

The frequency and fitness consequences of communal breeding in a natural population of burying beetles: a test of reproductive skew

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Abstract. 1. Reproductive cooperation occurs in diverse taxa and a defining characteristic of these social systems is how reproduction is shared. Both male and female burying beetles (*Nicrophorus* spp.) facultatively form associations to bury a carcass and rear a single brood, making burying beetles a model system for testing skew theory.

2. In this study, 50% of 40–45 g carcasses and 75% of 55–60 g ones were buried by more than one male and/or female *Nicrophorus tomentosus*.

3. Females were significantly more likely to cooperate on 55–60 g carcasses than on 40–45 g ones.

4. Analysis of parentage of 13 broods using microsatellite loci as genetic markers showed that maternity analysis of only 2% of the young excluded all females captured leaving the brood chamber after burial. Males previously mated with resident females or displaced by resident males fathered 7% of the young.

5. The male and female remaining the longest were usually the parents of the most offspring, and reproductively dominant individuals also tended to be the largest.

6. Although all but two or three individuals that helped to bury the carcass produced some offspring, reproduction was often not shared equitably. Reproduction of females was significantly skewed on six of nine 40–45 g carcasses but shared fairly equitably on all three 55–60 g ones. Reproduction was skewed among males on 7 of 10 broods.

7. Both males and females relinquished a greater proportion of the brood as the days of assistance from all conspecifics increased.

Key words. Bidding gene, burying beetles, communal breeding, *Nicrophorus*, parentage analysis, parental care, reproductive skew.

Introduction

Reproductive cooperation where more than one male or female provide care to young occurs in taxa as diverse as birds, mammals, and social insects. Communal breeding, in which parentage of offspring is shared, is somewhat less common. Models of helping behaviour and reproductive skew (reviewed in Johnstone, 2000) allow us to view cooperatively breeding species as lying along a continuum of despotic to egalitarian associations. Evolutionary theory predicts that subordinates should join a group when the net fitness gains of

joining are greater than the costs of dispersal and independent breeding; dominants should allow it when net fitness gains are greater than the costs of sharing resources or eviction. The factors expected to influence the evolution of communal breeding and how reproduction is shared among group members are degree of relatedness among cooperating individuals, the ecological constraints that limit independent breeding, the degree to which group reproduction is enhanced by assistance, and the ease with which one individual can dominate others. The relative importance of these factors and their consequences are expected to vary and to affect the degree to which reproduction is shared. Transactional models predict that dominants and subordinates “agree” on the level of reproductive skew that induces subordinates to join. Predictions differ when the dominant is assumed to have complete

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control (Vehrencamp, 1983a, b; Reeve & Ratnieks, 1993) or when the subordinate has more options (Reeve, 1998).

The assumptions of transactional models have been questioned (Clutton-Brock, 1998; Field *et al.*, 1998, but see Emlen *et al.*, 1998) and new models have been developed to examine the effects of biological and ecological variables on reproductive skew when dominants have limited control (Cant, 1998; Reeve, 1998; Reeve *et al.*, 1998; Johnstone & Cant, 1999). Some of the predictions from these models differ from those of the earlier ones. In tug-of-war models, no individuals have complete control and the outcome of how reproduction is shared depends on the costs and benefits of exerting control (Beekman *et al.*, 2003). When dominants have limited control, the subordinate's share of reproduction is expected to be insensitive to both relatedness and ecological constraints (Reeve *et al.*, 1998). Tests of the different predictions of these models allow us to examine the extent of control of reproduction by the dominant (Beekman *et al.*, 2003).

Thus the distribution of lifetime reproductive success among group members is a key measure to describe the outcome of reproductive cooperation and competition and to understand its evolution (Sherman *et al.*, 1995). Therefore measuring reproductive success, by establishing parentage, is essential for understanding the evolution of communal breeding and evaluating the outcome of reproductive decisions. Parentage analyses have been carried out for many species of vertebrates that display reproductive cooperation (Jennions & Macdonald, 1994; Westneat & Webster, 1994) but there are relatively few such studies for natural populations of insects (Evans, 1998; Field *et al.*, 1998; references in Reeve *et al.*, 1998; Scott & Williams, 1998; Seppa *et al.*, 2002; Sumner *et al.*, 2002; Heg *et al.*, 2006). This study examines the natural frequency of communal breeding, the composition of breeding groups, the duration of assistance provided by each adult, the fitness consequences, and the distribution of reproductive success among group members of a natural population of burying beetles. We evaluate the fitness consequences of reproductive decisions in the light of models of reproductive skew and postulate the degree to which the dominant breeders can control how reproduction is shared.

Natural history

Burying beetles (*Nicrophorus* spp.) use small vertebrate carcasses as a resource for breeding. Carcasses that are relatively small for a given species of beetle are buried and prepared by a single male and female, the winners of the intrasexual competition that occurs if more than one male or female discover the carcass (Pukowski, 1933). Relatively larger carcasses, however, are often buried and prepared by more than one male and/or female that rear a single brood and the propensity to do so varies with species (Eggert & Müller, 1992; Trumbo, 1992; Trumbo & Wilson, 1993; Scott, 1994). The fur or feathers are removed and the carcass is buried and rolled into a ball. *Nicrophorus tomentosus* Weber females lay eggs in the soil nearby 14–36 h after discovery of a carcass. These hatch 3–4 days later and larvae make their way to the carcass where they are fed by all adults remaining in the brood chamber. All adults present in the brood chamber also continue to preserve the carcass. Larval development is complete

6–8 days later and the carcass has generally been fully utilised. Thus in the present study, communal breeding refers to instances of more than one member of the same sex remaining long enough during carcass preparation to contribute genetically to the brood; they may or may not remain long enough to feed the larvae.

A carcass is a rich resource for many organisms, including bacteria, fungi, flies, and especially other burying beetles. Resident beetles consume fly eggs, continually clean microbes from the carcass and defend it from other congenics (Scott, 1990; Trumbo, 1991). Competition from other beetles and flies or the high probability of total nest failure have been proposed as the important selective force for communal breeding in different species (Trumbo & Wilson, 1993; Scott, 1994; Trumbo & Fiore, 1994; Trumbo, 1995; Eggert & Sakaluk, 2000). Groups of *N. tomentosus* are often better able to defend the carcass and to destroy fly eggs than pairs so that more young are reared or the brood has a higher probability of survival. However the dominant male and female, which in other circumstances would drive off others of the same sex, must share a limiting breeding resource. Several laboratory studies have estimated the proportion of offspring produced by each male and female in cooperative associations. These have used random amplified polymorphic DNA (RAPD) genetic markers (*N. tomentosus* Scott & Williams, 1993), phenotypic polymorphisms (*N. vespilloides* Eggert & Müller, 1992) and individually recognisable dyed eggs (*N. tomentosus*, *N. vespilloides* Scott, 1997; Eggert & Müller, 2000). These studies suggest that reproduction may be shared equitably by communal *N. tomentosus* females on large carcasses, skewed in favour of the male and female providing the longest care on medium carcasses, and not shared on small ones. In this species, reproductive skew is achieved primarily through differential ovicide and to a lesser extent by larger females that are more fecund (Scott, 1997).

Methods

The frequency of communal breeding and the duration of associations

Pots, 22 cm in diameter and 27 cm high, were filled with cores of forest soil and sunk into the ground so that they were level with the surface. A 40–45 g, previously frozen chick or mouse (medium carcass) or a 55–60 g previously frozen chick (large carcass) was placed on top of each. A domed, 50 × 50 cm piece of chicken wire with holes about five times the width of the beetles covered the pot to exclude vertebrate scavengers. Five pots were placed at 25 m intervals at the edge of each of two nearby hay fields in Jaffrey, New Hampshire. Ten new pots and carcasses were put out at roughly 1 week intervals during late August and early September. They were checked daily and when the carcass was completely buried, they were brought to a central place outside. Since females begin to oviposit 14–24 h after they discover a carcass, any beetles that would otherwise have arrived after pots were picked up would not have contributed to the brood nor would they have been allowed to join (Scott, 1994). Each pot was then placed inside a taller pot 30 cm in diameter that was covered with clear plexiglas. These pots were checked daily. Thus, when beetles left the brood chamber in the smaller pot,

they were captured in the larger pot and identified to species, sexed and measured (pronotal width). About a week after larval development was complete, the contents of the pot were examined; all larvae were found and weighed. All adults and larvae were frozen at -20°C until they could be transferred to a -80°C freezer.

Analysis of parentage

The DNA of larvae of 13 broods (10 reared on 40–45 g carcasses and three reared on 55–60 g ones) and all potential parents was analysed by obtaining genotypes for microsatellite loci (Queller *et al.*, 1993) in order to ascertain the parents of each of the larvae (Table 1, 58 adults and 268 larvae in total). These broods were chosen as representative examples of the range of group size and composition and duration of attendance (residence times). DNA was extracted from the flight muscles of adults and whole bodies of larvae, which had purged their guts after leaving the carcass. Samples were incubated overnight at 37°C in extraction buffer (10 mM Tris, pH 8.0; 2 mM EDTA, pH 8.0; 10 mM NaCl; 1% SDS; 8 mg ml⁻¹ DTT; 0.4 mg ml⁻¹ Proteinase K). DNA was extracted with phenol–chloroform and chloroform and precipitated with 0.1 M NaCl and 100% EtOH at -20°C for 2 h and resuspended in 50 μl TE.

A primary genomic library was constructed from 300–600 bp fragments of RsaI digested DNA (Pulido & Duyk, 1994). An enriched library was then constructed by primer extension of uracil-substituted single-stranded DNA (ssDNA) with a CA₁₀ primer. This secondary library was plated and screened with the same CA₁₀ oligonucleotide. Positive clones were sequenced and candidate microsatellite loci selected. Primers were designed using the Pipeline program (Whitehead Institute, Cambridge, MA, U.S.A.), synthesised (Operon, Alameda, CA, U.S.A.), and tested against a multi-individual panel of DNAs. Primers were tested for five loci (accession numbers: G31352, G31350, G31351, G31348, G31349 for NIC 1–NIC 5 respectively) of which two were invariant in *N. tomentosus*.

DNA was amplified with the polymerase chain reaction in 20 μl volume (Promega buffer, 2.5 mM MgCl₂, 0.2 mM each dNTP,

0.25 μM each primer, 1 U Taq DNA polymerase and 2 ng DNA template) at 95°C for 1 min, 50°C (NIC 3 and NIC 5) or 55°C (NIC 1) for 2 min and 72°C for 2 min for 24–28 cycles. PCR products were loaded on a 6% denaturing polyacrylamide gel in an ABI 373A sequencing system (Applied Biosystems, Foster City, CA, U.S.A.). Amplification products of all three loci for one individual were run in a single lane and could easily be distinguished by their different sizes and fluorescent labels. Fragment size information for each lane was recorded by ABI's GeneScan Collection software and later analysed using GeneScan Analysis software that identified fragment length through comparison with the size standard. Fragments within ± 0.25 bases were grouped as an allele.

The population frequencies of the alleles in 68 adults from the wild population of the three variable loci were examined. NIC 1 (226–237 bp) had 11 alleles ($H = 0.723$); NIC 3 (166–188 bp) had 15 alleles ($H = 0.89$); NIC 5 (276–292 bp) had five alleles ($H = 0.642$). Ambiguous DNA samples were amplified independently several times to reduce the probability of genotyping errors (Hoffman & Amos, 2005). No locus deviated from Hardy–Weinberg equilibrium (GenePop, <http://genepop.curtin.edu.au>).

Maternity or paternity of some larvae could not be determined either because two putative parents of the same sex had some of the same alleles and could not be distinguished or, with large assemblages, maternal and paternal alleles could not be distinguished. When a definite maternity (6.7% of larvae) or paternity (6.8% of larvae) assignment could not be made, the most likely candidate was identified based on the proportion of previously identified offspring of the uneliminated candidates and the proportion of alleles not shared by the other uneliminated candidates (i.e. the probability that its young could be identified). For example, if 4 of 16 larvae could not be definitely assigned to either of two possible fathers, if male 1 had already been assigned eight offspring and one allele at each of three loci was unique but male 2 had been assigned four offspring and had only one unique allele, $1 - 0.5^3$ of the probable offspring [i.e. $8/(1 - 0.5^3) = 9.1$ offspring] of male 1 could be identified but $1 - 0.5$ of those [i.e. $4/(1 - 0.5) = 8$] of male 2 could be identified. Unidentified offspring were assigned to males 1 and 2 in the proportion of $(9.1 - 8):(8 - 4)$ or, in this case, one to male 1 and three to male 2.

Table 1. Composition of adults, duration of their care (days), and number of larvae in broods analysed for parentage.

Brood	Carcass size (g)	No. of females [duration of care]	No. of males [duration of care]	No. of larvae [no. analysed if different]
A2	40–45	2 [3,5]	3 [1,1,1]	21
A22	40–45	2 [7,8]	1 [2]	31
A25	40–45	2 [1,7]	3 [1,1,1]	14
A27	40–45	2 [2,7]	1 [7]	12
A29	40–45	2 [2,7]	0	33 [31]
A30	40–45	1 [11]	2 [1,6]	25
B12	40–45	5 [1,1,3,4,9]	5 [1,2,2,3,9]	21 [20]
B13	40–45	2 [3,6]	1 [3]	16
B19	40–45	2 [1,8]	2 [1,3]	22
D10	40–45	4 [2,3,3,7]	4 [1,1,1,4]	28 [26]
B1	55–60	3 [2,2,2]	0	15
B24	55–60	3 [2,4,8]	2 [1,6]	16
C18	55–60	2 [3,11]	2 [1,5]	42 [19]

If an adult captured leaving the brood chamber had a genotype compatible with the genotype of a larva, it was assumed that it was a parent. However, a beetle not captured but with the same combination of alleles as the putative parent could be the true parent. Thus the mean probability of false inclusion was calculated from the population frequencies of each of the alleles shared by each larva and parent. The mean for each brood was calculated from the probabilities of false inclusion of each larva–parent pair. For most larva–parent pairs ($n = 268$), the probability of false inclusion was small; the mean probability for all the broods was $p = 0.013$, range 0.035–0.000.

Calculation of reproductive skew

The distribution of offspring in a brood among mothers or fathers were evaluated in two ways. An index of skew was calculated following Reeve and Ratnieks (1993), making no adjustments for parents not captured. The index ranges from 0 (equitable) to 1 (not shared) and the indices for our communally reared broods ranged from 0.01 to 0.87 (Table 2). Goodness-of-fit tests with Williams' corrections were also used to compare the actual number of offspring attributed to each (including those assigned by likelihood) to the number expected if parentage was shared equitably. Thus the null hypothesis was that resident males and females would be the parents of all the brood and in equal proportion. However, when some offspring were produced by adults not captured, the null hypothesis was adjusted. For these broods, the actual number of offspring of resident males and of males not cap-

tured was compared with the expected proportion of the brood if the males not captured produced 0.07 (the proportion of extra-group paternity) and the captured males share the rest equitably. When females not captured were the mother of some young, the null hypothesis was that these females produced 0.02 (the proportion of extra-group maternity) and the residents shared the remainder equally. If the probability from the goodness-of-fit tests was >0.05 , it was concluded that there was no significant skew of reproduction (Scott, 1997).

Factors contributing to reproductive success

The factors contributing to reproductive success were examined using multiple regressions. This allowed the effects of beetle size and residence time on reproductive success to be examined simultaneously. For reproductive success, the square-root transformed number of young assigned to each male or female present was used. This transformation made the count data more normally distributed (Zar, 1999). Because we were interested in the *relative* differences in body size among adults within each brood, we standardised pronotal width by mean deviation [(pronotal width – mean for that brood)/SD for that brood].

Results

The frequency of communal breeding in the field

Of 120 carcasses put out, some were lost to vertebrates in spite of the protective covering; some were never buried but

Table 2. Allocation of larvae by brood and two evaluations of the degree of reproductive skew.

Brood	Females						Males					
	Allocation of larvae		G_{adj}	d.f.	p	Skew index	Allocation of larvae		G_{adj}	d.f.	p	Skew index
Definite	All larvae	Definite					All larvae					
A2	9,12	9,12	0.42	1	0.51	0.038	2,3,3,10	2,3,5,11	5.36	3	0.16	0.061
A22	18,7	23,8	7.45	1	0.006	0.375	31	31				
A25	6,8	6,8	0.28	1	0.60	0.038	1,6,7	1,6,7	5.36	2	0.07	0.111
A27	5,7	5,7	0.32	1	0.57	0.010	4,8	4,8	7.32	1	0.007	0.207
A29	5,26	5,26	15.34	1	<0.001	0.632						
A30	25	25					1,6,18	1,6,18	6.41	2	0.04	0.232
B12	0,2,10,0,6	0,2,10,1,7	19.63	4	0.001	0.261	1,1,5,8,2	1,1,6,9,3	11.61	4	0.02	0.045
B13	4,5,7	4,5,7	13.70	2	0.001	0.021	7,9	7,9	16.93	1	<0.001	0.028
B19	6,16	6,16	4.61	1	0.03	0.349	9,11	10,12	0.18	1	0.67	0.020
D10	2,4,10,10	2,4,10,10	8.36	3	0.04	0.043	1,3,6,11	1,5,7,13	12.30	3	0.006	0.063
B1	2,0,5,5	2,2,5,6	6.35	3	0.10	0.034						
B24	2,3,5	4,7,5	0.83	2	0.66	0.121	1,15	1,15	14.25	1	<0.001	0.873
C18	6,10	7,12	1.30	1	0.25	0.127	3,0,14	3,0,16	23.32	2	<0.001	0.755

Allocation of larvae is given both as those definitely identified and all larvae including those assigned through likelihood. Larvae for which all captured males or females were eliminated are shown in bold. Larvae allocated to each parent are listed in ascending order of the duration of care by that parent. The degree of reproductive skew of maternity and paternity is evaluated with goodness-of-fit tests with Williams corrections and with the skew index from Reeve and Ratnieks (1993) which goes from 0 (equitable) to 1 (not shared). Goodness-of-fit tests were carried out grouping all larvae into sibships, including those assigned through likelihood and those assigned to adults not captured. $p < 0.05$ suggests that reproduction was not shared equitably.

utilised by flies and fed on by burying beetles; a few carcasses were buried by other *Nicrophorus* species (*N. defodiens* 18 and *N. orbicollis* 3) and most of these (76%) were abandoned, usually to flies and/or fungi. Only six carcasses (8%) were buried then abandoned by *N. tomentosus*. Burying beetles have no preference between bird and mammal carcasses (Kozol *et al.*, 1988) and there were no differences in frequency of communal breeding or reproductive success between mouse ($n = 8$) and chick ($n = 28$) 40–45 g carcasses. Therefore these data were pooled for analysis. *Nicrophorus tomentosus* reared broods on 36 40–45 g carcasses and 32 55–60 g ones. Forty to forty-five gram carcasses were buried after 2.0 ± 0.1 days (mean \pm SE) and 55–60 g ones were buried after 3.3 ± 0.4 days. There was no correlation between the total number of adult beetles and the number of days before 40–45 or 55–60 g carcasses were buried after they were put out ($n = 36$, $r = -0.21$, $p = 0.22$ and $n = 32$, $r = -0.19$, $p = 0.29$ respectively). The presence of additional beetles does not reduce burial time in other *Nicrophorus* species (Scott, 1990) and, more surprisingly, the arrival of more beetles does not cause beetles to begin burial sooner.

More than one male and/or female helped to bury and prepare the carcass and were still present when the pot was collected from the field for 18 (50%) of the broods reared on 40–45 g carcasses and 24 (75%) of those reared on 55–60 g carcasses (see fig. 3, Scott, 1996). There were (means \pm SE) 1.6 ± 0.2 females (range 1–5) and 1.4 ± 0.2 males (range 0–5) on 40–45 g carcasses and 2.8 ± 0.3 females (range 1–7) and 1.4 ± 0.2 males (range 0–4) on 55–60 g carcasses. Thus there was a significant increase in the probability that females, but not males, would breed communally on a 55–60 g carcass than on a 40–45 g one (Fisher's Exact tests, females: $n = 67$ broods, $p = 0.006$; males: $n = 51$ broods, $p = 0.78$). There was a strong positive correlation between the number of females and the number of males burying both 40–45 and 55–60 g carcasses ($n = 36$, $r = 0.71$, $p < 0.001$ and $n = 32$, $r = 0.50$, $p = 0.004$ respectively). Beetles were not distributed on the carcasses in random group sizes: the total number of beetles burying a carcass did not fit a Poisson distribution on either 40–45 g ($G_{\text{adj}} = 25.44$, d.f. = 8, $p = 0.001$) or 55–60 g ($G_{\text{adj}} = 16.03$, d.f. = 8, $p = 0.04$) carcasses, with more carcasses than expected buried by fewer than three or more than nine beetles. However, this effect is primarily due to the non-random distribution of females on 40–45 g carcasses ($G_{\text{adj}} = 12.09$, d.f. = 4, $p = 0.01$). This suggests that on 40–45 g carcasses females were able to prevent other females from joining up to a point and then they lost control.

Duration of communal associations

Although a few same-sex associations lasted until larvae were fairly mature, most (70% of female associations and 84% of male associations) ended before larvae arrived on the carcass. At natural environmental temperatures, eggs were expected to hatch on about the fourth day after burial on 40–45 g carcasses. They hatch on the fifth day on 55–60 g carcasses because these take longer to bury and prepare, and oviposition is delayed (Scott & Panaitof, 2004). Therefore we predicted that communal associations might be more likely to continue longer on 55–60 g

carcasses than on 40–45 g ones but this was not the case. The penultimate female to leave remained 2.7 ± 0.5 days ($n = 13$) (complete burial = day 0) on 40–45 g carcasses and 3.1 ± 0.3 days ($n = 24$) on 55–60 g ones (t -test assuming unequal variance, $t = 0.77$, d.f. = 23, $p = 0.22$, one-tailed) and the penultimate male to leave remained 1.6 ± 0.4 days ($n = 12$) on 40–45 g carcasses and 2.5 ± 0.7 days ($n = 13$) on 55–60 g ones ($t = 1.21$, d.f. = 18, $p = 0.12$). However female associations lasted longer than those among males on 40–45 g carcasses ($t = 1.91$, d.f. = 22, $p = 0.03$, one-tailed) but not on 55–60 g ones ($t = 0.76$, d.f. = 17, $p = 0.23$). Relatively few adults were still present in the brood chamber on the fourth day to participate in parental care (Fig. 1). The most common condition at that time was one female and no males on both 40–45 g carcasses (47%) and on 55–60 g carcasses (31%).

The mean duration of attendance (residence time) from the time of burial to departure by the females remaining longest on 40–45 g ($n = 35$) and 55–60 g ($n = 32$) carcasses was 8.3 ± 0.8 and 8.1 ± 0.6 days respectively ($t = 0.21$, d.f. = 61, $p = 0.41$). The mean residence time by the males remaining longest on 40–45 g ($n = 26$) and 55–60 g ($n = 25$) carcasses was 4.8 ± 0.6 and 5.7 ± 0.9 days respectively ($t = 0.85$, d.f. = 41, $p = 0.20$).

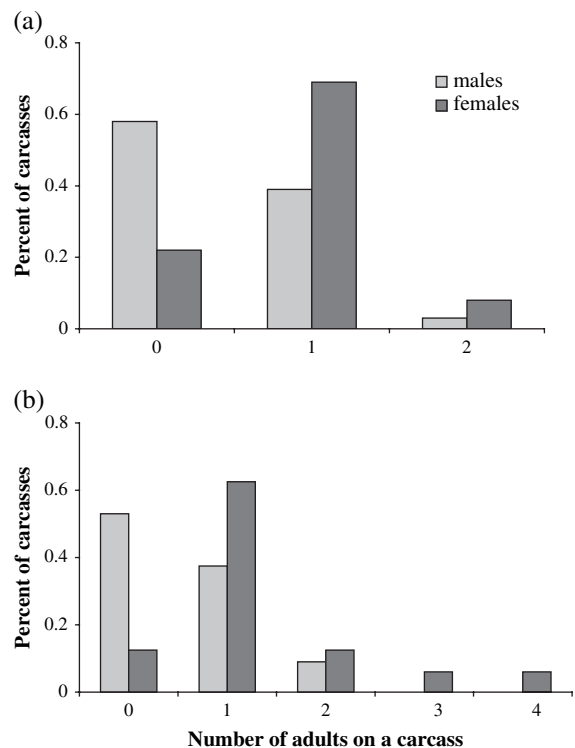


Fig. 1. The number of male (light) and female (dark) *Nicrophorus tomentosus* that were present at least 4 days after burial of (a) 40–45 g ($n = 36$) and (b) 55–60 g carcasses ($n = 32$). All adults were captured when they left the brood chamber. Larvae hatch and arrive on the carcass on the fourth day after burial on 40–45 g carcasses and on the fifth day on 55–60 g carcasses, therefore adults remaining longer than 4 or 5 days respectively were present to participate in parental care.

Single females remained significantly longer than the longest-remaining female in a group on 55–60 g carcasses (11.6 ± 0.7 vs 6.9 ± 0.6 days, $t = 4.81$, d.f. = 19, $p = 0.000$) but not on 40–45 g ones (9.1 ± 1.2 vs 7.1 ± 0.6 days, $t = 1.42$, d.f. = 28, $p = 0.08$, one-tailed). Single males also remained longer than the longest-remaining male in a group on 40–45 g carcasses: (5.8 ± 0.9 days vs 3.6 ± 0.7 days respectively, $t = 1.95$, d.f. = 23, $p = 0.03$) but not on 55–60 g carcasses (5.7 ± 1.6 vs 6.1 ± 1.1 days, $t = 0.21$, d.f. = 20, $p = 0.41$).

Consequences of communal breeding

Multiple females did not rear significantly more young than single females on either 40–45 g (20.2 ± 2.3 vs 23.4 ± 2.7 , $t = 0.90$, d.f. = 19, $p = 0.19$ one-tailed) or 55–60 g (26.3 ± 4.3 vs 21.2 ± 3.8 , $t = 0.89$, d.f. = 19, $p = 0.19$) carcasses. Nor was there a significant correlation between number of adults present and number of larvae reared on either 40–45 or 55–60 g carcasses ($r = -0.06$, $n = 36$, $p = 0.73$ and $r = 0.03$, $n = 32$, $p = 0.87$ respectively). The mean number of larvae reared on 40–45 and 55–60 g carcasses was 22.1 ± 1.8 and 25.2 ± 3.5 respectively ($t = 0.80$, d.f. = 40, $p = 0.21$). Although total failure to rear brood was rare and not more likely on 55–60 g than 40–45 g carcasses (one-tailed Fisher's Exact test $p = 0.42$), the variance in the number of young reared was very large, especially on 55–60 g carcasses. Three of the six cases of total failure may have been due to excessive numbers of beetles in the brood chamber (11–18 males and females) consuming the resource, causing social disruption and reducing the reproductive payoff for any one individual.

Analysis of parentage

Estimates of within-sex, within-group relatedness were made using Relatedness 4.2 (Goodnight and Queller). Neither cooperating males nor females appeared to be related in most groups ($r \leq 0.15$). However, $r = 0.35 \pm 0.38$ (estimate of standard error through a Jackknife procedure) was calculated for one group of females (A22) and $r = 0.53 \pm 0.47$ for one group of males (A30) both of which showed significantly skewed reproduction. (Skew theory predicts more skew with higher relatedness.) However we do not believe that these adults were in fact close relatives for several reasons. First, the standard errors were high. Second, these values for r could be achieved by chance as suggested by $r = 0.56$ for the relatedness of females to males in one group (A27). Third, the population is large (200 beetles can be captured at a single site in 2–3 days) and vagile (the recapture rate of marked individuals was only 0–4% depending on the time interval, M. P. Scott, unpublished data) and there is no reason to believe that relatives could maintain proximity with each other through the season.

Parentage analysis confirmed that the adults captured leaving the brood chamber were the parents of most of the larvae (Table 2). However some males and females that were not captured did produce some offspring. One of the females captured from the brood chambers was identified as the mother of 91.1% of

the larvae and all females captured for were excluded another 2.2% of larvae ($n = 268$). These apparent cases of parasitism occurred in two broods and in both cases the young could be attributed to a single additional female that had oviposited and departed immediately. It was more common to exclude all captured males as the fathers of some young (7.6%, $n = 222$). Sperm from previous matings could be used or a male could leave or be driven off soon after mating. At least one additional male fathered young in four of nine broods reared on 40–45 g carcasses and one of two broods reared on 55–60 g carcasses with one or more males present (Table 2). At least two additional males fathered young in brood A27 and a minimum of three additional males fathered young in B13. Not all of these males were necessarily at the carcasses as all females are inseminated within a week or two after they emerge (M. P. Scott, unpublished data). Likelihood was used to assign maternity ($n = 18$) and paternity ($n = 15$) of unassigned larvae (Table 2).

Reproductive skew

Maternity was shared equitably in only three of the nine broods reared by multiple females on 40–45 g carcasses but in all three of those reared on 55–60 g carcasses (one-tailed Fisher's Exact test, $p = 0.09$). Paternity was shared equitably in only 3 of 10 broods with multiple male parents (Table 2).

Factors contributing to reproductive success

Results from the multiple regression analyses with transformed number of larvae as the dependent variable indicate that there was a significant interaction between relative size and residence time (females: $n = 31$, multiple $R^2 = 0.52$, interaction $p = 0.017$; males: $n = 23$, multiple $R^2 = 0.36$, interaction $p = 0.048$). Thus reproductive success can be predicted from residence time (independent effects were stronger) but it depends on relative size as well. However from the beetles' perspective, this can be interpreted in the following way – relative size is a strong factor in reproductive dominance and dominant males or females remain longer with the brood.

If reproductively dominant females oviposited earlier than others, causing their young to hatch earlier or if they differentially fed larvae, their young would be larger at the end of development than young of other females. Analysis of young definitely assigned to each female (excluding those assigned by likelihood) suggested that this rarely was the case (Table 3). Only the young of the larger, longer-remaining, reproductively dominant female of brood C18 reared on a 55–60 g carcass were significantly heavier than young of the other female and the directions of trends in the other broods were very mixed. Since most males mated with all or many resident females and departed before larval care began, we did not expect, and did not see, any differences in mass of larvae with different paternity.

The female remaining the longest for each brood may relinquish reproduction in exchange for assistance from other females. There was a significant negative relationship between the

Table 3. Mass (g) of larvae definitely assigned to communally breeding males and females (mean \pm SE). Statistical tests are Kruskal–Wallis tests. Females and males are listed in the same order as shown on Table 2 and sample sizes are shown therein. Missing values indicate that parentage was not shared in that brood.

Brood	Females		Males	
A2	0.19 \pm 0.02	$H_1 = 3.1566, p = 0.08^*$	0.14 \pm 0.01	$H_2 = 2.6749, p = 0.44$
	0.16 \pm 0.01		0.16 \pm 0.02	
A22	0.17 \pm 0.01	$H_1 = 1.7729, p = 0.18^\dagger$	0.18 \pm 0.02	
A25	0.20 \pm 0.01		0.15	
A27	0.17 \pm 0.01	$H_1 = 0.4167, p = 0.52$	0.18 \pm 0.01	$H_2 = 2.0735, p = 0.35$
	0.20 \pm 0.00		0.18 \pm 0.00	
A29	0.10 \pm 0.10	$H_1 = 2.6466, p = 0.10^\dagger$		
A30	0.12 \pm 0.01			
B12	0.11 \pm 0.02	$H_1 = 0.0462, p = 0.83$	0.19 \pm 0.01	$H_1 = 2.7395, p = 0.25$
			0.16 \pm 0.01	
B13	0.13 \pm 0.02	$H_2 = 3.8145, p = 0.15^\ddagger$	0.16	
	0.19 \pm 0.01		0.14	
B19	0.16 \pm 0.01	$H_3 = 1.9419, p = 0.58$	0.20 \pm 0.02	$H_4 = 3.1686, p = 0.53$
			0.16 \pm 0.01	
D10	0.13 \pm 0.01	$H_1 = 0.9700, p = 0.62$	0.15 \pm 0.01	$H_1 = 0.5209, p = 0.47$
	0.13 \pm 0.00		0.12 \pm 0.01	
B1	0.12 \pm 0.01	$H_2 = 0.1692, p = 0.92$	0.12 \pm 0.01	$H_3 = 2.2420, p = 0.52$
	0.12 \pm 0.01		0.14	
B24	0.14 \pm 0.04	$H_3 = 1.9419, p = 0.58$	0.17 \pm 0.01	
	0.17 \pm 0.01		0.15 \pm 0.01	
C18	0.15 \pm 0.01	$H_2 = 1.0909, p = 0.58$	0.16 \pm 0.01	$H_1 = 1.0159, p = 0.92$
	0.16 \pm 0.01		0.15 \pm 0.00	
	0.21 \pm 0.02	$H_1 = 3.8118, p = 0.05^\dagger$		

*Larvae of the smaller, earlier-departing female were heavier.

†Larvae of the larger, longer-remaining female were heavier.

‡Larvae of the reproductively dominant female were heavier. She was the largest but not the longest-remaining female.

proportion of the brood parented by the female remaining the longest and the total days of assistance she received from other females (Fig. 2, $n = 12$, $r = -0.77$, $p = 0.003$). There was also a significant negative relationship between the proportion of the brood parented by the male remaining the longest and the total days other males were present (Fig. 2, $n = 8$, $r = -0.81$, $p = 0.01$). This negative relationship may be caused by females and males relinquishing reproduction to gain the assistance from conspecifics or be caused by secondary individuals with more young remaining longer with the brood. There was a significant positive relationship between the proportion of the brood parented by all females leaving before the last female and her residence time ($r = 0.52$, $n = 20$, $p = 0.01$) but no such relationship for males ($r = 0.35$, $n = 15$, $p = 0.20$).

Discussion

Communal breeding

Some of the costs and benefits to communal breeding may be different for burying beetles than for other communal breeders like birds, mammals, and wasps. The carcass is a fixed resource and, except for quite large carcasses, is usually fully consumed. Thus more helpers do not supply more food to the young. Nor do more helpers beyond a pair improve the survival of the brood (Scott, 1994). Nevertheless, female and male *N. tomentosus* engage in a high frequency of communal breeding on medium and large carcasses in nature. Females, but not males, are significantly more likely to cooperate to bury and prepare larger carcasses than smaller ones. However, in the field, most

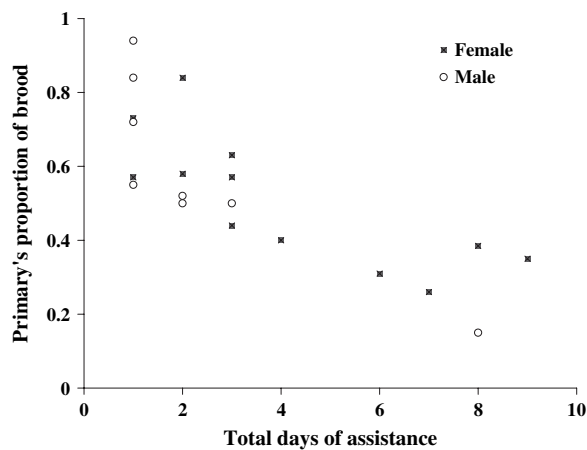


Fig. 2. The relationship of the proportion of the brood of the female (or male) remaining the longest and the total days of assistance she received from all other females (or males). For each brood, the number of days each consensual remained are summed but since larvae were only present after 4 or 5 days, on 40–45 g carcasses and 55–60 g carcasses respectively, they were not necessarily there to provide parental care. Females $n = 12$, $r = -0.77$, $p = 0.003$; males $n = 8$, $r = -0.82$, $p = 0.01$. Data were arcsin-transformed for analysis, back-transformed data are plotted.

same-sex associations end before larvae hatch. The propensity of females to breed communally on large carcasses supports the predictions of the game-theoretical model of Robertson *et al.* (1998) that for all conditions (e.g. different degrees of benefit to cooperation, size differences between females, probability of finding a new carcass, and opportunity for brood parasitism), reproductive tolerance between unrelated females is more likely on large resources. Females provide longer care than males and their cooperative associations last longer. A willingness to form cooperative associations, especially on large carcasses, has been demonstrated in the field for other populations of burying beetles (*N. orbicollis* and *N. defodiens* in Michigan, Trumbo, 1992, *N. defodiens* in Canada, Eggert & Sakaluk, 2000) and in laboratory studies of *N. tomentosus* (Michigan, Trumbo & Wilson, 1993; New Hampshire, Scott, 1994, 1997) and of *N. vespilloides* in Germany (Müller *et al.*, 1990; Eggert & Müller, 1992, 2000).

Although some cooperative associations lasted well into the parental-care stage, many were short lived. This raises the question of whether individuals that do not provide care to young should be considered to be brood parasites (Müller *et al.*, 1990). Preparation of the carcass is parental investment if not parental care. Females must assist in carcass preparation for vitellogenesis and oviposition to occur (Scott & Traniello, 1987; Trumbo *et al.*, 1995) and therefore demonstrate some cooperation. Females that leave after only a few days have an increased incidence of injury and appear to have been driven off rather than to have deserted (Trumbo & Wilson, 1993). On the other hand, males that leave after 1 or 2 days may not have contributed to carcass preparation. However, it is likely that they were in the brood chamber to interact with females and a carcass is a powerful stimulus for beetles to contribute to its preparation. Beetles leaving after 5 or 6 days had certainly been in the brood chamber to provide parental care. They leave covered with phoretic mites that reproduce on the carcass and disperse on departing adults (Brown & Wilson, 1992).

There was a strong relationship between reproductive dominance and residence time that was especially clear in smaller than larger assemblages. Residence time was also positively associated with reproductive dominance for males. The close relationship of reproductive success and residence time is also demonstrated by the fact that single females, which have confidence of maternity, provided longer care than the longest remaining female of a group. Single females do not require longer to prepare the carcass and oviposit almost as quickly as the reproductive dominant of a pair (Scott, 1997). Single males, on the other hand, have somewhat lower confidence of parentage than single females and in this study did not provide longer care than the longest remaining male of a group. A previous laboratory study (Scott & Williams, 1993) revealed a positive correlation between parentage and duration of stay of the subordinate male and female in groups of four. Thus even subordinates may gage their relative reproductive success and depart accordingly.

Reproductive skew

Dominant female and male *N. tomentosus* do exclude consensuals on small carcasses (Scott & Traniello, 1990) and presumably, although it may be more difficult, are able to do so as well on larger carcasses. However, there is a trade-off between the costs of sharing a large carcass and benefits of cooperation; and reproduction is not necessarily shared equitably. It is often significantly skewed in favour of the longest remaining female on 40–45 g carcasses but shared more equitably on 55–60 g ones. A comparison of skew on 40–45 and 55–60 g carcasses allows us to examine the models in light of their predictions when conditions change. Although some of the factors, like relatedness or the effects of body size, are the same on medium and large carcasses, others, like productivity and perhaps the degree of ecological constraint, differ.

Transactional models of reproductive skew that assume control by dominants (Vehrencamp, 1983a, b; Reeve & Ratnieks, 1993) indicate that we should expect groups of unrelated individuals to share reproduction more equitably than groups of relatives. The fact that burying beetles are not related and breed communally sharing reproduction supports these models. Studies of cooperatively breeding birds and mammals have shown that when subordinates are related to the dominant, as with most helpers-at-the-nest, they do not generally produce offspring (Reeve *et al.*, 1990; Jones *et al.*, 1991; Haig *et al.*, 1994; but see Rabenold *et al.*, 1990). As the indirect benefits decrease, subordinates are more likely to produce offspring on their own (Burke *et al.*, 1989; Creel & Waser, 1991; Jamieson *et al.*, 1994; Jennions & Macdonald, 1994; McRae, 1996). The effect of relatedness on reproductive skew by social insects is mixed. Many studies support the prediction of the transactional models that reproduction will be skewed when queens are closely related (reviewed in Reeve *et al.*, 1998, 2000). However other studies (Bourke & Heinze, 1994; Evans, 1996, 1998; Bernasconi *et al.*, 1997; Field *et al.*, 1998; Bernasconi & Strassmann, 1999; reviewed in Nonacs *et al.*, 2006) have found that relatedness either has no association with skew or has a negative one. These findings may support

models of limited control by the dominants (Reeve *et al.*, 1998) or may just reflect the high rate of queen turnover in many wasps and some ants (Peters *et al.*, 1995; Evans, 1998; Field *et al.*, 1998).

Skew theory also predicts that few opportunities for independent breeding will allow the dominant to monopolise reproduction to a greater extent. We do not know the probability of finding a carcass but presume it to be very low (Scott & Gladstein, 1993) and when one is found individuals should always try to breed. The fact that reproduction was often skewed, in spite of limited opportunities for the subordinate, suggests that other factors may come into play, such as the limited ability of dominant females to reduce oviposition of other females or, in the case of males, to prevent access to females.

A third prediction made by skew theory is that an increase in the disparity of fighting ability (e.g. larger difference in size) should increase control by the dominant and increase reproductive skew. Relative size has been a good predictor of the outcome of intrasexual competition in burying beetles: larger beetles exclude smaller ones on a carcass (Pukowski, 1933; Wilson & Fudge, 1984; Bartlett & Ashworth, 1988; Otronen, 1988; Scott, 1990) and, in laboratory studies, become dominant in communal associations (Müller *et al.*, 1990; Eggert & Müller, 1992; Scott & Williams, 1993; Trumbo & Wilson, 1993; Scott, 1997). However, a previous laboratory study found that the degree of reproductive skew was not affected by the difference in their size (Scott, 1997). Results of this field study do suggest that relative size does contribute to reproductive dominance. Studies of skew in paper wasp cofoundresses also found no relationship between size ratio (Field *et al.*, 1998; Reeve *et al.*, 2000).

The most interesting application of skew theory to communal breeding by burying beetles concerns the predicted effects of the increase in reproductive productivity by groups. When the dominant controls how reproduction is shared, greater productivity promotes higher skew (Reeve & Ratnieks, 1993) but when the subordinate has a choice of other groups to join or other means to exert control over the division of reproduction, an increase in group productivity should increase equality (Reeve, 1998). Many studies on burying beetles have shown that groups of females have greater productivity than single females on large carcasses (although the reproductive success *per capita* is less) whereas, on medium carcasses, there is little increase in productivity of a group over that of a single female (Eggert & Müller, 1992; Trumbo & Wilson, 1993; Scott, 1994; Trumbo & Eggert, 1994; Trumbo & Fiore, 1994) and on small carcasses a group may be even less productive than a single female (Scott, 1989). Reproduction tends to be shared equitably by females on large carcasses but not on medium ones. This suggests that the dominant female must yield a greater share of the reproductive output and some version of the *bidding game* (Reeve, 1998) is going on. In fact, on both medium and large carcasses, the additional young reared by two females is almost exactly offset by the subordinate female's share (Scott, 1997). Thus it is the dominant, not the subordinate, that is at the break-even point in this evolutionary strategy. This situation may result because the dominant female cannot fully utilise a large carcass herself (Trumbo, 1992; Scott, 1994). A limit to the maximum size of the broods of individual females is one of the factors predicted

to promote reproductive tolerance on large carcasses but not on smaller ones (Robertson *et al.*, 1998).

Contrary to our expectations, in this study multiple females did not rear more young than single females on either medium or large carcasses (Trumbo, 1994). We also expected that large carcasses would yield more young, especially when buried by more than one female. In fact in this field study there was very large variation in reproductive success on large carcasses. The delay in burial in the field compared with immediate burial in the laboratory may have increased the number of social interactions. The frequency of female group size does not follow a Poisson distribution, although males appear to be randomly distributed, and the number of males and females is highly positively correlated. Females, especially, tend either to exclude all conspecifics or allow them somewhat indiscriminately, which can result in fairly large groups burying a carcass.

The increase of reproductive productivity on large carcasses does not affect males as it does females. Males are no more likely to share reproduction equitably on large than medium carcasses. Whereas a female loses less by sharing a large carcass than a medium one because she cannot fully utilise the former, a male can inseminate all the females on any size carcass.

Females, and perhaps males as well, appear to be relinquishing some reproduction in exchange for assistance from conspecifics. The negative relationship between their proportion of the brood and the days of assistance demonstrates this trade-off. Secondary females that produce more young remain longer. This coupled with the data that female associations are longer, and the reproduction more equitably shared on large carcasses, are highly suggestive of a *bidding game* (Reeve, 1998) whereby a subordinate female is able to gain a large share of the additional young that her assistance produces.

The advantage of joining a cooperative association for a subordinate male or female is clear in this study. Beetles probably have few opportunities to breed in their 4–6 week reproductive lifespans (Scott & Gladstein, 1993) and they benefit from joining even if they rear only a few offspring. All beetles that produced less than 10% of the young made relatively little investment in time. Only one, possibly two, females and one male captured presumably leaving the brood chamber failed to produce some offspring and many subordinates gained quite a high share of the young.

Thus, although there was considerable variation in this field study, communal associations of burying beetles are good models for examining the assumptions of skew theory. Dominant individuals relinquish some reproduction, especially on large carcasses and subordinate females appear to have some control over the division of reproduction in spite of limited opportunities to breed.

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