

## Attraction of a Kleptoparasitic Sphaerocerid Fly (*Norrbonmia frigipennis*) to Dung Beetles (*Phanaeus* spp. and *Canthon* sp.)

E. Petersson<sup>1,3</sup> and J. Sivinski<sup>2</sup>

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*Norrbonmia frigipennis* (Diptera: Sphaeroceridae) is phoretic on dung-feeding scarab beetles (Coleoptera: Scarabaeidae). In this study we investigate the attractiveness of three beetle species, *Phanaeus ignius*, *P. vindex*, and *Canthon pilularis*, to the fly. Stationary, moving-dead, and live beetles were used. More flies were attracted to *Phanaeus*. However, this attractiveness may be due to the larger average size of *Phanaeus*. A preference for larger individuals was found within *Phanaeus*, though not within *C. pilularis*. Flies mounted beetles on the thorax and the elytra at similar rates. *Phanaeus* males that possessed horns did not attract more flies than did hornless ones, and there was no effect of host sex on attractiveness. In horned *Phanaeus*, about 11–16% of the flies mounting those beetles landed on the horn.

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**KEY WORDS:** visual attraction; dung beetles; Sphaeroceridae; *Norrbonmia frigipennis*.

### INTRODUCTION

A few members of the dipteran family Sphaeroceridae have been reported to ride on larger arthropods. The first record of such a fly was *Ceroptera rufitaris* (Meigan), clinging to the sacred scarab *Scarabaeus sacer* L. (Lesne, 1896). Since then phoretic sphaerocerids have been noted in North Africa (Chobaut, 1896), Central Africa (Roubaud, 1916; Villeneuve, 1916), Ceylon (Fletcher,

<sup>1</sup>Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden.

<sup>2</sup>USDA, Agriculture Research Laboratory, Insect Attractants, Behavior and Basic Biology Laboratory, P.O. Box 14565, Gainesville, Florida 32604.

<sup>3</sup>To whom correspondence should be addressed.

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1909; Collin, 1910), Australia (Monteith and Story, 1981), and North America (Moulton, 1880; Knab, 1915; Steyskal, 1971; Lloyd, 1979; Sivinski, 1983; Marshall and Montagnes, 1988). In the southeastern United States four species of Sphaeroceridae are phoretic kleptoparasites. Females oviposit in the buried dung caches of scarab beetles, most commonly those of *Phanaeus*, *Canthon*, *Geotrupes*, *Mycotrupes*, *Pelotrupes*, and *Onthophagus* species. Individuals of these genera often gather at high densities at animal droppings, thereby providing flies with opportunities for host choice. The sphaerocerids reach subterranean oviposition sites by riding on beetles near dung and following their host underground (Sivinski 1983). Males apparently ride to encounter females. Flies are frequently observed mating while riding on beetles (Sivinski, 1984).

Both male and female *Norrbombia frigipennis* (Spuler) arrive at dung and the surrounding area, where they either sit on nearby foliage or move about in the crevices of the faeces. Flies are attracted to sites of beetle activity but will occasionally land on stationary hosts. Boarding typically occurs on the ground, but *N. frigipennis* can fly up to and mount a beetle hovering over dung (Sivinski, 1983). On average, *Phanaeus* species are the most frequently ridden hosts (Sivinski, 1983), but it is not known whether flies are more attracted to *Phanaeus* or if some other factors are responsible. In this study we investigate the difference in attractiveness between *Phanaeus vindex*, *P. ignius*, and *Canthon pilularis*, the three most abundant diurnal drug-feeding hosts of *N. frigipennis*. We also present some data on the significance of beetle size and horns for attractiveness.

## MATERIALS AND METHODS

Four experiments were performed to investigate the attractiveness of the two beetle genera.

### Experiment I. Attraction to Stationary Dead Beetles in the Field

In the field four beetles (of two species) of about the same size were placed 10 cm from a small pile of pig manure (250 ml) (cf. Fig. 1). The four beetles were always arranged so that one faced north, one south, one west, and one east. The number of flies mounting the beetles was counted in 15-min (occasionally in 30-min) periods. After each such period the beetles were rotated clockwise. This study was made on 11–30 September 1992 and 14 May–8 July 1993, at a cattle pasture near Newberry, Alachua County, Florida, and along a road, near Shell Mound State Preserve, Levy County, Florida. *N. frigipennis* made up the majority of the flies mounting beetles; only occasionally were two other species observed [*N. fulvipennis* (Marshall and Norrbomb) and *Ceroptera sivinskii* Marshall].

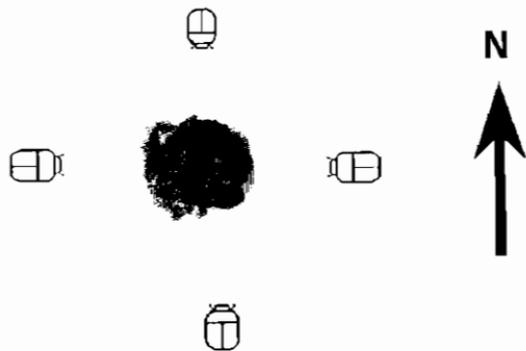


Fig. 1. Arrangements of dead beetles around a pile of pig manure (experiment I; see text).

### Experiment II. Attraction to Live Caged Beetles

Four to seven flies were presented with five beetles in plastic cylinders (cf. Fig. 2). Up to six vials were used at each trial and 25 trials were made on 18 September–23 October 1992 and 14 May–10 June 1993. Before the experiments the beetles were gently washed with a wet, soft toothbrush, to remove dung or mud remaining on the cuticula. Ten conditions were presented: single *Phanaeus* sp. or *C. pilularis*, a pair of either species (one large and one small beetle), pairs containing one of the three mixes of *P. vindex*, *P. ignitus*, and *C. pilularis*, and a beetle-less control. The vials were kept outdoors in the shade for approximately 6 h and were checked eight times during that time. We noted the number

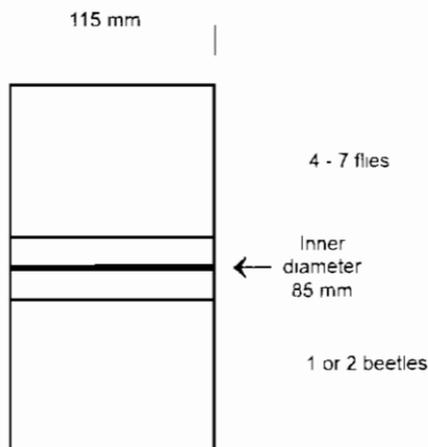


Fig. 2. The setup for the experiments with live beetles (experiment II; see text).

of flies in the top and bottom halves of the vials, as well as the number of flies riding and on which beetle(s) they rode. A beetle's activity was measured as the proportion of the checking times it was moving. After the experiment the vials were placed in a freezer. The next day the sex ratios of the flies were obtained, and the body length of the beetles (to the nearest 0.5 mm, using a ruler) and beetle wet weight (to the nearest 0.01 g) were determined.

### Experiment III. Attraction to Dead Moving Beetles

A pair of dead beetles was presented to 40 flies (20 males and 20 females) in a chamber. The beetles were glued on a transparent plastic sheet (circular, 60-mm diameter) on which a string was fastened. The beetles were pulled by hand on a layer of sand in a plastic transparent cylinder (cf. Fig. 3). We noted the number of flies that landed on each beetle, as well as whether the flies rode on the abdomen, the thorax, the head, or the horn (if present) or just followed the beetles. The beetles were pulled back and forth four times during each presentation (total length, about 2.4 m) at an average speed of  $0.0191 \pm 0.00097$  m/s (min = 0.0158 m/s, max = 0.0210 m/s;  $n = 256$ ), which is close to the maximum walking speed in the field. Eight combinations of beetles were used: large and small *C. pilularis*, large and small *Phanaeus*, *Phanaeus*, and *C. pilularis* (of about equal size), one of each *Phanaeus* species, and *Phanaeus* with and without horn (beetles of about equal size); in all cases the locations of the two beetles were alternated. One set of flies was thus presented with eight pairs of beetles, in a randomized sequence. Between each presentation the beetles were washed with a wet tooth brush, to remove dust and substances that might be placed on the beetles by the flies. This experiment was carried out indoors, and in total 32 trials were made, 7 December 1992–15 January 1993 and 26 May–9 June 1993.

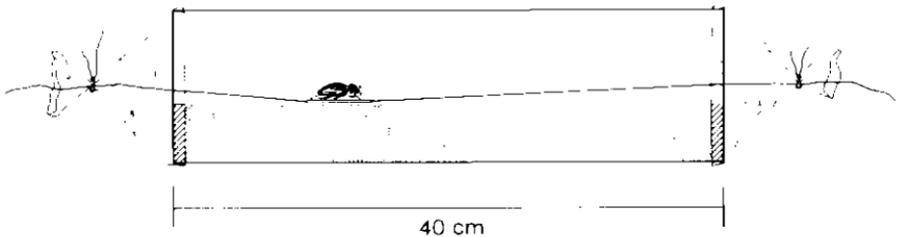


Fig. 3. The setup for the experiment with dead beetles that were pulled by hand (experiment II; see text). The inner diameter of the transparent plastic tube was 9.5 cm, the total volume was 69.4 cm<sup>3</sup>, and the free air space was 39.9 cm<sup>3</sup>. At both ends of the tube pieces of stockinette were fastened with a rubber band. The stockinette was knotted around the pulling string to prevent the flies from escaping.

### Experiment IV. Attraction to "Fly-Smelling" Beetles

In order to investigate whether the flies place some substance on the beetles that might attract or repel other flies, flies were presented with a pair of dead beetles (*P. vindex*, beetles of about the same size), one that had been mounted previously by flies and one "clean." The dead beetles were glued on a plastic sheet (as described in experiment III). One of the beetles was covered with a small plastic cup and the beetles were put in a small cage (15 × 15 × 15 cm) with about 100 flies for about 20 min. After that the beetles were taken out and the experiment was done using the cylinder described above (Fig. 3). Thirty-six to fifty flies (50% mated females and 50% mated males) were used, and each setup of flies was presented to beetles six to eight times during 8 hr. Between each trial the beetles were washed with 70% ethanol and were allowed to dry for at least 20 min before being reexposed to the flies in the cage. The locations of the two types of beetle were alternated. Numbers of flies landing on a beetle were counted, and the analysis was calculated on the proportion of the total number of flies mounting beetles. This experiment was carried out indoors, and in total 11 setups of flies were presented to pairs of beetles, 26 February–22 April 1993.

### Miscellaneous and Statistical Methods

Throughout the second, third, and fourth experiments, only laboratory-reared flies were used. The flies had no experience of beetles and were 3–5 days old. Before experiments III and IV and after experiment II, the beetles were dissected to establish beetle gender (the three most posterior sternites were carefully removed; the elytra was not affected by this). After that (not experiment II) the beetles were soaked first in methylene chloride and then in ethanol, for at least 12 h each, to remove environmental compounds that might influence host choice. The beetles were then dried at room temperature for 24 h.

Statistical analyses were made using SAS software for personal computers (SAS Institute, 1987), except Wilcoxon matched-pairs signed-ranks test (Siegel 1956), and Dunn's test (Hollander and Wolfe, 1973). Nonparametric methods were used for most of the analyses, due to nonnormal distributions. For the same reason the highly skewed data are presented as median (first quartile, third quartile). In a few cases residuals from linear regressions were used to adjust the data for a variable. The data were then arcsin-transformed before the computation of the linear regression and the adjusted values were back-transformed before reanalyses. In other analyses values from different pairwise comparisons were combined. Because some medians of these pairs differ, the data were standardized prior to analysis. All tests are two-tailed.

**Table 1.** Number of *Norrhombia frigidipennis* Flies per Minute and Beetle Landing on Dead Beetles Arranged Around a Pile of Pig Manure (cf. Fig. 1)<sup>a</sup>

Beetle species pair	No. flies/min/beetle	<i>n</i>	<i>z</i>	<i>P</i>
<i>Phanaeus vindex</i> <i>Canthon pilularis</i>	0.047 + 0.050 0.024 ± 0.042	72	2.31	<0.021
<i>Phanaeus ignius</i> <i>Canthon pilularis</i>	0.054 ± 0.051 0.017 ± 0.034	70	2.81	<0.006
<i>Phanaeus vindex</i> <i>Phanaeus ignius</i>	0.060 ± 0.046 0.056 + 0.043	69	0.56	ns

<sup>a</sup>Statistical test. Wilcoxon two-sample test. *n* = number of observation periods (15 min; occasionally, 30 min).

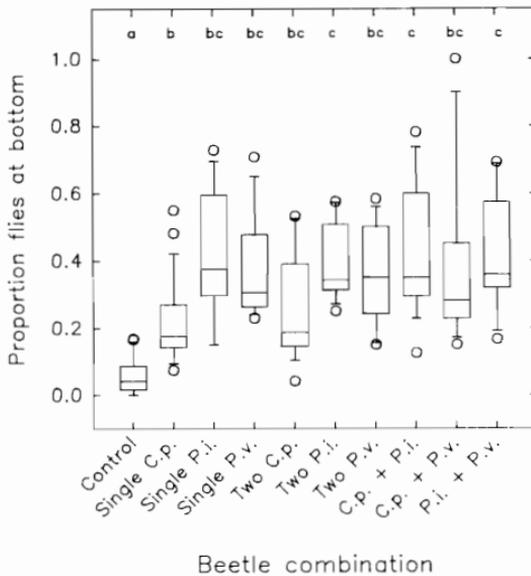
## RESULTS

### Experiment I. Attraction to Stationary Beetles in the Field

On average, the number of flies mounting per beetle and minute was greater for *Phanaeus* than for *C. pilularis* (Table 1). However, the distributions were highly skewed to the right, and for all three species the median equaled zero. No differences were found due to date, time of day, site, *Phanaeus* species, or cardinal points.

### Experiment II. Attraction to Live Caged Beetles

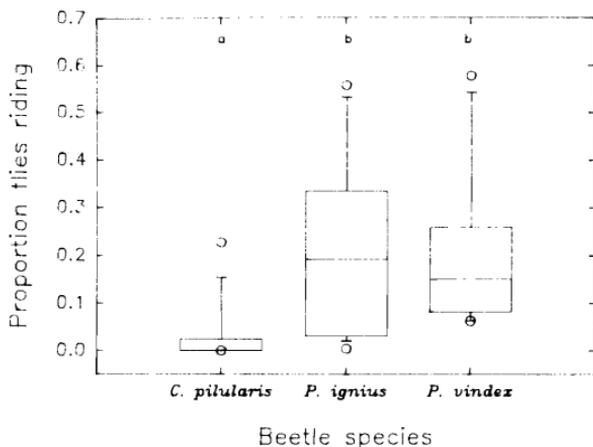
All vials that contained beetles had on average proportionally more flies in the bottom section, where the beetles were, than the control vials (no beetles). Beetle combinations containing any *Phanaeus* attracted on average more flies than those that contained only one *C. pilularis* specimen, although not always significantly (Fig. 4). A single *Phanaeus* sp. attracted more flies than a single *C. pilularis* (cf. Fig. 5). This difference between the "single-beetle vials" was eliminated if the data were adjusted for beetle size (body length; *Phanaeus* was on average larger than *C. pilularis*). However, within single *Phanaeus* sp. and single *C. pilularis*, no correlations were found between beetle size and proportion of flies in the bottom section [ $r_s = 0.104$  (ns) and  $r_s = 0.191$  (ns), respectively;  $n = 18$  in both cases]. On average, *Phanaeus* moved around more than did *C. pilularis* in the single vials ( $z = 2.34$ ,  $P < 0.02$ , Mann-Whitney *U* test; no difference between the two *Phanaeus* species,  $z = 0.98$  ns). However, *Phanaeus* was found to attract more flies even if the data were adjusted for this ( $z = 1.83$ ,  $P < 0.034$ , Mann-Whitney *U* test; no difference between the two *Phanaeus* species,  $z = 1.06$  ns). Similarly, more flies rode on *Phanaeus* sp. than on *C. pilularis* in the single-beetle vials ( $z = 3.90$ ,  $P < 0.001$ , Mann-



**Fig. 4.** Mean proportions of flies that were observed in the bottom section of the vials in the experiment with live beetles (experiment II; see text). Horizontal lines: medians, the upper and lower quartiles are the upper and lower edges of each box, respectively, and the end of the lower whiskers denotes the tenth percentile and the upper one the 90th percentile. Extreme values are marked with a circle. Boxes with the same letter are not significantly different according to Dunn's test; experimental error rate = 0.1.

Whitney  $U$  test; no difference between the two *Phanaeus* species,  $z = 1.21$ , ns), and this was true even if the data were adjusted for beetle activity ( $z = 2.87$ ,  $P < 0.005$ ). If the data were adjusted for beetle size (body length, using residual from linear regression), there was no difference in the proportion of flies that rode on *Phanaeus* or *C. pilularis* ( $z = 0.016$ , ns, Mann-Whitney  $U$  test; no difference between the two *Phanaeus* species,  $z = 0.003$ , ns).

In the vials containing different pairs of the three beetle species the flies ride more often on *Phanaeus* sp. than on *C. pilularis* (Table II). In none of the combinations did the two beetles differ in activity. The *P. vindex/C. pilularis* size ratio (body length) was  $1.23 \pm 0.22$  and the *P. ignius/C. pilularis* size ratio was  $1.14 \pm 0.19$ . There was a correlation between size difference and the difference in proportion of flies that rode on the two beetles ( $r_s = 0.608$ ,  $n = 13$ ,  $P < 0.02$ , and  $r_s = 0.576$ ,  $n = 12$ ,  $P < 0.03$ , respectively), i.e., the bigger *Phanaeus* was compared to *C. pilularis*, the more flies rode on *Phanaeus*. When the data were adjusted for this (using residuals from linear regression), still more flies rode on *Phanaeus* than on *C. pilularis* (*P.v.* versus *C.p.*,  $T =$



**Fig. 5.** Mean proportion of flies riding on beetles of the vials containing single beetles (experiment II; see text). Horizontal lines: medians, the upper and lower quartiles are the upper and lower edges of each box, respectively, and the end of the lower whiskers denotes the tenth percentile and the upper one the 90th percentile. Extreme values are marked with a circle. Boxes with the same letter are not significantly different according to Dunn's test; experimental error rate = 0.1.

**Table II.** Proportion Flies Riding on Beetle in the Pairs of Live Beetles; Experiment II<sup>a</sup>

<i>N</i>	Medium (1st and 3rd quartiles)		<i>t</i> value	<i>P</i>
13	Large <i>P. ignius</i> 0.086 (0.050, 0.125)	Small <i>P. ignius</i> 0.031 (0.000, 0.075)	61	<0.005
12	Large <i>P. vindex</i> 0.113 (0.031, 0.324)	Small <i>P. vindex</i> 0.063 (0.000, 0.100)	58	<0.012
15	Large <i>C. pilularis</i> 0.000 (0.000, 0.063)	Small <i>C. pilularis</i> 0.021 (0.000, 0.083)	29	>0.46
12	<i>P. ignius</i> 0.059 (0.035, 0.203)	<i>P. vindex</i> 0.073 (0.027, 0.181)	37	>0.38
12	<i>P. ignius</i> 0.058 (0.036, 0.200)	<i>C. pilularis</i> 0.010 (0.000, 0.025)	68	<0.01
13	<i>P. vindex</i> 0.036 (0.025, 0.125)	<i>C. pilularis</i> 0.021 (0.000, 0.025)	88	<0.001

<sup>a</sup>The results are given as the median (first and third quartiles). Number of beetle pairs to the far left. Wilcoxon matched-pairs signed-ranks test.

14,  $n = 13$ ,  $P < 0.05$ ; *P.i.* versus *C.p.*,  $T = 16.5$ ,  $n = 13$ ,  $P < 0.05$ ; Wilcoxon matched-pairs signed-ranks test). The size ratio of *P. vindex* to *P. ignius* was  $1.09 \pm 0.24$ , but there was no correlation between size ratio and the difference in proportion riding flies ( $r_s = 0.201$ ,  $n = 12$ , ns). If, however, the size ratio was calculated as large *Phanaeus*/small *Phanaeus* (i.e., regardless of the species, this always gives a value equal or greater than 1.0), there was such a correlation ( $r_s = 0.599$ ,  $n = 12$ ,  $P < 0.02$ ).

In the vials that contained two beetles of the same species, more flies rode on the larger one in the *Phanaeus* vials but not in the *C. pilularis* vials (Table II).

### Experiment III. Attraction to Dead Moving Beetles

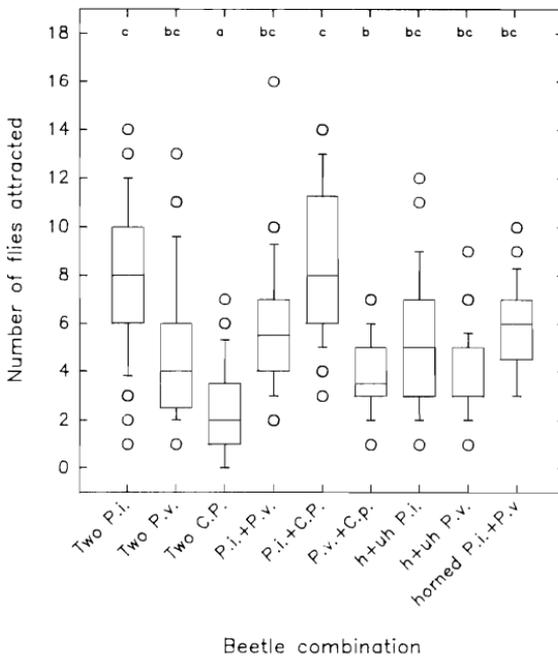
The combinations containing *Phanaeus* beetles attracted significantly more flies than those that contained only *C. pilularis* beetles (Fig. 6). However, in the pairs that consisted of one *P. vindex* and one *C. pilularis* of about equal size, there was no difference in attractiveness, whereas *P. ignius* was more attractive than *C. pilularis* (Table III). In the pairs that consisted of one large and one small beetle of the same genus, the larger *Phanaeus* attracted more flies than the smaller one, but for *C. pilularis* no such difference was found. No difference was found between the two *Phanaeus* species (Table III). In the pairs that consisted of one horned (always a male) and one hornless *Phanaeus* (mostly females), no difference was found in attractiveness. When only beetle gender was regarded, no difference was found between the sexes in the proportion flies mounting [*P. vindex*—males, 0.111 (0.086, 0.187),  $n = 34$ , females, 0.104 (0.078, 0.187),  $n = 28$ ;  $z = 1.11$ , ns; *P. ignius*—males, 0.354 (0.122, 0.476),  $n = 26$ ; females, 0.389 (0.186, 0.452),  $n = 20$ ;  $z = 1.23$ , ns; *C. pilularis*—males, 0.050 (0.050, 0.100),  $n = 10$ ; females, 0.050 (0.025, 0.050),  $n = 12$ ,  $z = 0.14$ , ns; Mann-Whitney *U* test].

On average, the flies equally preferred to mount the beetles on the thorax or the elytra (Fig. 7). *C. pilularis* was never mounted on the head, as were hornless *Phanaeus*. No flies mounted horned *Phanaeus* on the head; rather, those beetles were mounted on their horn. Proportionally more flies mounted horned *P. vindex* on the horn compared to *P. ignius* ( $\chi^2 = 8.98$ ,  $df = 3$ ,  $P < 0.05$ ).

In this experiment no effects were found concerning the date, time of day, or the sequence of presenting the beetle pairs.

### Experiment IV. Attraction to "Fly-Smelling" Beetles

No difference in attractiveness was found between beetles that had been mounted by flies and unmounted beetles ( $T = 27$ ,  $n = 11$ , ns; Wilcoxon matched-



**Fig. 6.** Total number of flies that mounted any of the beetles in each combination of the pairs in the experiment with dead moving beetles (experiment III; see text). Horizontal lines: medians, the upper and lower quartiles are the upper and lower edges of each box, respectively, and the end of the lower whiskers denotes the tenth percentile and the upper one the 90th percentile. Extreme values are marked with a circle. Boxes with the same letter are not significantly different according to Dunn's test; experimental error rate = 0.1.

pairs signed-ranks test). Previously mounted beetles attracted on average  $0.055 \pm 0.034$  fly at each trial, and  $0.058 \pm 0.033$  unmounted fly. Nor did we find any effects concerning the date, the time of day, or the number of flies used.

## DISCUSSION

The results in this study show that the sphaerocerid fly *N. frigipennis* was attracted to *Phanaeus* and *C. pilularis* dung beetles. Because the dead beetles had soaked in both methylene chloride and ethanol, it is unlikely that any attractant volatile substance remained. Thus, the attractiveness in the experiments with dead beetles was mainly visual. Apparently dead stationary beetles attracted fewer flies than dead moving beetles, which attracted fewer flies than living

Table III. Proportion Flies Mounting Beetles in the Pairs of Dead Beetles; Experiment III<sup>a</sup>

<i>N</i>	Medians (1st and 3rd quartiles)		T value	<i>P</i>
22	<i>P. ignius</i> (horned) 0.200 (0.125, 0.375)	<i>P. ignius</i> (unhorned) 0.250 (0.150, 0.400)	51	ns
21	<i>P. vindex</i> (horned) 0.050 (0.025, 0.100)	<i>P. vindex</i> (unhorned) 0.050 (0.025, 0.075)	78	ns
33	Large <i>P. ignius</i> 0.475 (0.150, 0.650)	Small <i>P. ignius</i> 0.350 (0.175, 0.475)	61	<0.01
41	Large <i>P. vindex</i> 0.125 (0.050, 0.200)	Small <i>P. vindex</i> 0.100 (0.050, 0.150)	184.5	<0.02
22	Large <i>C. pilularis</i> 0.050 (0.050, 0.100)	Small <i>C. pilularis</i> 0.050 (0.025, 0.050)	47.5	ns
30	<i>P. ignius</i> 0.400 (0.350, 0.600)	<i>P. vindex</i> 0.475 (0.225, 0.525)	133	ns
24	<i>P. ignius</i> (horned) 0.200 (0.125, 0.350)	<i>P. vindex</i> (horned) 0.200 (0.125, 0.275)	104.5	ns
25	<i>P. ignius</i> 0.575 (0.175, 0.650)	<i>C. pilularis</i> 0.250 (0.100, 0.400)	37	<0.01
41	<i>P. vindex</i> 0.075 (0.050, 0.100)	<i>C. pilularis</i> 0.075 (0.025, 0.100)	240	ns

<sup>a</sup>The results are given as the median (first and third quartiles). Number of trials to the far left. Wilcoxon matched-pairs signed-ranks test.

beetles. Thus, the movement of the beetles probably is important to the flies, either as a cue for recognizing the beetles or for deciding whether to mount an already recognized beetle. We attempted to investigate whether the flies were attracted to the sound of flying beetles, but no response to the sound were noted. Nor did flies seem to "mark" beetles with chemicals, because "smeared" and "clean" dead beetles were equally attractive. Nevertheless, living beetles most likely gave flies additional cues, which might still be either olfactory, acoustic, or some additional visual cue, or any combination of all three.

The experiments in this study provide evidence that *Phanaeus* is more attractive to the flies than *C. pilularis*. Most of this greater attractiveness is due to the larger average size of *Phanaeus*. However, in the experiment with live beetles, where the flies were allowed to choose between the two genera, *Phanaeus* on average attracted more flies than *C. pilularis*, even when the effect of beetle size was considered. In the experiment with dead stationary beetles (which were of about the same size), more flies landed on *Phanaeus* than on *C. pilularis*. Only in the experiment using dead moving beetles was there no significant

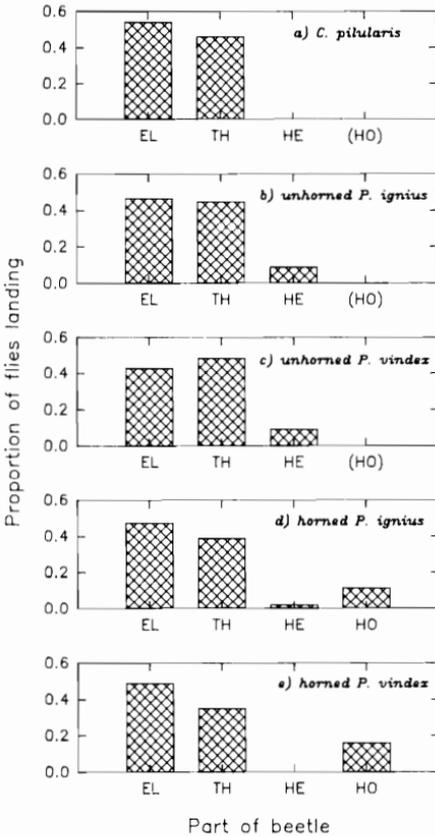


Fig. 7. The frequency of flies mounting different parts of the beetle bodies. Data from the experiment with dead moving beetles (experiment III; see text). EL, elytra; TH, thorax; HE, head; HO, horn.

difference between the number of flies choosing *Phanaeus* and that choosing *C. pilularis*, although the values were higher for *Phanaeus*. No difference between the two *Phanaeus* species could be detected. It is, however, our impression from the field that *P. vindex* attract more flies than do *P. ignius*. According to the result in this study, this might be an effect of the greater average size of *P. vindex*.

On average, *Phanaeus* attracted about 10% more flies than did *C. pilularis*. Some data from the field show a much greater difference, Sivinski (1983) found that about 40% of the flying *Phanaeus*, but only 7% of the flying *C. pilularis* carried flies. This discrepancy between laboratory and field results may suggest that *Phanaeus* and *C. pilularis* are about equally attractive to the flies when walking on the ground but that *Phanaeus* are preferred when flying. The cuticula of *C. pilularis* is smoother than that of *Phanaeus*, which probably make *C. pilularis* harder to ride on in the air. Thus *Phanaeus* is more likely to be important to the flies for dispersal, while both beetle genera are probably about equally

useful to the flies for getting access to mates (males) or egg-laying opportunities (females). This is consistent with earlier findings. Sivinski (1984) found that flying scarabs carried proportionally more female flies than walking beetles, i.e., female flies use beetles for dispersal and for reaching new egg-laying sites. Such a phoretic relationship is not unusual within the insects, and it is rather common among entomophagous insects (Clausen, 1976), mites (Mitchell, 1970), and pseudoscorpions (Beier, 1948; Zeh and Zeh, 1992). What makes these sphaerocerid flies curious is that they are kleptoparasitic, whereas the other arthropods mentioned are parasitic or parasitoids or simply use their host for transportation, i.e., dispersal. A few other kleptoparasitic and phoretic dipterans have been reported to ride on spiders (Sivinski, 1985). In these species the majority of the riding flies is also female. It is, however, unlikely that those flies are using the relatively stationary spiders for dispersal. Alternative explanations might be that the flies on flying beetles are "old groups" from which males have been chased or that males do not feed on spider prey and thus this is a non-resource-based mating system.

In both the experiment with live beetles and the experiment with dead moving beetles, the larger beetle attracted more flies than the smaller one in the *Phanaeus* pairs but not in the *C. pilularis* pairs, although, on average, the size ratios in all pairs were statistically the same. This might suggest that the relationship between attractiveness and the possibility of being detected and beetle size is not linear. It might be that, above a certain beetle size, the flies are more able to judge the difference in size. Another explanation might be that the size of a *C. pilularis* beetle is not important; the resource available to the flies is about the same, independent of beetle size. In *Phanaeus*, on the other hand, larger beetles may gather a larger amount of manure, which means that the flies get access to a larger resource as well. A third possibility is that the attractiveness of the beetles to the flies has some adaptive background. When arriving at the dung pile *Phanaeus* land close to the dung and usually go under the dung. *Canthon pilularis*, on the other hand, land at a longer distance and climb up on the dung pile and start to make a ball of the dung. This means that *C. pilularis* is exposed to the flies for longer periods.

There was no difference in attractiveness between horned and hornless *Phanaeus*, which shows that there is no difference between the sexes of *Phanaeus* (only males possess horns, although there are hornless males as well). The flies, however, frequently mounted horned *Phanaeus* on their horn (cf. Fig. 7). Sivinski (1983) reported that this behavior may be more common in male flies, probably enabling them to occupy a better outlook for mate searching.

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