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**BEHAVIOR AND ACTIVITY PATTERNS OF THE BLACK SCAVENGER
FLY, *SEPSIS PUNCTUM* (DIPTERA: SEPSIDAE),
NEAR A PERMANENT DUNG SOURCE**

Beth E. Leuck¹

ABSTRACT

The behavior of the black scavenger fly *Sepsis punctum* (L.) (Diptera: Sepsidae) was studied on satellite resource (dung) patches established near a pig pen. Flies were most numerous on the patches when ambient temperature and light conditions were high. Females were commonly found on the patches and males occupied boards surrounding the patches where they displayed vigorously to other males and females. Approximately four times as many females as males occurred on the patches. Females were larger than males, and paired males were larger than unpaired males. Males did not exhibit precopulatory guarding as reported in *Sepsis cynipsea* (L.) and European populations of *S. punctum*, and copulatory encounters appeared to be brief. The permanency of pig dung utilized by this population of *S. punctum* compared to the transience of cow pats utilized by *S. cynipsea* may influence differences in sex ratios, precopulatory guarding, copulation duration, and male aggressive behavior in the two species.

Flies of the family Sepsidae (order Diptera) commonly inhabit mammalian feces (Steyskal 1987). Sepsids are small (2-6 mm in length), dark, shiny flies that characteristically flip their wings when walking (Steyskal 1987). Females oviposit in dung, and both larvae and adults feed on dung (Meier 1996). Many species are sexually dimorphic, and males have enlarged bristles on the forelegs used to grasp the base of females' wings during copulation (Steyskal 1987, Allen and Simmons 1996, Blanckenhorn et al. 1998).

The field behavior of only one species, *Sepsis cynipsea* (L.), a specialist on cow dung, is relatively well studied (Allen and Simmons 1996; Blanckenhorn et al. 1999; McLachlan and Allen 1987; Parker 1972a, 1972b; Ward 1983; Ward et al. 1992). Both sexes arrive soon after deposition. Many males arrive so there is a high degree of competition for access to females (Parker 1972a). A male climbs on a female's dorsum prior to oviposition and adopts a "passive phase" while the female oviposits (Parker 1972a). The female then walks off the dung into the surrounding vegetation where the male copulates with her (Parker 1972a, 1972b). Males with symmetrical features are better able to clasp females than are asymmetrical males and are thereby indirectly selected for by females (Allen and Simmons 1996, Blanckenhorn et al. 1998). Larger males also are more successful at clasping females (Parker 1972a, 1972b; Ward 1983; Blanckenhorn et al. 1998), and there is evidence that large body size is highly heritable and indicative of "good genes" in males (Blanckenhorn et al. 1998, Blanckenhorn et al. 2004).

Unlike *S. cynipsea*, *Sepsis punctum* (L.) is a fecal generalist, having been reported on the dung of many mammal species, on carrion, and on rotting vegetation (Meier 1996). The species seems to prefer moister conditions than *S. cynipsea* because it is rarely found in dry pastures (Meier 1996). Parker (1972a) and Schulz (1999) reported precopulatory guarding in *S. punctum* in Europe, but Schulz (1999) did not observe precopulatory guarding in North American populations of *S. punctum*. European males are dimorphic with larger males mounting females on dung while smaller males wait in the surrounding vegetation to intercept

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females (Meier 1996). "Take-overs" by large males of females clasped by small males are common (Meier 1996). Large males may establish territories on dung and spend much of their time attempting mountings or take-overs of females arriving to oviposit in the dung (Meier 1996). Although both *S. punctum* and *S. cynipsea* males compete for females, *S. punctum* males appear to be more aggressive than *S. cynipsea* during intrasexual encounters (Parker 1972a, Meier 1996).

Observations of *S. punctum* behavior have been reported in the literature but no field studies have been conducted on North American populations. The purpose of this study was to quantify several aspects of the ecology and behavior of a North American population of *S. punctum*.

METHODS

A population of *S. punctum* living in and around a pig pen located at the Central Michigan University Biological Station on Beaver Island, MI, was monitored during the summer months of 1996 and 1997. Three pigs have inhabited the 10m x 6m pen from May until September every year since 1990. The presence of *S. punctum* was noted in 1992. Adults, which hibernate during the winter (Meier 1996), have appeared on pig dung and wire fencing of the pen and in the surrounding vegetation by mid-May every year since 1992.

Because of the difficulty of studying small flies in a pen with three pigs, I created five satellite resource patches within 5 m of the periphery of the pen, four to observe fly behavior and a fifth to sample for moisture content. Each patch consisted of approximately 700 ml of moist pen substrate (a mix of dung, dead vegetation, food, and sand) deposited in the center of a 1m x 1m plywood board. A fresh patch was placed on each board every morning before observations began and was left undisturbed for the remainder of the day. The small area occupied by the patch and large area occupied by the board allowed for unobstructed observations of flies attracted to these patches.

Patches were established between 7:30 am and 8:30 am on 28 days from 25 May to 29 July over 1996 and 1997. Observations were made at the four patches from one to six times on a given day, usually one or two hours apart. During an observation period I recorded the time, light intensity, relative humidity and temperature on the board. Because the pig pen and boards were intermittently shaded by surrounding trees, light intensity, relative humidity and temperature were partially dependent on ambient shade conditions. A sample was removed from the fifth patch during each observation period, and moisture content was determined by weighing the sample, drying it for 48 h at 105°C, and reweighing the sample.

During each observation period I noted the number of *S. punctum* males and females on each dung patch and board. Females could usually be distinguished from males by their larger size, swollen abdomens, slower movement, and lack of display behavior. Males had thin, curved abdomens and moved and displayed vigorously. When individuals on the patches were too numerous to count accurately I counted the number of flies on one quarter of the patch and multiplied by four for an estimated total.

Behavior of both sexes on the satellite resource patches and in the surrounding vegetation was recorded and quantified using *The Observer* behavioral software. Males were observed for 50 3-min periods, and a focal male's behavior was recorded during each 3-min period. The focal male often changed during an observation period because the original male flew off, but the behavior of only one male was recorded at a time. Behavioral categories recorded included sitting, walking, grooming, displaying, and fighting. Twenty-five observations were done on males on the boards and 25 observations on males in the vegetation surrounding the pig pen. Females were observed for 45 3-min periods. Behavioral categories recorded included sitting, walking, shaking the abdomen (usually when a

male was nearby), shaking a male from the dorsum, displacing another fly, and ovipositing. Again, the focal individual sometimes changed if the fly under observation flew off. Fifteen observations were done on females on patches, 15 on females on boards, and 15 on females in the vegetation surrounding the pig pen.

Sweep-netting was done in the surrounding vegetation on several occasions, and I also captured paired flies throughout the study period. Flies were preserved in 70% ethanol, and their sex was noted and wing length was measured using an ocular micrometer. Under the microscope, enlarged bristles on the forelegs of males were readily visible. Females lacked these wing clamps, so the characteristic was used to confirm the sex of measured specimens. For this study the wing lengths of 67 unpaired females, 60 unpaired males, and 25 pairs were measured.

Data on wing length, behavior, and numbers of males and females on patches and boards were analyzed using the statistical and graphing software packages *StatMost 32* from DataMost Corporation and *ProStat for Windows* from Poly Software International. For the purpose of analysis the times at which observations took place were pooled by the hour in which they occurred yielding 13 time periods ranging from 8:00 am – 8:59 am and 8:00 pm – 9:00 pm EDT.

RESULTS

The number of males and females on both patches and boards was positively correlated with ambient temperature and light conditions but not correlated with time of day, humidity conditions, or age of patch (soil moisture content) (Spearman rank correlation, $r = 0.58$, $P < 0.001$ for temperature; $r = 0.59$, $P < 0.001$ for light). The highest temperature and light conditions tended to occur near mid-day, so there were more flies on patches and boards between 12:00 pm and 4:00 pm than at other times (Fig. 1). Flies were more common in late June and early July, and their numbers decreased in late July (Fig. 2).

Females were more numerous than males at the satellite resource patches at all times of the day (Fig. 1). The differences were especially pronounced during the middle of the day when the total number of flies was high. Although females were always more numerous than males, the number of males and females on or near patches became less equitable later in the summer. Female numbers remained high while the number of males decreased at the end of June (Fig. 2). When compared to an expected 1:1 sex ratio, the observed data were highly significantly different ($\chi^2 = 2480.7$, $P < 0.0001$), but they did not vary from a 1:4 ratio ($\chi^2 = 0.2$, $P = 0.66$). On the other hand, the sex ratio among flies swept from the vegetation surrounding the pig pen did not differ from a 1:1 ratio ($n = 127$, $\chi^2 = 0.19$, $P = 0.66$).

The two sexes maintained different spatial distributions. Males were rarely found on patches regardless of ambient conditions but were instead located on the boards (Fig. 3). Differences between the number of males on and off patches were highly significant during all observation periods ($n = 28$ days; Mann-Whitney U-test, $P < 0.001$). In fact, usually no males were found on the dung patches. Even when the population of *S. punctum* on patches was large, such as in June and early July and during mid-day hours (Fig. 1), males were no more common on patches than when the population was smaller.

Females were found significantly more often on patches than on the boards (Fig. 3; $n = 28$ days; Mann-Whitney U-test, $P < 0.001$). These differences were noticeable in all ambient conditions, but particularly during the middle of the day. At 1400, there were, on average, five times as many females on patches as on boards (12.3 females per patch vs. 2.5 females per board).

Males on the boards and in the vegetation surrounding the pig pen spent 15-20% of their time displaying to conspecifics (Table 1). This display consisted of walking toward another fly while rapidly vibrating the wings and swinging the abdomen from side to side. If the conspecific did not fly away, the displaying

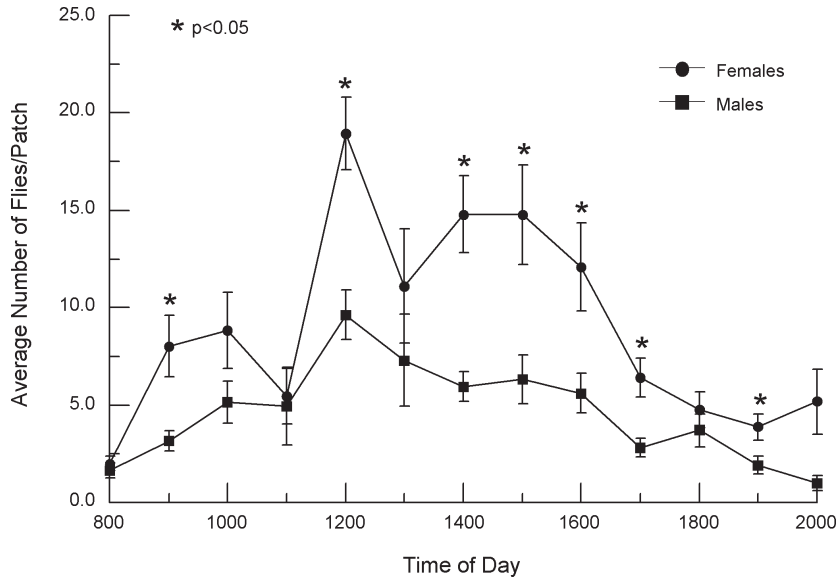


Figure 1. Average number of *S. punctum* males and females observed at a satellite resource (dung) patch at different times of the day. Four patches were established on 1 m × 1 m boards near a pig pen. Significant differences between the number of males and females at a given time (Mann-Whitney U tests) are marked with asterisks. Vertical lines represent standard errors.

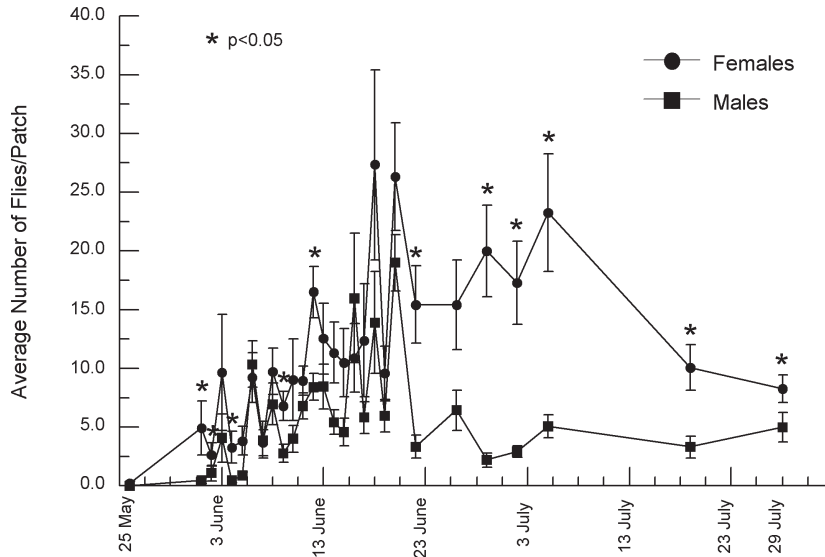


Figure 2. Average number of *S. punctum* males and females observed at a satellite resource (dung) patch on different dates. Four patches were established on 1 m × 1 m boards near a pig pen. Significant differences between the number of males and females on a given date (Mann-Whitney U tests) are marked with asterisks. Vertical lines represent standard errors.

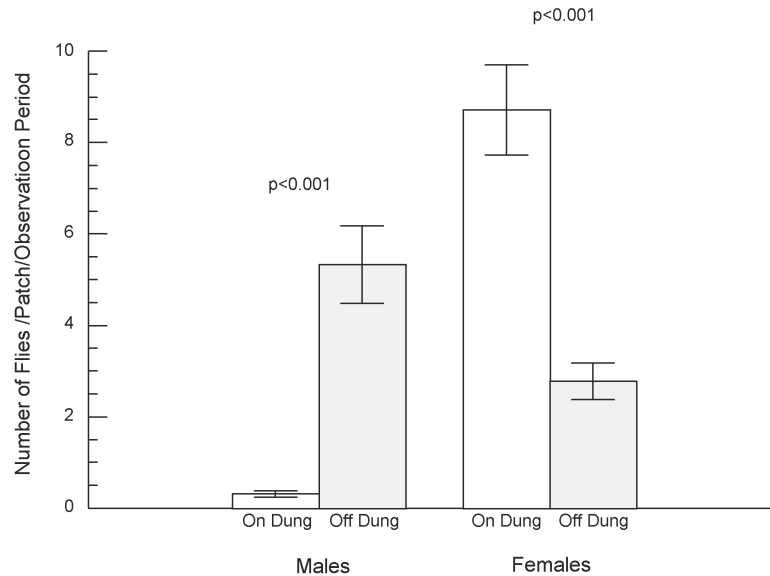


Figure 3. Comparison of the average number of males and females on and off satellite resource (dung) patches. Four patches were established on 1 m × 1 m boards near a pig pen. *P* values of Mann-Whitney U tests are listed above the categories compared to each other. Vertical lines represent standard errors.

fly stopped walking and continued to swing its abdomen and vibrate its wings. If the challenged fly was a male, he either displayed, which often ended with both flies grappling on the substrate until one flew, or he turned away from the challenger and raised his abdomen prior to flying. The “winner” of the contest remained on the leaf or portion of the board and walked rapidly around on the substrate. If the challenged fly was a female, she shook her entire body from side to side, which caused the male to pause his display. If the female stopped shaking, the male resumed his display. This exchange usually continued for five or six bouts until the male jumped on the female’s dorsum. The female then usually flew off and the male continued patrolling the substrate. Patrolling (walking) consumed 51% of a male’s time on the board or in the vegetation surrounding the pig pen (Table 1).

Females were not as active as males; they spent up to 84% of their time sitting on the patch, board, or vegetation, or ovipositing on the patch (Table 1). They exhibited little aggression toward conspecifics (“displace” in Table 1), and their only display was shaking in response to males’ displays (Table 1). Shaking was more common on the board where male numbers were higher than they were in the vegetation or on patches (Table 1).

Wing lengths of 85 males and 92 females were compared as an indicator of body size. Females had significantly longer wings than males (mean female wing length = 2.91 ± 0.26 mm; mean male wing length = 2.73 ± 0.27 mm; Mann-Whitney U test, *P* < 0.001). Single (unpaired) males had a mean wing length of 2.67 ± 0.28 mm, and paired males had a mean wing length of 2.85 ± 0.22 mm. These lengths were significantly different from each other (Fig. 4; Mann-Whitney U test, *P* = 0.006). Unpaired vs. paired females showed no difference in wing length (Fig. 4; mean length of unpaired females = 2.89 ± 0.24 mm; mean length of paired females = 2.95 ± 0.28 mm; Mann-Whitney U test, *P* = 0.18), and paired males had wing lengths similar to all females (*P* = 0.12).

Table 1. Percent time spent in each recorded activity by *S. punctum* males and females on plywood boards, on satellite resource (dung) patches on the boards, and in vegetation surrounding a pig pen. Males were observed for 150 min and females for 135 min. Males were not observed on patches.

	Males			Females		
	On boards	In vegetation		On dung	On boards	In vegetation
Sit	20.8	20.0	Sit	52.9	76.5	83.9
Walk	51.9	51.1	Walk	21.3	17.5	14.4
Groom	2.2	7.5	Shake	0.2	5.3	1.1
Display	19.6	14.6	Shake off male	0.0	0.5	0.5
Fight	5.5	6.7	Displace	0.1	0.2	0.1
			Oviposit	25.5	0	0

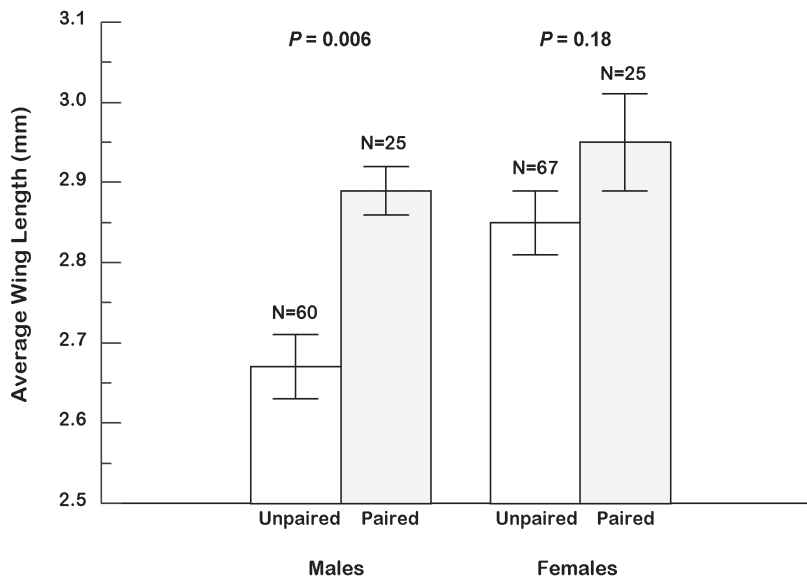


Figure 4. Average wing length in mm for males and females captured singly or paired with a member of the opposite sex. There was a significant difference in wing length between single and paired males but not in females (Mann-Whitney U test). *P* values are listed above the compared categories, and sample sizes are listed above each bar. Vertical lines represent standard errors.

Of 9002 flies counted, only 18 pairs were observed at the satellite resource patches. Five of these pairs (28%) were seen on patches, and 13 pairs (72%) occurred on boards. Another seven pairs were captured from the vegetation surrounding the pig pen for a total of 25 pairs. One copulation event was recorded on video; the pair spent 13.1 s in copula. The male jumped on the female's dorsum and remained there for 0.6 s. The female shook violently and succeeded in removing the male from her dorsum, although she dragged him around for another 12.5 s still presumably attached to her by his genitalia. Both flies then separated, and the male displayed to the female while the female shook her abdomen in response to the male's displays.

DISCUSSION

A positive correlation of number of flies on dung patches with ambient temperature has also been observed in *S. cynipsea* by Blanckenhorn et al. (1999). Laboratory studies indicate that higher ambient temperatures lead to decreased larval development time, longevity and adult body size among *S. cynipsea*, but higher temperatures also lead to greater sexual dimorphism in body size between males and females (Blanckenhorn 1997). If development time is shortened by higher ambient temperatures, then as temperatures increase throughout the summer, more cohorts will visit patches simultaneously, which would explain the increase in total number of *S. punctum* observed on satellite resource patches in late June and early July. However, it does not explain the rapid decrease in the number of these flies during July. Ambient temperatures were still high and remained high through August. Blanckenhorn (1997) and Blanckenhorn et al. (1999) observed a decrease in *S. cynipsea* numbers in August, which correlated with a decrease in ambient temperature. Blanckenhorn et al. (1999) found no variation in clutch size in *S. cynipsea* over the course of their study (June – September) and were only able to correlate a decline in fly numbers with a decline in ambient temperature. The *S. punctum* population in my study seemed to have decreased for reasons other than ambient temperature changes, but these reasons are unknown. The species richness of dipterans on the dung in the pig pen increased during July, so it may be that the decline in *S. punctum* was due to interspecific competition among various dung-utilizing fly species.

Sepsis cynipsea, a specialist on cow dung, tends to desert cow pats as they age and dry during the course of a day (Parker 1972a, Ward 1983, Blanckenhorn et al. 2000a). Parker (1972a) found that the number of *S. cynipsea* males decreased from approximately 175 to 75 in the first hour after dung deposition, and the arrival rate of females decreased from approximately 1.4 per min to fewer than 0.2 per min over the same period. *Sepsis punctum* does not show the same trend in this study. Even though the experimental patches lost an average of 14.8% of their moisture content over the course of a day, the number of black scavenger flies on patches did not correlate with this change in resource quality. Because *S. punctum* is a generalist (Meier 1996), it may tolerate a wider range of dung moisture than *S. cynipsea*.

Sepsis punctum males were more frequently found on boards than they were on dung patches, but females tended to congregate on the patches. Parker (1972a) reported a similar distribution of *S. cynipsea* males, with the highest percentage of males in a zone 0 to 10 cm from the edge of the cow pat. Parker (1972a) found approximately 17% of *S. cynipsea* males on a cow pat, but only 6% of *S. punctum* males were found on patches in this study. Also, most of the females on dung in Parker's study were carrying males on their dorsa, but I observed mostly unescorted females on patches. Parker did not record numbers of unescorted (single) females during his study because of difficulty distinguishing them from swarming males at a cowpat (Parker 1972a).

Populations of *S. cynipsea* are male-biased (Parker 1972a, Blanckenhorn et al. 1999, Blanckenhorn et al. 2000a), but the sex ratio of the *S. punctum* population

around the satellite resource patches in this study was highly skewed in favor of females (1:4 ratio). Schulz (1999) reported similar female-biased populations of *S. punctum* in Arizona and Idaho. The skew associated with patches in this study was not indicative of the general *S. punctum* population because the sex ratio of flies swept from the vegetation surrounding the pig pen did not differ from a 1:1 ratio. The sex ratio of flies on patches and boards may have been skewed in favor of females due to differences in the aggressive behavior of males and females. The density of females on patches was high due to a lack of female-female interactions, but high levels of male aggression led to a reduced number of males on the boards at any given time because males chased each other away. Blanckenhorn et al. (2002) reported that *S. cynipsea* males rarely exhibited any aggressive behavior toward each other, unlike the *S. punctum* males in this study. This lack of aggression in *S. cynipsea* could explain the different sex biases seen in populations of *S. cynipsea* and *S. punctum*; *S. cynipsea* males are not chased off by other males so their numbers at dung sources are higher.

Although the location and numbers of males and females around dung sources and male-male aggression appear to differ between *S. cynipsea* and *S. punctum*, size relationships of the sexes do not. Females of both *S. cynipsea* and *S. punctum* are larger than males (Parker 1972b, Ward 1983, Allen and Simmons 1996, Blanckenhorn 1997, Martin and Hosken 2002, Mühlhäuser and Blanckenhorn 2002) so females are capable of accepting or rejecting mates. To reject a male that has mounted her, a female sepsid shakes vigorously from side to side (Parker 1972a, 1972b; Ward et al. 1992; Allen and Simmons 1996; Blanckenhorn et al. 2000b). *Sepsis cynipsea* females that shake the longest and most vigorously are most likely to dislodge a male that has mounted them (Ward et al. 1992). Larger males may have higher reproductive success because they can better grip the females' wings during shaking (Ward 1983, Allen and Simmons 1996, Blanckenhorn et al. 2000b). Males' ability to remain clasped to a female may be particularly important in sepsid populations that exhibit escorting (precopulatory guarding). Schulz (1999) found that males in an escorting population of *S. punctum* were significantly larger than females, but in nonescorting populations there was no difference in size between males and females. Although the population of *S. punctum* in this study appeared to be primarily nonescorting, males were significantly smaller than females based on wing length. However, there was no significant difference in wing length between females and mounted males, implying that larger males were more successful at mounting females than were smaller males.

The 18 pairs of escorting flies found on the satellite resource patches during the study comprised only 0.4% of all dung flies observed. Only five pairs were seen on patches. Observations of *S. punctum* in the vegetation surrounding the pig pen indicated that escorting behavior was a rare phenomenon in this population of *S. punctum*. Only seven pairs of flies were captured in the vegetation during the study, and 225 min of focal-animal observations yielded only one instance of copulatory behavior. The rarity of paired flies on the satellite resource patches, in the pig pen and in the surrounding vegetation, and the single brief copulation event captured on video suggest that *S. punctum* has an extremely short male-female association time. Schulz (1999), who also studied nonescorting populations of *S. punctum*, stated that nonescorting flies have lower levels of male-male competition than escorting populations in which escorting males are constantly challenged by rivals at oviposition sites. She believed there has been little selection for "specialized male competitive behaviours" in nonescorting populations (Schulz 1999). However, in the population of *S. punctum* that I studied, males demonstrated competitive behavior in the form of visual displays. In spite of the apparent female-biased sex ratio on the satellite resource patches, males were highly aggressive toward each other and spent approximately one-fifth of their time displaying to and fighting with potential competitors.

Schulz (1999) suggested that because populations of nonescorting *S. punctum* are female-biased around oviposition sites, males may be searching for females at other locations in the environment. However, no flies were ever observed at two compost piles 10 m from the pig pen or on flowering plants [mostly *Chrysanthemum leucanthemum* (L.) and *Silene vulgaris* (Moench)] in the vicinity of the pig pen in spite of checking both locations every day that observations were made. Although the sex ratio of flies on the satellite resource patches was 1:4, the sex ratio of flies in the vegetation surrounding the pig pen was approximately 1:1. If male association with a female is very brief, as indicated by the one observation of copulatory behavior made during this study, then more frequent contact among unpaired flies occurs than in a population where males have prolonged guarding of females. Aggressive displays toward other males may improve a male's chance of copulating with a female by removing competitors from the vicinity and have therefore been selected for in this population of *S. punctum*. It would be interesting to investigate changes in male aggressive behavior at different times of the day to determine if males adjust their behavior to fluctuating numbers of potential mates and competitors.

All detailed studies of sepsid dung flies in the literature have concentrated on the behavior and life history characteristics of *S. cynipsea*, which utilizes cow dung. Cow pats are relatively small, ephemeral resources (Mohr 1943). Observations indicate that both male and female *S. cynipsea* arrive within a few minutes of deposition, reach peak numbers in less than an hour, then decline as resource quality decays (Parker 1972a, Ward 1983, Blanckenhorn et al. 2000a). *Sepsis cynipsea* individuals inhabiting cow pastures must skip constantly from one resource patch to another to obtain matings and/or oviposition sites. On the other hand, the pig dung in this study was a permanent resource during the *S. punctum* mating season. Although I used satellite resource patches to observe individuals, the dung in the pig pen was a constant for the population of black scavenger flies around the pen. The dependability of the critical resource needed by females for oviposition may have contributed to the presence of competitive display behavior by males. The predictability of the location of females was high, making it unnecessary for males to search widely for females. Instead, males congregated near a single oviposition site where the close proximity of males to each other led to strong male-male competition in the form of aggressive visual displays and fighting. Therefore, even though North American populations of *S. punctum* appear to be nonescorting, males may exhibit aggressive behavior depending on local habitat conditions. The *S. punctum* populations studied by Schulz (1999) were found on cow dung or cow dung bait, which may have led to different behavioral responses by males than those observed in this population, which lives near a permanent dung source.

In conclusion, the population of *S. punctum* in this study is characterized by a highly female-biased sex ratio at the oviposition site, no precopulatory guarding, brief copulation, and aggressive visual displays by males. These traits may be correlated with local habitat conditions that favor the congregation of females around a permanent dung source which in turn attracts males to compete for access to females.

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