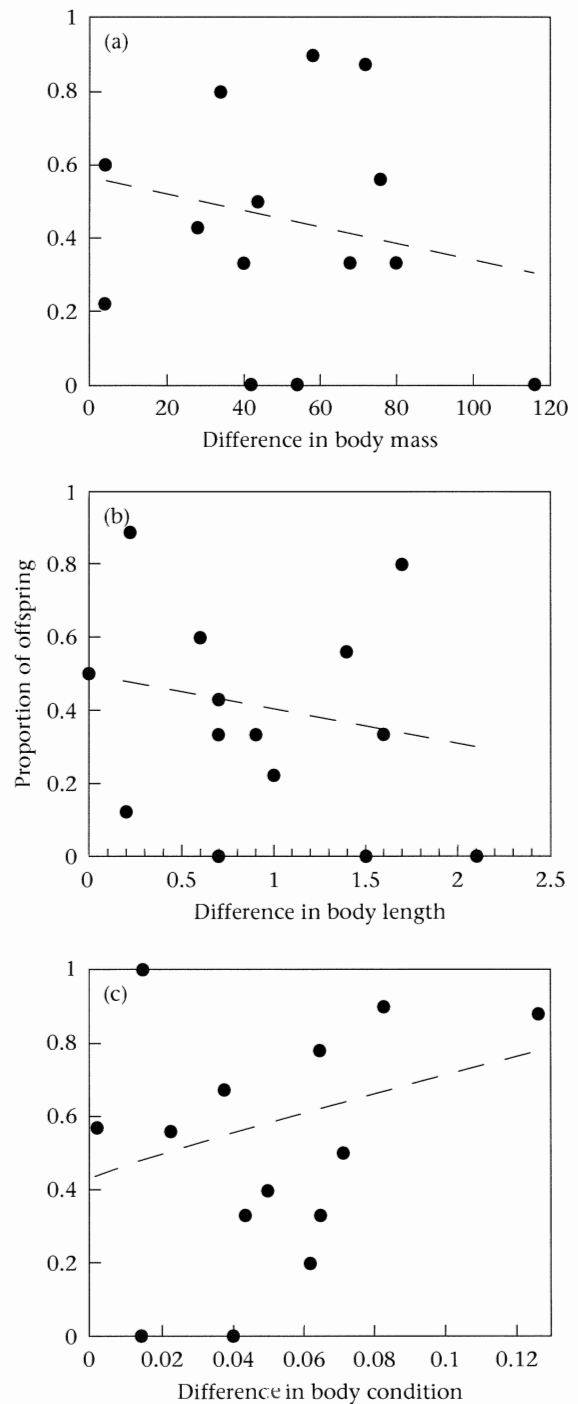


Figure 3. Proportion of offspring attributed to (a) heavier, (b) larger and (c) better body condition female in relation to the difference in (a) body mass, (b) body length and (c) body condition between the two females, respectively (larger value – lower value). See text for statistical tests; the nonsignificant weighted logistic regression curves are indicated in the graphs: coefficients for constant \pm SE: (a) 0.253 ± 0.294 , (b) -0.012 ± 0.420 , (c) -0.255 ± 0.383 ; coefficients for X axis \pm SE: (a) -0.009 ± 0.005 , (b) -0.378 ± 0.389 , (c) 11.970 ± 6.771 .

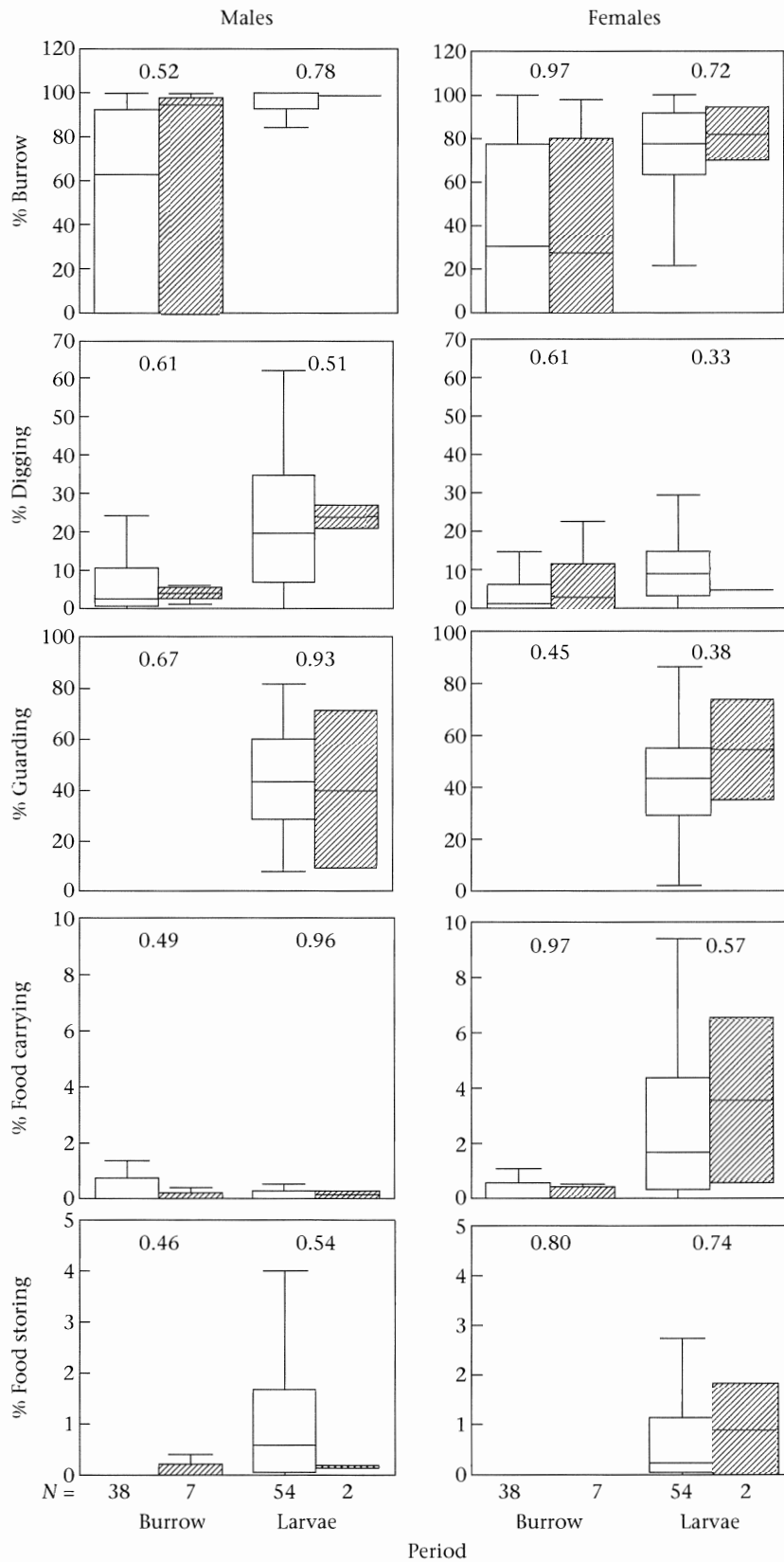


Figure 4. Percentage time spent in the breeding hole and in four parental behaviours of males and females during two periods (burrow: burrow construction; larvae: larval feeding), comparing monogamous pairs with communally breeding trios (in trios only data of first female presented, sample sizes are shown below the graph). The *P* values of separate Mann-Whitney *U* tests are indicated above the two bars being compared.

of the communally breeding females, although the larger female usually had the larger share in reproduction (Scott 1997). In *P. armaticeps* there was a nonsignificant tendency for females in better body condition to take a larger share of reproduction. In another laboratory study, we have shown that monogamous females in better body condition produce more offspring, probably because they produce more larvae to start with (Heg & Rasa 2004). Hence, the higher share of reproduction taken by communally breeding females could simply be a side-effect of their good condition, and have nothing to do with active control or suppression of reproduction of the competing female. In fact, we have found no evidence whatsoever for active female control or suppression: no female–female aggressive interactions were seen during pair formation, egg laying and afterwards, and both females were able to enter and leave the breeding burrow unhindered by the competing female (and the male). These results compare well with those in a study on joint-nesting oystercatchers, *Haematopus ostralegus* (Heg & van Treuren 1998), where also no aggression was seen, but contrast with those in a study on joint-nesting *Nicrophorus* beetles. In these beetles competition is overt and, as a consequence, same-sized joint-nesting females have more bodily injuries than dissimilar-sized females (Trumbo & Wilson 1993). An increase in the reproductive skew with an increase in the female size ratio in two paper wasps has been hypothesized and tested; like those on beetles, both studies failed to find support for this hypothesis (*Polistes bellicosus*: Field et al. 1998; *P. carolina*: Seppa et al. 2002; see also Nonacs et al. 2004).

Reproduction in the two communally breeding *P. armaticeps* females seemed to be shared randomly, and on average communal breeding groups showed low reproductive skew. In this respect, there are clear parallels with other animal species, where lack of dominant control seems to be the major reason why reproduction is shared equally, or where the benefits of group size override the costs of shared reproduction to the dominant female or male (e.g. banded mongoose, *Mungos mungo*: De Luca & Ginsberg 2001; spotted hyaenas, *Crocuta crocuta*: Engh et al. 2002; *Melanerpes formicivorus*: Haydock & Koenig 2002). In contrast, other studies have reported high skew, suggesting either that dominants control reproduction, or that subordinates refrain from reproduction, maybe to avoid eviction from the group (e.g. a Malaysian hover wasp, *Liostenogaster flavolineata*: Sumner et al. 2002; laughing kookaburra, *Dacelo novaeguineae*: Legge & Cockburn 2000; stable groups in white-winged choughs, *Corcorax melanorhamphos*: Heinsohn et al. 2000; Seychelles brush warbler, *Acrocephalus sechellensis*: Richardson et al. 2002; a cichlid fish from Tanganyika Lake, *Neolamprologus pulcher*: Dierkes et al. 1999). No evidence has been found for active female control in lions, *Panthera leo*, probably because of the costs of exerting control and the large mutualistic benefits of females staying in the group (Packer et al. 2001). Dominants also do not seem to control the reproduction of subordinate female Damaraland mole-rats, *Cryptomys damarensis* (Clarke et al. 2001); rather, female subordinates seem to avoid inbreeding (Cooney & Bennett 2000; Faulkes & Bennett 2001).

It is unlikely that lack of control causes the low reproductive skew in *P. armaticeps*. In the cases where the male was confined with two females and mated monogamously with one of the females, usually the larger female was easily able to chase the second female from the breeding burrow, and the latter did not try to intrude into the burrow during egg laying or afterwards (D. Heg, personal observation). However, things might be different in the field situation, where females have to travel further to gather food and bring it to the burrow and, hence, cannot guard the entrance against second females intruding in the meantime. Nevertheless, males do the guarding when females are absent, and are highly aggressive against intruders of either sex, probably because of the risk of being evicted from the breeding burrow by an intruding breeding pair. If males want to breed with a second female, they would have to enlarge and maintain a larger breeding burrow, and the costs of doing so might outweigh the benefits of attracting a second breeding female. Pupae in particular need a lot of space within the burrow, and have to be turned regularly. The facts suggest that males, on average, have not much to gain from accepting and breeding with second females. Our laboratory results also suggest no benefits to the males, in terms of increased reproductive success or reduced paternal effort, from the presence of a second female in their breeding burrow.

We did not test the effect of relatedness on reproductive skew in *P. armaticeps*, but relatedness might influence the amount of communal breeding and skew, and the social system in general (e.g. Johnstone 2000). These Kalahari beetles form aggregations in the hot, dry nonbreeding season: large groups of beetles huddle together inside burrows during the daytime, and thereby reduce water loss (Rasa 1994, 1995, 1997; Rasa & Endrody-Younga 1997). Some of these groups may consist of parents and their offspring maintaining prolonged associations, although some individuals are known to disperse over considerable distances, and individuals do not necessarily use the same burrow all the time (Rasa 1997). Finally, the failure to find a positive effect of communal breeding on the per capita reproductive success, as found in, for example, the paper wasp *Polistes dominulus* (Tibbetts & Reeve 2003), might be caused by our laboratory setting. In nature, communally breeding insects might benefit from each other's presence because of cooperative nest defence against intraspecific competitors (e.g. Gamboa 1978), parasites (e.g. Garófalo et al. 1992; but see Smith 1982) and predators (e.g. Kukuk et al. 1998), and cooperative nest maintenance (e.g. Strassmann et al. 1988), but these environmental influences have been ruled out in our experiments. The effects of relatedness and ecological factors on the costs and benefits of communal breeding and reproductive skew in our study species remain to be tested in detailed behavioural and genetic field studies.

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