Ecological Entomology (1983) 8, 419–426

The natural history of a phoretic sphaerocerid Diptera fauna

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ABSTRACT. 1. Three species of phoretic Sphaeroceridae kleptoparasitize the dung caches of scarab beetles in north Florida. *Ceroptera sivinskii* Marshall intercepts beetles under dung, then accompanies them into their burrows. *Borborillus frigipennis* (Spuler) rides on ball rolling and tunnelling scarabs. It perches on beetles both underground and in flight. *B.singularis* (Spuler) is similar in habits but is principally nocturnal.

2. Kleptoparasitism is probably a means of escaping environmental decay and competition in 'parent' faeces. Nonscarab competitors and predators are less abundant in beetle stored dung, and *Borborillus* spp. are among the few spaerocerids that flourish when large, rapidly developing calypterate flies are abundant.

3. Since oviposition in *B.frigipennis* occurs only underground, phoresy is an inexpensive and safe means to maintain contact with hosts. Males ride in order to find mates.

Key words. Sphaeroceridae, Scarabaeidae, Sarcophagidae, kleptoparasitism, phoresy, competition, *Borborillus, Ceroptera, Pterogramma.*

Introduction

A few small flies ride about on relatively gargantuan fellow arthropods. Mounts range from New Guinean asilids to giant African millipeds, but the first record of such a fly, and the first animal to be dubbed 'phoretic', was a sphaerocerid, *Ceroptera rufitarsis* (Meigan) (= *Limosina sacra*), clinging to the sacred scarab *Scarabaeus sacer* L. (Lesne, 1896). Since then, sphaerocerids riding dung feeding scarabs have been noted in North Africa (Chobaut, 1896), Central Africa (Roubaud, 1916; Villeneuve, 1916), Ceylon (Fletcher, 1909; Collin, 1910), Australia (Monteith & Story, 1981), Central America (G. Fritz, personal communication) and North America (Moulton, 1880; Knab, 1915; Steyskal, 1971; Lloyd, 1979). Considering the novelty of phoretic flies surprisingly little is known of their biology. The presumably universal *raison d'être* of sphaerocerid symbiosis, oviposition in the beetles' buried caches, has been observed in only a pair of old world species (Roubaud, 1916; Monteith & Story, 1981). The following describes hosts, activity patterns, actions aboard beetles, development, and sex ratios for a common southeastern United States phoretic sphaerocerid *Borborillus frigipennis* (Spuler) (see Fig. 1). Brief contributions to the bionomics of two less abundant species, *Borborillus singularis* (Spuler) and *Ceroptera sivinski* Marshall, are made and the evolution of phoresy discussed. The advantages of kleptoparasitism are examined through the oviposition patterns of a sympatric 'facultatively kleptoparasitic' sarcophagid *Ravinia derelicta* (Walker).

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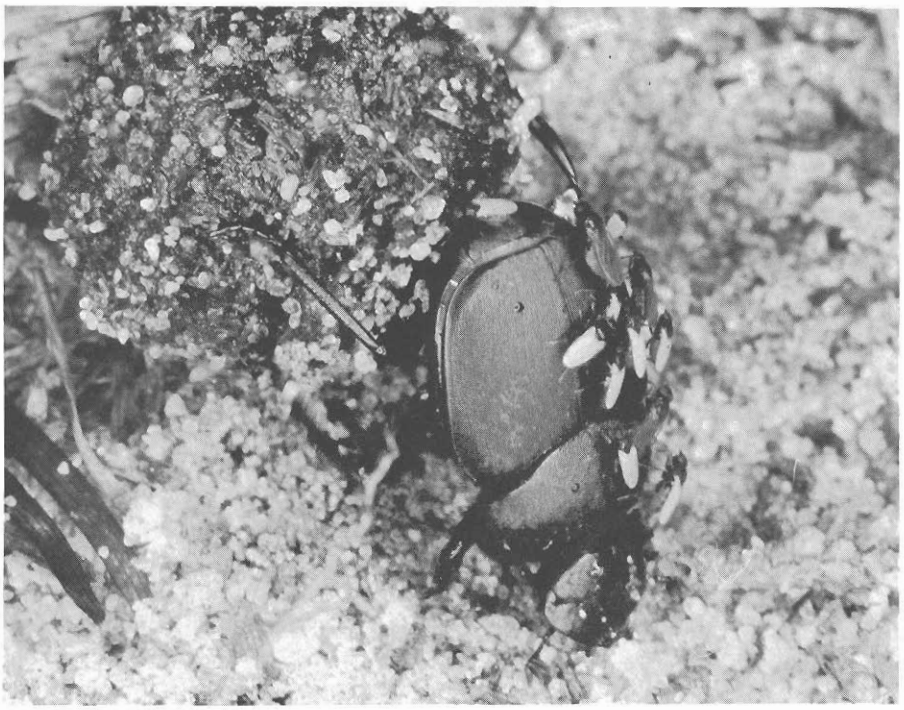

FIG. 1. *Borborillus frigipennis* and *B.singularis* (large darker flies) mounted on the ball rolling scarab *Canthon pilularius*. (Photograph by J. E. Lloyd.)

Methods

Field observations were made primarily in Alachua and Levy Cos., Florida. Underground behaviours were observed by confining flies and hosts in 11 cm × 13 cm × 1.5 cm plexiglass sandwiches containing soil and dung. Flies were reared in plastic cups containing damp, sterile sand at a constant temperature (25 ± 1°C).

Arthropod diversity and abundance in 140 beetle dung caches and the seventy-eight cattle excrements from which the caches originated were compared in Alachua Co., Florida. When dung 'balls' were collected, a similar size sample was taken from an estimated or known site of cache construction on the 'parent' scats. A small core of the ball and parent sample was removed, weighed, dried at 100°C for 24 h, and weighed again. The water content of the core was calculated and used to estimate the dry weight of the complete sample. After weighing, the major samples were placed on damp sand in a plastic cup and kept at a constant temperature (25 ± 1°C). Cups were checked daily for insect emergence for periods of at least 21 days.

The facultative kleptoparasitism of sarcophagids can illuminate the evolution of obligate kleptoparasitism in sphaerocerids. In order to examine these flies, pig faeces were frozen to destroy any previously present arthropods. These were placed in a deciduous forest in Manatee Springs State Park, Levy Co., Florida. When a ball-rolling scarab, *Canthon pilularius* (L.), had completed construction of its ball, rolled it away and begun burial, the dung ball was collected and samples of the construction site and of the adjacent area of the experimental scat were immediately taken. These were obtained by pressing a small round plastic container into the faeces. The resulting sample had a similar surface-to-volume ratio as a dung ball, thereby standardizing the larvi-positional opportunities per gram of the three corresponding samples (on the average for every cm^2 of ball surface there is 3.4 cm^3 of dung volume). Ten sets of balls and samples of the parent scat were examined for water content and insect fauna.

Results

In north Florida, four species of Sphaeroceridae kleptoparasitize the buried dung caches of scarabs, i.e. lay eggs in the food or brood stores of the beetles. Of these four flies, three are phoretic (an undescribed *Pterogramma* sp. follows 1–3 cm behind dung moving scarabs; see Table 1).

(a) *Ceroptera sivinskii* is an unusual, virtually subterranean fly, and the sole representative of its genus in North America (Marshall, 1983). It waits under dung to intercept scarabs burying stores under or at the edge of faeces (i.e. *Geotrupes egeriei* Germar, *Copris minutus* (Drury) and *Phanaeus vindex* MacLeay), although a single male was taken from the back of *Canthon pilularius*, a species that forms a spherical dung ball which it rolls *c.* 1–10 m before burial. A specimen was reared from the dung cache of a *Copris* sp. and a mating pair was discovered on the back of an unearthed *Phanaeus vindex*. *C.sivinskii* rides principally on the dorsal surface or on the pygidium. Its eyes are reduced (greatest diameter = half height of head), a common condition in sphaerocerids living underneath droppings. Of forty-seven nonphoretic flies taken from under dung, thirty (64%) had eyes with diameters of 0.5 or less the height of the head. Only three (2%) of 168 sphaerocerids from the dung surface had reduced eyes. It appears that the dung habitat is sub-divided, and that underdung specialists have trogophile-like eye reductions. The known period of activity of *C.sivinskii* spans January to May. Specimens have been seen on both diurnally and nocturnally active hosts in Alachua Co., Florida.

(b) *Borborillus frigipennis* is evident in north Florida from spring through to autumn (see Fig. 1). Adults were absent only in the months of December, January and February (however, no extensive searches were made during December). Flies of both sexes arrive at dung and the surrounding area, where they either sit on surrounding foliage or 'investigate/feed' in the crevices of faeces (see Fig. 2). Scarabs encountered on dung and ridden by *B.frigipennis* are the burrowers *Phanaeus vindex*, *P.igneus* MacLeay and *Onthopagus* spp. (including the recently imported exotic, *O.taurus* Schreber) and the rollers *Canthon pilularius* and *Boreocanthon depressipennis* (Le Conte). They are attracted to sites of beetle activity, but will land on a stationary host (although apparently not in the numbers or with the same alacrity as on an active one). Several once mounted an inappropriate beetle, a large green cetonine scarab crawling past faeces. Boarding typically occurs on the ground, but *B.frigipennis* can fly up to and mount a beetle hovering over dung (seen only in the case of flying *Phanaeus vindex*). On walking beetles, flies spend most of their time on the dorsal surface. When on *Canthon* spp. and other rollers which push dung caches with the posterior tilted upward, flies tend to aggregate on the highest (hindmost) point of the host. Frame by frame analysis of a film of

TABLE 1. Scarab hosts of kleptoparasitic Sphaeroceridae in Florida.

Fly	Beetle
Borborillus frigipennis	*Boreocanthon depressipennis* *Canthon pilularius* *Phanaeus vindex* *Phaneus igneus* *Onthophagus* spp.
Borborillus singularis	*Copris minutus* *Canthon pilularius*
Ceroptera sivinskii	*Geotrupes egeriei* *Copris minutus* *Phanaeus vindex*
Pterogramma sp. (non-phoretic)	*Canthon pilularius* *Glaphyrocanthon v. viridis* *Phanaeus igneus*

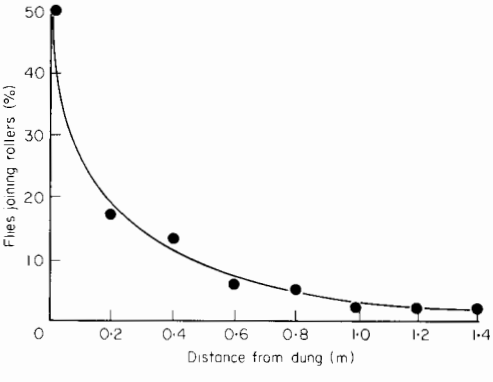

FIG. 2. Distance from dung at which 101 *Borborillus frigipennis* mounted rolling scarabs. Numbers on *x* axis are meant to include all distances between it and the lower adjacent value.

four *B.frigipennis* riding a more level dung pusher, *Phanaeus igneus*, showed 1292 instances of flies on the host's thorax (29% of total), 2596 instances on the anterior elytra (58%) and 591 instances on the posterior elytra (13%). *B.frigipennis* and other sphaerocerids often move to the posterior and sometimes underneath burrowing beetles. Sexual dimorphism in location is not typical, but males are found more often on the horns of male *Phaneus* spp. (perhaps occupying high ground for better mate searching) and females after being pursued by males sometimes spend unusual amounts of time on the sides or underneath hosts. *B.frigipennis* rides beetles in flight. They are usually located on the posterior margin of the thorax, although if the thorax is crowded, some will move forward. Such flies are often those that have ridden a beetle underground, then regained their seats as the scarab left the area. *Phanaeus vindex* and *P.igneus* are the most commonly ridden hosts. Of 261 flying *Phanaeus* spp. surveyed specifically for riders, 104 (40%) carried flies, for an overall average of 1.2 flies per flying scarab. Of 321 flying *Canthon pilularius*, only twenty-three (7%) bore phoretics, for a mean of 0.1 flies/beetle (census during spring 1980, Alachua Co., Florida).

Scarabs seldom react to the presence of phoretic passengers. It is difficult to imagine an effective defence. Flies are agile, tenacious, and of a rubbery constitution that makes them difficult to crush. The very magnitude of their abilities to maintain contact suggests an evolutionary past when relations between kleptoparasite and host were less restrained (however, scarabs scrape perching calypterate flies from their backs using their mid-legs; see Discussion).

Both sexes of *B.frigipennis* accompany scarabs underground. Observations in the laboratory suggest that once a beetle has blocked its burrow with earth, adult flies do not (cannot?) dig to the surface. If they leave, they do so in the company of their host (this in contrast to newly eclosed adults, which can squeeze through soil). The amount of time a fly spends underground depends on the species and sex of its host and whether the cache will be used by the scarab for food or oviposition. Among the more common mounts, male *Phanaeus* spp., when not feeding, often spend less than an hour in subterranean sexual searches, and in *Canthon pilularius*, food balls take *c.* 1–3 days to consume, but brood balls are quickly abandoned (see Matthews, 1963). Individuals of *Copris* spp. stay buried with larvae throughout the development of their offspring (see Halffter & Matthews, 1966).

In samples of manure from the field, fifty-two *Borborillus frigipennis* have been reared from scarab dung caches, but none from parent dung masses. Note the attenuated fauna of buried dung (Table 2), these reductions may be important in the evolution of kleptoparasitism (see discussion section 'Advantages of kleptoparasitism'). In the laboratory *B.frigipennis* can be consistently reared from arthropod-free cow faeces and in the absence of a scarab, showing that larvae feed on faecal material and are not predators or parasitoids of host beetles. Oviposition occurs underground (see Discussion section 'The advantages of phoresy'). At 26°C, larval development requires a minimum 7 days, with the pupal stage lasting a minimum of another 7 days. Interestingly, the developmental period exceeds the 'life expectancy' of common dung caches. The food balls of *Canthon pilularius*, for example, rarely last more than 3 days. It seems likely that larvae continue development on the 'scraps' of the dung cache smeared into the soil and associated bacteria. Newly mated females kept on a surfeit of arthropod-sterile cow manure produced a mean of 47.3 offspring over a lifetime (n = 7, range 84–28, s = 22.0). Adults in captivity seldom lived longer than 10 days.

The sex ratio of *B.frigipennis* reared in captivity is significantly female biased (410:528, 0.44 male; H_0:sex ratio is even, χ^2 14.84, $P < 0.005$). Field collections are female biased as well; from the backs of walking scarabs, 578:624, 0.48 male; from the backs of flying scarabs, 60:105, 0.36 male; from the surface of dung 60:91, 0.40 male. There is no sexual dimorphism in adult size (the mean body length of twenty-four randomly chosen males was 0.999 that of thirty-one females; the mean of thirty-one male wing lengths, 1.17 mm, is essentially identical to a mean of thirty-eight female wing lengths, 1.16 mm).

(d) *Borborillus singularis* is sympatric with

TABLE 2. The numbers of various arthropod types and their per gram frequency as reared from above ground ungulate faeces (control) and buried caches of *Canthon pilularius*, *Onthophagus* spp., *Phanaeus vindex* and *Copris minutus*. Insects were categorized as belonging to the suborder Nematocera of the Diptera, nonphoretic sphaerocerids, phoretic sphaerocerids of the genus *Borborillus*, the suborder Cyclorrhapha (Diptera) exclusive of Sphaeroceridae, insects believed to have predaceous larvae, insects believed to have parasitoid larvae. The right-hand column is the ratio of arthropods per gram dry-weight control faeces (No./gC) divided by the number of arthropods per gram dry-weight reared from the cache of dung feeding scarabs (No./gDB).

	Buried dung balls (412 g)	Control (342 g)	No./gC / No./gDB
Nematocera	38 0.09	350 1.02	11.3
Nonphoretic Sphaeroceridae	51 0.12	282 0.82	6.8
Phoretic *Borborillus* spp.	70 0.17	0 0	0
Cyclorrhapha (Diptera)	154 0.37	370 1.08	3.7
Predators	2 0.005	10 0.03	6.0
Parasites	12 0.03	30 0.09	3.0

B.frigipennis in Alachua Co., Florida. It is distinguishable from *B.frigipennis* even at a distance by its brownish colour and darker wings and seems likely to be one of the unidentified phoretic species mentioned by Moulton (1880). *B.singularis* is principally nocturnal, but can be active during the day, particularly in spring and autumn. At these times it constituted *c.* 2% of the phoretic *Borborillus* fauna. During the day it was found only on the rolling scarab *Canthon pilularius*. Individuals were reared, however, from the dung cache of a nocturnal burier, *Copris minutus*. *B.singularis* was never found on a flying scarab.

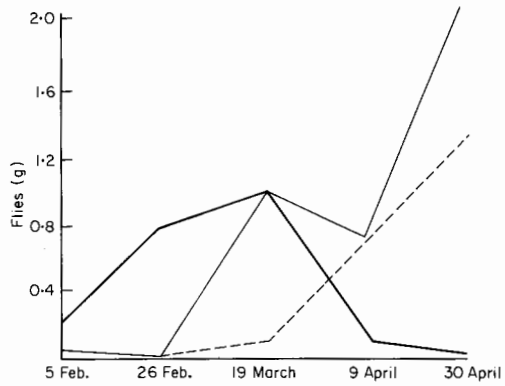

FIG. 3. Numbers of various dipteran taxa reared from dung (both the 'parent' faeces and beetle cache samples whose inhabitants are listed in Table 2) over time. The heavy black line represents nonphoretic sphaerocerids, the dashed line phoretic sphaerocerids of the genus *Borborillus* (i.e. *B.frigipennis* and *B.singularis*), and the thin solid line calypterate flies, principally Sarcophagidae. Data are from 1980 in Alachua Co.

Discussion

The advantages of kleptoparasitism

The obligatory theft of resources from a much larger animal presents problems. Hosts may defend their goods and the number of resource patches is decreased, since only those in the host's possession are available for use. However, avoidance of environmental decay and competition are advantages to kleptoparasitism that could overcome its costs.

(a) *Avoiding environmental decay*. As dung loses moisture, it becomes a hostile environment for immature Diptera (see Oldroyd, 1964, for a discussion of moisture's importance

to flies). In particular, the dry, hard crust of aging faeces might prevent larvae or eggs from reaching the more hospitable and stable interior of a dropping.

Scarabs, especially rollers, expose soft, moist dung faeces during cache preparation. Such surfaces are useful to flies, as is suggested by the larviposition habits of Sarcophagidae that facultatively kleptoparasitize scarabs. *Ravinia derelicta* follows, rides and larviposits in beetles' dung balls, principally those of the roller *Canthon pilularius*. When numbers of adult flies emerging from beetle caches and different sites on the parent faeces were compared, significantly more flies were reared from dung balls and samples from the scarabs' work face than in the adjacent surface of faeces (Table 3). The greater number of flies obtained from the dung balls and working surfaces could be due to the fact that both offer soft sites for larviposition.

An alternative explanation, that flies intend larvae to end up in dung caches and place juveniles near construction sites, seems unreasonably complex, since there is no obvious interference competition between females ovipositing directly on the ball.

(b) *Escape from competition.* Dung, particularly its large bacterial component, is rich food that attracts large numbers of diners (e.g. Bartholomew & Heinrich, 1978; human faeces are about half bacteria by volume, Rabkin & Silverman, 1979). Certain scarabs have evolved means of avoiding competition by moving faecal fragments away from concentrations of competitors, a 'motive' reflected in the depths at which various types of beetles bury their caches. Those that bury caches at the edge or under dung often put dung 10 cm or more underground (Halffter & Mathews, 1966; Woodruff, 1973). Rollers, on the other hand, have shallower burrows. *Canthon pilularius* buries dung balls at only *c.* 2 cm, but the shallow burrows are often several metres from the parent dung mass (Mathews, 1963). Shallow and deep digging is consistent with avoidance of competition. Rollers escape horizontally and need only cover their caches from view and scent. Buriers escape vertically and put distance between their stores and competitors' by constructing deep burrows. As might be expected, the numbers of potential competitors reared from the dung stores of scarabs are much less numerous than those raised from parent dung masses (recall Table 2).

Kleptoparasitic sphaerocerids have gained access to these undercolonized faecal fragments, and one large competitor, the beetle, replaces the many smaller. The effect of a scarab on *Borborillus frigipennis* fecundity is considerable. Numbers of adults emerging decrease by a mean 63% when a *Canthon pilularius* is added to a cup containing a female fly and faeces. However, seasonal distribution of Sphaeroceridae suggests that the competition of the scarab is not the equal of the summed appetites of other competitors. The Diptera fauna of north Florida changes during the late winter and early spring (Fig. 2). Nematocera, particularly Sciaridae, and non-kleptoparasitic Sphaeroceridae become less numerous. At the same time, calypterates, principally Sarcophagidae, increase. It is possible that the large, rapid-growing flesh flies competitively exclude the smaller Diptera (the sarcophagid *Ravinia derelicta* in the laboratory goes from larvae deposited by the female to pupae in 3 days, less than half the development time required by sphaerocerids).

TABLE 3. Differences in the number of Sarcophagidae reared from the dung caches of *Canthon pilularius*, the site of the ball's construction, and the adjacent faecal surface. All samples are of pig manure and were taken in deciduous forests in Levy Co., Florida.

	n	Sarcophagids	Dry weight of summed samples (g)	Flies/g
Canthon pilularius dung balls	10	298	32.1	12.9
Construction site	10	229	19.6	11.6
Sample from adjacent area of dung mass	10	131	17.6	7.4

Competitive exclusion would account for kleptoparasitic species of *Borborillus* surviving the general decline of their family. By ovipositing in scarab dung, contact with most calypterates is avoided.

The advantages of phoresy

The above are the advantages and disadvantages of kleptoparasitism but do not account for the evolution of phoresy. This cannot be addressed without an explanation for long-term associations with beetles. Prolonged contact seems unnecessary for oviposition in the dung. Why do sphaerocerids spend most of their time upon beetles rather than searching for more oviposition sites? The first part of an answer is that oviposition does not occur above ground. *Borborillus frigipennis* were only reared from dung caches that had been buried for at least 4 h (three of nine dung balls associated with adult flies and dug up after 4 or more hours produced flies, none of twenty-two balls collected earlier produced adults). Why females wait to oviposit is unclear. Perhaps eggs on the surface of a roller's dung ball or in a burier's manipulated fragment might be damaged as they roll along or are packed in burrows (sarcophagid larvae, on the other hand, can rapidly burrow into the safe interior). *Trichocypsela longiseta* and *T.nasuta*, sphaerocerid kleptoparasites from central Africa, ride rolling scarabs. They do not go underground with dung balls, but oviposit in the faeces as they are being buried (Roubaud, 1916). This last-minute deposition suggests a compromise between the dangers facing eggs and advantages of adult freedom. If females must maintain contact with beetles in order to reach particular oviposition sites at specific times, it seems energetically less expensive to ride than to walk, and easier to ride on the beetle than on a tumbling bit of manure.

Riding could also be safer than walking. Spiders, reduviids, asilids, staphylinids and odonates commonly hunt in the vicinity of dung (e.g. the reduviid *Apiomerus crassipes* Fab. approaches faeces from downwind and lands directly on them, suggesting it uses faecal odours to locate hunting grounds.) A predator pursuing sphaerocerid flies may not be able to glean prey from a larger scarab, and an animal attacking a dung beetle might not exert itself to capture associated small flies (note that Old World *Ceroptera* spp. ride underneath scarabs, suggesting a predator capable of capturing them from a host's dorsum).

The presence of dung haunting predators may help explain the spatial distribution of *Borborillus frigipennis* around faeces (see again Fig. 2). Only 54% of flies mount scarabs on dung; others are found intercepting hosts as they leave dung at distances of up to 1.5 m. Since the concentration of ball rolling beetles is greatest at dung, and faeces are the only predictable location for finding burying scarabs, the presence of these outlying individuals seems odd. Perhaps distant individuals have fewer opportunities to locate hosts, but also face less danger from predators. Many small dung breeding flies mate away from the dung, perhaps because of predators lurking on faeces (particularly the predaceous dung-breeding fly *Scatophaga stercoraria*; Borgia, 1979).*

While females ride to oviposit, males ride to obtain mates. Sexual activity is common on scarabs, and females can spend up to 70% of their riding time in repeated copulation with a single male. Couplings also occur underground and males invest heavily with their time to continue sexual activity with buried females. Recall that, by accompanying a beetle into its burrow, a male can easily be prevented from encountering new mates for 30% or more of his reproductive life. These self-imprisonments are probably a means of winning sperm competitions. In many insects, the last male to mate before oviposition obtains the majority of fertilizations (Parker, 1970; Walker, 1980). Since oviposition occurs underground, final inseminations will also be subterranean. Males would be constrained to

* A braconid of the genus *Aphaerete* (probably *allipes*) is frequently recovered from faeces, often accompanied only by the flesh fly *Ravinia derelicta*, suggesting that the wasp is a parasitoid of the fly (see Krombein *et al.*, 1979). The ratio of *Aphaerete* sp. to sarcophagid is positively density dependent. Flies in the densely inhabited dung balls of *Canthon pilularius* and ball construction sites suffered significantly more parasitization than those that were larviposited on a dung surface away from beetle activity. The parasitoid apparently tracks accumulations of flesh fly larvae, perhaps by noting beetle activity.

forego fresh mates in order to obtain high quantity, final copulations with already familiar females.

Acknowledgments

I would like to thank J. E. Lloyd and T. J. Walker for advice and comments, P. Sivinski for translations and B. Hollien for typing the manuscript. S. Marshall provided expeditious identifications and W. Ploss kindly allowed me the run of his ranch. Florida Agricultural Experiment Station Journal Series No. 4393.

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Accepted 11 May 1983