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COMPARATIVE BEHAVIOR OF *PYRELLIA CYANICOLOR* (DIPTERA: MUSCIDAE) ON THE MOSS *SPLACHNUM AMPULLACEUM* AND ON SUBSTRATES OF NUTRITIONAL VALUE[1]

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Entomophily is commonly associated with flowering plants and their pollen vectors, but also occurs in other groups of plants. Among fungi, several genera of Phallaceae offer food rewards to calliphorid and muscid flies, which inadvertently disperse the fungal spores (Ingold 1964). Bryhn (1897) first noted a relationship between various species of Diptera and members of the moss family Splachnaceae. The nature of this interaction has been the subject of much speculation (Bequaert 1921, Erlanson 1935, Crum et al. 1972, Koponen and Koponen 1977), but no experimental evidence has been collected.

In an earlier study, *Pyrellia cyanicolor* Zetterstedt was observed visiting the sporophytes and transporting the spores of the moss *Splachnum ampullaceum* Hedw. in northern Michigan (Cameron and Troilo, in press). *P. cyanicolor* is distributed throughout North America, but few details of its biology are known. Adult females are reported to prefer carrion for oviposition sites but will utilize dung when carrion is not available. The larvae are general scavengers (Cole 1969). *Splachnum ampullaceum* occurs throughout the cold, temperate regions of North America (Crum and Anderson 1981) and is restricted to organic or organically enriched substrates (dung). Rarely, it has been collected from soil (Crum et al. 1972).

The sporophytes of the moss possess many presumed adaptations for entomophily. These include the production of a distinct, dung-like odor, and an expanded, brightly pigmented capsule base (the apophysis), both of which are believed to be adaptations for attracting dispersal agents. The occurrence of completely recurved peristome teeth and the capsule walls which shrink upon drying are thought to be important in spore presentation. Adhesive spores are believed to be an adaptation for attachment to the dispersal vector.

The purpose of this study was to determine (1) if *S. ampullaceum* is attractive to *P. cyanicolor*, and (2) if a food reward is obtained by the flies visiting the sporophytes. To this end, behavior exhibited by the flies on substrates of nutritional value was examined and quantitatively compared to behavior displayed by the flies while on the *S. ampullaceum* sporophytes.

METHODS

The study site was located in a black spruce (*Picea mariana* A. Dietr) swamp on the northwest shore of the Stutsmansville Lake Bog, Emmet County, Michigan (T35N, R6W, Sec. 24). A total of 19 hours was spent observing flies from 12 July to 3 August 1980. Observation periods began at 1000 hrs and ended at 1500 hrs EDT.

The behavior of *P. cyanicolor* was observed on four substrates presented in the field: (1) sporophytes of *S. ampullaceum;* (2) carbohydrate food reward (~5 ml 0.5 M sucrose solution containing apple bits) provided on red, yellow, and blue petri dishes, one dish/color, spaced ~1 m apart; (3) red squirrel (*Tamiasciurus hudsonicus* Erxleben) carrion, a protein food source and substrate for oviposition; (4) commercial fly medium (Ralston-Purina), an alternate food source and possible oviposition site. Substrates were presented and observed individually without competition from other substrates.

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Stopwatches and hand tally event recorders were used for data collection. Behaviors measured for the four substrates were (1) visit frequency and duration, (2) proboscis behaviors, and (3) grooming. Proboscis behaviors were divided into two categories, feeding and sampling. Feeding was noted when the proboscis was extended and left in continual contact with the substrate for longer than 3 sec. or when the proboscis, while remaining fully extended, was tapped on the substrate surface continuously for at least 3 sec. Sampling was seen as the rapid extension and withdrawal of the proboscis from the substrate surface. The criterion for these categories is based largely on the work of Dethier (1976). Grooming behavior was recorded when the front tarsi were rubbed together, with or without drawing the tarsi over the head region, and when the rear tarsi were rubbed together.

RESULTS

Flies were most active on sunny and warm (24–32°C) days. This was also the period when sporophytes of *S. ampullaceum* produced the strongest odor.

Typically, flies approaching the moss patch flew directly to the sporophytes. Occasionally they landed on a neighboring plant or other substrate, oriented toward the moss, and then walked or flew directly to the sporophytes (Fig. 1). When an individual on the moss was chased away, it often returned after a short flight to a neighboring plant or fallen log.

The total number of visits observed, hours of observation time, mean length of visits, and average visits per observational hour are presented for each substrate in Table 1. On the average, *S. ampullaceum* is visited nearly as frequently as the carrion and more so than the carbohydrate nutrient source or the fly medium.

A one-way ANOVA for visit duration on the four substrates indicates that the means were not equal ($P < 0.0001$). Duncan's multiple range test (Table 1) indicates that the mean visit duration on *S. ampullaceum* was significantly shorter ($P < 0.01$) than the carrion and commercial fly medium but not significantly different from the carbohydrate substrate. This test also demonstrates that the mean visit duration for the carrion and fly medium (both protein sources) were not significantly different.

In the color preference experiment, *P. cyanicolor* preferred the yellow petri dishes containing carbohydrate food reward. For a sample size of 22, red was never visited, blue was visited twice, and yellow 19 times (χ^2 test, $P < 0.01$).

Proboscis behaviors were categorized as either feeding or sampling. The number of individuals falling into each of these categories for each of the substrates is summarized in Table 1. Proboscis behaviors associated with feeding do not take place on *S. ampullaceum;* only sampling behavior was observed.

The carbohydrate, carrion, and fly medium were grouped as a category representing food rewards ($n = 46$). This group was then compared to *S. ampullaceum* in terms of the frequencies of proboscis behaviors by χ^2 analysis. Proboscis behavior on *S. ampullaceum* was determined to be significantly different from that shown on substrates with nutritional value ($P < 0.01$).

Table 1 also shows the number of individuals grooming on each of the substrates. A χ^2 2×2 contingency analysis showed that the number of flies grooming on *S. ampullaceum* was significantly lower than the carbohydrate and the carrion ($P < 0.01$ for both tests). The fly medium was excluded in the χ^2 analysis, because the expected frequency generated was too low. Comparison of the carrion with the carbohydrate showed no significant difference in terms of the number of flies grooming on each ($P > 0.05$).

DISCUSSION

Splachnum ampullaceum is indeed attractive to adult *Pyrellia cyanicolor*. In terms of the number of visits per observational hour, *S. ampullaceum* is at least as attractive as carrion. Furthermore, *S. ampullaceum* is more attractive than either carbohydrate or fly-medium substrates. Observations concerning orientation of individual flies to the moss sporophytes and the immediate return of chased individuals adds further evidence to the attractiveness of *S. ampullaceum.*

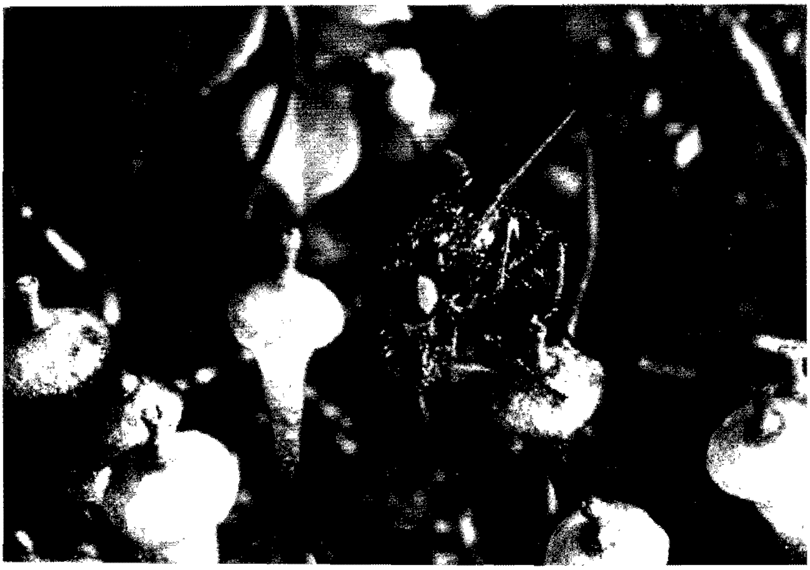

Fig. 1. *Pyrellia cyanicolor on Splachnum ampullaceum* sporophytes (~ 10x). Note the left mesotarsus resting on the capsule mouth.

The significance of a yellow color preference in carbohydrate feeding suggests the yellow color of the sporophytes is important to the relationship, possibly as a short distance attraction cue (Kugler 1956). The odor emitted by the sporophytes, presumably a long distance cue, undoubtedly plays an important role in attraction.

Apparently, flies do not obtain a food reward from the moss sporophytes. Two observations point to this conclusion. First, visit duration on *S. ampullaceum* is significantly shorter than on protein-supplying substrates. Also, the analysis of proboscis behavior indicates that feeding was probably not taking place on the S. ampullaceum sporophytes. However, we could not rule out the possibility that spores were being ingested. Proctor and Yeo (1972) have pointed out that many flies which normally feed on exposed liquids are capable of ingesting small solid particles, including pollen grains and spores. A moisture reward cannot be ruled out either.

Nevertheless, the short visit duration and the lack of continuous proboscis extension by *P. cyanicolor* on *S. ampullaceum* makes the occurrence of a significant food reward improbable. Furthermore, the number of flies grooming on *S. ampullaceum* was significantly lower than for substrates of known nutritional value. The reduced frequency of grooming on *S. ampullaceum* suggests an abscence of feeding, although the exact relationship between feeding and grooming incidence is not known. It most likely functions as a means for cleaning contact chemoreceptor hairs located on the tarsi and labellum.

From the results of this study and that of Cameron and Troilo (in press), we suggest the following relationship between *S. ampullaceum* and *P. cyanicolor*. *Splachnum ampullaceum* sporophytes are attractive to *P. cyanicolor* apparently through mimicry of visual and olfactory cues normally provided by nutrient resources. When a fly visits *S. ampullaceum* sporophytes, it senses the substrate with its tarsal chemoreceptor hairs and, less frequently, with its labellar sensory hairs. Upon determining that no food is present, it quickly leaves. While there, however, it may inadvertently pick up spores from the capsules (Cameron and Troilo, in press). These spores may then be deposited on nutrient sources for the fly, where

Table 1. Visit duration, proboscis behavior, and grooming behavior of *Pyrellia cyanicolor* on *Splachnum ampullaceum* and substrates of nutritional value.

Substrate	Observations Hours	Observations Numbers	Duration (sec.) $\overline{X} \pm S^2$	Mean visits/ observ. hour	Proboscis behavior Feeding	Proboscis behavior Sampling	Number Grooming
S. ampullaceum	7	59	25.8 ± 35.8^a	8.4	0	16	11
Carbohydrate	8	19	36.4 ± 37.0^a	2.7	22+	0	13[c]
Carrion	2	17	99.5 ± 64.8^b	8.5	17	0	3
Fly medium	2	7	94.8 ± 77.4^b	3.5	0	0	0

[a, b] Means with the same letter not significantly different.
[c] n = 22.

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the spores are able to develop. This relationship may be termed commensal. The moss benefits from the fly-mediated spore dispersal, while the fly seems to derive neither harm nor benefit from the interaction.

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