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Effects of different animal manures on attraction and reproductive behaviors of common house fly, *Musca domestica* L

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Abstract Insects rely mainly on their well-developed and highly sophisticated olfactory system to discriminate volatile cues released from host and nonhost substances, mates, oviposition substrates, and food sources. Onset of first mating, mating duration, and onset of first oviposition, oviposition period, fecundity (number of eggs laid by a female), and longevity of freshly emerged Musca domestica L. (Diptera: Muscidae) adults were observed in the presence of different animal manures: cow, horse, donkey, poultry, and an artificial diet. The M. domestica adults exposed to horse manure showed a delay in onset of first mating and first oviposition, prolonged mating duration, and reduced fecundity compared to the artificial diet (control). Likewise, the fecundity was reduced in the presence of donkey manure as compared to artificial diet. The onset of first mating was delayed and duration of first mating was shortened in the presence of cow manure as compared to artificial diet and no oviposition was observed throughout the duration of the experiment. However, the reproductive behaviors and all fitness measures in adults exposed to poultry manure were similar or even better, compared to the artificial diet. Surprisingly, in a free-choice

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³ Department of Chemistry, COMSATS Institute of Information Technology, Abbottabad 22060, Pakistan attraction assay, the highest numbers of adult flies were attracted toward the cow manure as compared to all other manures as well as the artificial diet. However, the numbers of flies captured in all other types of manures were not different than the artificial diet (control). Furthermore, chemical analysis of headspace samples of manures revealed qualitative differences in odor (volatile) profiles of all manures and artificial diet, indicating that behavioral differences could be due to the differences in the volatile chemistry of the adult ovipositional substrates and larval growth mediums. This study may contribute toward both understanding the linkage between ecological adaptations and host selection mechanisms and the development of pest management strategies against this serious pest of medical and veterinary importance.

Keywords House fly \cdot Manures \cdot Chemicals \cdot Attraction \cdot Behaviors

Introduction

Insects have highly sophisticated sensory systems that facilitate discrimination between the host and nonhost substrates and also the host of different quality (Benton 2006; De Bruyne and Baker 2008; Taylor and Krapp 2007). Among the sensory modalities, olfaction (sense of smell) is the most important for determining innate behaviors, including selection of mates, oviposition substrates, and food sources (De Bruyne and Baker 2008). Chemical cues released by host and nonhost odor sources may have the ability to influence these behaviors (Azeem et al. 2013; Azeem et al. 2015; Binyameen et al. 2013).

The common house fly, *Musca domestica* L., is an economic pest of many leading industries, including food processing units, livestock, and poultry farms (Malik et al.

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2007). It has also been classified as an insect pest of public health and veterinary importance, as it is a mechanical vector of more than 100 diseases in humans and other animals (Fasanella et al. 2010; Forster et al. 2007; Vazirianzadeh et al. 2011). Poor hygienic conditions combined with a hot and humid environment serve as ideal conditions for *M. domestica* breeding (Hogsette 1996). Manure heaps in poultry, pet, and livestock farms serve as suitable breeding sites for *M. domestica* (Moon et al. 2001b). Food contamination and quality deterioration of poultry and livestock products are the major problems due to M. domestica (Clavel et al. 2002; Taylor et al. 2012). Meat and milk spoilage and egg spotting are major effects that are directly linked with high population density of M. domestica (Khan et al. 2012). Expanding urbanization in rural areas and public health concerns about flies associated with livestock facilities often results in societal problems, such as neighborhood confrontation and/or even litigation (Gerry et al. 2005).

Application of pesticides is the most common pest control tactic used to prevent economic losses due to pests and vectors (Khan 2009). Although chemical control has proven to be a cost-effective (one invested dollar returns \$4 benefits) pest management strategy, its indirect environmental costs, which are estimated to be \$10 billion annually, cannot be neglected (Pimentel 2005). According to the World Health Organization (WHO), about 20,000 people die annually due to adverse effects of pesticide exposure, while 3 M are poisoned, and there are nearly 750,000 new cases of chronic pesticide exposure every year (Ortiz et al. 2002). Importantly, injudicious pesticide application and lack of safety equipment has raised serious public health concerns in less developed countries (Hazell and Wood 2008), as the numbers of deaths due to pesticide food poisonings are more than those of infectious diseases (Ortiz et al. 2002). Moreover, excessive pesticide application has led to the development of resistance in target pests (Abbas et al. 2015), as well as the destruction of natural enemies (Hajek 2004). There are more than 600 species of arthropods reported to be resistant to different pesticides, and *M. domestica* is ranked as the 20th most resistant species of the world (Whalon et al. 2008). Tellingly, chemical control has been used as the principal control measure to overcome *M. domestica* problems during the last century but is currently limited due to resistance problems (Scott et al. 2000). Recently, it has been reported that M. domestica can develop resistance to almost all chemical classes (Abbas et al. 2014; Kristensen and Jespersen 2003; Shah et al. 2015; Tang et al. 2002). Usually, resistance results in increased application rates of insecticides with short frequent intervals, environmental pollution, and ultimately failure of the products (Khan et al. 2013a). Therefore, there is an urgent need, to explore ecofriendly management methods as an alternative to chemical control (Mann et al. 2010; Siriwattanarungsee et al. 2008).

Research aimed at behavioral manipulations has gained importance as an insect pest management tool to counter reliance on synthetic chemicals (Witzgall et al. 2010). Ecofriendly management tools such as "push-pull" strategies have positively contributed to current insect pest management approaches (Cook et al. 2006). A number of studies have been conducted to evaluate the effect of manures and manureoriented volatiles on the development and behavior of the house fly (Cickova et al. 2012; Cosse and Baker 1996; Foster and Harris 1997; Khan et al. 2012; Larrain and Salas 2008; Moon et al. 2001a). But, information on the impact of volatiles released from different livestock and poultry manures on the reproductive behaviors of M. domestica has not been studied so far. Therefore, the current study was performed to observe the effects of manures from cow, horse, donkey, and poultry on reproductive behaviors and fitness measures of M. domestica adults. Additionally, the attraction of M. domestica adults toward cow, horse, donkey, and poultry manures and a control was examined. Furthermore, headspace volatiles from these sources were analyzed to determine qualitative differences in volatile chemical profiles of the manures and artificial diet. Results are discussed in an ecological context, considering selection of adult oviposition sources and larval growth mediums. Moreover, the possible effect of different manure volatiles toward house flies attraction and oviposition behaviors is also discussed.

Materials and methods

Insects

A sample population of *M. domestica* adults (same proportion of male and female) was captured from a butcher's shop in Multan (30° 12' 0" N, 71° 25' 0" E) with the help of sweep nets. Afterward, the collected flies were brought to the laboratory and reared according to the procedure developed by Abbas et al. (2014). Briefly, the adults were kept in meshcovered plastic cages provided with milk, sugar mixture (1:1), and ad libitum hydrated cotton pads in petri dishes. For larval diet, 75 mL of water was added to make a paste of milk, sugar, wheat bran, rice straw, and yeast (3:3:40:10:10 g), respectively (Bell et al. 2010). Laboratory reared adults were used in the experiments to avoid preexposure effects to any of the manures used. Adults were anesthetized by chilling and the sexes were separated immediately after emergence. The newly emerged (<12 h old) adults were used in no-choice reproductive behavior bioassays, and 3-5-day-old adults in free-choice attraction bioassays. Insect rearing and all other experiments were done at standard laboratory conditions: temperature at 27±2 °C, relative humidity at 70 ± 5 %, and under photoperiod conditions of 12 h light:12 h dark.

Animal manures and their standardization

$$C = \frac{A - T}{A}$$

A is the grams of air-dried sample, and *T* is the grams of the sample after complete drying in the oven.

After determining the moisture content of air-dried manures, the moisture level of air-dried manure was adjusted to 70 % by adding water. For obtaining the desired moisture content, the amount of water added was determined according to the following formula:

$$X = \frac{(Y)(D)}{1-y} - C$$

where

- X the amount of water (ml) required to be added to 100 g of air-dried manure sample
- *Y* desired proportion of the water in the manure
- D oven dried weight of 100 g of the air-dried weight
- C grams of water in the 100 g of air-dried manure

We used the procedure of adding water to the air-dried manure because the physical characteristics of the manure were maintained in a more natural state than if we used the alternative of adding water to oven-dried manure.

Reproductive behavior bioassays (no-choice assay)

Reproductive behavior bioassays were performed according to Binyameen et al. (2013). Comprehensively, newly emerged single pairs (male/female) of M. domestica adults were shifted into porous plastic cages (14×9 cm). A muslin cloth was fastened with a rubber band at the open end of the adult cage. The milk + sugar mixture (1:1) and hydrated cotton pad were provided as adult diet. Five grams of manure was weighed and provided in a petri dish in each plastic cage. The manure was replaced with fresh substrate every other day. The manure of each animal was considered as a separate treatment, and each pair of M. domestica was regarded as one replicate. Each treatment was replicated five times. The time until onset of first mating was observed for 12 h daily in the light for the first 10 days. Mating observations were recorded at 10-min intervals for 10 days from the start of experiment. The manure samples were taken out of experimental cages, and the males and females were shifted to separate cages during the next 12 h of the dark period. The insect pairs surviving at least 3 days after the start of experiment were included in data of reproductive behavior including onset of first mating, mating duration, onset of oviposition, oviposition period, and fitness measures, i.e., fecundity and longevity. For fecundity and longevity, eggs laid by each female and the numbers of dead adults (males and females), respectively, were counted daily. Fecundity and longevity (both male and female) were recorded for 18 consecutive days.

Attraction bioassay (choice assay)

Attraction bioassay was performed following the methodology of Khan et al. (2013b) with some modifications. Briefly, the free choice arena was comprised of the prescribed four types of manures and a positive control (artificial diet) kept in meshed wooden box $(91.44 \times 45.72 \times 60.96 \text{ cm})$. The order of the placement of glass jars containing manures in each replicate of the free choice experiment was determined by using a random number table. Every type of manure was considered as a separate treatment, and 150 g of manure sample was used in each treatment. Each treatment was replicated thrice. The manure samples were placed in a glass jar having a plastic funnel at the open end to avoid the escape of flies after entry. There were 25 pairs used per cage (replicate) and 75 pairs in the whole experiment. The numbers of captured flies were counted and removed from the jar at 6-h intervals during the day-time and 12 h after darkness. For lighting in the experimental room, we used one light bulb (Philips, Model # 929676000902) in each corner of the room and one in the middle of the room. Cage positions were changed by moving one position forward after each

observation to rule out the possibility of position effects. The experiment was run until >75 % (usually about 4 days after the beginning of the experiment) of the exposed flies were captured.

Collection of volatiles

In order to analyze volatile organic compounds emitted by manures and artificial diet, the samples were prepared and treated in the same way as in the behavioral bioassay and then stored at -20 °C in a freezer until volatile chemical analysis using head space, solid phase micro extraction (SPME) fiber, and gas chromatography-coupled mass spectrometry (GC-MS).

Frozen manure samples were thawed until reaching room temperature $(22\pm2 \text{ °C})$, and 5 g of each was precisely weighed in a 100-ml Erlenmeyer flask covered with aluminum foil. The collection of volatiles was carried out by using methodology described by Azeem et al. (2015) with modifications; briefly, the flask headspace (HS) was equilibrated with manure volatiles for at least 2 h prior to headspace volatile collection using SPME fiber. The SPME fiber (stable flex, 65 µm polydimethylsiloxane/divinylbenzene, Supelco, USA) was conditioned at 250 °C for 30 min before first time use as advised by the manufacturer. For the collection of volatiles, the SPME needle was introduced into the flask through a pin hole in the aluminum foil, and the SPME fiber was exposed to the HS volatiles for 40 min at room temperature without shaking; after volatile collection, the fiber was retracted into the needle and injected immediately into the gas chromatograph (GC) at 235 °C. The SPME fiber was cleaned at 235 °C under a stream of helium gas for 5 min before each collection of volatiles.

Identification of volatiles

Separation and identification of volatiles were carried out on PerkinElmer Clarus 600 gas chromatograph (GC) connected with PerkinElmer Clarus 600 C mass spectrometer (MS). The GC was equipped with a split/ splitless injector (splitless mode, 60 s); the carrier gas was helium, with a constant flow of 1 ml/min through the column. The GC was equipped with an Elite 5-ms capillary column (30 m, 0.25 mm ID, and 25- μ m film thickness, PerkinElmer, USA). The temperature program of the GC oven was 40 °C for 1 min increasing in temperature at a rate of 5 °C min⁻¹ up to 160 °C and maintained at 160 °C for 1 min then increasing at a rate of 20 °C min⁻¹ until 240 °C and maintained for 5 min. The injector temperature was isothermally set at 235 °C, and the transfer line connecting the GC to the MS was isothermally set at 250 °C. The MS ion source temperature was 150 °C; mass spectra were obtained at 70 eV with a mass range of 40 to 400 m/z. Retention indexes of separated compounds were calculated by injecting hydrocarbon standard solution (C₉-C₂₅) into the GC-MS under the same parameters as those used for samples. Identification of separated compounds was initially carried out by comparing their mass spectra to the Finnigan NIST-05 (National Institute of Standard and Technology, USA) MS library. The final authentication was made by comparing their retention indexes and mass spectra with published literature as well as by injecting synthetic compounds, where available (purchased from Sigma-Aldrich and having 99 % GC-purity) to the GC-MS using the same parameters as those used for the samples. Relative concentration of each identified compound found in the headspace of a sample was determined by comparing peak area of the compound to the sum of all peaks' area in a total ion current (TIC) chromatogram.

Data analysis

The data of reproductive behaviors—delay in onset of first mating, first mating duration, mean mating duration, time until onset of first oviposition, oviposition period, and fitness measures—fecundity (numbers of eggs laid by a female), and longevity of *M. domestica* adults exposed to cow, horse, donkey, and poultry manures were compared with that of control (artificial diet) using Kruskal–Wallis one-way analysis of variance (ANOVA) followed by a post hoc test, Dunn's multiple comparison test at $P \le 0.05$ due to nonnormal distribution of the most of the parameters (Shapiro–Wilk test, P < 0.05) employing an analytical software, IBM SPSS Statistics 21 (Anonymous 2005).

Hedges' method of unbiased effect sizes following the Hedges and Olkin (2014) was used to assess the effect of different treatments on reproductive behaviors and fitness measures compared to the control. Effect size is a unit less measure of treatment effect that is obtained by dividing the difference among the means of control and treatment by pooled standard deviation (Nakagawa and Cuthill 2007). An effect size of 0.2, 0.5, and above 0.8 is regarded as small, medium, and large effect, respectively (Nakagawa and Cuthill 2007).

For attraction bioassay, ANOVA was done and means of different treatments were compared using a post hoc test, least significant difference (LSD), at $P \le 0.05$ using an Analytical software, Statistix 8.1 (Anonymous 2005). Binomial confidence intervals (95 %) were calculated following Newcombe (1998) with IBM SPSS Statistics 21 (Anonymous 2005).

Results

Reproductive behaviors

Time until onset of first mating

The medians (inter quartile range) of time until onset of the first mating of *M. domestica* females exposed to cow, horse, donkey, poultry, and control were 120 (180), 98 (13.65), 63 (24.9), and 27 h (28), respectively (Fig. 1). The time until onset of the first mating differed significantly across the treatments (H=14.378, df=4, P=0.006). Pairwise comparisons with adjusted P values showed that there were nonsignificant differences for the time until onset of first mating of the pairs including poultry-control (P=1), poultry-donkey (P=0.578), poultry-cow (P=0.578), control-donkey (P=1), control-cow (P=0.384), donkey-cow (P=1), and horse-cow (P=1), but a significant difference was observed for that of the pairs including poultry-horse (P=0.016), control-horse (P=0.016), and donkey-horse (P=0.016). Effect size calculations also showed that compared to the control mating was strongly delayed in the presence of cow effect size (95 % confidence interval) |1.24| (-0.11-2.60) and horse manures |2.77| (1.03-4.50), while medium effect by donkey |0.61| (-0.65-1.88) manures, while mating started earlier |-0.82| (-2.12-0.47), in the presence of poultry manure.

Duration of first mating and duration of all matings

The medians (inter quartile range) of duration of the first mating of *M. domestica* females exposed to cow, horse, donkey, poultry,

and control were 3 (5), 25 (47.25), 20 (26.75), 15 (24.75), and 15 min (0), respectively (Fig. 2). There was an extreme score in the control. The median duration of first mating was significantly different among the treatments (H=11.11, df=4, P=0.025). Pairwise comparisons with adjusted P values showed that there were non-significant differences for the median of duration of first mating of *M. domestica* females for the pairs—cow-control (P=0.646), cow-poultry (P=0.369), control-poultry (P=1), control-donkey (P=1), control-horse (P=0.820) and poultrydonkey (P=1), poultry-horse (P=1), and donkey-horse (P=1)—but a significant difference was observed for that of the pairs—cow–donkey (P=0.036) and cow–horse (P=0.003). Effect size calculations also showed that compared to the control, mean duration of first mating was longer in the presence of horse effect size (95 % confidence interval) [1.32] (-0.05-2.69) and donkey manures |1.19| (-0.15-2.54), while mating duration in poultry manure was having very low effect |0.39| (-0.86-1.65) compared to control. However, mating duration was much shorter in the presence of cow manure |-3.70| (-5.74–(-1.66) compared to control.

The medians (inter quartile range) of duration of the all matings of *M. domestica* females exposed to cow, horse, donkey, poultry, and control were 5 (14), 25 (47.25), 20 (26.75), 20 (25.25), and 15 min (0), respectively (Fig. 3). There was an extreme score in the control. The median duration of total matings was significantly different among the treatments (H=14.691, df=4, P=0.005). Pairwise comparisons with adjusted P values showed that there were non-significant difference for the median of duration of total mating time of *M. domestica* females



Fig. 1 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles of time until onset of first mating of *M. domestica* adults under the effect of different animal manures



Fig. 2 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles and extreme scores (*) for duration of first mating of *M. domestica* adults under the effect of different animal manures

for the pairs including cow-control (P=0.646), cowpoultry (P=0.369), control-poultry (P=1), control-donkey (P=1), control-horse (P=0.820) and poultry-donkey (P=1), poultry-horse (P=1), and donkey-horse (P=1), but a significant difference was observed for that of the pairs including cow-donkey (P=0.036) and cow-horse (P=0.003). Effect size calculations showed that compared to the control, mean duration of all matings was longer in the presence of horse |effect size| (95 % confidence interval) |1.19| (-0.15-2.54) and donkey manures |1.19| (-0.15-2.54). Poultry manure has had medium effect |0.48| (-0.78-1.74) on mating duration as compared to the control. However, mating duration was short in the presence of cow manure |-0.97| (-2.28-0.34).



Fig. 3 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles and extreme scores (*) for duration of total matings of *M. domestica* adults under the effect of different animal manures



Fig. 4 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles and extreme scores (*) for time until onset of first oviposition period of *M. domestica* adults under the effect of different animal manures

Time until onset of first oviposition

The medians (inter quartile range) of time until onset of first oviposition period of M. domestica females exposed to cow, horse, donkey, poultry, and control were 432 (0), 180 (60), 144 (84), 73 (27.25), and 120 h (60), respectively (Fig. 4) .There was an extreme score observed both in the cow and control treatments. The median time until onset of first oviposition period was nonsignificantly different among the treatments (H=9.380, df=4, P=0.62). Post hoc test was not performed because analysis of variance (KW test) showed the nonsignificant difference among treatments. Effect size calculations showed that compared to the control, oviposition was delayed differently (from strong to small effect) in the presence of horse |effect size| (95 % confidence interval) |1.45| (-0.02-2.93 and donkey |0.43| (-0.90-1.76) manures, while oviposition started earlier |-1.53| (-3.02–(-0.04), in the presence of poultry manure.

Oviposition period

The medians (inter quartile range) of duration of oviposition period of *M. domestica* females exposed to cow, horse, donkey, poultry, and control were 0 (0), 60 (78), 60 (78), 96 (120), and 24 h (198), respectively (Fig. 5). There was an outlier in the control. The median duration of oviposition period was significantly different among the treatments (H=17.161, df=4, P=0.002). Pairwise comparisons with adjusted P values showed that there were nonsignificant differences for the median of duration of oviposition period of *M. domestica* females for the pairs including poultry–control (P=1), poultry– donkey (P=1), poultry–horse (P=0.181), control–donkey (P=1), control–horse (P=1) and donkey–horse (P=1), donkey–cow (P=0.277), and horse–cow (P=1), but a significant difference was observed for that of the pairs including poultry–cow (P=0.001) and control–cow (P=0.044). Effect size calculations showed that compared to the control, mean oviposition period was shorter in the presence of cow manure |effect size| (95 % confidence interval) |-1.38| (-2.84-0.08). Horse |-0.51| (-1.84-0.83) and donkey manures |-0.50| (-1.84-0.83) have medium effect on the oviposition period, while the effect of poultry manure |0.13| (-1.45-1.18) was similar to control.

Fitness measures

Fecundity

There was no oviposition in the cow manure. The medians (inter quartile range) of fecundity (number of eggs laid per female) of *M. domestica* females exposed to cow, horse, donkey, poultry, and control were 0 (0), 11 (19), 25 (13), 59 (33.75), and 48 (34), respectively (Fig. 6). The median duration of oviposition period was significantly different among the treatments (H=17.161, df=4, P=0.002). Pairwise comparisons with adjusted *P* values showed that there were nonsignificant differences for the median fecundity of *M. domestica* females for the pairs including poultry–control (P=1), poultry–donkey (P=1),



Fig. 5 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles and outliers (0) for time until onset of first oviposition period of *M. domestica* adults under the effect of different animal manures

poultry-horse (P=0.181), control-donkey (P=1), controlhorse (P=1) and donkey-horse (P=1), donkey-cow (P=0.277), and horse-cow (P=1), but a significant difference was observed for that of the pairs including poultry-cow (P=0.001) and control-cow (P=0.044). Effect size calculations showed that female fecundity was very low in the presence of cow |effect size| (95 % confidence interval) |-3.47| (-5.55-(-1.40), horse |-2.41 (-4.14-(-0.69)|, and donkey manure |-1.71| (-3.25–(-0.18), while fecundity was slightly more in poultry manure than control |0.24| (-1.08–1.56).

Longevity

The medians (inter quartile range) of male longevity of *M. domestica* females exposed to cow, horse, donkey, poultry, and control were 240 (168), 384 (240), 360 (312), 336 (240), and



Fig. 6 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles for fecundity (eggs/female) of *M. domestica* adults under the effect of different animal manures

288 h (300), respectively (Fig. 7). The median male longevity was significantly different among the treatments (H=17.584, df=4, P=0.001). Pairwise comparisons with adjusted P values showed that there were nonsignificant differences for the median male longevity of M. domestica females for the pairs including cow-horse (P=1), cow-donkey (P=0.761), horse-donkey (P=1), horse-control (P=0.248), horse-poultry (P=0.15), donkey-control (P=1), donkey-poultry (0.914), and control-poultry (P=1), but a significant difference was observed for that of the pairs including cow-control (P=0.009), cow-poultry (P=0.005). Effect size calculations showed male longevity in the presence of cow |effect size (95 % confidence interval) |-0.14 (-1.10-1.39), horse |-0.10 (-1.34-1.14), donkey |0.21(-1.03-1.46), and poultry manures |0.11 (-1.35-1.13).

The medians (inter quartile range) of female longevity of *M. domestica* females exposed to cow, horse, donkey, poultry, and control were 336 (216), 432 (216), 432 (12), 360 (186), and 288 h (108), respectively (Fig. 8). The median female longevity was not significantly different among the treatments (H=1.072, df=4, P=0.899). Post hoc test was not performed because analysis of variance (KW test) showed the nonsignificant difference among treatments. Similarly, female longevity in cow |0.14| (-1.10–1.39), horse |-0.05| (-1.28–1.19), donkey |0.39| (-0.86–1.64), and poultry treatments |0.39| (-0.86–1.65) was not different than the control (artificial diet).

Attraction bioassay

The highest number of flies (both sexes) was captured in cow manure (P=0.0297) compared to those captured in other

treatments including control (Fig. 9). The numbers of flies captured in all other manures were not different than control.

Chemical analysis of volatile

Overall, thirty-one volatile compounds were identified in the headspace of manure samples and artificial diet (Table 1). Chemical analysis revealed the identification of ten, 17, 11, eight, and six compounds in the headspace of artificial diet, donkey, horse, poultry and cow manure, respectively. Artificial diet mainly emitted different esters, whereas manure samples emitted mixtures of hydrocarbons, ketones, and alcohols (Table 1). The most abundant volatile compounds found in the headspace of cow, horse, donkey, poultry, and artificial diet were 4,7-dimethylundecane, aromadendrene, 2,6,10trimethyl-1,5,9-undecatriene, 3-octanone, and ethyl hexanoate, respectively (Table 1). However, these compounds were not identified in the chemical profiles of any other manure or artificial diet, except one compound, aromadendrene. which was found in both horse and donkey manures. Interestingly, 2-methylbutyl hexanoate, ethyl octanoate, 2methylpropyl hexanoate, 3-methylbutyl 2-methylpropanoate, 2-methylpropyl 2-methylpropanoate, ethyl butanoate, and 3methyl-1-butanol were present only in artificial diet.

Discussion

Selection of food sources and oviposition substrates has a direct impact on fitness and successful reproduction in insects.

Fig. 7 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles for male longevity of *M. domestica* adults under the effect of different animal manures



Fig. 8 Box-plots displaying the group medians, first and third quartiles, 10th and 90th percentiles for female longevity of *M. domestica* adults under the effect of different animal manures

The present study investigates the role of chemical cues in the selection of adult oviposition substrate and larval food source in *M. domestica*. Furthermore, behavioral attraction and host-choice selection were studied to understand their link to reproductive behaviors and fitness measures, which are considered to be necessary for a biologically successful life.

The present study reveals that reproductive behaviors of *M. domestica* were negatively affected by the presence of cow manure compared to the control. Although the onset time of first mating in *M. domestica* adults was delayed (nonsignificant statistically) compared to the control, the duration of first mating and the mean mating duration were reduced (an extreme score in control, i.e., individual variations rendered

them statistically nonsignificant) compared to the control (artificial diet). Previously, it has been reported that environmental chemical volatiles have great ability to modulate the reproductive behaviors of insects positively or negatively depending on ecological conditions (Jactel et al. 2011; Jactel et al. 2001; Papadopoulos et al. 2006; Shelly and Villalobos 2004; Sutherland 1977; Zhang et al. 2007). Insects may dedicate their olfactory sensory system to locate oviposition sites with ample provisions of quality resources required for the successful development of their offspring and also free of survival threats (Binyameen et al. 2013; Lam 2010).

Interestingly, females exposed to cow manure showed no oviposition activity at all; this might possibly be due to unique



Fig. 9 Attraction of adult flies toward different oviposition sources. Bars with different letters are significantly different (LSD test, $P \le 0.05$)

 Table 1
 Percentage composition

 of volatile compounds detected in
 the headspace of cow, horse,

 donkey, and poultry manure and
 artificial diet samples, values

 represented as relative amount
 based on GC-MS data

Compound name	RI ^{**}	Cow	Horse	Donkey	Poultry	Artificial
3-Methyl-1-butanol*		_	_	_	_	4.1
Pentyl lactate		_	—	_	3.5	_
1,3,5-Cycloheptatriene		61.6	19.3	1.2	5.3	-
Ethyl butanoate*		-	-	-	-	14.2
Butyl ether		12.7	5.8	0.6	1.5	_
Nonane	900	-	-	0.3	0.3	_
2-Heptanone	903	-	-	3.0	-	_
3-Methyl-6-heptene-1-ol	928	-	9.9	0.5	-	_
3,7-Dimethyl-1,6-octadiene	943	-	13.2	2.6	-	_
2-Methylpropyl 2-methylpropanoate*	960	-	-	-	-	0.7
3,7-Dimethyl 2-octene	967	-	4.0	8.2	-	_
3-Octanone*	998	-	-	-	58.2	_
Ethyl hexanoate*	1010	-	-	_	-	70.5
3-Ethyl-2-methyl-1,3-heptadiene	1017	-	2.4	0.3	-	-
2-Ethyl-1-hexanol	1054	-	15.1	0.7	24.5	-
3-Methylbutyl 2-methylpropanoate*	1064	-	-	_	-	4.2
3-Methyl-1-hexanol	1095	7.8	5.9	_	-	-
Acetophenone*	1098	-	-	17.4	-	-
2-Methylpropyl hexanoate*	1159	-	-	_	-	0.4
Phenol*	1167	-	-	_	6.5	-
Ethyl octanoate*	1204	_	—	_	_	3.6
2-Methylbutyl hexanoate*	1260	_	—	_	_	0.8
Tridecane	1301	_	—	0.2	0.3	0.8
α-Cubebene*	1378	_	—	0.4	_	-
Ethyl decanoate	1403	4.8	3.4	_	_	0.8
2,6,10-Trimethyl-1,5,9-undecatriene*	1406	_	—	61.8	_	-
Aromadendrene	1423	_	18.0	0.8	_	-
2,3,5,8-Tetramethyl-decane	1462	-	-	0.9	-	-
β-Himachalene	1483	_	_	0.6	_	_
4,7-Dimethylundecane*	1805	4.8	_	—	-	_
8-Methyl-1-decene	1848	8.4	3.0	0.1	-	_

* The unique compounds for each analyzed sample

** Retention index was calculated by analyzing C9–C25 alkanes at the same parameters as those used for manure samples

volatiles that were released from only cow manure but not by other manures as well as artificial diet. Surprisingly, in the attraction bioassay, the highest numbers of adult flies were attracted toward cow manure as compared to horse, donkey, and poultry manures, and control. These results are in agreement with studies performed by Larsen et al. (1966) and Ascher (1958), where the most attractive substrate was not the most optimal oviposition substrate. So, it may be concluded that attraction toward the cow manure in our study is not strictly relevant to oviposition behavior, as the final decisions for acceptance or rejection of an oviposition substrate depend mainly on contact cues instead of sense of smell (Lam 2010).

Meanwhile, cow manure may possibly contain some volatile cues that have attracted more flies than all other substrates but may also have some nonvolatile compounds that caused significant delay in the onset of mating and also inhibited female oviposition. Similar observations have been reported by Zakir et al. (2013), where onset of mating in a polyphagous pest moth, *Spodoptera littoralis* (Bois.) was delayed in the presence of volatiles released from poor quality hosts. However, further studies are needed to test the hypothesis that some nonvolatile compounds are responsible for this inhibition.

Insects show variation in their reproductive behaviors in the presence of different manures due to difference in their nutritious value and phago-stimulating factors (Khan et al. 2012; Larrain and Salas 2008; Myers et al. 2008). *M. domestica* females exposed to horse manure showed a delay in onset of first mating, significantly prolonged duration of first mating as well as all

matings (an extreme score in control, i.e., individual variations rendered them statistically nonsignificant) as compared to control. Similar findings were reported by Binyameen et al. (2013), where mating duration of S. littoralis was the longest in the presence of volatiles released from leaves of a nonhost tree species, Picea abies which they hypothesized to be the effect of high amount of toxic terpenes, that might disable the insect from decopulation once mating has started. It could be assumed that volatiles released from the horse manure may have had some negative impact on the sensory system of mated pairs leading to higher mating duration. Furthermore, the number of eggs laid by females exposed to horse and donkey manures was significantly less in comparison to control. The reduced fecundity in the presence of poor quality oviposition substrate has been reported in S. littoralis (Anderson and Alborn 1999; Binyameen et al. 2013). An aversion trend in fecundity of Plutella xylostella (L.) has been observed on poor-quality peas (Zhang et al. 2007). The reduced egg laying could be the outcome of the survival strategy adopted by mother insects to save their progeny from threat of food shortage or more predation (Zhang and Schlyter 2004). These negative variations in reproductive behavior could possibly be linked with the poor quality of these manures for house fly breeding (Khan et al. 2012; Larrain and Salas 2008), since house fly females presumably prefer to lay eggs in the manure that serve as best developmental medium for their offsprings (Lam et al. 2009).

Our results showed that reproductive behaviors of M. domestica including onset of first mating, mating duration, onset of first oviposition, oviposition duration, and fecundity in the presence of poultry manure were similar or even positively affected compared to control. It may be concluded that poultry manure is a suitable substrate for house fly breeding (Khan et al. 2012; Larrain and Salas 2008). These results are consistent with those of Binyameen et al. (2013) and Sadek and Anderson (2007), in which S. littoralis showed optimum reproductive behavior on a suitable host, i.e., cotton, compared with nonhost plants. Additionally, one of the possible reasons for M. domestica optimal reproductive response in poultry manure could be its lower carbon/nitrogen ratio compared with the cow and horse manure (Moon et al. 2001a). Normally, lower carbon/nitrogen ratios enhance the microbial activity in larval substrates which is essential for larval growth and development (Ferrar 1987).

There were ten compounds identified from the analyses of volatile samples of control (artificial diet); eight compounds, including 3-methyl-1-butanol, ethyl butanoate, 2-methylpropyl 2-methylpropanoate, ethyl hexanoate, 3-methylbutyl 2-methylpropanoate, 2-methylpropyl hexanoate, ethyl octanoate, and 2-methylbutyl hexanoate, were unique compared to the four manures. Previously, Becher et al. (2012) reported that baker's yeast, *Saccharomyces cerevisiae*, is sufficient for *Drosophila melanogaster* attraction, oviposition, and larval development; baker's yeast was also an ingredient of the artificial diet used as a control in our study and may

indicate suitability of artificial diet for housefly reproduction. Moreover, ethyl hexanoate and 3-methyl-1-butanol were common in the chemical profile of volatile samples in both studies. We identified six and eight compounds in cow and poultry manure, respectively. Additionally, the 4,7-dimethylundecane was identified as unique in cow manure. Although the role of 4,7-dimethylundecane in determining the insect behavior is not well studied, it was previously identified in the volatiles of an entomopathogenic fungus, Isaria fumosorosea (=Paecilomyces fumosoroseus) (Hussain et al. 2010). The chemical profile of volatiles released from poultry manure contains two unique compounds including 3-octanone and phenol. The two phenolic compounds (4-ethyl-phenol and 4-methyl-phenol) and an alkane isomer (3-methyl-dodecane) identified in the current study have also been previously reported by Huang et al. (2007) from the manures of the same animals, poultry and cow, respectively. Cosse and Baker (1996) also recorded electrophysiological responses in female house flies to these phenols. Previously, oviposition substrates with enhanced microbial activity were reported to be preferred by dipteran females and production of volatiles such as phenols was also associated with these substrates (Jeanbourguin and Guerin 2007). Moreover, Quinn et al. (2007) detected esters in the chemical profile of molasses, and their presence was associated with microbial activity. The 3-octanone was known to be associated with the composted mushroom that serve as an ideal breeding source for a dipteran fly, Megaselia halterata (Wood) (Pfeil and Mumma 1993). Moreover, the 3-octanone was found in the frass of the soybean looper and was reported to be attractive to its parasitoid Microplitis demolitor (Ramachandran et al. 1991). Thus, it could be concluded that enhanced microbial activity was the probable reason for the volatiles of poultry manure and also make it suitable medium for house fly larval development. There were 11 and 17 compounds identified in the volatiles released from horse and donkey manure, respectively. There were only three unique compounds including 2,6, 10-trimethyl-1,5,9-undecatriene, α -cubebene and acetophenone identified in the chemical profile of donkey manure. Previously, Tawatsin et al. (2006) reported that 2,6,10trimethyl-1,5,9-undecatriene was the chemical constituent of the Houttuynia cordata Thunb that act as the oviposition deterrent against different species of mosquitoes. Moreover, the α cubebene was known to be associated with pathogenic fungal volatiles (McLeod et al. 2005). Additionally, α -cubebene was identified as the antennally active compound for the Agrilus planipennis Fairmair (Tawatsin et al. 2006). According to Jonfia-Essien et al. (2007a) and Jonfia-Essien et al. (2007b), acetophenone has positive impact on the growth and development of the Tribolium castaneum (Herbst) and Lasioderma serricorne (Fabricius), and also was antennally active compound for the T. castaneum. However, to understand the ecological implications of these compounds on house fly reproduction, further studies are needed in the future.

In conclusion, the current study implies that *M. domestica* populations should be managed more carefully in poultry farms, and proper manure management practices should be adopted in all kinds of farmhouses. Furthermore, based on current information about reproductive behaviors of *M. domestica*, in the future, there should be focus on the role of volatile compounds identified in this study and on the identification of nonvolatile compounds from both cow and poultry manures that may result in better management of this pest by using natural behaviorally active semiochemicals.

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Author's contribution RMS, MB, and SAS designed the experiments. RMS, FA, and MA performed the experiments. RMS, MB, and MA analyzed the data and wrote the manuscript. MB and SAS supervised the experiments. WBW provided the technical help for the preparation of final manuscript including English language and scientific-content editing.

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