

Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*

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Alternative reproductive tactics can be maintained through different evolutionary avenues. They can be genetically or stochastically determined, in which case they must yield equal fitness, or their use can be conditional, in which case the fitness payoff of alternatives may differ. We attempted to assess the reproductive success of alternative reproductive tactics employed by wild male and female burying beetles in natural associations on carcasses placed in the field. A beetle's reproductive tactic was defined by its potential involvement in care of larvae, and parentage was assessed using oligolocus DNA fingerprinting of offspring and potential parents. Both in males and in females, alternative tactics yielded significantly different reproductive benefits: subordinate females (brood parasites) and males (satellite males) had considerably lower reproductive success than dominant or uncontested individuals. Joint breeding was too infrequent for statistical inferences, generating intermediate offspring numbers. About 15% of offspring were sired by males not present on the carcass, suggesting that mating away from reproductive resources can produce reproductive benefits to males. Our results, in concert with the observation that beetles using one tactic can be manipulated into employing the alternative, support the notion that *Nicrophorus vespilloides* uses alternatives conditionally, opportunistically employing lower-benefit tactics when more profitable tactics are not available, or as additional "on-the-side" tactics to bolster reproductive success. *Key words:* alternative tactics, brood parasitism, burying beetles, communal breeding, DNA fingerprinting, *Nicrophorus*, parentage, satellite males. [*Behav Ecol* 18:196–203 (2007)]

The evolutionary maintenance of alternative reproductive behaviors has been a challenge to the optimality-centered field of behavioral ecology (Hamilton 1979; Thornhill and Alcock 1983; Austad 1984; Gross 1985, 1996; Eberhard and Gutiérrez 1991; Andersson 1994; symposium edited by Austad and Howard 1984). Game theory emphasized frequency-dependent selection as an explanation of such behavioral variation. The confusion caused by deviating definitions of "strategy" in game theory and behavioral ecology in general (Austad and Howard 1984) led Dominey (1984) and, more than a decade later, Gross (1996) to publish some explicit definitions of terms, defining strategy as a genotypically based sets of rules stipulating which alternative behavior will be adopted, and tactics as simple behavioral phenotypes. Alternative tactics are alternative strategies if the respective individuals are genetically polymorphic. If they are genetically monomorphic, there is only a single strategy. A strategy is referred to as "mixed" if it specifies a probabilistic (stochastic) use of tactics and as "conditional" if it specifies use of tactics based on environmental or physiological conditions (Dominey 1984; Gross 1996). In some systems, genetically different strategies seem likely (Zimmerer and Kallman 1989; Shuster and Wade 1991; Ryan et al. 1992; Lank et al. 1995; Sinervo and Lively 1996), but the majority of alternative reproductive behaviors are employed conditionally (Andersson 1994; Gross 1996).

In order to distinguish between the various possible modes of maintenance, information on the reproductive benefits of tactics

is required: alternative or mixed strategies require equal average fitness, whereas tactics within a conditional strategy may differ in their average fitness. Most studies of the success of alternative tactics to date have used surrogate measures of reproductive success, such as number or length of copulations (e.g., Alcock 1996; Lanctot et al. 1998; Sauer et al. 1998; Denoel et al. 2001; Lidgard et al. 2001). Compared with the extensive use of DNA markers to determine parentage in the field in many birds, mammals, and fish (Avice 1994; Hughes 1998; Richardson et al. 2001; Avice et al. 2002), genetic data on the success of alternative tactics are still relatively rare (fish: Fu et al. 2001; Garant et al. 2003; lizards: Zamudio and Sinervo 2000; shrews: Stockley et al. 1994; bats: Heckel and von Helversen 2002; pinnipeds: Lidgard et al. 2004). In insects, molecular parentage analysis is largely restricted to social hymenoptera (e.g., Bourke et al. 1997; Queller et al. 2000; Seppä et al. 2002; Brown et al. 2003; Paxton et al. 2003) although some other orders have been studied (Saccheri and Bruford 1993; Simmons and Achmann 2000; Bonizzoni et al. 2002; Liewlaksaneeyanawin et al. 2003). A laboratory study with laboratory-reared dung beetles used DNA fingerprinting to study the reproductive success of alternative phenotypes (Simmons et al. 2004), but in the field, the fitness benefits of alternative tactics in insects have not previously been assessed with molecular markers. The present study provides such an assessment in a biparental insect with male and female alternative tactics, the burying beetle *Nicrophorus vespilloides* Herbst (Coleoptera: Silphidae).

Burying beetle reproduction

In all *Nicrophorus* species studied to date, both sexes are capable of providing parental care (Eggert and Müller 1997; Scott

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Received 17 October 2005; revised 19 September 2006; accepted 22 September 2006.

1998). Adult beetles inter small vertebrate carcasses as the sole food source for their larvae and prepare the buried carcass for the young larvae by removing its fur or feathers, shaping it into a ball, and then keeping the carrion ball moist as well as removing fungi from it (Pukowski 1933). During the burial process and the subsequent oviposition period, resident males and females mate frequently (Müller and Eggert 1989). Ovarian development is completed only after a carcass has been detected (Wilson and Knollenberg 1984; Scott and Traniello 1987; Trumbo et al. 1995), and monogamous *N. vespilloides* females begin to oviposit about 12 h after carcass detection (Eggert and Müller 2000). Oviposition continues for a day or 2, and once the larvae have begun to hatch and crawl to the carcass, the adults chew an opening at the top of the carrion ball and feed regurgitated carrion to the larvae crowding in this opening. As they grow, the larvae increasingly feed on the carcass by themselves, hollowing out the carrion ball from the inside. Parental beetles with larvae attack burying beetles that might enter the crypt, as well as any predatory insects like rove beetles, in an apparent attempt to defend the carcass and their larvae (Pukowski 1933). Females can perform all these tasks by themselves, staying with the brood until larvae disperse. If a male is present, he contributes to parental care, leaving a few days prior to the female's departure (Bartlett 1988; Scott and Traniello 1990).

When several same-sex conspecifics are present on an unburied carcass, they engage in fights (Pukowski 1933; Otronen 1988), and after only a few fights, subordinates begin to act more furtively, lurking in the soil off the carcass for long periods of time (Dressel 1987; Bartlett 1988; Bartlett and Ashworth 1988; Dressel and Müller 1988; Müller et al. 1990). Their attempts to access the carcass are usually curtailed by the dominant's attacks. Subordinates leave the carcass before larvae hatch and do not participate in the feeding and defense of young (parental care in the narrow sense, Clutton-Brock 1991). Based on this differential participation in parental care, Müller et al. (1990) labeled subordinate females "intra-specific brood parasites"; subordinate males have been described as "satellite" males (Dressel and Müller 1988; Eggert and Müller 1997).

Especially when carcasses are relatively large for the species in question, same-sex conspecifics may act less aggressively. Two females may be present near the carcass until well after the larvae have hatched. Joint parental care has been demonstrated for a number of species (Eggert and Müller 1992; Scott and Williams 1993; Trumbo and Wilson 1993). Associations of multiple adults that extend into the larval period have been referred to as communal breeding (Trumbo 1992), cooperative breeding (Trumbo and Wilson 1993), joint breeding (Eggert and Müller 1992), or cobreeding (Eggert and Müller 2000). The phenomenon appears to occur in both sexes (Trumbo 1992; Scott and Williams 1993; Scott 1994). Trumbo (1992) reported finding 12 broods in which several same-sex *Nicrophorus orbicollis* cared for larvae in the field, and this sample, although not differentiated by sex in the publication, included 6 groups of males (Trumbo ST, personal communication).

Males can also sire young by inseminating females away from reproductive resources. Such encounters may occur on feeding carcasses or be mediated by male pheromones (Müller and Eggert 1987; Eggert and Müller 1989a, 1989b; Eggert 1992). Sperm in the female's spermatheca can remain viable for weeks (Eggert 1992) and can fertilize eggs if she detects a suitable carcass.

Alternative tactics and reproductive success

The reproductive success of dominant and subordinate males and females in brood-parasitic (Müller et al. 1990; Scott and

Williams 1993), satellite-male (Bartlett 1988; Müller et al. 1991; Eggert 1992), or joint-breeding (Eggert and Müller 1992, 2000; Scott and Williams 1993) associations has been assessed in the laboratory. Generally, individuals providing longer care were found to produce more offspring in the majority of the above studies. However, the sterilized-male method (Bartlett 1988) did not allow for an exact determination of parentage, the study using randomly amplified polymorphic DNA (Scott and Williams 1993) had a total sample size of 10, pooling brood-parasitic and joint-breeding associations, and the remaining studies (Müller et al. 1990, 1991; Eggert 1992; Eggert and Müller 1992; Trumbo and Wilson 1993) relied on the use of inbred color strains, which might have deviated in some aspect of their biology from members of naturally occurring populations. None of these studies investigated naturally occurring associations, relying instead on beetles that were selected and placed on the carcass by the experimenter. None of the numerous published field studies (Wilson and Fudge 1984; Müller et al. 1990; Scott and Traniello 1990; Eggert 1992; Trumbo 1992; Hoferer et al. 1996) provides data on individual reproductive success.

Here we report the results of a study that assessed the benefits of alternative tactics by establishing the parentage of broods produced in natural breeding associations of burying beetles (*N. vespilloides*) in a southern German population. Tactics used by candidate parents were identified based on the duration of their stay on the carcass under standardized conditions, and paternity and maternity were assigned after oligonucleotide fingerprinting (Benken et al. 1998).

METHODS

We studied the locally abundant *N. vespilloides* Herbst in a deciduous forest ("Mooswald") in southern Germany near the city of Freiburg (48°00'N 07°51'E). We did not include other species in our study, because *N. vespilloides* is by far the most abundant species of *Nicrophorus* at our study site: catch-and-release pitfall trapping in an area adjacent to our study site in 1999 and 2000 yielded 10 869 *Nicrophorus* specimens and 10 198 (93.6%) of these were *N. vespilloides*. To avoid the potentially confounding effects of variation in carcass size, we used carcasses of a single mass (25 g). A total of 52 previously frozen carcasses of laboratory mice (*Mus musculus*) weighing between 24.9 and 25.4 g were placed on the forest floor during the summer of 1999 (June 16 through September 26). For each carcass, a large plastic tube (inner diameter 15 cm, length 25 cm) was sunk into the ground vertically such that its upper rim was 5 cm above the surrounding area. The tube and its associated soil core were then pulled out, and sufficient material removed from the hole thus created to allow placing the tube back inside the hole such that its rim was flush with the surrounding forest floor, but so that the level of the material inside was about 5 cm lower. A freshly thawed carcass was placed inside the arena-like area at the top of the tube between 09:00 AM and 11:00 AM Central European Summer Time, a time of day during which *N. vespilloides* are not active in the field (Müller and Eggert 1987). Scavenging vertebrates were excluded by covering the entire setup with sturdy coarse hardware cloth (mesh size 1 cm). The site was revisited daily at the same time to assess the condition of the carcass. If the carcass was found completely buried at one of these visits, the entire tube was pulled up from the soil (the core remains intact during this procedure) and placed standing up inside a large plastic box (20 × 20 × 6 cm), covered with a transparent Plexiglass disk, and transferred to the laboratory.

We chose to transport the containers into an environment with controlled temperature in order to facilitate the identification of tactics. Temperature strongly affects the duration

of embryonic and larval development and parental care (Müller JK, unpublished data), and in the field, daytime highs can easily vary by 15 °C (between 15 °C and 30 °C). In the laboratory at 20 °C, in contrast, we can predict the timing of larval hatching fairly precisely based on our own laboratory experiments (Müller 1987; Eggert and Müller 2000). We do not think that the transport of containers (5 min on foot, 20 min by car) was traumatic to the beetles, as it did not appear that oviposition was delayed or that beetles in monogamous associations abandoned carcasses prematurely.

In the laboratory, the tubes were stored inside an environmentally controlled chamber at 20 °C on a photoperiod corresponding to the photoperiod in the field at the time of the study (light from 05:30 AM to 09:30 PM). The next morning, a small piece of transparent plastic tubing was inserted into a previously plugged circular opening (diameter 3 cm) near the top of each tube, level with the inside surface. From then on, beetles were able to leave the carcass. Thus, we denied beetles the opportunity to abandon the carcass for 24 h, which may have slightly delayed the departure time of some subordinates. However, we do not think this had a major impact on reproductive tactics or success because subordinates still had 36 h to leave the carcass before they would have been considered joint breeders (see below).

Beetles leaving the carcass through the exit tube were trapped inside a *Drosophila* tube with a plaster-of-Paris bottom that was kept moist to prevent beetles from dehydrating. We assumed that beetles had arrived on the carcass during their daily activity period in the late afternoon or evening (Müller and Eggert 1987) the day before the carcass was found buried. The *Drosophila* tube was first checked and emptied the evening after the tube had been opened, about 2 days after beetles had discovered and begun to bury the carcass. Beetles found in the tube at that time (08:00 PM) were considered to have a departure time of 2.0 days, which really means they stayed on the carcass for somewhere between 1.5 and 2.0 days. Thereafter, the tube was checked every 12 h (at 08:00 AM and 08:00 PM). The pronotum width of beetles leaving the carcass was measured under a Wild stereomicroscope equipped with an ocular micrometer. Fifteen days after the carcass had been moved into the laboratory, the lid was removed and the soil searched systematically for larvae or pupae. Any offspring found were counted, weighed, and frozen for subsequent analysis of parentage.

Analysis of parentage

Parentage of offspring was determined using DNA fingerprinting rather than microsatellite DNA, because the protocol for this method had already been established in our laboratory, as described in detail by Benken et al. (1998). Genetic fingerprints were produced by isolating chromosomal DNA and digesting it with a restriction enzyme (*HaeIII*). The resulting fragments were separated electrophoretically. After being transferred to an immobilizing membrane, certain fragments were labeled using a probe that binds specifically to a certain base sequence. The probe (GATA)₄ was used because it yields highly polymorphic patterns when used in combination with a number of restriction enzymes but especially with *HaeIII* (Benken et al. 1998). The patterns were analyzed by eye or with the help of an image analyzing system (Gerascan, Gera, Germany). Samples from offspring and potential parents were always run on the same gel to enable reliable comparison of bands. Bands produced by *HindIII*-digested, digoxigenated λ DNA were used as size standards.

Accuracy of parentage analyses

To assign parentage to a maximum number of offspring, several individual (diagnostic) bands should be present in a fin-

gerprint pattern. A total of 1061 offspring were recovered from the 42 successful broods. Analyzable band patterns were obtained from 1050 (99.0%), and maternity could be unequivocally assigned in 1022 (96.3%) of all young. The 39 offspring (3.7%) that could not unequivocally be assigned to one of the females were ascribed to their potential mothers in the ratio of their unequivocal offspring.

In female-only groups ($N = 6$), 101 offspring (9.5% of the entire sample of 1061 offspring) were reared. For such broods without parental males, our results can only provide a minimum estimate of the number of sires contributing to the offspring produced. Analyzable band patterns were obtained from 950 (99.0%) of the remaining 960 offspring and paternity could be assigned in 934 (97.3%). In the remaining 16 instances, either the mother shared one band with both of the potential fathers and there were no additional bands or the offspring's fingerprint patterns contained maternal bands exclusively. All 26 offspring (2.7%) whose fathers could not be unequivocally identified were assigned to their potential fathers in the ratio of their unequivocal offspring. However, 57 of the 934 offspring that yielded unequivocal band patterns were fathered by males that had not been recovered from the carcass (see Results). As in the female-only broods, we could only estimate the minimum number of males involved in siring these offspring.

Identification of brood parasites, satellite males, hosts, and joint breeders

We identified reproductive tactics based on an individual's departure time from the carcass relative to the hatching of larvae. In multifemale groups of *N. vespilloides*, the first eggs are usually laid about 20 h after the females' first contact with the carcass (Eggert and Müller 2000) and larval development takes about 56 h (Müller 1987), such that the first larvae hatch after an average of 76 h. Therefore, we define females in polygynous associations that leave before larvae hatch (3 days or sooner) as noncaring females (brood parasites), and females that stay until larvae are present (3.5 days or more) as caring females (hosts or joint breeders). Brood-parasitic associations, then, consist of exactly one caring female and one or more noncaring ones. Analogously, satellite-male associations contain exactly one caring male and one or more noncaring ones, and male or female joint-breeding associations contain 2 or more caring individuals of the same sex.

Statistics

For several variables, nonparametric methods were used because the data deviated significantly from a normal distribution (Shapiro–Wilk tests, all $P < 0.01$): number of females and males on a carcass and number of offspring of brood parasites and satellite males (last parasite/satellite). For some variables with nonnormal distributions, we present the mean value in addition to the median.

RESULTS

Problem broods with missing parents

There were 2 broods in which DNA analysis revealed that 2 of 25 and 1 of 39 offspring, respectively, were the offspring of females that were not recovered from the respective carcass. These females must have been present on the carcass to lay eggs, and we are including them in the total number of females on the carcass. Our failure to recover these females could have resulted from either of 2 events: they could have abandoned the carcass before we retrieved the soil core or

Table 1
Number of females present and producing offspring

Number of females with offspring	Number of females present					Total
	1	2	3	4	6	
1	14	1	2	0	1	18
2		10 ^a	4	1	0	15
3			4 ^a	2	1	7
4				2	0	2
Total	14	11	10	5	2	42

^a Includes the cases in which one of the females was not recovered.

they could have been inside the core and died there. If they left early, they were brood parasites by our definition. If they died in the container, they probably were brood parasites as well because this is the role with the highest injury risk (Eggert and Müller 1992). Thus, we are classifying these missing mothers as brood parasites.

The third missing parent was a male. He had sired 1 and 2 offspring, respectively, with each of the 2 females on the carcass and thus, he must have been present there. This male could have also left early or died inside the soil core, and analogous to the missing females, we are classifying him as a satellite male.

Number of females producing young on a carcass

Successful breeding associations ($N = 42$) contained between 1 and 6 females, but no more than 4 females actually produced offspring on the same carcass (Table 1). On 43% (18) of the carcasses, a single female produced offspring, on the remaining 57% (24), several females did. The mean number of females present on a carcass was 2.3; the mean number producing offspring was 1.8.

Reproductive benefits of female tactics

Females in monogynous groups

There were a total of 14 monogynous groups: 4 single females, 8 monogamous pairs, and 2 polyandrous groups with 1 female and 2 males. All analyzable young ($N = 278$) in these broods were the resident female's offspring. Monogynous females reared a mean of 19.9 offspring (see Table 2).

Hosts and brood parasites

Our sample included 21 brood-parasitic associations and 2 groups that contained both joint breeders and brood parasites. For the following analyses, we excluded the 2 broods with joint breeders and brood parasites. Host females, which exhibit greater parental investment, produced significantly more offspring than their brood parasites (each host com-

pared with the average of her parasites: Wilcoxon MPSR, $T_- = 0$, $P < 0.0001$; see Table 2). This was true even when hosts were compared with the longest-staying brood parasite, that is, the female closest to the host in departure time (Wilcoxon matched-pair signed-rank test [MPSR], $T_- = 0$, $P < 0.0001$; mean number of last parasite's offspring = 5.4, standard deviation [SD] = 6.4, range = 0–22, $N = 21$; median = 3, $Q_1 = 0.75$, $Q_3 = 9.25$). When several brood parasites left the carcass at the same time, each was assigned an equal share of their combined offspring for the above and the following analyses. To assess whether a brood parasite's reproductive success depended on the time at which she abandoned the carcass, we selected broods in which parasites left at different times and compared offspring numbers for the last parasites to leave a carcass and for the ones leaving earlier. In these 10 broods, the longest-staying parasites did not have significantly more offspring than the earlier-leaving ones (last: mean = 3.5, SD = 4.9, range = 0–15, $N = 10$ broods, median = 1.8, $Q_1 = 0$, $Q_3 = 3$; earlier: mean = 3.1, SD = 3.6, range = 0–9, $N = 10$ broods, median = 1.5, $Q_1 = 0$, $Q_3 = 6$; Wilcoxon MPSR for the 7 broods in which the values are not identical: $T_- = 12$, $P = 0.735$, $N = 7$).

In laboratory studies, brood parasites have been found to reduce their host's reproductive success by reducing the number of offspring produced (Müller et al. 1990; Eggert and Müller 1992). We found no such detrimental effect in the field: the hosts in brood-parasitic associations did not have fewer offspring than females in monogynous associations (Table 2; Mann–Whitney U test, $U = 130.5$, $P = 0.578$).

Joint breeders

Few quantitative statements can be made about joint breeding because of the small number of broods in which the phenomenon was observed. Our sample included 4 joint-breeding associations and 2 groups with joint breeders and brood parasites. In 3 of the 6 joint-breeding groups, the last female to leave produced the most offspring, in 2 another female did, and in 1 the last 2 females left simultaneously. The last female to leave had a mean of 13.3 offspring, the second last one a mean of 8.5 offspring; the largest female had a mean of 16.2 offspring, and the next smaller cobreeder 8.2.

The largest brood size in a joint-breeding association was 39, in a group with 2 joint-breeding females, a brood parasite, and 2 males. This brood also exhibited very little reproductive skew between the joint-breeding females (18 young were the offspring of the female that provided longer care and 20 were the offspring of the female that left earlier).

Number of males producing young on a carcass

The number of males present on a carcass varied between 0 and 6, whereas the number of present males producing offspring varied between 1 and 4 (Table 3). On 47% (17) of the 36 carcasses with males, a single male had offspring, whereas on the remaining 53% (19), several males did. When

Table 2
Female reproductive roles and number of offspring they yielded

Reproductive role	N_{females}	Total offspring	N_{broods}	Offspring per female		
				Mean \pm SD	Median ($Q_1 - Q_3$)	Range
Monogynous uncontested	14	278	14	19.9 \pm 10.6	18.5 (9 – 28)	7–43
Dominant: parasite hosts	21	432	21	20.6 \pm 6.9	21 (16.5 – 23.5)	8–33
Subordinate: parasites	43	167	21	3.9 \pm 5.2	1 (0 – 7)	0–22
Tolerant: joint breeders	14	146	6	10.4 \pm 9.6	7.5 (3 – 18)	0–31

One brood in which several females were present but none stayed to provide care was disregarded.

Table 3
Number of males present and producing offspring

Number of present males with offspring	Number of males present					Total
	1	2	3	4	5/6	
1	14	2	0	0	1	17
2		12 ^a	2	0	0	14
3			1	1	0	2
4				2	1	3
Total	14	14	3	3	2	36

The number of males producing offspring does not include absentee fathers (see text).

^a Includes the case in which one of the males was not recovered.

all 42 carcasses are considered, the mean number of males present on a carcass was 1.8 and the mean number of present males with offspring was 1.5. When only carcasses with males are considered ($N = 36$), the mean number of males present was 2.1 and the mean number producing offspring 1.8.

Reproductive benefits of male tactics

Males in monandrous groups

By definition, monandrous groups include only a single male. There were 14 monandrous associations (8 monogamous pairs and 6 polygynous groups), which produced 389 young. In contrast to females in monogynous groups, not all these young were the resident male's offspring. The resident male did sire all of the offspring in 4 of these 14 groups. In each of the remaining 10 broods, some offspring (total $N = 35$) were not the resident male's. When only a single male was present on the carcass, he sired a mean of 25.3 offspring (91% of the brood, see Table 4).

Dominant males and satellite males

Our sample included 20 satellite-male associations and one group that contained both joint breeders and satellites. For the following analyses, we excluded the brood with joint breeders and satellites. Dominant, caring males produced significantly more offspring than satellites (each dominant male compared with the average of his satellites: Wilcoxon MPSR, $T_- = 22.5$, $P = 0.002$). This was true even when dominant males were compared with the longest-staying satellite, that is, the male closest to the dominant in departure time (Wilcoxon MPSR, $T_- = 22.5$, $P = 0.002$; mean number of last satellite's offspring = 6.4, SD = 7.5, range = 0–35, $N = 20$; median = 5.5, $Q_1 = 2.5$, $Q_3 = 6.5$). When several satellites left the carcass at the same time, each was assigned an equal share of their combined offspring for the above analyses. Similar to the situation in brood-parasitic associations, there was no significant

difference in offspring numbers between males in monandrous groups and dominant males in satellite-male associations (Table 4, Mann–Whitney U test, $U = 273$, $P = 0.327$).

Joint breeders

In the one instance in which the timing of the males' departure from the carcass suggests joint breeding, paternity of the brood was shared between the 4 males on this carcass, with the 2 cobreeders siring 13 and 5 offspring and the 2 satellite males siring 2 and 1 offspring, respectively.

Absentee fathers

More than half of the successful broods (22/42) in our study contained some offspring of males that were not present on the carcass, totaling 14.9% of all young (158/1061). All offspring on carcasses without males ($N_{\text{offspring}} = 101$, in 6 broods) and some offspring on carcasses with males ($N_{\text{offspring}} = 57$, in 16 of 36 broods) were sired by absentee fathers. This means that the respective females used sperm that they had received in earlier matings and stored in their spermathecae. Offspring of absentee males were found in relatively fewer polyandrous (27%, 6/22) than monandrous broods (71%, 10/14; chi-square test, $\chi^2 = 6.756$, $P = 0.009$).

Individual broods with tending males usually had few offspring sired by absentees. Broods with absentee offspring contained a median of 2 such young ($N = 16$, median = 2, $Q_1 = 1$, $Q_3 = 4$, mean = 3.5; SD = 3.7, range = 1–15). In one exceptional case, more than half of the offspring (15/25) were sired by at least 3 different absentee males. When no male was present, absentee offspring were often sired by more than one male. In the 6 breeding groups without males, a minimum of 2–5 males contributed to the paternity of the female's brood (2, 2, 3, 4, 4, and 5). In groups with males, the minimum estimate of absentee fathers was typically 1 (in 7 broods) or 2 (in 5 broods); however, in 3 broods at least 3 absentee males sired some offspring and in 1 brood at least 4 males did.

DISCUSSION

Our results corroborate laboratory studies indicating that burying beetles can achieve some reproductive success in a variety of roles. Males and females were frequently found uncontested or in agonistic associations (brood-parasitic and satellite-male groups); female joint breeding was found in 6 groups, male joint breeding in 1. Alternatives in both males and females yielded vastly different reproductive benefits. Brood parasites and satellite males produced fewer offspring than uncontested or dominant beetles; reproductive success in joint-breeding groups was intermediate. Brood parasitism and satellite-male behavior are clearly less beneficial tactics that appear to be employed conditionally by individuals to whom the superior options are not available.

Table 4
Male reproductive roles and number of offspring they yielded

Reproductive role	N_{males}	Total offspring	N_{broods}	Offspring per male		
				Mean \pm SD	Median ($Q_1 - Q_3$)	Range
Monandrous uncontested	14	354	14	25.3 \pm 14.3	24.5 (13 – 35)	7–54
Dominant: satellite hosts	20	382	20	19.1 \pm 7.8	21 (15.5 – 23)	1–30
Subordinate: satellite males	33	138	20	4.2 \pm 6.5	2 (0 – 6)	0–35
Tolerant: joint breeders	2	18	1	9	9	5–13

Broods in which no males were present ($N = 6$) and one brood in which several males were present but none stayed to provide care are not considered.

Reliability of methods

A potential problem of our experimental design arises from the fact that beetles arriving on the carcass in the first 12–16 h could have come and gone without being noticed. Especially when estimating the frequency of female-only broods, the idea that males might have left the carcass before we retrieved it is worrisome. However, we are confident that males were not present in the breeding associations we describe as female-only. An earlier study at the same field site with a design (one-way access to the carcass) that prevented any beetles from leaving the container unnoticed (Hoferer et al. 1996) yielded a slightly higher frequency of female-only broods than the present one (11 of 45 broods vs. 6 of 42 in the current study), indicating that the open-access design does not overestimate the frequency of female-only broods. As breeding carcasses are very scarce (Eggert and Müller 1997; Scott 1998), neither sex stands to gain anything by simply abandoning the carcass before oviposition. Monogamous males participate in parental care and ensure their paternity by mating very frequently during the first 48 h on the carcass (Müller and Eggert 1989). In many hundreds of broods of burying beetles, we (J.K.M., A.K.E.) have never seen uncontested sexually mature males or females abandon a carcass before eggs are laid. It is also not likely that uncontested males died in the containers because deaths in monogamous associations are extremely rare (Müller JK and Eggert A-K, unpublished data).

The only beetles that, in our opinion, had any appreciable probability of being missed because of early departure, or because of death inside the container, were subordinates in agonistic associations. They are the only ones that might have had an incentive for early departure, and they are by far the most likely to die as a consequence of fatal injuries inflicted by dominants. We may have missed males or females that died inside the container, although we should have recovered some of the exoskeleton, especially the brightly colored elytra. In successful females, we would have found evidence of their presence in the offspring, whereas in males, we would have attributed offspring to absentee fathers. Given that both sexes fight vigorously, death or early departure should have been equally likely in both sexes. The fact that we did not find many cases of missing mothers in our sample suggests that we missed few beetles overall. Another argument for the validity of our methods is the similarity in paternity rates to laboratory estimates. In the present study, *N. vespilloides* males in monandrous groups sired 91% of the offspring raised, and in the laboratory, *Nicrophorus* males mated to previously inseminated females sired 92% of the offspring they helped raise in both *N. vespilloides* (Müller and Eggert 1989) and *N. orbicollis* (Trumbo 1991; Trumbo and Fiore 1991).

Brood parasitism and satellite-male associations in laboratory and field experiments

Brood-parasitic associations were far more frequent in our study than monogynous associations or joint breeding. In female dyads in the laboratory, the larger female always acted as the host, that is, was last to abandon the carcass and had the most offspring (Müller et al. 1990). Consistent with this finding, the current study revealed that the last female to depart from the carcass in brood-parasitic groups (i.e., the host) had the most offspring. In laboratory experiments with 2 females on 15-g carcasses, the brood parasites' reproductive success amounted to 21% of the hosts' (5.8 and 28.0 offspring; Müller et al. 1990). In the current study on 25-g carcasses, parasites' offspring amounted to 19% of the hosts' (3.9 and 20.6 offspring, Table 2).

For males, agonistic polyandrous associations were by far the most frequent associations. In satellite-male associations

of 2 males in the laboratory, the larger male always assumed the role of dominant, that is, was last to abandon the carcass and had the most offspring (Bartlett 1988; Dressel and Müller 1988; Müller et al. 1991). Consistent with this finding, the current study revealed that the last male to depart from the carcass in satellite-male groups (i.e., the dominant) had the most offspring. In laboratory experiments on 15-g carcasses, satellite males sired a median of 10% of the offspring (Eggert 1992). In the current study on 25-g carcasses, median offspring numbers for satellites amounted to 10% of median offspring numbers for dominants (2 and 21 offspring, Table 4).

Our own laboratory experiments have shown that individuals that act as satellites or brood parasites in the presence of a larger same-sex conspecific can be manipulated to act as a dominant by placing them on a carcass with a smaller conspecific (Müller JK, personal observation). In the absence of competitors, females never act like brood parasites, but always provide care (Müller et al. 1990), as do males (Müller JK, unpublished data). Both facts show that tactics are reversible and not genotypically fixed.

Joint breeding in laboratory and field experiments

In laboratory studies with dyads of females on large carcasses (25 g, 30 g, 35 g), reproduction was not strongly biased in favor of the larger female, and both females usually stayed with the brood past the time of larval hatching (Eggert and Müller 1992, 2000). The present study confirmed that in the population studied, some breeding associations will contain multiple females that stay near the carcass until well after the larvae have begun to hatch. There were too few joint-breeding groups to allow for reliable statistical inferences, but the data suggest that the reproductive success of joint-breeding females is intermediate between that of hosts and brood parasites. Compared with a laboratory study on 25-g mice, the current study yielded smaller brood sizes and greater reproductive skew (Eggert and Müller 1992: a mean of 28.6 offspring for the larger and 21.8 for the smaller female; this study: a mean of 16.2 offspring for the largest female and 8.2 for the next smaller cobreeder).

Male joint breeding in *Nicrophorus* has not been studied in the laboratory, and the present study only identified a single case of male joint breeding in which the secondary male stayed barely long enough to encounter larvae (3.5 days). It is conceivable that there are sex differences in the propensity to breed jointly: the 6 male cobreeding groups of *N. orbicollis* Trumbo (1992) found on very large carcasses in the field (Trumbo ST, personal communication) and our one group of *N. vespilloides* constitute the only published field observations of male joint breeding in *Nicrophorus*. In *Nicrophorus tomentosus*, males were also less tolerant of each other than females on 35–40 g carcasses, and subordinate males usually left before larvae hatched (Scott and Williams 1993; Scott 1994).

Joint-breeding groups are not well understood. Tolerance does not imply true cooperation, as mutual infanticide of larvae is rampant in groups of jointly breeding females (Eggert and Müller 2000). Beetles become more tolerant on larger carcasses (Eggert and Müller 1992; Trumbo 1992; Trumbo and Wilson 1993), but we do not know why. High takeover rates (Trumbo 1992, 1995) cannot explain reproductive tolerance in our population because takeovers are rare at our site (Haas 2003). Attempts to find group benefits to communal breeding have failed (Eggert and Müller 1992; Scott 1994; Trumbo and Fiore 1994; Eggert and Sakaluk 2000). Differences in the dominant's ability to influence skew may contribute to the transition from agonistic to tolerant behavior with carcass size (Robertson et al. 1998), but to date, the

ultimate cause of tolerant versus agonistic behavior remains obscure.

Use of stored sperm in laboratory and field studies

The current study revealed that stored sperm are frequently (15% of offspring) used by females in breeding attempts and that matings away from reproductive resources can result in some reproductive success for males. Earlier studies had provided evidence that pheromone emission without reproductive resources serves as an additional mate-finding tactic for males (Eggert and Müller 1989a, 1989b; Eggert 1992; Beeler et al. 1999). The reproductive benefits of single matings away from breeding carcasses are likely to be minute, but the widespread use of stored sperm by females, even in mixed-sex groups, suggest that such benefits are greater than zero. Compared with the search for carcasses, pheromone emission is likely a low-benefit, low-cost alternative that can be employed as an on-the-side option by most males and may be the only option available to males with low energy reserves.

Even when paired monogamously in the laboratory, previously inseminated females fertilize some of their eggs with stored sperm (Müller and Eggert 1989; Trumbo 1991; Trumbo and Fiore 1991). There are no other field data on the incidence of absentee offspring in breeding groups with males, but in all of the populations studied to date, all-female groups constitute a significant portion of all breeding groups. In an earlier study of the population in Freiburg that used 15- and 30-g carcasses (Hoferer et al. 1996), the frequency of female-only broods was 35% (8/23) on the smaller and 14% (3/22) on the larger carcasses. In an earlier study in northern Germany using 15-g mice, 39% (101/258) of all breeding groups contained only females (Eggert 1992). In New Hampshire, field studies yielded frequencies between 22% and 39% for different species (Scott 1996—*N. tomentosus*: 18/68 = 26%; Scott and Traniello 1990—*Nicrophorus defodiens*: 7/18 = 39%, *N. orbicollis*: 8/36 = 22%, *N. tomentosus*: 8/28 = 29%). In northern Michigan, one beetle (which would usually be a female, as males attract females via pheromone emission) was found on 31% (52/166) of all carcasses with *N. defodiens* and on 15% (15/102) of carcasses with *N. orbicollis* and in southern Michigan, on 33% (31/94) of carcasses with *N. orbicollis* (Wilson and Fudge 1984).

Alternative tactics in dominant and subordinate *N. vespilloides* on carcasses

This paper confirms that dominant and subordinate males and females on carcasses exhibit alternative reproductive tactics. Tactics are reversible and depend on the actual competitive situation on the carcass; losing fights inevitably results in brood-parasitic/satellite-male behavior. Although genotypically fixed strategies may theoretically coexist with a conditional strategy (Plaistow et al. 2004), such does not appear to be the case here. Instead, these alternative tactics appear to be components of the same conditional strategy that is exhibited by all individuals in the population.

We would like to dedicate this article to Professor K.P. Sauer (University of Bonn) on the occasion of his 65th birthday. We thank Anne Houde, Scott Sakaluk, Steve Trumbo, and 2 anonymous reviewers for helpful comments on the manuscript and Theo Benken for technical assistance. The work was supported by grants from the Deutsche Forschungsgemeinschaft to J.K.M. (Mu 1175/1-1, 1-2 and 3-1).

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