






*We dedicate this paper to Reuven Heinik, manager of kibbutz Kissufim dairy farm, and the Israeli and Thai dairy farmers and workers who were murdered, kidnapped or otherwise hurt by Hamas terrorists on 7–9 October 2023 on 16 dairy farms near the Gaza border.*

## Population dynamics of common filth flies (Diptera: Muscidae) on dairy farms: Importance of manure removal and mass release of parasitoids

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### ABSTRACT

In the dairy industry confined cattle produce large amount of manure in a short time, thus providing optimal conditions for the breeding of the common filth fly pests (Diptera: Muscidae), mainly houseflies *Musca domestica* Linnaeus and stable flies *Stomoxys calcitrans* (Linnaeus). Filth-fly control relies largely on manure management practices, mass trapping, use of insecticides, and augmentative release of chalcidoid pupal parasitoids. The effectiveness of the last measure was variable and mostly limited in previous studies performed over limited temporal and spatial scales. The objectives of the current study were to follow the population dynamics of these two major pests on dairy farms, and to test the effect of natural parasitism and mass-released parasitoids on fly populations over a larger scale. In two consecutive years, we monitored fly numbers on ten dairy farms in south-western Israel and released *Muscidifurax raptor* Girault & Sanders (Hymenoptera: Pteromalidae) and *Spalangia cameroni* Perkins (Hymenoptera: Spalangidae) parasitoids (ca. 1:1 ratio) on five of the farms in the second year. In both years and on all the farms, housefly numbers were ten-fold higher than those of stable flies. Although the populations sizes of both fly species differed significantly among farms, they showed similar seasonal dynamics with significant differences among sampling dates. Housefly populations started to peak in April in both years, with a decline in June and mid-July in the first and second years, respectively. Stable fly numbers decreased from April to July, probably reflecting an earlier population peak that preceded the monitoring period in this study. These temporal population dynamics of the flies may reflect changes in manure moisture levels. The clearing frequency of the manure pits on the study farms had an inconsistent effect on fly

numbers. The release of parasitoid wasps did not affect adult housefly abundance significantly, possibly because the wasps were released too late in the season. The study provides useful information on temporal occurrence of two fly species on dairy farms, which is essential for the employment of site-specific preventive control measures to suppress fly populations.

**KEY WORDS:** Dairying, housefly, stable fly, *Musca domestica*, *Stomoxys calcitrans*, biological control, parasitoid wasps, population dynamics, *Muscidifurax raptor*, *Spalangia cameroni*.

### תקציר

במשקי רפת החלב פרות מייצרות כמות גדולה של זבל בזמן קצר, ובכך מספקות תנאים אופטימליים להתרבות זבובים מזיקים ממשפחת הזבוביים (Diptera: Muscidae), בעיקר זבוב הבית, *Musca domestica*, זבוב האורווה, *Stomoxys calcitrans*. ריסון אוכלוסיות הזבובים מסתמך במידה רבה על שחרור של צרעות טפיליות ממשפחת הפטרומליטיים (Pteromalidae) ומשפחת הספלנגיטיים (Spalangiidae), טפילות גלמי זבובים, שהראו רמות שונות של יעילות במחקרים קודמים. עם זאת רוב המחקרים בוצעו בזמנים ומרחבים מוגבלים. מטרת המחקר הנוכחי היא לעקוב אחר דינמיקת האוכלוסייה של שני מיני הזבובים המזיקים העיקריים ברפתות, ולבדוק את ההשפעה של טפילות טבעית ופיזורי הצפה של טפילים על אוכלוסיות הזבובים באזור נרחב יותר. במשך שנתיים רצופות, עקבנו אחר אוכלוסיות זבובים בעשר רפתות בדרום-מערב ישראל, ושחררנו בשנה השנייה את הפרזיטואידים תוקפי הגלמים *Muscidifurax raptor* ו-*Spalangia cameroni*, בחמש מהחוות. בשתי השנים של המחקר ובכל החוות אוכלוסיות זבוב הבית היו גבוהות פי עשר מאוכלוסיות זבוב האורווה. למרות שגודל האוכלוסיות של שני המינים היה שונה באופן מובהק בין החוות, הן הראו דינמיקה עונתית דומה עם הבדלים מובהקים בין תאריכי הדגימה. אוכלוסיות זבוב הבית החלו להגיע לשיא באפריל, עם ירידה ביוני ובאמצע יולי בשנים הראשונה והשנייה, בהתאמה. אוכלוסיות זבוב האורווה פחתו מאפריל עד יולי, כאשר שיא האוכלוסייה היה כנראה מוקדם יותר, לפני תקופת הניטור במחקר זה. דינמיקת אוכלוסיות הזבובים שנצפתה עשויה להיות מושפעת משינויים בלחות היחסית לאורך תקופת המחקר. לא נמצאה השפעה עקבית או מובהקת של תדירות הפינוי של בורות הזבל על אוכלוסיות הזבובים. שחרור צרעות טפיליות לא השפיע באופן מובהק על אוכלוסיות זבובי הבית הבוגרים, אולי בגלל שהצרעות שוחררו מאוחר מדי בעונה. המחקר הנוכחי מספק מידע שימושי על דינמיקה העיתית של שני מיני הזבובים ברפתות, מידע חיוני לדיכוי אוכלוסיותיהם. מילות מפתח: זבוב הבית, זבוב האורווה, זבוב שוקיים, צרעה טפילית, טפיל, גולם, הדברה ביולוגית.

### INTRODUCTION

Common filth flies (Diptera: Muscidae), the housefly *Musca domestica* Linnaeus, 1758 and the stable fly *Stomoxys calcitrans* (Linnaeus, 1758) in particular, are among the most important pests of farm animals worldwide. These synanthropic flies vector numerous pathogens of animals and humans and cause major nuisance which leads to impaired cattle productivity (reviewed in Rochon *et al.* 2021; Nayduch *et al.* 2023). The economic damage inflicted by these fly species in the USA alone is estimated at hundreds of millions to over two billion dollars per year (Taylor *et al.* 2012; Machtinger *et al.* 2021).

To effectively control filth flies, an integrated pest management (IPM) approach should be taken, combining mass trapping, release of biological control agents and selective use of insecticides (Farkas & Hogsette 2000; Machtinger *et al.* 2015a). However, the elimination of fly breeding sites must be incorporated in any such management program; houseflies develop mostly in moist manure whereas stable flies typically develop in more fibrous substrates, such as soiled straw bedding, manure mixed with straw or hay and rotting vegetation (Farkas & Hogsette 2000).

Dairy farms are arguably the principal breeding ground of filth flies in Israel, with about 120,000 cows held on 659 dairy farms distributed across the country as reported by Israel Dairy Board (2022). The massive amounts of produced manure combined with the warm climate provide ideal habitat for the development of filth flies. Manure is treated in various ways, such as tilling, piling, covering and removal. Yet filth flies still attain high population densities, in spite of these substantial management efforts.

Biological control programs of filth flies on animal farms rely largely on augmentative releases of pteromalid pupal parasitoids of the genera *Muscidifurax* Girault & Sanders, 1910 (Hymenoptera: Pteromalidae) and *Spalangia* Latreille, 1805 (Hymenoptera: Spalangiidae). Species of these genera are prevalent in most parts of the world and are closely associated with muscid flies, although they attack also flies from other families (e.g., Tephritidae and Drosophilidae) (Kapongo *et al.* 2007; Tormos *et al.* 2012; Noyes 2019). The effectiveness of augmentative releases of these parasitoids varies greatly; mass releases of parasitoids have led to high parasitism rates and great suppression of fly populations in certain studies, whereas little or no impact has been recorded in others (summarized in Machtinger *et al.* 2015a). These inconsistent outcomes may be attributed to various factors such as climatic conditions, substrate qualities (e.g., manure from different animals that vary in physical and chemical properties), insecticides used, as well as parasitoid identity, and the amount and timing of release. Nonetheless, the vast majority of these studies have been performed in North America and Europe, and none in the Middle East, including Israel, which is characterized by Mediterranean, semi-arid and arid climatic conditions. In the latest survey, nine housefly parasitoid species were found in Israel: five *Spalangia* species, two *Muscidifurax* species, *Pachycrepoideus vindemmiae* (Rondani, 1875) (Pteromalidae) and *Dirhinus giffardii* Silvestri, 1913 (Chalcididae) (Chiel & Kuslitzky 2016).

The main objectives of the present study are to quantify the importance of manure removal frequency and the mass release of parasitoids on the two main filth fly pests on dairy farms, namely *M. domestica* and *S. calcitrans*. Toward these goals, it has been important to record the population dynamics of the target fly species and to document the presence of any naturally occurring parasitoid species.

## MATERIALS AND METHODS

### Study design

The study was carried out from April to October of 2011 and 2012 on ten dairy farms located in the north-western Negev area of Israel (Fig. 1). This area is characterized by a semi-arid climate, with several farms affected by Lumpy skin disease outbreaks, a sickness mechanically transmitted by biting flies (Kahana-Sutin *et al.* 2017; Paslaru *et al.* 2021). The ten farms were of similar size with about 300 cows per farm and differed in their clearing frequency of manure pits: once per week



**Fig. 1:** Location of dairy farms used in the study in south-western Israel. Insert shows paired parasitoid release farms in green and control, no-release farms in yellow, in 2012.

(Gevulot [4.3 ha], Nizzanim [3.0 ha] and Urim [2.3 ha]), once per month (Ziqqim [5.0 ha], Dorot [5.0 ha], Gevim [3.8 ha] and Kissufim [3.6 ha]), and once every two months ('En Zurim [5.0 ha], Gevar'am [3.4 ha], 'Alumim [3.6 ha]), according to the farmers' reports. Climatic conditions in our study area were obtained from the Israel Meteorological Service (2024).

In the first year of the study, the fly population dynamics were recorded without any introduction of parasitoids. In the second year, parasitoids were introduced on five of the ten farms, and fly populations and parasitism rates were monitored. This experimental design enabled us to: (i) monitor the temporal dynamics of fly populations over two consecutive seasons; (ii) associate fly population densities with clearing frequency of manure pits; (iii) assess natural activities on fly predators and parasitoids; and (iv) compare fly populations and parasitism rates on the release vs. non-release farms on the second year.

### **Assessment of adult fly populations**

Adult fly populations were monitored using sticky cylindrical traps made of a white plastic tube covered with a clear nylon sheet (40×40 cm) coated with clear sticky paste for trapping moths and flies (polyisobutene 80 %; RIMIFOOT™; Rimi Chemicals Co. Ltd, Petah Tiqwa, Israel). Every two weeks, two traps were positioned vertically on each farm, one next to the manure pit near a cowshed, and the other on the opposite side of the same pen. Trapped flies were identified and counted on site 24 hours after trap setting. To detect seasonal trends obscured by the high variance in fly populations among farms, we standardized the number of captured flies by dividing the number of flies trapped on each sampling date by the number of flies trapped on the first sampling date in the same trap (i.e., baseline). Houseflies and stable flies can fly several kilometers per day, thus the possibility of flies moving between the experimental dairy farms cannot be ruled out (Nazni *et al.* 2005).

### **The effect of mass-released parasitoids on fly populations**

On the second year of the study, augmentative releases of parasitoids were performed on five farms, leaving the other five as unreleased control. To reduce geographic-driven variation, proximal farm pairs were randomly assigned as release and no-release control farms. Parasitoids were supplied by 'Biologic' (Alonim, Israel) and released in the corresponding farms every two weeks, between May and October 2012. On each release, 35,000–40,000 *Muscidifurax raptor* Girault & Sanders, 1910 and *Spalangia cameroni* Perkins, 1910 (about 1:1 ratio of the two species and sex ratio of 60–70 % females in both species) were dispersed by the farmers (after initial guidance) near main fly breeding sites, the manure pit, the path leading from the milking parlor to the sheds, and the fermenting feed. Hence, the average release rate was 0.88 wasp per m<sup>2</sup> (range 0.7–1.1). The parasitoids were supplied as parasitized housefly puparia mixed with wood shavings in nonwoven fabric bags, and at the time of dispersal some of the wasps had already emerged, and the rest emerged gradually over about 10 days.

The effect of parasitoids' mass-releases on fly numbers was evaluated both by adult trapping (as detailed above) and by measuring parasitism rates of sentinel pupae (see below) three times in 2012: on 15 April (before the first release of parasitoids), 12 June (mid-season) and 15 October (late-season). The sentinel pupae approach consisted of one hundred, 24 hour-old housefly pupae that were placed in 10×10 cm screen nylon pouches. Screen density allowed the entry of parasitoids and prevents the escape of emerging adult flies. Ten sentinel pouches were placed on each of the ten study farms, in locations that match the distribution of indigenous pupae (Sercovich 2014), hidden under a 2–3 cm layer of loose dry manure, to mimic natural pupal micro-habitat. The pouches were not disturbed for seven days, then retrieved to the lab for individual incubation in ventilated plastic cups at 25 °C for 30–45 days to allow the emergence of all adult flies and parasitoids. Subsequently, each puparium was scored either as a dead pupa (intact puparium), puparium with a fly emergence hole, puparium with a parasitoid emergence hole, mechanically crushed puparium, and puparium that was preyed upon by other arthropods such as ants. The intact puparia were dissected for the presence of dead parasitoids, if found it was added to the 'puparia with a parasitoid emergence hole' category.

### Data analysis

Homogeneity of variance was tested using Levene's and Barlett's tests and, when needed, data were log- or square root transformed to achieve homogeneity of variance. Data were then subjected to ANOVA, and a Tukey test was performed to compare treatment means. When ANOVA pre-requisites were not met, a non-parametric Wilcoxon test was used. JMP® (7.0.2, 2007, SAS Institute Inc.) was used for all statistical analyses. To resolve possible autocorrelation between data from different sampling dates on the same farm, the numbers of trapped flies were normalized by presenting them as percentage of the number of flies trapped on the first sampling date on the respective farms. This way, fly numbers were standardized across farms.

## RESULTS

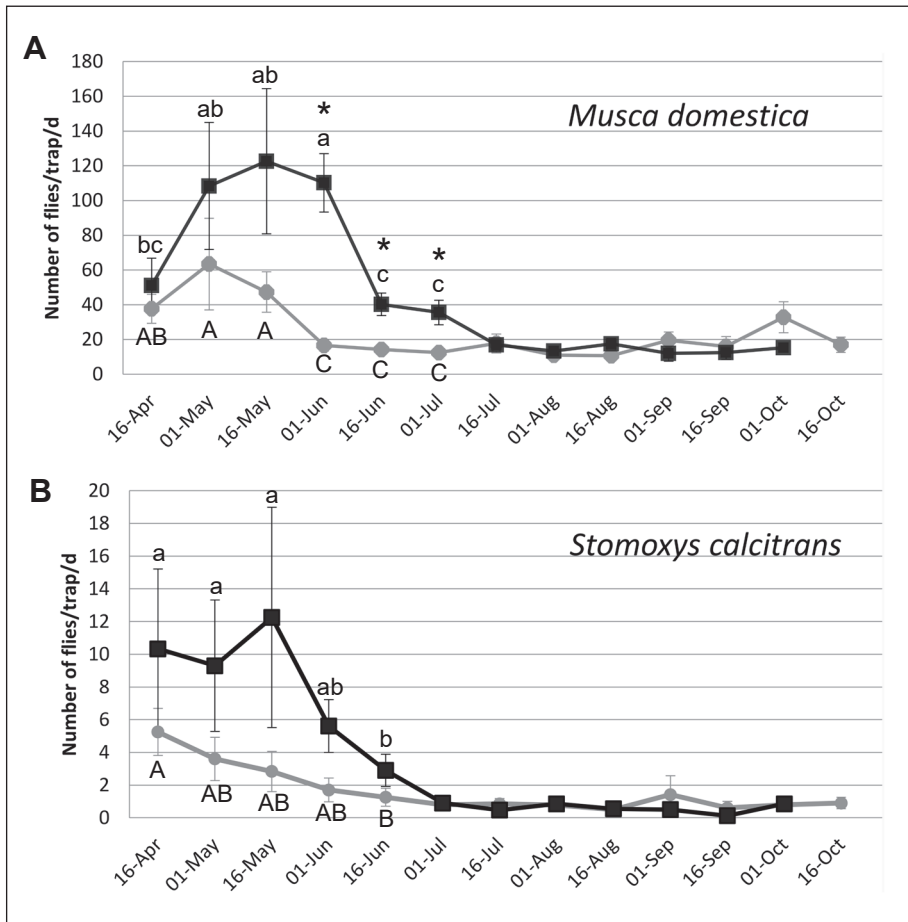
### Population dynamics of adult flies

Overall, housefly counts in traps differed significantly among farms (2011:  $F_{9,244}=10.42, p<0.0001$ ; 2012:  $F_{9,227}=10.25, p<0.0001$ ), yet they all showed a similar seasonal trend. Much like the housefly, stable fly counts differed significantly among dairy farms (2011:  $F_{9,242}=7.45, p<0.0001$ ; 2012:  $F_{9,218}=6.81, p<0.0001$ ), yet they too showed a similar seasonal trend. For analyses and presentation, therefore, counts of each fly species were pooled across farms.

A total of 5,963 and 10,178 adult houseflies were caught in the sticky traps in 2011 and 2012, respectively; the difference between the two years was significant only on 1 and 16 June, and on 1 July (Fig. 2). In both years, fly trapping differed significantly among sampling dates (2011:  $F_{12,241}=3.71, p<0.0001$ ; 2012:  $F_{11,214}=15.38, p<0.0001$ );

fly populations peaked in spring, with a possible second smaller increase in fall of 2011 (Fig. 2, top panel).

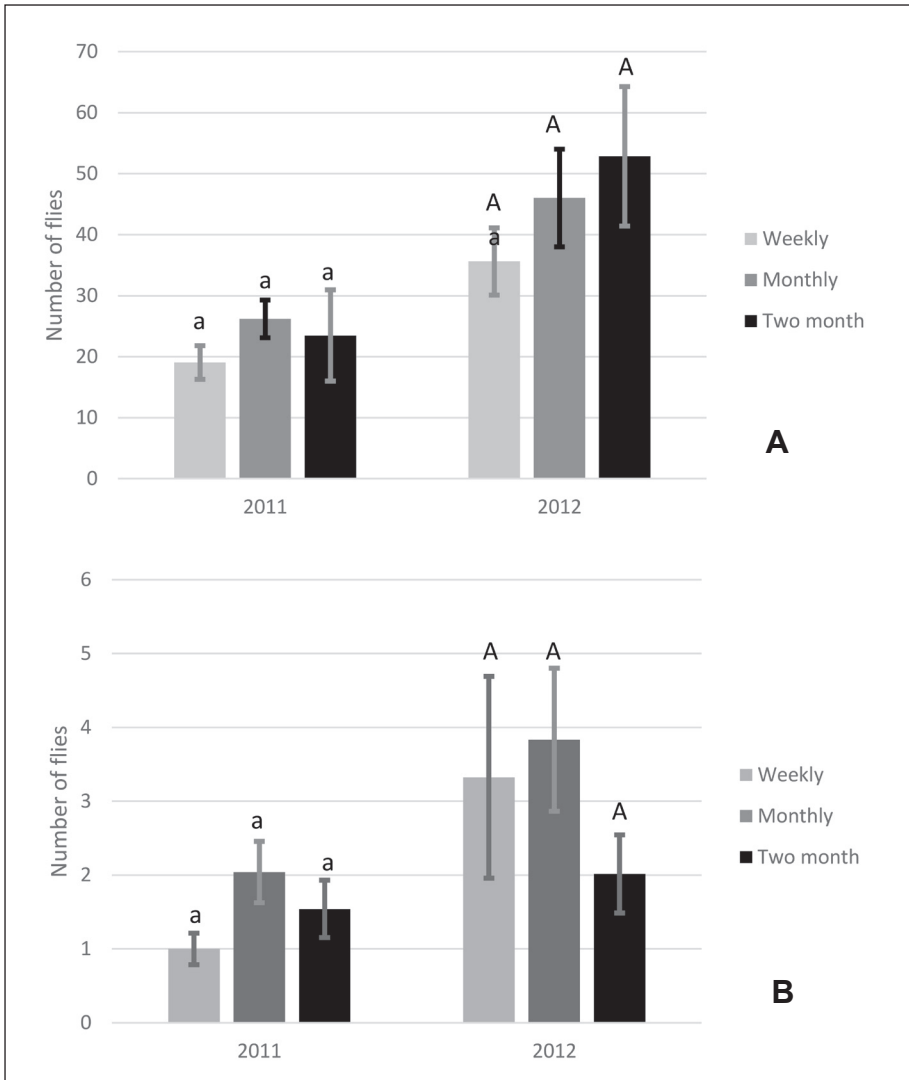
A total of 398 and 712 adult stable flies were caught in sticky traps in 2011 and 2012, respectively, yet this difference was not statistically significant ( $F_{1,458}=1.76$ ,  $p=0.18$ ). Populations of the stable fly differed significantly among sampling dates (2011:  $F_{12,239}=2.80$ ,  $p=0.001$ ; 2012:  $F_{11,216}=6.22$ ,  $p<0.0001$ ); higher numbers were trapped at the beginning of the sampling period with a significant subsequent decline in both years (Fig. 2, bottom panel).



**Fig. 2:** Average number ( $\pm$ SE) of adult houseflies *Musca domestica* (A) and stable flies *Stomoxys calcitrans* (B) in sticky traps placed on ten dairy farms in 2011 (in grey) and 2012 (in black). Data points with shared letter within panel and year do not differ significantly; asterisks indicate significant difference between years on a particular date (ANOVA & Tukey test,  $p<0.05$ ). Note the different scales in the Y axes.

### Effect of clearing frequency of manure pits

Density of housefly populations varied over the season and differed among dairy farms (see above). In both years, adult housefly populations were not affected significantly by the clearing frequency of manure pits (2011:  $F_{2,208}=0.12, p=0.88$ ;



**Fig. 3:** Mean number ( $\pm$ SE) of adult houseflies (A) and stable flies (B) trapped per day per trap placed on ten dairy farms with weekly, monthly or fortnightly clearing of manure pits in 2011 and 2012. Means within panel and year do not differ statistically (ANOVA & Tukey test,  $p < 0.05$ ).

2012:  $F_{2,183}=0.40, p=0.69$ ), with no significant interaction between pit clearing frequency and sampling date (2011:  $F_{24,208}=1.09, p=0.37$ ; 2012:  $F_{22,183}=1.09, p=0.39$ ). Nonetheless, in general and in both years of the study, fewer adult houseflies were trapped overall on farms with more frequent manure removal practice (Fig. 3A).

Much like the houseflies, no significant effect was detected, on both years, of clearing frequency of manure pits on adult stable fly populations (2011:  $F_{2,207}=0.11, p=0.90$ ; 2012:  $F_{2,186}=0.10, p=0.90$ ). Here too, the interaction between pit clearing frequency and sampling dates was not significant (2011:  $F_{24,207}=1.41, p=0.13$ ; 2012:  $F_{22,186}=1.49, p=0.11$ ). The low numbers of trapped adult stable flies and the associated high variance did not allow the detection of a clear trend in the data (Fig. 3B).

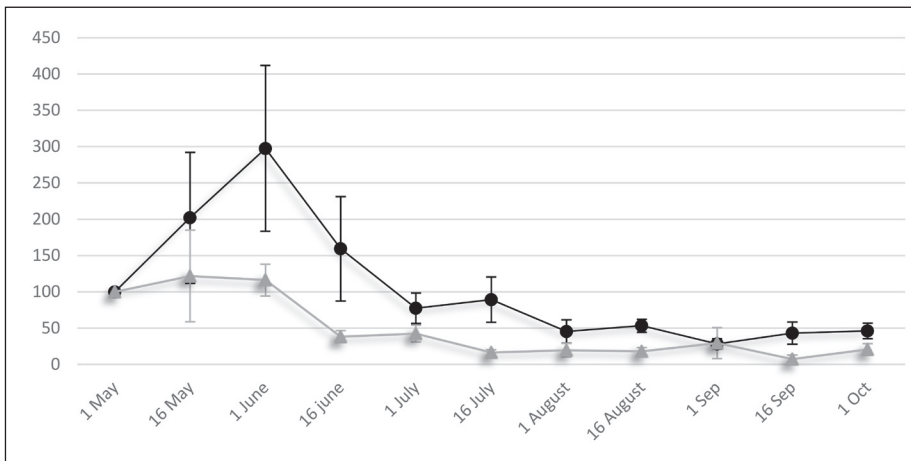
**Effect of parasitoid release on fly populations:**

Parasitoid releases in 2012 did not affect the number of trapped adult houseflies significantly ( $F_{1,90}=2.14, p=0.18$ ). However, fewer houseflies were trapped on parasitoid-release than non-release farms, especially from mid-May to mid-June (Fig. 4).

A comparison of housefly trapping on the wasp-release farms between the two years showed no significant difference on four of the five farms; on the fifth farm (Gevulot), and contrary to expectation, significantly fewer houseflies were trapped in 2011 (before wasp release) than in 2012 ( $F_{4,91}=5.17, p<0.001$ ).

**Parasitism rate and fate of housefly puparia**

In 2012, a total of 11,099 fly pupae were collected from the wild populations on six farms, four of which were parasitoid-release farms and two no-release controls. Of all the pupae collected until mid-June (corresponding to the first sampling date



**Fig. 4:** Percentage (Mean ± SE) of adult houseflies, normalized to the numbers captured on the first sampling date on each farm, on parasitoid-release farms (grey) and no-release farms (black) in 2012.

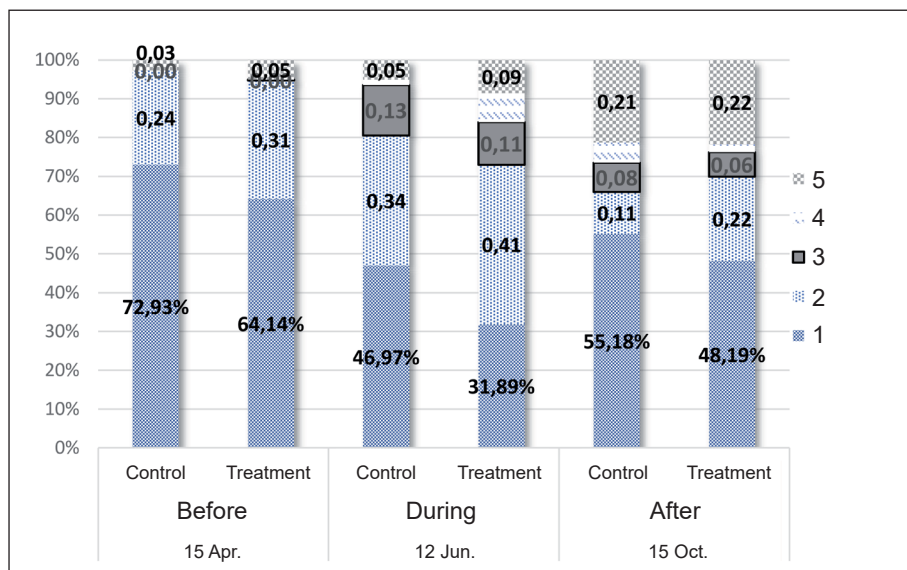
of bagged sentinel pupae essay), 14.05 and 9.33 % were parasitized in no-release and parasitoid-release farms, respectively. In the second half of the season, 14.38 and 14.49 % of the pupae were parasitized on no-release and parasitoid-release farms, respectively.

A total of 1,476 parasitoid wasps were recovered from the collected pupae, of which, 44.9 % were *Muscidifurax* spp., 23.8 % *Spalangia* sp., 10.8 % *Dirhinius* sp. and 21.1 % other parasitoids, possibly hyperparasitoid species. The three genera were mostly active during mid and late season (June–October). Much like the parasitoids, predatory arthropods, mostly pseudoscorpions, were also observed at filth fly breeding sites mainly after June.

In the bagged sentinel pupae essay, parasitism rates were similar in parasitoid-release and no-release farms. In the 12 June assay, 13.05 and 10.99 % of the pupae were parasitized in the no-release and parasitoid-release farms, respectively. Somewhat lower parasitism rates were recorded in the 15 October assay (7.51 and 6.27 % on no-release and parasitoid-release farms, respectively) (Fig. 5).

#### DISCUSSION

In both years of the study and on all the farms, an order of magnitude more houseflies were trapped compared to stable flies. Similar results were reported in Brazilian poultry houses (de Lima Bicho *et al.* 2004), but the reverse was found on Canadian dairy farms (Lysyk 1993*a, b*) and population of both species fluctuated on pig farms



**Fig. 5:** Fate (%) of sentinel fly pupae on control and parasitoid-release dairy farms, before, during and after wasp release in 2012 (n=5): 1 – fly eclosure, 2 – unclosed puparia, 3 – parasitoid emergence, 4 – physically destroyed puparia, 5 – preyed upon.

(Birkemoe & Sverdrup-Thygeson 2011). More adults of the two species were trapped in 2012 than in 2011. This difference could be attributed to drier spring conditions in 2011 (62 % RH between 16 April and 1 May) than in 2012 (71 % RH) (Sercovich 2014). Such conditions are known to affect immature fly survival and thus have a direct impact on adult populations (Skoda 1992). Indeed, rainfall is the main factor influencing stable fly population dynamics (Mullens & Meyer 1987; Cruz-Vázquez *et al.* 2004; Issimov *et al.* 2020) and housefly development (e.g., Noorman & Otter 2002). However, comparisons between the capture numbers of the two fly species should be taken with caution, because their attraction to traps may differ (Black & Krafur 1985; Birkemoe & Sverdrup-Thygeson 2011).

The population dynamics of both fly species also appeared to respond to changes in seasonal conditions; populations peaked during May and declined in June. Relatively few adults were trapped during the hot and dry summer at our study areas, and into fall. The importance of ambient temperature for fly population dynamics is evidenced from the positive relations between timing of peak populations and latitude; populations of these fly species increased gradually during spring and remained high until September in Florida (LaBrecque *et al.* 1972), peaked in early July and in August in Iowa (Black & Krafur 1985), and were abundant during August and September in Alberta, Canada (Lysyk 1993*a, b*). These seasonal dynamics correspond with the highest *M. domestica* activity at 30 °C, with decreased activity at higher and lower temperatures (Schou *et al.* 2013).

In this study, we did not detect statistically significant effect of manure pit clearing frequency on fly populations. Nonetheless, a trend was observed; fewer flies were trapped on farms with frequent pit clearing practices. Several factors appeared to have contributed to the high variation in the obtained data, thus hampering our ability to detect significant effects of waste management on fly populations. First, the stated frequency of pit clearing was an approximation; the actual clearing was often done at somewhat greater intervals. Second, it was suggested that a more frequent elimination of breeding materials, such as manure, may be needed to reduce housefly population size (Pickens *et al.* 1967). Third, clearing manure was often incomplete, leaving behind some waste, thus allowing some larvae to complete their development. Fourth, some farmers mixed the waste in the manure pit daily; this practice moves the larvae from the surface to greater depths, thus killing them. Fifth, random events that impacted immature survival; for example, water gushing from a broken pipe flooded the manure pit, thus creating anaerobic conditions and high larval mortality. Likewise, water was used in some cases to clean the pit, thus maintaining high moisture levels favorable to the larvae.

*Muscidifurax* sp. and *Spalangia* sp. were the commonest parasitoid taxa in our study. Similar results were reported in farms in Denmark (Skovgård & Jespersen 1999). In an earlier study in the same region of Israel, *Spalangia* sp. was reported to be the most abundant pupal parasitoid and no *Dirhinus* sp. were found (Havron & Margalit 1991). It is hard to conclude if the *Muscidifurax* and *Spalangia* spp. found in

our samples are offspring of naturally occurring local populations or of the introduced wasps. In the survey by Chiel and Kuslitzky (2016), *S. cameroni* was hardly found in the same geographical area, *M. raptor* was found in considerable numbers in spring, and a third species, *Pachycrepoideus vindemmiae*, was the dominant species in fall. Both *M. raptor* and *P. vindemmiae* appear to act as primary parasitoids of flies and as hyperparasitoids of con- or hetero-specifics. There is no information on the long-range dispersal of these parasitoids, but it is likely that they tend to stay in their eclosed habitat as long as there are sufficient fly hosts, which is the case on such dairy farms. Taken together, results suggest that the wasps recovered from the sentinel pupae are offspring of the mass-released wasps. The mortality of houseflies in the sentinel bags may be attributed to host-feeding by parasitoids, in addition to abiotic factors, such as physical condition and exposure to pesticide.

No significant effect of parasitoid release on adult housefly populations was detected. This might be attributed to the relatively late release time of the wasps (May). At that time, housefly populations were already at their peak, too late for the wasps to suppress. Indeed, pupal parasitism rate was relatively low (12.31 %) and similar to that reported by Skovgård and Jespersen (1999), who asserted that parasitoids should be released early in the season to effectively control fly populations. Higher parasitism rates were reported in some other studies (Havron & Margalit 1991; Skovgård 2004). Yet parasitism rate may be overestimated because parasitized hosts are more likely to be collected when time to parasitoid emergence is longer than that of the flies; 17–33 d vs. 4–5 d, respectively (Skovgård 2004). An additional factor that might affect our results is that typically, these wasp species have low dispersal rate (Machtinger *et al.* 2015b; Skovgård 2002). This factor, however, was unlikely to lead to the recorded low parasitism rates because the sentinel pupae were placed very close to the parasitoids release spots.

*Muscidifurax* and *Spalangia* sp. accounted for 45 % and 24 % of the parasitoids recovered from the sentinel pupae, respectively. This difference could be attributed to (i) placing the sentinel pupae in the upper stratum of the manure, where *Muscidifurax* sp. tend to forage for hosts whereas *Spalangia* sp. tend to forage in deeper strata (Legner 1977; Rueda & Axtell 1985; Geden 2002; Skovgård 2006) and (ii) *Muscidifurax* sp. parasitize and kill fly hosts parasitized by *Spalangia* sp. (Wylie 1971, 1972).

Moreover, higher parasitism rate was sometimes the result of attributing pupal mortality to parasitoid stinging, oviposition and host-feeding (Petersen *et al.* 1992). If a similar assumption was applied to our data, parasitoid-inflicted mortality would vary between 28 and 52 % on parasitoid-release farms compared to 18–47 % on the no-release farms. We believe, however, that attributing all (or most) pupal mortality to parasitoid activity is not unwarranted at this stage.

It should also be noted that clearing the manure pits is likely to have a substantial adverse effect on parasitoid populations (Skovgård 2004). This practice has a greater impact on the parasitoids than on the host pupae because of the extended

development time of the former. It is proposed therefore that some remnant manure is left at moist locations on the farm to support parasitoid populations (Petersen *et al.* 1992).

### CONCLUSIONS

The obtained results may advance our ability to manage filth fly populations on dairy farms. First, the similarity in population dynamics of adult flies may allow implementation of effective, single preventive measures, before the populations peak. Second, manure clearing from pits and alleyways seems to reduce mostly the numbers of houseflies, likely because stable flies reproduce in other sites on dairy farms; manure clearing frequency in 2012 had a substantial, though not statistically significant, effect on housefly numbers. Third, release of parasitoids should employ high enough numbers (to inundate hosts) and should commence as early as possible in the season to compensate for the reproductive advantages of the flies (fly fecundity is an order of magnitude higher and their generation time is much shorter compared to that of their parasitoids). Therefore, conservation biological control programs should be developed to harness these natural enemies for filth fly control on dairy farms, in combination with optimized manure clearing; the advantage of fly population suppression against the disadvantages of excess operational costs and the hampering of parasitoid populations build-up.

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