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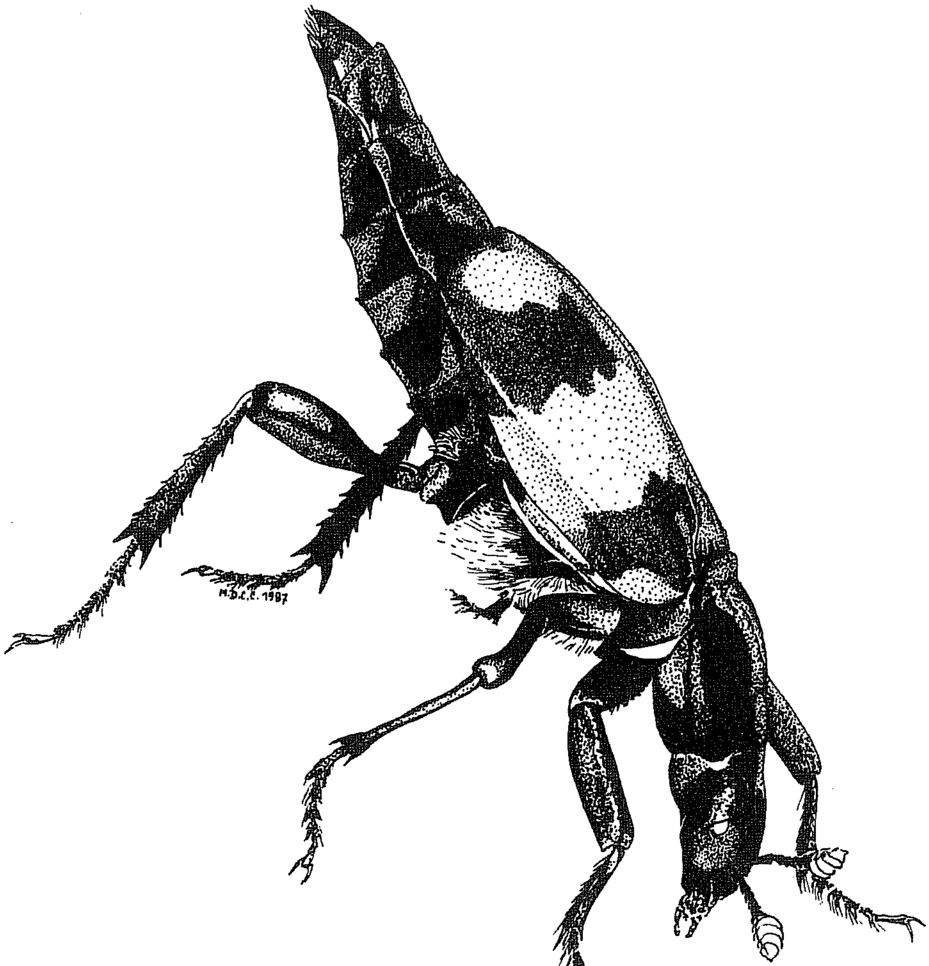

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Alternative male mate-finding tactics in burying beetles

Male burying beetles, *Nicrophorus vespilloides* Herbst (Coleoptera: Silphidae), use two alternative mate-finding tactics: males can (1) search for carcasses that serve as oviposition sites or (2) attract mates via pheromone emission. In the laboratory, all males tested used both tactics, but there were significant differences among males in the time they spent employing either tactic. These differences appear to be partially genetically based. Time of day also affected the tactic used. A comparison of the benefits of the two tactics, based on field and laboratory experiments, suggests that the search tactic results in higher reproductive success than the attraction tactic. However, pheromone emission may be favored toward the end of the activity phase, when female activity is high but carcass availability may be lowest. Females readily mate with pheromone-emitting males even though this tactic is less profitable than mating with a male that has already found a carcass. However, it is likely that females can distinguish between males with and without a carcass only after physical contact. Also, fresh sperm permits females to rear offspring if they find a carcass without a conspecific male. *[Behav Ecol 3:243–254]*

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Behaviors deviating from those considered typical of a species began drawing the interest of biologists in the 1970s, shortly after the evolutionarily stable strategy (ESS) concept had been developed. Such behaviors, termed "alternative behaviors," "tactics," or "strategies" (see Austad, 1984; Cade, 1980; Dominey, 1984), seemed to be a widespread phenomenon, particularly in the context of reproduction. Alternative male mating behaviors have been documented in a variety of arthropod and vertebrate species (e.g., Arak, 1988; Austad and Howard, 1984; Ryan and Causey, 1989; Thornhill and Alcock, 1983; van Rhijn, 1983). Many of these alternative behaviors have turned out to be conditional on factors such as body size or age; this has mostly been interpreted as the less competitive individuals "making the best of a bad job" (Dawkins, 1980). In other cases, different tactics are employed at different times of day (Fincke, 1985; Waltz and Wolff, 1988) or at different population densities (Greenfield and Shelly, 1985). Only rarely have the alternatives been documented as due to genetic differences between individuals; in those instances, the different strategies are employed by genetically distinct morphs of different body size (Gross, 1985; Shuster, 1989; Zimmerer and Kallmann, 1989).

The burying beetle (*Nicrophorus vespilloides*) reproduces on small carcasses that adult beetles bury in the ground. (The species that is referred to as *Nicrophorus vespilloides* Herbst in this paper is equivalent to *Nerophorus vespilloides* Herbst in the author's earlier publications.) Carcasses have long been regarded as the only place for male and female burying beetles to meet and mate ("rendez-vous sites": Niemitz, 1980; Pukowski, 1933). Recent studies, however, have shown that males, besides searching for a carcass, also have the option of using a second type of behavior to obtain mating partners: they can attract females by emitting a pheromone without having found a carcass (Eggert and Müller, 1989a,b; Müller and Eggert, 1987). Because these two behaviors are discrete and mutually exclusive (a male can, at any one time, either fly around in search of a carcass or stay put to emit the pheromone) but serve the same function, they can be considered alternative mate-finding tactics.

In this paper, I address the following questions: (1) Do individuals differ in their use of the two tactics, and, if so, are the differences caused by genetic differences between individuals? (2) Is the use of the two tactics influenced by environmental conditions? (3) What is the benefit to males of each of the two tactics, and why do the two tactics coexist? (4) How and why do females contribute to the maintenance of the two tactics?

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Natural history of burying beetles

Species in the genus *Nicrophorus* are well known for the parental care that adults perform (Fabre, 1899; Pukowski, 1933). Oviposition and parental care take place exclusively on the carcasses of small vertebrates. Adult beetles of both sexes fly around and locate carcasses suitable for reproduction. A carcass may be detected by a beetle of either sex; if a female is the first to find the carcass, she moves about the carcass for a while and then starts to bury it (Pukowski, 1933). Unless a male arrives in the meantime, the female uses the sperm stored in her spermatheca to fertilize her eggs and raises the brood without the help of a mate. A male that is the first to detect a carcass may or may not start to bury the carcass. At a time of day that is species specific, the male begins emitting a pheromone if no conspecific female has yet arrived (Pukowski, 1933; Wilson and Fudge, 1984). These pheromones attract primarily conspecific females (Müller and Eggert, 1987). When the male has succeeded in attracting a mate, the two beetles bury the carcass together and prepare it for the larvae. The pair mate repeatedly during this process (Müller and Eggert, 1989; Pukowski, 1933), and the female subsequently lays her eggs singly in the soil near the carcass. The larvae approach the carcass on their own; they are fed and guarded by both adults for several days. The male leaves the brood a few days earlier than the female (Bartlett, 1988; Schwarz and Müller, 1989; Scott and Traniello, 1990).

If several beetles meet on an unburied carcass, fights occur between members of different species and between conspecifics of the same sex (Pukowski, 1933). The outcome of these fights largely depends on the relative body size of the contestants (Bartlett and Ashworth, 1988; Otronen, 1988; Pukowski, 1933); the fights continue until only one female or one conspecific pair occupies a "central" position, that is, spends most of its time directly on the carcass or in close proximity to it. Escalated fights can lead to severe injuries (Müller et al., 1990a); even fatal fights occur (Scott, 1990).

For *N. vespilloides* it has been shown that losers can also gain some reproductive success from the lost carcass: female losers can stay in the vicinity of the carcass for several days and lay eggs of their own, and some of their larvae will be raised by the winning female (Müller et al., 1990a); loser males can achieve some reproductive success through sneaky matings with the female(s) (Bartlett, 1988; Dressel, 1987).

Several phenomena indicate that carcasses are rare and valuable resources that are used for reproduction whenever possible: Individuals engage in risky fights for the chance of producing a few offspring (Müller et al., 1990a); carcasses of very small size (down to a mass of 1 g) are used for reproduction by *N. vespilloides* (Müller et al., 1990b); if their first clutch is lost, females will produce a replacement clutch if there is still carrion left (Müller, 1987).

For a male burying beetle, there are two possible ways of finding a mate. One of these is to search for mates by searching for potential oviposition sites, small carcasses to which females will also be attracted (search tactic). Males and females locate these carcasses by orienting to the odors of the carrion. Once a male has found a carcass, he can increase the chances of attracting females to the same carcass by emitting a pheromone. Mating with females near oviposition sites is a tactic used by males of several insect species, among them many dung or carrion breeders (Thornhill and Alcock, 1983). The reproductive success that a male *N. vespilloides* can achieve through this tactic depends on his chances of finding a suitable carcass, the number of larvae raised on the carcass, and the proportion of the brood sired by the male.

Alternatively, a male can emit a pheromone and thereby attract females without having found an oviposition site (Eggert and Müller, 1989b; Müller and Eggert, 1987). In this case, each female is inseminated just once by the male; afterwards, the female leaves the male (Eggert and Müller, 1989a). When the attraction tactic is used, male reproductive success depends on the number of females attracted and inseminated per unit time, the females' chances of finding a carcass, the number of offspring raised, and the proportion of larvae fathered by the male. Although pheromone emission ultimately occurs in both contexts, this paper deals with the alternatives for a male that has not detected a carcass, which are to search for a carcass or to attract and inseminate females.

METHODS

In all laboratory studies except the paternity experiments, the beetles used were first-generation offspring of beetles trapped in a deciduous forest near Bielefeld in northwestern Germany. I kept the beetles under a 16 h light: 8 h dark cycle at 20°C and maintained them on a diet of dead mealworms.

Interindividual differences and time of day

I held 70 males separately immediately after their emergence as adults; I observed them daily at 10-min intervals during the last 4 h of the light phase, when pheromone emission in *N. vespilloides* occurs (see Figure 1). The beetles were observed on 50 consecutive days from the first observed pheromone-emitting behavior. From these observations I obtained two values: the total number of observations per day during which a male showed the posture typical of pheromone emission (Eggert and Müller, 1989b) and the number of observations during which a male simply moved about the container or attempted to fly.

I assumed that locomotory activity indicates the search for a carcass (the search tactic). Support for this assumption comes from the fact that the daily pattern of locomotory activity in the laboratory is consistent with the daily activity pattern as derived from catches in carrion-baited pitfall traps (Cordes R-G and Eggert A-K, unpublished data; Müller and Eggert, 1987). Another observation also supports the assumption that locomotory activity in the laboratory actually indicates a search for reproductive opportunities rather than for food. If male activity was mainly a search for food, hungry males should be more active than well-fed ones. This is the case with immature males, but not with sexually mature ones (Cordes R-G, unpublished data), indicating that immature males are active mainly to search for food, whereas mature males mainly search for mating opportunities. In contrast to mature males, immature males hardly show any locomotory activity when well fed (Cordes R-G, unpublished data).

I also observed the same 70 males throughout three entire light periods (16 h each) to determine how time of day affects the frequency of the two tactics. Again, each male was checked every 10 min. As there were no obvious differences between the results obtained on these 3 days, I present only the results from one light period.

Observations were not made during the dark phase because pheromone emission and locomotory activity end soon after dark. In the laboratory, fewer than 5% of the males continue to emit pheromones 1 h after dark (Eggert, 1990), and in the field, *N. vespilloides* is not active during the night (Müller and Cordes, 1987).

Genetic basis of interindividual differences

To test whether the daily amount of time spent on each of the two tactics is affected by genetic differences between individuals, I estimated narrow-sense heritability of both the daily duration of pheromone emission and locomotory activity.

From the 70 males observed throughout the experiment on interindividual variation, 8 were selected. Three of these males had regularly emitted pheromones for most of the daily observation period and thus had high values for the character "duration of pheromone emission." Three others had low values for this character, and the remaining two had intermediate durations of pheromone emission. These males were each allowed to inseminate an unrelated virgin female; each female then reared her own brood. Males were not involved in rearing their offspring, so paternal effects could not affect offspring performance.

Male offspring (7–12 per male) were observed on 18 successive days, from day 34 to 51 after adult emergence. At this age, all males emit pheromones, and there is no effect of age on the duration of pheromone emission (Eggert, 1990). The values used for calculating the regression were means of the daily duration of pheromone emission derived from repeated measurements: 18 days for sons (days 34–51), and 40 days (the last 40 observation days) for fathers. Because there is no time course, the two means should not differ except in how exact an estimate of the true mean for a male they yield.

Because the number of sons per family was not equal, I used weighted offspring means to calculate the offspring-on-sire regression (Falconer, 1989). Weights were derived from the number of sons per family and the intraclass correlation coefficient, a measure of similarity between members of the same family (Falconer, 1963). I then calculated the heritability estimate as $2 \cdot b$, twice the regression coefficient; the standard error of the estimate was similarly determined as $2 \cdot \mathrm{SE}(b)$, twice the standard error of the regression coefficient.

Laboratory experiments on paternity

When two males compete for a carcass, it is likely that the less competitive male also gets some matings with the female and fathers some of the larvae reared on the carcass (Bartlett, 1988; Dressel, 1987). We studied the relative paternity of two males competing for a carcass using males from two laboratory strains with differently colored elytra (Müller and Eggert, 1989).

The two laboratory strains derive from field-caught animals, and they both differ with respect to the normal coloration of this species. In the "light" strain, all of the individuals have wing covers that are mostly red-orange in the posterior half, whereas in the "dark" strain, all of the beetles have wing covers with an extremely wide black band in the posterior half. In some dark individuals, the posterior part of the wing covers is entirely black. If a female from one of the strains is mated to a light and a dark male, the two males' offspring will be clearly distinguishable from one another. Within-strain matings (male and female from the same strain) result in offspring that show the parents' color, whereas across-strain matings result in offspring that are intermediate in coloration and resemble the wild type, which has a narrow black band across the wing covers. From a total of 579 offspring in the study, 577 (99.7%) could clearly be attributed to one of the potential fathers; the remaining two individuals were not considered in the analysis.

Ten triads consisting of a female and two differently colored males each were supplied with a mouse carcass (15 g weight) in a peat-filled flower pot (height 16 cm, diam 16 cm). Once the carcass was buried, the beetles could leave the container through a narrow (diam 3 cm), transparent plastic tube. About 20 days after the parents had left the carcass, their offspring emerged from the pupal chambers and also left the container. Paternity could then be determined from the offspring's elytral coloration.

The paternity of a male using the attraction tactic was estimated by allowing males a single copulation with a female whose spermatheca was filled with sperm from a male from the other color strain. The experiment was designed this way because pheromone emitters usually get to mate only once with each female attracted (Eggert and Müller, 1989a), and reproductively active females usually carry fertile sperm in their spermatheca (Müller and Eggert, 1989).

I first kept each female together with a male from one of the strains for 24 h, during which time pairs mate frequently, resulting in the female's spermatheca being filled with motile sperm (Müller and Eggert, 1989). Two or 3 days later, the females were allowed to approach and mate with a pheromone-emitting male of the other color type in an observation arena. Thus, the last male to mate with a female was always a pheromone emitter. Each pair of males was used twice: with one female, the dark male got to mate first and the light male mated second; with another female, the same two males were used in reverse order.

I isolated the females after they mated with the second male. The following day, I provided the females with a carcass to induce oviposition. Some of the larvae from large clutches were raised by foster-mothers because caring adults are known to cull large broods (Bartlett, 1987). I excluded those cases from the analysis in which less than 10 offspring survived to adult emergence and excluded those in which one of the males proved to be sterile. These restrictions left 23 of the 32 replicates for analysis.

Field experiment

To find out how often females raise their brood in the absence of conspecific males and how many males are usually present on a carcass buried for reproduction, I placed 300 mouse carcasses (14–16 g weight) in a deciduous forest near Bielefeld, Germany (latitude 52°01′ N, longitude 8°23′ E) between 15 May and 1 September 1988. I checked the mice for burial every 24 h, and the container on which they had been placed was searched for beetles and their eggs 24 h after the carcass had been found buried (for a more detailed description of the method, see Müller et al., 1990b).

Sperm longevity

To test how long sperm stored in the female's spermatheca retain their capacity for fertilizing eggs, females were made to lay eggs at different times after insemination. Out of 60 females that had each been kept together with a male for 24 h, 10 were supplied with a carcass immediately, another 10 were not given a carcass until a week after insemination, and another 10 each were given a carcass 2, 3, 4, and 6 weeks after insemination, respectively. After oviposition, I collected eggs from the substrate and stored them until the larvae hatched. I regarded eggs as fertilized if a larva hatched or if features of a developed larva were visible inside an egg that had failed to hatch. Females that had produced unfertilized eggs only were dissected after the experiment to check the content of their spermathecae.

RESULTS

Effects of time of day

Time of day strongly affected the use of the two tactics: early in the afternoon most males engaged in locomotory activity or made attempts to fly, whereas later in the afternoon they turned to pheromone emission (Figure 1). Five hours before dark, no male was observed in the pheromone-emitting posture, whereas by the end of the light phase, more than 90% of the males had assumed this posture. Most males showed both types of behavior during the last 9 h of the light phase (the main activity period of the species). The more time a male spent in locomotory activity, the shorter the period of pheromone emission (Spearman rank correlation, $r_s = -.50$, $n = 70$, $p < .001$). The negative correlation becomes stronger when only the last 4 h of the light phase are considered ($r_s = -.81$, $n = 70$, $p < .001$). During these 4 h, most males were active, performing either one of the two behaviors.

Intra- and interindividual variation

Both the search and the attraction tactic are regular components of the reproductive behavior of male *N. vespilloides.* All 70 males observed showed the typical pheromone-emitting posture as well as locomotory and flight activity. In most males, the daily duration of pheromone emission increased during the first 10 days after it first appeared. Therefore, the following analysis is based on the last 40 observation days exclusively, when the daily duration of pheromone emission was stable.

Sixty-one of the 70 males showed the pheromone-emitting posture on each of these 40 days; most of the remaining 9 males failed to do so on 1 or 2 days only (median = 1.3 days). However, there were significant interindividual differences in the daily amount of time a male spent emitting pheromones, accounting for 46% of the overall variation in the daily duration of pheromone emission; the remaining 54% was due to intraindividual variance (Table 1, Figure 2). Similarly, of the overall variation in the daily duration of locomotory activity, 43% was due to inter- and 57% to intraindividual variance (Table 1).

Genetic basis of interindividual variation

The weighted regression of mean offspring values on fathers' values indicated significant heritability for both the duration of locomotory activity and the duration of pheromone emission (Table 2). These heritability estimates were calculated using mean values derived from repeated measurements of the same individuals, and thus measure the proportion of interindividual variance that is due to the additive effects of genes. In other words, the estimates describe the heritability of the mean duration of the two tactics. The standard error for the heritability estimates is smaller than expected ($\mathrm{SE}_{\mathrm{exp}} = 2 \cdot \sqrt{N}$) because sires were selected from both ends of the distribution (Falconer, 1989; Hill and Thompson, 1977).

To obtain a measure of the heritability of the overall (inter- and intraindividual) phenotypic variance observed, repeatability as a measure of intraindividual variance should be multiplied by the heritability estimates obtained above (Butlin and Hewitt, 1986). Repeatability is a measure derived from quantitative genetics theory that is generally regarded as an upper limit for the heritability of a character. Repeatability describes the extent to which multiple measurements on the same individuals vary in relation to measurements on several individuals; it is determined by a model-II ANOVA as the proportion of the observed overall variance in the sample that is due to interindividual differences. These values (46% and 43%, respectively), previously

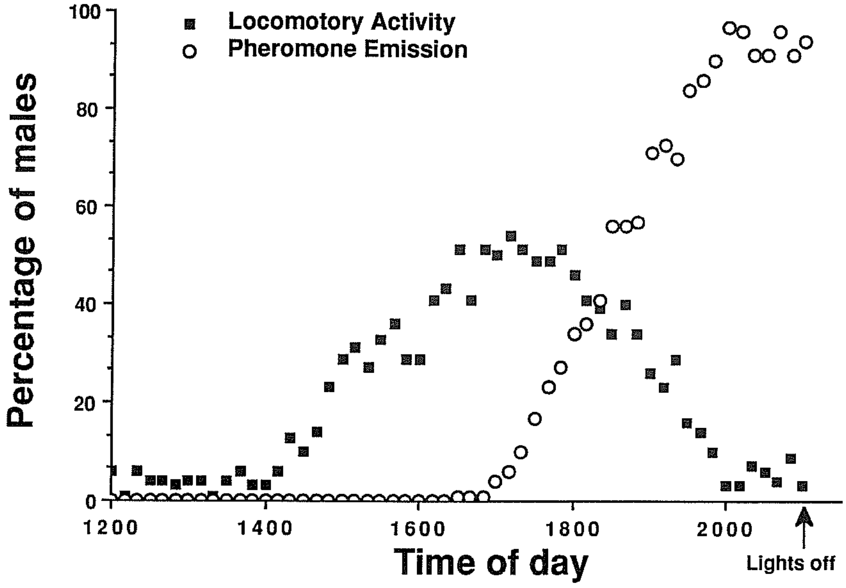

Figure 1
Percentage of males ($n = 70$) exhibiting pheromone-emitting or locomotory behavior at different times of the day. Percentages graphed refer to observations on a single day; parts of the day with activity levels below 5% were deleted.

Table 1
One-way ANOVA of the daily amount of pheromone emission and locomotory activity in the last 4 h of the light phase

Source of variation	df	SS	MS	*F*	*p*
Pheromone emission					
Between males	69	32,441.8	470.2	34.63	<.001
Within males	2730	37,070.2	13.6		
Total	2799	69,511.9			
Locomotory activity					
Between males	69	33,410.0	484.2	31.13	<.001
Within males	2730	42,459.9	15.6		
Total	2799	75,869.9			

SS = sum of squares; MS = mean squares.

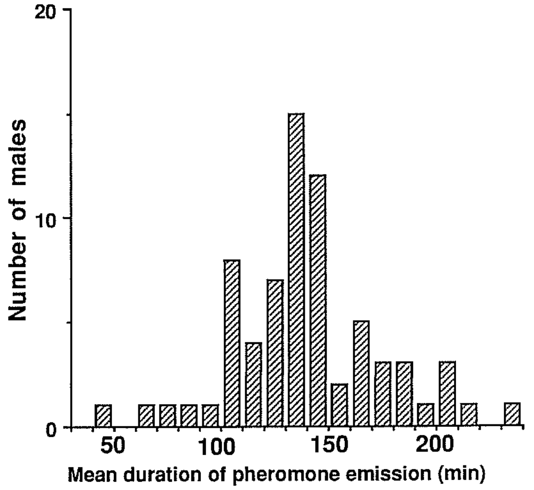

Figure 2
Frequency distribution of the mean duration of pheromone emission (minutes out of the last 4 h of the day); the mean value for each of the 70 males derived from 40 successive observation days.

determined in the first section (intra- and interindividual variation), yielded heritability estimates of 0.36 for both characters when multiplied by the values in Table 2. These values estimate the heritability of single measurements of pheromone emission duration rather than the heritability of means (Falconer, 1989).

Paternity of males using the search tactic

The laboratory experiment with two males and a female on a carcass showed that the loser male, that is, the male that left the carcass first, sired some offspring in 7 of 10 cases. The percentage of offspring fathered by losers ranged from 0% to 35% (median = 10%, n = 10 broods).

In the field, 258 carcasses were buried for reproduction by *N. vespilloides.* On 158 (61%) of these carcasses, males were present. In 84% of the 158 cases, only one male was found near the buried carcass, whereas two (15%) or three (1%) males were found on the remaining carcasses. This frequency distribution deviates significantly from a Poisson distribution with the same mean number of males (0.75) on carcasses (contingency table analysis, $p < .001$) because the first male to detect a carcass buries it, thereby reducing the probability of multiple discoveries below that expected by chance.

If the larvae raised on a carcass with n males were fathered exclusively by these males, average paternity for each of them would be $1/n$. However, not all the young raised on a carcass will be the offspring of the male on the carcass because females coming to a carcass usually carry viable sperm that compete with the sperm of the resident males (Müller and Eggert, 1989). Males that buried a carcass together with inseminated females in the absence of other males fathered no more than 92% of the larvae raised on these carcasses, despite a high mating frequency (Müller and Eggert, 1989); exactly the same relative paternity for males involved in parental care was found in another burying beetle, *N. orbicollis* (Trumbo, 1991). Because additional males on a carcass mate less frequently than the owner of the carcass (Bartlett, 1988; Dressel, 1987), it is likely that a higher number of males on the carcass does not significantly reduce the proportion of eggs fertilized by sperm from previous matings. For the following calculation, I assumed that total paternity for all the males on a carcass is invariably 92%. Thus, the expected paternity for a male on a carcass with a total of n males is $0.92 \cdot 1/n$, and average paternity for a male on a carcass would simply be a mean of paternities expected for the different numbers of males weighted by their relative frequencies in the field: $0.92 \cdot [1.0 \cdot 0.84$ (one male) $+ 0.5 \cdot 0.15$ (two males) $+ 0.33 \cdot 0.01$ (three males)$] = 0.84$. The average paternity for a successful searcher would thus be 84% of the brood raised on the carcass.

The frequency of carcasses with two or more males on them as derived from the field study must be regarded as a minimum estimate because the presence of beetles was only checked 1 day after burial. In a laboratory study, Schwarz and Müller (1989) found that males of male–female pairs never left the carcass on the first or second day after burial; on carcasses with two males, however, one of them often left before brood care started (Müller et al., 1991). Thus, my field study might underestimate the proportion of carcasses with two or three males on them. However, even assuming that this proportion was twice as high, my estimate of average paternity is still high (77%). This shows that the expected mean paternity of a successful searcher male is relatively robust to changes in the estimation of the numbers of males around carcasses.

Table 2
Estimates of heritability and their standard errors for the daily amount of pheromone emission and locomotory activity in the last 4 h of the light phase as determined from an offspring-on-sire regression (Falconer, 1989)

Character	h^2	SE (h^2)	p	n_{families}	n_{sons}
Daily amount of scent emission	0.78	0.31	<.05	8	89
Daily amount of locomotion	0.84	0.29	<.05	8	89

Paternity of males using the attraction tactic

Through a single copulation with a female whose spermatheca was filled with another male's sperm, the pheromone-emitting males achieved a median paternity of only 5.0% ($n = 23$ broods, interquartile range 0–17.4%). Müller and Eggert (1989) conducted a similar study in which the last male was also allowed a single mating only, but unlike the present study this male had not been emitting pheromones immediately before mating. This earlier study yielded a median paternity for the second male of 9.1% ($n = 13$ broods, interquartile range 5.0–15.6%) that was not significantly different from the one in the present study (Mann-Whitney U test, $p > .05$).

In the above experiment the pheromone emitters were the last males to mate with the female before oviposition. Under field conditions, the expected paternity for pheromone-emitting males is also affected by the females' subsequent matings. When mating frequencies are high and/or search time for a carcass is long, the probability is high for any pheromone-emitting male that a female he inseminates will subsequently mate with several other males. For each pheromone emitter, the degree of paternity then depends not only on the sperm precedence pattern but also on the number of times the female mates subsequently before she oviposits on a carcass.

A simple model can be used to describe how a pheromone emitter's expected paternity is affected by the number of times the female subsequently mates with other males. The model is based on several assumptions: (1) The female's spermatheca is already filled with sperm before mating with the pheromone emitter. This is a realistic assumption; mature females in the field mostly carry fertile sperm (Müller and Eggert, 1989). (2) The amount of sperm stored is constant, that is, some of the stored sperm are displaced in each new mating. (3) Sperm in the spermatheca mix. Paternity experiments never resulted in complete first- or last-male sperm precedence (Müller and Eggert, 1989), which means that there is at least some degree of sperm mixing. (4) The proportion of a brood fathered by a male depends only on the proportion of his sperm in the spermatheca. (5) The number of sperm transferred in each mating is equal. (6) Eggs are not laid until a carcass is found. This is realistic because the final stages of egg development are triggered only on a carcass (Wilson and Knollenberg, 1984).

The relationship between a pheromone emitter's paternity with one female, $p(m)$, and the number of times this female mates subsequently, m, is described by the function $p(m) = p_1 \cdot (1 - p_1)^m$ where p_1 is the paternity for a male that is the last to mate with a female. This function describes the paternity resulting from one particular mating. If the female's subsequent matings are also with pheromone emitters, the mean paternity of pheromone emitters from these matings is the sum of paternities, divided by n, the total number of matings the female had:

$$p(n) = 1/n \cdot \sum_{m=1}^{n} p_1 \cdot (1 - p_1)^m.$$

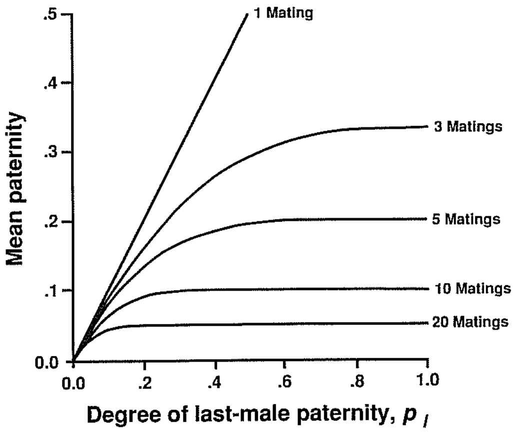

Figure 3
Expected mean paternity (proportion of brood fertilized) for pheromone emitters mating with nonvirgin females as a function of the degree of last-male paternity (proportion of brood fertilized by the last male to mate). For a description of the underlying model, see text. The different curves indicate the effect of the number of times that females mate before oviposition.

The model shows that with increasing last-male sperm precedence, it becomes more important for males to be last to mate with a female (Figure 3). Male *N. vespilloides* can increase the degree of last-male paternity by repeated mating (Müller and Eggert, 1989). However, for a pheromone-emitting male, it is impossible to predict how close a female he inseminates is to finding a carcass and ovipositing, so males could not possibly adjust their mating behavior to the number of subsequent matings the female will accept.

The model also shows that the degree of last-male paternity becomes less important the more often females mate before they finally lay eggs (Figure 3). The mating frequency of female *N. vespilloides* with pheromone-emitting males can be assumed to be as high as one to two times per day (Eggert and Müller, 1989a). Female search time for suitable carcasses is unknown but can be assumed to be long, resulting in a large number of matings before oviposition.

Frequency of uniparental care

The paternity of males that have previously inseminated a female will be strongly reduced when the female reproduces with the help of another mate (Müller and Eggert, 1989). The presence or absence of males on carcasses that females are using for reproduction is thus an important factor for the potential paternity

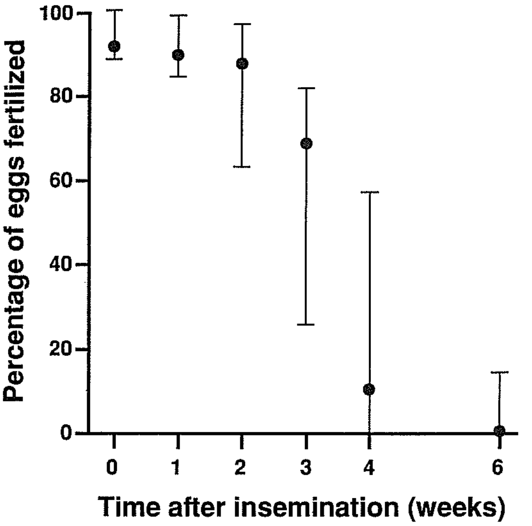

Figure 4
Percentage of fertilized eggs (median and interquartile range) in clutches produced at different times after insemination. Each female was permitted to produce a single clutch after insemination. Each interval between mating and oviposition was replicated with 10 females, of which at least 9 produced a clutch of 10 or more eggs.

of a pheromone emitter that inseminates a female. In the field study, the frequency of females raising their brood in the absence of males proved to be high: on 100 (39%) of the 258 mice buried, only females were found the day after burial. Lone males, in contrast, were rare: they were found on only 7 (3%) of the carcasses. It is not likely that sexually mature males had been present on the carcasses with females before the container was searched; in the laboratory, mature males that were given the opportunity to bury a carcass together with a female in the absence of any male competitors always stayed on the carcass for several days (Schwarz and Müller, 1989). In a field study on North American burying beetles, frequencies of single females ranged between 22% and 39% (Scott and Traniello, 1990). Uniparental care thus seems to be a regular phenomenon. If this were not the case, mating with females off carcasses by pheromone emitters would hardly yield any reproductive benefit for males.

Female benefits from multiple mating: sperm longevity

When females laid eggs immediately after several matings, the median percentage of eggs fertilized was 92% (Figure 4). The fertilization rates of clutches produced 1 or 2 weeks after insemination did not deviate significantly from this value (Mann-Whitney U test, $p > .1$ for both comparisons) but were more variable (Figure 4). However, 3 weeks after insemination, significantly fewer eggs were fertilized than immediately after insemination (U test, $p < .001$), and one of the clutches consisted of unfertilized eggs only. Out of the 10 clutches produced 6 weeks after insemination, only 2 contained any fertilized eggs; the fertilization rate in each of these 2 clutches was 30%. All of the females that laid unfertilized eggs only had large numbers of immobile sperm in their spermathecae.

The experiment shows that sperm stored in a female's spermatheca start to become infertile 3 weeks after insemination, even when the female has not produced eggs in the meantime. A female's total reproductive period is considerably longer under both laboratory and field conditions and lasts several months. This means that females, unless inseminated regularly, run the risk of not having sufficient viable sperm available.

DISCUSSION

Mate-finding tactics of *N. vespilloides* males

My data show that the two mate-finding tactics in *N. vespilloides* are best viewed as components of a conditional strategy. Within individuals, the switch from one tactic to the other is dependent on the time of day, with most males engaging in locomotory activity or flight attempts early in the afternoon and later turning to pheromone emission. This daily switch from one tactic to the other is consistent with the results of a field study with baited pitfall traps (Müller and Eggert, 1987): In carrion-baited traps, catches of males peak in the afternoon, whereas in traps baited with *N. vespilloides* males, catches (mainly of females) peak later in the evening.

All males use both tactics, but there are differences between individuals in the daily amount of time devoted to the respective tactics, and these differences are partially explained by genetic differences. This appears to be similar to what Cade (1981) described for male crickets (*Gryllus integer*). He found continuous interindividual variation in mean calling duration, and a selection experiment showed that the amount of calling had a genetic component (Cade, 1981).

The heritability estimates reported in the present study, though significantly different from zero, must be considered preliminary owing to the small sample sizes. In addition, estimates of heritability obtained under laboratory conditions that minimize environmental variation are likely to yield higher values than studies under field conditions (Falconer, 1989; Riska et al., 1989). However, for the character investigated here, as in most other heritability studies (Riska et al., 1989), field studies would not be feasible.

Benefits of alternative mate-finding tactics: paternity and number of mates

Although a lack of information on female mating frequencies and the availability of carcasses prevents a direct comparison of the fitness gains for each alternative mate-finding tactic, it is possible to compare two components of the reproductive success a male can achieve by using either alternative: (1) the paternity of successful males, i.e., males that find a mate by using one of the tactics, and (2) the probability of obtaining a mate through each tactic. For a successful searcher, the degree of paternity achieved with a given female will be high, but the number of mates he can obtain by using this tactic is small because of the long search time for a suitable carcass.

The attraction tactic, in contrast, allows males to inseminate a great number of females. In a field study in 1987, males employed the attraction tactic for an average of about 2 h per evening and attracted and mated with an average of 1.8 females per evening (Eggert and Müller, 1989a). It is highly unlikely that males using the search tactic encounter a comparable number of mates per day. However, each of the females with which a pheromone-emitting male mates is of relatively low value to the male because it is uncertain if and when these females will find a carcass to lay eggs on. It is possible that pheromone emitters can sometimes achieve a degree of paternity that is higher than suggested by the results of the paternity experiment because my experimental design maximized the number of competing fresh sperm in the female's spermatheca. For a realistic estimate of the benefit of the pheromone emission tactic, more information is needed on female mating behavior in the field and on the mechanism of sperm competition in *N. vespilloides.*

Comparison of the overall reproductive success of the two tactics

If carcasses were readily available for *N. vespilloides,* most matings would occur on carcasses. But because carcasses are probably rare, females will mostly mate off carcasses, such that practically all of the sperm stored in their spermathecae will stem from matings off carcasses. Single mothers will mostly raise the offspring of males using the pheromone emission tactic. On carcasses with male–female pairs, however, the successful searcher male is likely to father most but not all of the offspring. For the following calculation we assumed that males on a carcass sire 92% of the larvae raised on the carcass (Müller and Eggert, 1989; Trumbo, 1991), that the remaining 8% are offspring of pheromone emitters, and that all of the larvae raised by single females are the offspring of pheromone emitters. These assumptions lead to an estimated 55% of all larvae that are the offspring of searcher males ($0.61 \cdot 0.92$) and 45% that are the offspring of pheromone-emitting males ($0.39 \cdot 1.0 + 0.61 \cdot 0.08$). If all males use both tactics to obtain mates, it appears that, on average, males get an almost equal number of offspring using either tactic.

This estimate assumes that females arriving on carcasses carry the sperm of pheromone-emitting males only. However, matings can also occur on carcasses that are not suitable for reproduction (Wilson and Knollenberg, 1984), which decreases the relative success of the pheromone-emission tactic. In addition, single females are more likely than pairs to lose their brood to infanticidal congeneric intruders, but only when population density is high (Trumbo, 1990: *N. defodiens* in Michigan, but see Scott, 1990: *N. orbicollis* in New Hampshire). Therefore, pheromone emitters probably sire less than 45% of the surviving offspring.

To summarize, it appears that more than half of the larvae raised on carcasses are the offspring of males that used the search tactic. In the laboratory, males spend more than half of their daily activity emitting pheromones. If this is also true in the field, it means that pheromone emission without carcasses is less effective than searching for carcasses. However, it is probably also less energy expensive than the search flight. Chemical communication has been considered an energetically inexpensive form of communication because it only requires the production of small amounts of the pheromone (Alcock, 1989). Flight, in contrast, has been found to be a very energy-consuming activity for insects; during flight the metabolic rate can be elevated to as much as 50–100 times the resting level (Kammer and Heinrich, 1978).

Maintenance of tactics and genetic variation

I believe that both alternatives have been maintained because their success rates vary inversely with the time of day. The chances of attracting females via pheromone emission are much higher at the end of the daily activity period because female activity is low in the early afternoon and reaches a maximum later in the day (Cordes, 1990). The probability of finding a carcass, in contrast, is likely to decrease later in the day. Assuming that carcasses used by *N. vespilloides* become available throughout the day, carcasses should accumulate during the night and the morning, when *N. vespilloides* is not active (at our study site, *N. vespilloides* is by far the most abundant species, and the two co-occurring *Nicrophorus* species were found on only 11% of the carcasses buried in the field). In the course of the activity period of *N. vespilloides,* more and more carcasses are found and buried or at least concealed under the leaf litter, making detection by other beetles more difficult. Thus it probably pays males to search for carrion first and switch to pheromone emission later in the day.

Alternatively, the daily shift in tactics could be due to a change in environmental conditions such as air currents that favor chemical signaling, or it could be affected by interspecific competition from larger species. However, the largest species in my study area, *N. humator,* which is strictly nocturnal, shows the same sequence of mate-finding tactics (Müller and Eggert, 1987). Competition from congeneric competitors should not affect the activity pattern of this species, and it seems unlikely that air currents become more favorable when this species starts signaling (around midnight).

A similar daily shift from one mate-finding behavior to another occurs in the damselfly *Enallagma hageni* (Fincke, 1985). In this nonterritorial coenagrionid, males can use either of two mate-finding tactics. One of these, the waiting tactic, yields lower reproductive success than the alternative searching tactic. Nevertheless, most males use both tactics and turn from searching to waiting later in the day when fewer females are available for searchers.

However, in *N. vespilloides* there is also significant heritable variation in the amount of time males spend with either tactic or in the timing of the switch point. The fitness consequences of this variation are unknown. Even if males that spend more time searching produce more offspring per unit time, this need not translate into a higher lifetime reproductive success. For example, these males could experience reduced survival because of the greater metabolic stress during flight or because of an increased predation rate. Even if there are fitness differences, heritable variation in the switch point could have been maintained by a number of different mechanisms (Barton and Turelli, 1989). A likely candidate for the specific case of *Nicrophorus* would be a spatially or temporally fluctuating availability of carcasses.

The female point of view

In the context of alternative male mate-finding tactics, the females' interests should not be overlooked. If the alternative tactics differ in the cost or benefit they have for females, females can be expected to favor males using one of the alternatives. In the case of *N. vespilloides,* the question arises as to why females mate with males using the attraction tactic, despite the fact that these males have nothing but sperm to offer.

One aspect of this problem concerns why females react to pheromone-emitting males in the first place. Attraction of females to male-produced pheromones over long distances is rare among insects (Greenfield, 1981; Jacobson, 1972; Thornhill, 1979). Such exceptions from this typical sex attraction pattern occur when there is competition between females for valuable resources offered by pheromone-emitting males (Thornhill, 1979), when signaling is more costly than responding, or when the distribution of resources that are critical for female reproduction is extremely clumped so that females search for these resources anyway (Greenfield, 1981). *Nicrophorus* males emit pheromones both when they have found a carcass and when they have not, and it is likely that females cannot always tell whether a male is emitting pheromones on or off a carcass before the first physical contact with the male (Eggert and Müller, 1989a). Under these conditions, the benefit to females arising from their orientation to pheromone emitters must take both types of males into account. Even if a female does not benefit from meeting a pheromone emitter without a carcass, it pays her to approach every pheromone emitter she perceives unless the proportion of males that actually offer a breeding opportunity is so low that the female's chances of detecting a carcass are higher when she searches for a carcass on her own without responding to male pheromones.

The second problem is why females that encounter a pheromone emitter allow him to copulate. Hanging flies (Bittacidae) also have male-produced long-range sex attractants, and in at least one species, females discriminate against males that emit pheromones but offer only small prey items as nuptial gifts (Thornhill and Alcock, 1983). In *N. vespilloides,* in contrast, females allow males without a carcass to mate even though the time required to reject a male that attempts to mate is shorter than the duration of a copulation without female resistance (Eggert and Müller, 1989a). The benefit the female obtains from these matings are the sperm transferred by the male because an adequate sperm supply is important for females when they find a carcass on which no mate is present. Field studies have found that *Nicrophorus* females often raise their brood without a mate (19–39% of the carcasses used by a species: this study; Scott and Traniello, 1990). In this situation, females depend on sperm transferred in earlier matings for fertilization of their eggs.

Female *N. vespilloides* lay eggs on carcasses even when they are still virgin (Eggert A-K and Müller JK, personal observations), or when the supply of fertile sperm in the spermatheca is depleted (as in the sperm longevity experiment). Without sufficient fertile sperm, oviposition would mean a waste of considerable amounts of time and energy. The fact that this behavior occurs in the laboratory suggests that females either do not get any information about the content of their spermatheca, or they are unable to control oviposition. In the field, most females have stored at least some fertile sperm (93% of sexually mature females in a 1985 survey: Müller and Eggert, 1989). This shows that females do mate multiply and thus maintain a store of fertile sperm; therefore, the ability to respond to the actual condition of the sperm stores might not confer any benefit to females.

Although there are some insect species in which a single mating may suffice to fertilize the lifetime egg production of females (Parker, 1970), a recent review (Ridley, 1988) has found that multiple mating may often be necessary for female insects to ensure fertilization throughout the female's reproductive life. Maintaining a storage of viable sperm may generally constitute a more important benefit of multiple mating to female insects than previously thought.

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