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Activity and distribution of the mushroom phorid fly, *Megaselia halterata*, in and around commercial mushroom farms

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Abstract

The mushroom phorid fly, *Megaselia halterata* (Wood) (Diptera: Phoridae), is a key pest in mushroom farming in most parts of the world. Studies on the mushroom phorid fly have focused on its life history within mushroom growing houses, but little is known about the fly's activity outside mushroom growing houses. In this study, daily activity and distribution of adult *M. halterata* in the areas surrounding mushroom growing houses was studied using yellow sticky traps. Results suggest that *M. halterata* focuses its flight activity over turf areas rather than windbreaks and spent compost piles, possibly for mating purposes. Our study found no evidence of *M. halterata* breeding in turf areas surrounding mushroom growing houses. In addition, flight activity is highest in the afternoon until midnight at higher temperatures, yet at lower temperatures activity ceases after sunset. Establishing temperature and daylight thresholds for *M. halterata* flight activity may be useful in developing integrated pest management (IPM) tactics for this species. The most successful IPM tool that mushroom growers use at present is fly exclusion. Exclusion can be improved by focusing farm operations around temperature and daylight thresholds when fly activity is at its lowest.

Introduction

The mushroom phorid fly, *Megaselia halterata* (Wood) (Diptera: Phoridae), is a key pest in mushroom farming in most parts of the world (Richardson & Hesling, 1978; Keil, 2002). Studies on the mushroom phorid fly have focused on its life history within mushroom growing houses, but little is known about the activity of *M. halterata* outside mushroom growing houses, including nearby residential neighborhoods where the fly can become a serious nuisance to homeowners (Binns et al., 1979). Mushroom growing is performed inside growing rooms, where *M. halterata* populations fluctuate throughout the year. Mushroom growers in Chester County (PA, USA), where our study was performed, report that *M. halterata* populations begin to build up during the late summer months (June and July) and become a problem during autumn (from August to November), when they reach their highest levels. The populations then begin to decrease in December and remain low during the winter and spring months. Also, little is known about the activities and behavior of feral populations of this pest species. *Megaselia halterata* are obligate fungal feeders (Scheepmaker et al., 1996), and hence females are attracted to spawned mushroom compost (compost with active mycelial growth) (Tibbles et al., 2005). Some reports suggest that female phorids enter rooms at 'spawn run' (stage in the mushroom production process after which the compost has been 'seeded' and the mushroom mycelia are actively growing in the compost) either from outside the mushroom-growing house or from other growing rooms within the house (Hussey, 1960; Binns et al., 1979; Navarro et al., 2001). Once inside the mushroom house, females lay eggs on the mushroom mycelia growing in the spawned compost, where larvae feed on the mycelia (Keil, 2002).

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Activity patterns of *M. halterata* flies have been studied on commercial mushroom farms. Hussey (1965) trapped mushroom phorid flies outside mushroom growing houses with suction traps and concluded that phorid flight is governed by both temperature and daylight. He found that the critical threshold for flight outside growing houses is an air temperature of 12.8 °C; however, flight does not become 'general' until the air reaches a temperature of 15.5 °C. In morning hours after sunrise, phorid flies do not become active until air temperatures rise above 12.8 °C. In the evenings, flight is curtailed by sunset, even when the temperature may be above the threshold for flight (Hussey, 1965). Jess et al. (2007) studied *M. halterata* activity on mushroom compost wharfs (exterior open spaces where mushroom compost is processed) and found little to no activity of the flies in outside wharf areas where the mushroom compost is prepared and pasteurized (phase I and phase II composting areas), or at the bagging area where compost is placed into bags before being transported to the farms. They concluded that phase II mushroom compost (mushroom compost that has been pasteurized yet not spawned) is not a source of *M. halterata* for infestations within growing houses.

Anecdotal reports of *M. halterata* describe large numbers in what appear to be swarms outside of mushroom houses (Hussey, 1965). Our observations on mushroom farms in Chester County, PA, place this 'swarming' behavior over mowed turf areas on the farms. Swarms may indicate mating behavior as documented in other fly species such as chironomids (Fyodorova & Azovsky, 2003) or mosquitoes (Tuten et al., 2013; Hassan et al., 2014) or alternatively, these are just large populations of *M. halterata* leaving the mushroom houses and flying around before feeding, laying eggs, or dying. Hussey & Gurney (1964) reported that a period of flight is required for *M. halterata* before mating, although this reporting is from laboratory rearing studies. The mating status of flies within these large populations outside the houses has not been reported.

In addition to turf areas, other typical landscapes around mushroom houses may be associated with phorids. These include woody areas at the perimeters of the farm properties as well as collections of used ('spent') compost outside the houses. Some farms keep this spent compost, a waste product of production, on the farm premises for several days or more until it is transported off the farm. Spent compost has been anecdotally suspected of being a source of *M. halterata* infestations of subsequent mushroom crops.

The objectives of this study were to gain a greater understanding of the daily activity and distribution of adult *M. halterata* in the areas surrounding mushroom growing houses by determining where and when flies are found in the greatest numbers. Specifically, our objectives were (1) to compare *M. halterata* adult activity among turf areas, windbreak areas, and spent mushroom compost piles, all surrounding commercial mushroom growing farms; (2) to determine diurnal fly activity around the farms; and (3) to determine whether mushroom phorid fly larvae could be found in the turf areas surrounding the farms. Ultimately, results from the study may inform the development of new tactics to control infestations and reduce annoyances to surrounding residential neighborhoods.

Materials and methods

We used yellow sticky traps (Alpha Scents, West Linn, OR, USA) to determine the relative distribution of *M. halterata* adults in the following areas that typically surround mushroom growing houses: (1) grassy turf areas near the mushroom houses, (2) windbreak areas farther away from the houses, and (3) piles of spent mushroom compost immediately outside the houses. We also used yellow sticky traps to determine the daily *M. halterata* adult activity patterns outside the mushroom houses during 'early season' (in August), and during colder periods later in the season (in October). Finally, we observed the behavior of *M. halterata* adults during flights of large populations over turf areas to determine whether these flights were related to mating behavior or not.

Four mushroom farms were used in this study. All farms were located in Chester County, PA, and all were within 7–27 km of each other. Trapping experiments were conducted during two times of the year, a warm period from 22–26 August 2016, and a colder period from 5–7 October 2016. Each sticky trap used was a yellow panel (18 × 14 cm) with dry adhesive coating on both sides. The traps were deployed using short metal stakes pushed into the ground. The bottoms of the sticky cards were between 10 and 15 cm off the ground.

Trapping at differing sites and distances from mushroom houses

All four of the mushroom houses used for this study had areas of turf (mowed lawn-type grass) located 15 and 30 m (three farms) and 90 m (one farm) from the walls of the house. However, only two of the four mushroom houses had turf extending out to narrow windbreaks (10 m wide) containing several species of mature deciduous and evergreen trees as well as spent compost piles on the farm premises, so only these two farms were used for the trap-site comparison study in which we compared captures from compost piles, turf-near-mushroom-houses, and turf-near-windbreak areas. Thus, for this trap-site-difference test performed in August, on farms 1 and 2, two

yellow sticky cards were deployed on spent compost piles, on turf near the mushroom houses, and on turf areas at the edge of windbreaks, farther away from the houses. On farm 1 the distances from the house were: spent compost at 30 m, turf at 15 m, and turf at 90 m, at the edge of the windbreak. On farm 2, the distances from the house were: spent compost at 70 m, turf at 15 m, and turf at 30 m, at the edge of the windbreak.

After deployment, each trap was photographed 3× per day (visiting each trap at each time point), with a high-resolution digital camera to evaluate the outdoor time of flight activity of *M. halterata*. Traps were deployed at 16:00 hours on 22 August and photographed at 24:00 and 08:00 hours the next day. When traps were re-visited at 16:00 hours, the old traps were replaced with new traps. This procedure was repeated each day for the next 5 days. For the trap site comparison, phorid flies on each card were counted from the photos and the number captured per day on each of the two traps at each of the three sites on farms 1 and 2 was recorded.

Daily flight activity

In August, trap captures over the turf areas nearest the mushroom houses on all four farms were used for assessment of daily flight activity. The traps deployed on farms 1 and 2 were as described above, and on farms 3 and 4, two traps each were placed in three locations over turf areas on each farm. These traps were deployed 15 and 52 m from farm 3, and 15, 16, and 28 m from farm 4. The three capture periods assessed each day thus were from 16:00 to 24:00, 24:00 to 08:00, and 08:00 to 16:00 hours.

In October, we concentrated on assessing daily fly activity using turf areas near the mushroom houses on the same turf areas used during August on each of the same four farms. This adjustment was made in response to the preponderance of *M. halterata* captures on the turf areas closest to mushroom houses during the sampling in August. Four daily trapping intervals (instead of three as in August) were used in October to more finely dissect any differences in daily flight activity. The intervals used during October were 06:00 to 10:00, 10:00 to 16:00, 16:00 to 20:00, and 20:00 to 06:00 hours.

The October trapping test started on 5 October at 16:00 hours, with three yellow sticky traps being deployed on each of the four turf areas on the four farms. As in the August experiment, the sticky traps were placed at a height of 10–15 cm from the ground using metal stakes pushed into the turf. Traps were replaced with new, clean traps at each observation. Trapping stopped on 7 October at 10:00 hours. Collected traps were immediately covered in 'food wrap' plastic film and returned to the laboratory at Penn State for counting.

For the daily flight activity studies, the number of *M. halterata* flies captured only on traps on the 'turf near mushroom houses' on each of the four farms was used. For each time interval the number of *M. halterata* flies caught on each card was recorded.

Sampling of adults flying over turf for evidence of sexual activity

On 17 and 18 October 2016, between 17:00 and 19:00 hours, *M. halterata* adults were sweep-netted on or near turf on farm 2. The specimens that were netted were examined for pairs in copula. In addition, apparent in-flight pursuits by large numbers of flies following individual flies on the hood of our car (dark blue) parked next to the turf area were observed and video-recorded also between 17:00 and 19:00 hours.

Turf samples for immatures

During the October sampling dates, turf samples (ca. 3 l each) were taken from each of the same turf areas where the traps were placed for monitoring phorid fly larval activity. Three samples, approximately 5 m apart, were taken using a post hole digger. Turf samples were placed into sterile polyethylene bags. In the laboratory, each sample bag was opened and placed into an emergence cage (30 × 30 × 30 cm) with a single vinyl window (Raising Butterflies, Salt Lake City, UT, USA) housed in a growth chamber at 21 °C, 70% r.h., and L12:D12 photoperiod for 30 days. These conditions have been preliminarily tested for *M. halterata* emergence from mushroom compost. The cages were visually inspected for fly emergence on a daily basis. In addition, three random sub-samples were taken from these turf samples and dissected with forceps under a stereoscopic microscope for the presence of *M. halterata* immature stages.

Statistical analysis

For comparison of the number of mushroom phorid flies among sites outside mushroom houses (data gathered in August), we used a general linear model and Tukey's multiple comparison test for mean separation among sites. In order to compare time intervals tested for each month as well as the time intervals between months in August and October, the number of phorid flies per interval was converted to flies per h. For each month, the effect of time interval on phorid fly activity was tested with a mixed effects model with 'farm' as a random variable. Mean separations was performed with a Tukey's multiple comparison test. All statistical analyses were done in JMP v.13 (SAS, Cary, NC, USA). Temperature values from the nearest weather station (ca. 20–30 km from study sites) on 22–26 August and 5–7 October 2016 were obtained from the National Oceanic and Atmospheric Administration

(NOAA) (databases: Local climatological data hourly observations August 2016 – station: Wilmington New Castle Airport, DE, USA – and Local climatological data hourly observations October 2016).

Results

Flight activity in three locations

Significantly more *M. halterata* adults (mean ± SE = 8.1 ± 1.01) were caught on the traps placed over turf areas nearest the mushroom houses. Very few flies were caught on the traps placed over spent mushroom compost piles (1.0 ± 0.11) or near windbreaks (0.17 ± 0.2), and the mean captures for these two locations did not differ (Figure 1).

Flight activity during time intervals in August

The number of phorid flies caught between time intervals differed ($F_{1,11}$ = 38.12, P<0.05). More flies per h were caught between 16:00 and 24:00 hours (mean ± SE = 21.3 ± 1.9) than from 08:00 to 16:00 hours and 24:00 to 08:00 hours. The lower captures during the 24:00 to 08:00 and 08:00 to 16:00 hours (12.2 ± 1.2 and 9.9 ± 1.3, respectively) did not differ from each other. Likewise, fly captures differed among farms and time interval (P<0.05). More flies per h (21.3 ± 1.9) were captured between 16:00 to 24:00 hours on farms 2 and 4, whereas farms 1 and 3 fly captures deviated from the time pattern (Figure 2).

Flight activity during time intervals in October

Mushroom phorid fly captures differed between time periods in October ($F_{1,15}$ = 91.15, P<0.05). October diurnal flight patterns were similar to those of August except that night-time capture was drastically reduced. The greatest number of flies per h was caught between 16:00 and 20:00 hours (mean ± SE = 61.4 ± 15.5). Low levels (0.2 ± 0.03) were registered between 20:00 and 06:00 hours. The daytime intervals, 06:00 to 10:00 and 10:00 to 16:00 hours (29.2 ± 9.2 and 33.6 ± 14.3, respectively), did not differ from each other (Figure 3). Farm 4 deviated from the time pattern, with similar fly catches from 10:00 to 20:00 hours (Figure 3).

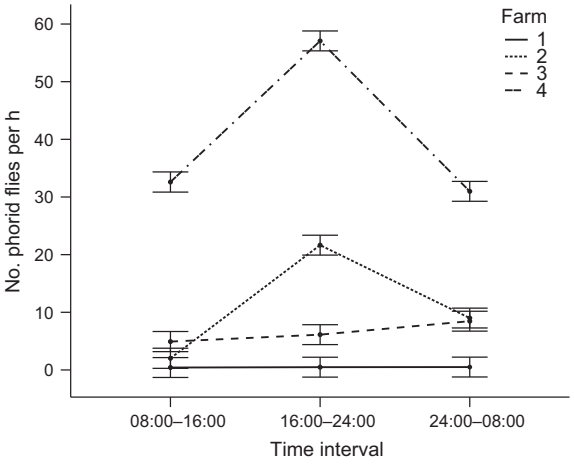

Figure 2 Mean (± SE) number of *Megaselia halterata* flies captured per h in August 2016, for each of the four farms and three time intervals.

Sampling of adults flying over turf for evidence of sexual activity

On both nights in October phorid flies began flying in great numbers over turf around 17:00 hours and this

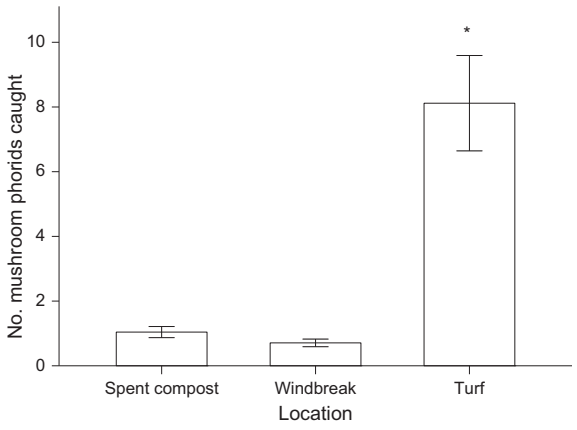

Figure 1 Mean (± SE; n = 30) number of *Megaselia halterata* flies captured on yellow sticky traps placed at multiple locations of the near surroundings of mushroom farms. Fly catches from two farms and three 5-day periods were pooled.

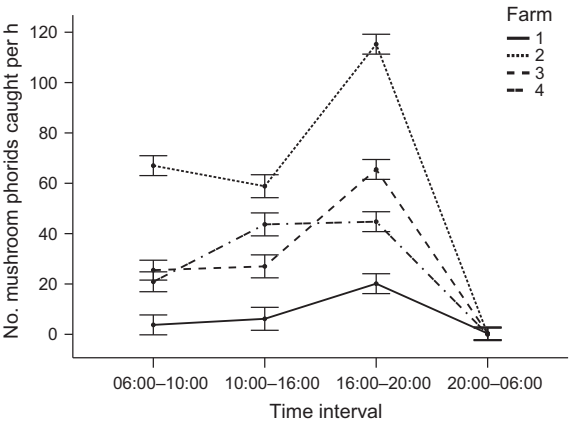

Figure 3 Mean (± SE) number of *Megaselia halterata* flies captured per h in October 2016, for each of the four farms and four time intervals.

activity lasted until sunset, which occurred at ca. 19:00 hours. After sunset all adult flight activity ceased over the turf areas we were observing. These assemblages of thousands of flies cruising at high speeds over grass were seen primarily at altitudes between 0.1–2 m over the same turf areas upon which the yellow sticky traps had been placed. Some flies appeared to achieve copulation aerially and pairs in copula could easily be observed in flight compared to singly flying, non-copulating adults. We estimated on both nights that roughly 30% of the flying adults were flying in copula within these turf areas at any given time.

Turf samples for immatures and adult emergence

Although we captured the greatest numbers of *M. halterata* over turf areas close to mushroom houses, we found no evidence that fly larvae were developing in the soil. Out of 12 samples taken during the heavy flight, 0 adults emerged from all the soil/turf samples over 4 weeks, and not a single egg, larva, or pupa was found in any of the dissected subsamples.

Discussion

The very low number of *M. halterata* fly catches on the sticky cards placed over spent mushroom compost piles in August indicates that this substrate is not attractive to mushroom phorid flies nor is it a source of adult emergence, and hence not a source of re-infestation of mushroom houses. Our results are in agreement with Hussey (1965), who caught no female mushroom phorid flies on traps placed over spent mushroom piles in England (UK). Previous studies have shown that *M. halterata* is an obligate fungal feeder that will not complete its development on a mushroom substrate lacking *A. bisporus* mycelia (Scheepmaker et al., 1996). Female *M. halterata* have been shown to be attracted to mushroom compost that has actively growing *A. bisporus* mushroom mycelia (Baker et al., 1982; Pfeil & Mumma, 1993; Tibbles et al., 2005) and hence will be most likely to enter mushroom growing rooms at the middle and end of spawn run (stage of active mycelial growth) of the crop (Richardson & Hesling, 1978). Steaming the mushroom compost at the end of the crop is a common agricultural practice employed in mushroom farming (Beyer, 2002). At such high temperatures, the *A. bisporus* mycelia that are present in the compost are killed, which should render the compost unattractive to *M. halterata* flies. The negligible number of *M. halterata* flies that we caught over spent mushroom compost piles supports this idea, and the few flies captured were most likely those flying around the general vicinity of the mushroom houses.

The low number of flies caught on the sticky traps near windbreaks could simply mean that *M. halterata* adults do not normally inhabit wooded areas even though many fungal species are present in the leaf litter, and the flies prefer to concentrate their activities over turf areas. Alternatively, the data may mean that flies emigrating out of the houses do not or cannot reach areas farther from the mushroom houses. All of the turf areas were at distances of 15–52 m from the mushroom houses, and so it seems likely that these data from the grass near the mushroom houses compared with windbreaks would mean that the flies captured in these locations originated from within the mushroom houses. Life histories and distribution of most phorid species in nature are unknown. *Megaselia halterata* has most often been reported in association with mushroom farms (Disney, 2006; Brown & Hartop, 2017), rather than with natural areas.

Megaselia halterata observed flying over the grassy areas and the sweep-netting of thousands of these flies strongly indicates that these grassy areas are sites for courtship and mating. Approximately 30% of the flies captured in aerial flight via sweep-netting were in copula. We observed many *M. halterata* in courtship pursuits on the hood of our car or in copula there. These findings are new evidence that *M. halterata* leave the mushroom houses to find mates during daylight. The fact that we found zero *M. halterata* eggs, larvae, or any adult emergence from our turf samples taken over several areas where we had trapped flies indicates that *M. halterata* are not using the grassy turf for egg laying. The females therefore must be flying somewhere else for oviposition, and this means they likely attempt to return to the mushroom houses to do so. Swarming behaviors in the family Phoridae have been reported, including *M. halterata* and other *Megaselia* species (Coyler, 1954). Hussey (1965) reported cases in which *M. halterata* were found outside mushroom houses where male-to-female ratios were found to be male biased and suggested that female flies leave the mushroom growing rooms in response to a pheromone-based stimulus from males. Although we did not record the sex ratio of the flies caught over turf areas outside mushrooms houses, our data suggest that flies are exiting the growing houses, concentrating over turf areas and mating. Mushroom production is an intensive farming system, in which one growing house may be in the final stages of production, whereas another house may be in the initial stages of the crop (stage of active growing *A. bisporus* mycelia in the compost). It is likely that the flies are re-entering these houses and infesting the compost at these earlier stages.

In August, as in October, the greatest number of flies were caught after 16:00 hours. However, the time effect in August was dependent on the density of flies; farms

2 and 4 showed a clear time pattern, whereas farms 1 and 3, due to very low fly catches, did not. In August, high fly numbers correspond to an interval from 16:00 to 24:00 hours eastern daylight time, where temperatures ranged between 27 and 17 °C, respectively. Sunset during this sampling period was at approximately 20:00 hours. According to Hussey (1965), *M. halterata* activity is curtailed by sunset, even if the temperature remains above the critical threshold for flight of 12.8 °C. We hypothesize that the flies caught during this August interval were mostly likely active before sunset, when temperatures before that hour were above 20 °C. In October, the high level of phorid fly activity was from 16:00 to 20:00 hours eastern standard time. This interval had temperatures ranging between 23 and 15 °C. Even though temperatures were above the critical flight threshold stated by Hussey (1965) for most part of this time interval, sunset was at approximately 19:00 hours, suggesting that flight was possibly curtailed by darkness even when temperatures were within a range conducive to fly activity for at least a portion of that time interval. Farm 4 deviated from this overall time pattern, with similar numbers between 10:00 and 20:00 hours. We cannot explain this deviation from our data, however – perhaps certain farm activities during this time period may have contributed to high fly numbers in the morning hours for this farm. During activities such as casing (when layer of peat moss is brought into the growing room) and harvesting, the doors to the growing rooms remain open for ca. 4 h and flies may exit the growing rooms causing outside fly catches to peak. Exiting flies at these stages of the crop may be mating outside and re-infesting new rooms (new crops) for oviposition.

Nocturnal fly activity was also low in both sampling occasions. Temperatures during the corresponding time interval in August ranged from 18 to 26 °C, as opposed to lower night time temperatures in October which ranged from 17 to 11 °C. The negligible fly numbers caught in October during the night hours as opposed to August could be due to these lower nighttime temperatures.

Establishing temperature and daylight thresholds for *M. halterata* flight activity may be useful in developing integrated pest management (IPM) tactics for this species. The most successful IPM tool that mushroom growers use at present is fly exclusion. There are three main stages in the mushroom crop cycle when exclusion is hindered due to the opening of the mushroom house doors for long periods of time: the day the mushroom house is filled or spawned, the day the compost is cased, and during the harvesting period. During these stages, the crop is susceptible to mushroom phorid fly invasions, which can be reduced by scheduling these activities during hours when outdoor mushroom phorid flight is minimal. Our data suggest that farm operations should be limited to nighttime hours possibly after sunset and should be avoided after 16:00 hours until sunset in order to enhance fly exclusion measures. Further studies are needed to determine with greater precision the activity of *M. halterata* in relation to daylight and temperature.

Further studies are needed in order to determine *M. halterata* critical flight times, especially with regard to this species' flight activity in relation to crop stages so it can be determined when it is most likely that flies will emigrate from the growing rooms to the outside. Our study showed that mushroom phorid flies are indeed active outside mushroom farms for a crucial part of their lifecycle – that of mating. This stage of the mushroom pest's life history can potentially be interrupted in a mushroom IPM program, targeting flies that leave the mushroom houses to mate with the use of premise sprays or pheromone mating disruption, hence reducing the pressure from flies that re-enter the growing rooms to deposit eggs on the spawned compost.

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