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Effects of Carrion-Independent Pheromone Emission by Male Burying Beetles (Silphidae: *Necrophorus*)

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With 4 figures

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Abstract

All former publications on the reproductive biology of burying beetles (genus *Necrophorus*) state that in these species copulations take place on carcasses only, this being the only place for the sexes to meet. Our laboratory investigations have shown that males emit pheromones if no carrion is around. We now present data from a field investigation showing the effects of pheromone emission by males that have not secured a carcass. Such males are successful in attracting conspecific females. But conspecific males and individuals of other species are also attracted by the scent. Possible benefits for attracted individuals of different species and sex are discussed.

Pheromone emission and attraction of conspecifics are restricted to a distinct species-specific period of the day in at least two of the common species.

Introduction

Sexton beetles of the genus *Necrophorus* reproduce on small carcasses. Both sexes are attracted to the carrion by the odour of decomposition. Several authors have stated that *Necrophorus* beetles copulate on carcasses only, this being the only opportunity for the sexes to meet (PUKOWSKI 1933; NIEMITZ 1978; WILSON & KNOLLENBERG 1984).

As early as in 1933, PUKOWSKI gave a detailed description of a behaviour exhibited by *Necrophorus* males which she called "Sterzeln". She stated this behaviour to occur only if a male remains alone on a carcass suitable for reproduction and suspected the male to emit a volatile substance attractive to females. In this paper we present findings concerning the effect of carrion-independent pheromone emission in the field, the attractiveness of pheromone-emitting males, species specificity of attraction, and sex ratios of attracted individuals.

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Methods

Field investigations were carried out using baited pitfall traps which were emptied every three days. The traps were placed in two parallel rows with a minimum distance of 20 m between two traps. Six of the traps were normal pitfall traps as described by MÜLLER (1984), and three of them were time-sorting pitfall traps of the type described by BARNDT (1982). The bait was placed in a small can hanging in the opening of the trap. A tea strainer covering the can prevented the attracted beetles from entering the can and the beetles serving as bait from escaping. Males of the investigated species (*N. humator*, *N. investigator* and *N. vespilloides*) and decaying carrion served as baits. The carrion bait consisted of two pieces of pig's lung, one of these being 0—3 days old, the other one being 3—6 days old. Whenever traps were emptied, the older piece was replaced by a fresh one. The males used as baits were fed during trap emptying; they were exchanged monthly. *N. investigator* and *N. humator* males were taken from field catches. *N. vespilloides* males were laboratory-bred, sexually mature individuals, their daily activity was synchronized with the natural light/dark cycle.

Trapping with carrion baits (three traps) was done from Apr. 7 to Oct. 10 in 1986. Male-baited traps (N = 3 for *N. humator* and *N. vespilloides*, N = 2 for *N. investigator*) were used only during the time of year when sexually mature males were active in the field (*N. humator*: Apr. 22 to Jul. 21; *N. vespilloides*: Apr. 22 to Oct. 1; *N. investigator*: Jul. 21 to Oct. 22). When numbers of trapped individuals from different types of traps are compared, they refer to the same number of traps.

Statistics: The data were analyzed using χ^2 test. Null-hypotheses for attractivity of different traps were equal distribution between lung- and male-baited traps and a 1 : 1 sex ratio.

Results

1. Natural History of the Investigated Species

Numerous publications deal with the reproductive behaviour of *Necrophorus* beetles (FLETCHER 1881; PUKOWSKI 1933; VON LENGERKEN 1954; MILNE & MILNE 1976). The best and most detailed description is given by PUKOWSKI. To summarize, the species of this genus have specialized in burying carcasses of small birds and mammals to raise their brood on them. If several individuals meet at a carcass, they start fighting until only one pair of one species remains. Larger individuals have better chances to win intra- and interspecific combats (PUKOWSKI 1933; NIEMITZ 1978). Both individuals bury the carcass and prepare it together. The female places the eggs near the carcass and waits for the larvae to hatch in order to feed them. A male coming to a carcass alone buries it superficially and emits a pheromone to attract females (PUKOWSKI 1933). A single female on a carcass buries and prepares it by herself and lays eggs immediately; she can reproduce without a male's assistance (PUKOWSKI 1933; WILSON & FUDGE 1984; pers. obs.).

The preferred habitats of the three investigated species are forests. *N. humator*, the largest species (18—26 mm), reproduces from Apr. to early Jul., new-generation tenerals appear from Jul. on and are active until Sep. These adults hibernate and do not become sexually mature before the following spring. *N. humator* is nocturnal.

N. investigator (12—22 mm) reproduces from Jul. to Oct. The prepupae hibernate; tenerals of the next generation appear in mid-Jun. of the following year and become sexually mature in a relatively short time. Main activity of this species on carrion baits is in the evening hours around sunset (20.00 to 22.00 h MESZ).

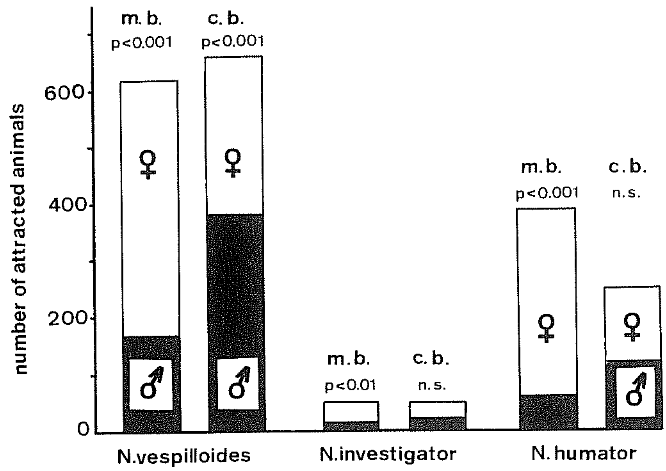

Fig. 1: Attraction of *Necrophorus* beetles to carrion baits (c. b.) and to scent-emitting conspecific males (m. b.). Sex ratios with statistical significance of the deviation from a one-to-one ratio (chi-square test)

The reproductive season of *N. vespilloides* (12—18 mm) ranges from Apr. to Sep. This period is sufficient for two successive generations. *N. vespilloides* hibernates as imago; it is unknown whether first-generation adults also survive the following winter. Individuals of this species are diurnal, maximum activity measured by means of carrion-baited traps is during afternoon and early evening (14.00 to 20.00 h MESZ).

2. Attractiveness and Sex Ratio

The trapping study shows that male *Necrophorus* beetles attract conspecifics of both sexes (Fig. 1). In an additional field experiment, females of *N. vespilloides* proved to be non-attractive for other burying beetles (unpubl. data). Males are at least as attractive baits for conspecifics as decaying carrion. Males are caught much more frequently in carrion-baited traps than in traps baited with conspecific males; the difference is statistically significant for the two most abundant species (*N. vespilloides* and *N. humator*: $p < 0.001$). In contrast, females of these two species are far more abundant in traps baited with conspecific males (*N. humator* and *N. vespilloides*: $p < 0.001$). In *N. investigator*, there are no significant trends for either sex.

There is a significant deviation from a one-to-one sex ratio in the male-baited traps of all three species (Fig. 1); it is most extreme in *N. humator*. In carrion-baited traps, the sex ratio was unbiased in *N. investigator* and *N. humator*, but male-biased in *N. vespilloides* (Fig. 1). For individuals that reacted to males of a different species (Fig. 2), the sex ratio is not always female-biased. The sex ratio of *N. humator* in traps baited with *N. investigator* males is still weakly ($p < 0.05$) female-biased, but in traps baited with males of *N. vespilloides*, there is no bias towards one sex neither in *N. investigator* nor in *N. humator*.

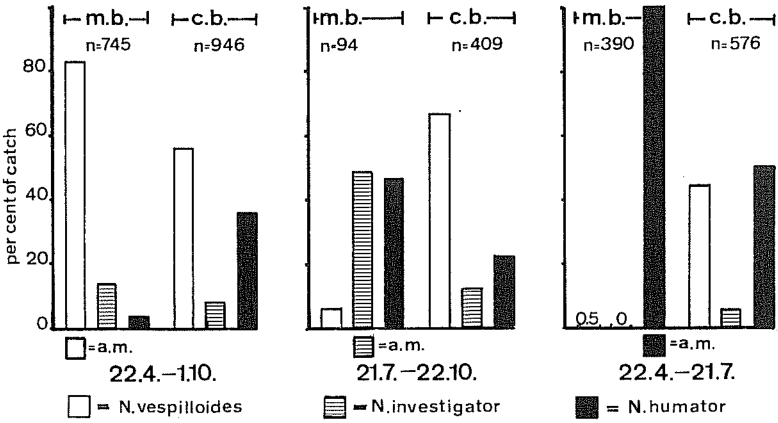

Fig. 2: Relative frequency of species attracted by *Necrophorus* males of different species (m. b.) and carrion bait (c. b.), respectively, in the same catching periods (a. m. = attracting species)

3. Species Specificity and Daily Rhythmicity

Attraction by pheromone-emitting males is largely species-specific, though individuals of different *Necrophorus* species are also attracted (Fig. 2). More than 80 % of the beetles attracted to *N. vespilloides* males are conspecifics; attraction by *N. humator* males is almost completely (> 99 %) restricted to members of their own species.

In the field, attraction to conspecific males occurs exclusively during certain periods of the day. The periods of male-mediated attraction in *N. humator* and *N. vespilloides* overlap very slightly (Fig. 3). Pheromone emission by males is

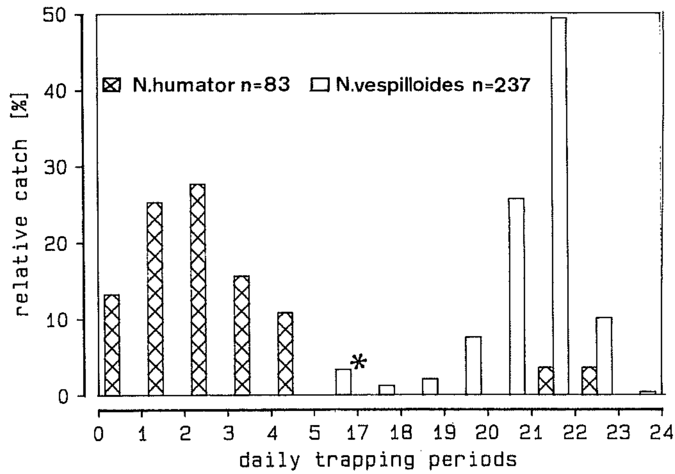

Fig. 3: Daily distribution of attraction of *Necrophorus* by conspecific males (asterisk: trapping period = 12 h; time given as MESZ)

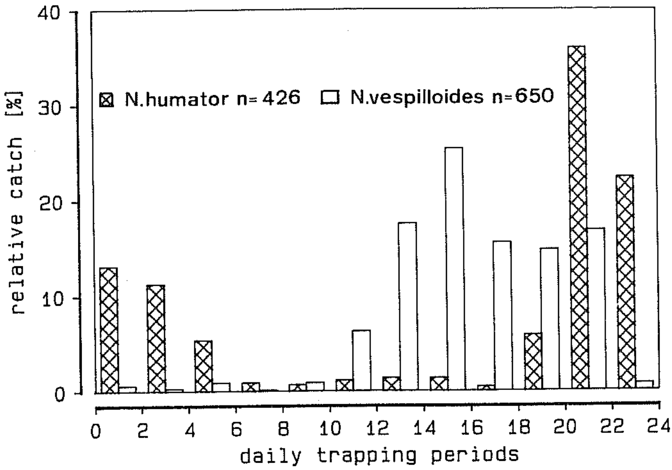

Fig. 4: Daily distribution of attraction of *Necrophorus* by carrion (time given as MESZ)

restricted to this period in *N. vespilloides* as well as in *N. humator*, as CORDES (unpubl. data) has shown from video recordings of single males.

Individuals of both species are active not only during the period of day when conspecific males emit pheromones (MÜLLER & CORDES 1987). *N. humator* flies around searching for carrion in the early evening; *N. vespilloides* is active mainly during afternoon and, in very small numbers, throughout the night. This can be seen from catches in carrion-baited time-sorting traps (Fig. 4). Since activity periods of both species overlap, opportunity for cross-attraction exists. Daily rhythms can account for specific attraction in these species only if individuals of both species are less responsive to male scent during the emission phase of the other species.

These reflections on species-specific attraction concern only two of the three investigated species. This is due to the fact that *N. investigator*, the third species, is a complete failure with respect to species specificity of male-mediated attraction (Fig. 2b). Half of the beetles caught in traps baited with males of this species are immature second-generation tenerals of *N. humator*. *N. investigator* seems to be very unspecific not only in scent emission, but also in its reaction to other species' scent signals: more than half of the *N. investigator* catches from male-baited traps had been attracted by *N. vespilloides* males.

One final result concerning species-specificity should be mentioned here. Remarkably, 'mis-reaction' to a pheromone-emitting male is more frequent if the reacting individual belongs to a larger species than the emittor (Fig. 2). The smallest species, *N. vespilloides*, is hardly attracted by males of different species, whereas a considerable proportion of *N. humator*, the largest species, reacted to males of *N. investigator* and *N. vespilloides*. *N. investigator*, a species of medium body size, was not found in traps baited with *N. humator* males, but was very abundant in traps baited with *N. vespilloides* males. These results are not due to different abundances of the three species (see Fig. 2). Attraction to scent-emitting males of a different species of larger body size is always less frequent than attraction to carrion. In contrast, species of larger body size than the sending male are overrepresented in male-baited traps. The only exception is *N. humator* that reacted to *N. vespilloides* males less frequently than to carrion baits.

Discussion

1. Attraction of Conspecifics by Pheromone-emitting Males

WILSON & KNOLLENBERG (1984) suggest that large carcasses as well as small ones represent mating opportunities for male sexton beetles. NIEMITZ (1978) even states that only carcasses serve as rendez-vous places for burying beetles. In contrast to these statements, our results strongly suggest that males without a carcass also emit pheromones in order to attract females. This applies to each of the three species we investigated. So in burying beetles, male scent emission does not depend on the presence of resources, as it does, for example, in scorpion flies (BORNEMISSZA 1964).

2. Benefits for the Calling Male (Sender)

The adaptive value for a male that employs scent emission in case he has stayed alone on a carcass is obvious. The 'sending' male can hide the carcass he has found from competitors (conspecific males, individuals of congeneric species, flies, small carrion-feeding vertebrates) and yet attract a conspecific female that enables him to reproduce on this carcass. Since females are actually attracted by the male scent, the benefit for a scent-emitting male without a carcass is obvious, too. If one of the females he has inseminated finds a carcass by herself and raises her young on it without a male's assistance, part of her eggs will probably be fertilized by sperm from the scent-emitting male she has copulated with before. This would mean an increase of the male's reproductive success without requiring his investment in parental care.

3. Possible Benefits for Attracted Individuals (Receivers)

The chance of finding a carcass might motivate the receivers' reaction to the scent under the condition that the attracted individuals are unable to distinguish between males that have secured a carcass and males that have not. If this is the only reason for attraction, then a minimum proportion of all scent-emitting males at a given time and place should have to be sincere in signalling they have found a carcass. Otherwise conspecific females could more profitably search for carcasses by themselves than fly to scent-emitting males. But obvious preferences for conspecific males indicate that attracted individuals of the sender's species can benefit even if the sender has not found a carcass.

a. Conspecific Females

Females of the sender's own species have the best chance to gain a benefit if they approach the sender. If the scent-emitting male has not found a carcass, the female gains a fresh sperm storage from copulation with the male. If he has found a carcass females can reproduce or, at least, feed on the carcass.

b. Conspecific Males

If the sender emits his scent near a carcass, the attracted male can reproduce there only if he manages to defeat the present 'owner' and to attract a conspecific female. So the male's chance of successful reproduction on another male's carcass is much smaller than it is for females. Like conspecific females, conspecific males might also gain a benefit if a male that has not found a carcass is the sender: (1) Males attracted to conspecifics could stay near the luring male without emitting pheromones themselves, waiting for an opportunity to intercept females arriving at the place and to copulate with them. A similar kind of behaviour has been found in *Anthonomus grandis* (HARDEE et al. 1969). (2) Several males might also emit pheromones together in order to amplify the signal. Efficiency of joint signalling is discussed by THORNHILL & ALCOCK (1983).

c. Individuals of Different Species

We assume that the attraction of different species is not simply due to 'errors' in the recognition of conspecific males. This means that the attracted individual must gain some benefit from its reaction to a male of a different species. This benefit can only be the detection of a carcass that can be used for reproduction or, at least, as a food source. Since individuals of different species must fight the resident male regardless of their own sex (interspecific fights are not exclusively intrasexual), males and females could be expected to react to different species in approximately the same numbers.

The chance to feed or reproduce on a scent-emitting male's carcass decreases greatly if the attracted individual is smaller than the sender. This would explain why hardly any individuals of smaller species are attracted by males of *N. investigator* and *N. humator*. On the other hand, individuals of larger species have good chances to repel the sender. Probably this is why *N. investigator* males attract considerable numbers of immature *N. humator* during autumn: A male of *N. investigator* is probably unable to keep a *N. humator* from feeding on the carcass. From this point of view it is astonishing that only very few individuals of *N. humator* reacted to *N. vespilloides* males. As the body sizes of the two species differ considerably, it is possible that they utilize different kinds, especially sizes, of carcass. So maybe carcasses of *N. vespilloides* males are not appropriate for the reproduction of *N. humator*.

When considering the benefits for attracted individuals that do not belong to the sender's species, one must keep in mind that trapping numbers can be strongly influenced by their life histories (daily activity patterns, reproductive seasons).

4. Species Specificity of Attraction and Isolating Mechanisms

One mechanism to achieve species specificity is a specific daily rhythm of pheromone emission and responsiveness to the scent. This phenomenon is described by HENDRIKSE (1977), ROELOFS & CARDE (1974), and other authors. In *N. vespilloides* and *N. humator*, specificity might be achieved by this mechanism (Fig. 3), if the females' responsiveness is restricted to the emission period of their own species. Their responsiveness must then change in the course of the day or according to their reproductive status. *Necrophorus* females obviously do adjust their responsiveness to different odour sources to their own reproductive status (WILSON & KNOLLENBERG 1984). But specificity can still be due to the use of different chemicals. In *Necrophorus*, specific long-range attraction cannot be interpreted as a pregamic isolating mechanism since individuals of different species meet on carcasses. So additional isolating mechanisms must exist.

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