Biology of *Phygadeuon fumator* Gravenhörst (Hymenoptera: Ichneumonidae), a pupal parasitoid of house and stable flies (Diptera: Muscidae) in Manitoba

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We examined the preferred stage of host attacked, seasonal dynamics, and methods for laboratory rearing for *Phygadeuon fumator* Gravenhörst, a potential biological control agent of house flies and stable flies in Manitoba. Of 50,842 live sentinel house fly pupae retrieved at two Manitoba dairies in 1996, *P fumator* parasitized 1,998. A total of 4,691 naturally occurring house fly and stable fly pupae were collected, of which 9.4% were parasitized by *P. fumator*. *Phygadeuon fumator* attacked only pupae in the field. When individual females were exposed to pupae and 3rd instar house fly larvae in the laboratory, 52.2% and 5.8% of observations were taken when females were in contact with containers of the pupae and larvae, respectively. At 22°C, males of *P. fumator* had significantly shorter development times (24.8 ± 0.1 days, 14 to 35 days; n=615) than females (26.5 ± 0.2 days, 18 to 35 days; n=147). Some *P. fumator* did not emerge immediately and entered a state of larval diapause. A greater proportion of *P. fumator* in sentinel pupae entered larval diapause (75.8%) than those in naturally occurring pupae (29.5%). *Phygadeoun fumator* has considerable potential as a biological control agent of house flies and stable flies, but factors influencing diapause induction and laboratory rearing must be determined.

INTRODUCTION

The genus *Phygadeuon* is a large one, most species of which parasitize pupae of cyclorrhaphous Diptera. There are some inconsistencies in the literature about the species of *Phygadeuon* which attack various filth flies, and the stage of host attacked. Legner and Olton (1968) examined parasitoids of the house fly, *Musca domestica* L., the stable fly, *Stomoxys calcitrans* (L.) and species of *Fannia* Robineau-Desvoidy, *Muscina* Robineau-Desvoidy and *Ophyra* Robineau-Desvoidy (Diptera: Muscidae) throughout the Palaearctic. A species of *Phygadeuon* parasitized *S. calcitrans*, *Fannia* and a species of Syrphidae (Diptera) in Ireland. *Phygadeuon* was also found in the Ethiopian and Pacific regions. Depner (1968) reared a *Phygadeuon* sp. from field-collected horn fly, *Haematobia irritans* (L.) (Diptera: Muscidae), pupae in Alberta. Floate *et al.* (1999) also found a *Phygadeuon* sp., presumably *Phygadeuon fumator* Gravenhörst (Hymenoptera: Ichneumonidae), attacking house flies and stable flies in Alberta feedlots. A species of *Phygadeuon* has also been reported to attack *M. domestica* in Denmark (Mourier 1972), and in the US (Legner *et al.* 1967; Miller and Rutz 1990; Smith and Rutz 1991*b*). Legner and Olton (1968) concluded that the activity of *Phygadeuon* sp. is greatest at higher latitudes in the Northern Hemisphere where other parasitoids are scarce or absent.

In a previous study, McKay and Galloway (1999) found that *P. fumator* was an important parasitoid of naturally occurring house fly pupae collected in two eastern Manitoba dairy barns. Although there is substantial information on the distribution of *Phygadeuon* spp., little is known about their biology, and there is confusion about what host and life stages it prefers. For example, Müller (1971) stated that *P. fumator* attacked the larval and pupal stages of *Delia brassicae* Bouché, but also attacked the pupae of the onion and turnip flies. Legner *et al.* (1976) and Rueda and Axtell (1985) concluded that *Phygadeuon* spp. attacked the larval stages of filth flies. Blanchot (1988), who was the first to describe the biology of *P. fumator*, found this species to attack pupae of *M. domestica.* Floate *et al.* (1999) reared a *Phygadeuon* sp. from puparia of sentinel house flies that had been placed in feedlots in Alberta. Of the 22,401 freeze-killed sentinel pupae retrieved from eight dairies in Manitoba, only one pupa was parasitized by *P. fumator* (McKay and Galloway 1999). It was not known if *P. fumator* rejected sentinel pupae because they had been freeze-killed or if it was because it was a larval parasitoid. Therefore, the main objective of this study was to determine if *P. fumator* in Manitoba was a larval or pupal parasitoid.

As secondary objectives, we wanted to investigate the basic biology of *P. fumator* in the field and under laboratory conditions, and to determine whether a laboratory colony could be established. In 1995, many *P. fumator* that were present in naturally occurring pupae had entered what was assumed to be a larval diapause and did not emerge from house and stable fly puparia after 60 days (McKay and Galloway 1999). Smith and Rutz (1991*a*) also found *P. fumator* frequently entered larval diapause. It is critical to understand the nature of this larval diapause to be able to assess the potential of *P. fumator* as a biological control agent of house flies and stable flies in Canada.

MATERIALS AND METHODS

Locations. Two farms, the Stengel and Staerk dairies, located near Beausejour (50 04'N, 96 30'W) and Whitemouth (49 58'N, 95 59'W), Manitoba, were chosen to examine the biology of *P. fumator*. The Stengel and Staerk dairies, with approximately 40 and 20 milking cows, respectively, had similar manure management and were selected on the basis of the numbers of *P. fumator* found in parasitoid surveys conducted in 1994 and 1995. Of eight dairies examined in 1995, *P. fumator* made up the majority of parasitoids reared from house and stable fly pupae at these two locations (McKay and Galloway 1999).

Sentinel pupae and larvae. Live sentinel pupae, reared from a laboratory house fly colony, were used to determine the presence of *P. fumator*. Three 450 ml plastic containers, each holding a minimum of 100 live one-day-old house fly pupae and two containers (450 ml) holding at least 100 third instar lab-reared house fly larvae were placed twice weekly at each farm from the 13 May to 17 October, 1996. Containers were nestled into the surface of known fly breeding sites (calf pens, under feed troughs) and protected from livestock. Adult *P. fumator* frequently penetrated deeply into the medium in the containers. After larvae and pupae were exposed in the barns for 4 days, containers were covered before being taken to the lab to prevent adult *P. fumator* from escaping. Each container was then carefully examined and all *P. fumator* found were placed into a plastic cage (16.5 x 16.5 x 16.5 cm) with access to a dilute honey solution and water to establish a laboratory colony. House fly pupae and larvae remaining were held in separate cages (32 x 32 x 32 cm) at 22 ± 1 C (16 hours light:8 hours dark) until all adult flies had emerged. Empty and intact puparia were then counted. Individual puparia were placed in single wells in Falcon® 96-well Micro Test III tissue culture plates and incubated at 25 ± 1 C (16L:8D), then examined each day for the emergence of *P. fumator*. The sex of all emerged *P. fumator* was determined and adults were transferred to the colony. After 60 days, intact puparia were dissected and the per cent parasitism of *P. fumator* determined. If an unemerged *P. fumator* was found, the stage of development (larva, pupa or adult) was recorded. A ^{2} statistical test was used to determine if the proportions of *P. fumator* in the various developmental stages were the same for both locations.

Naturally occurring pupae. House fly and stable fly puparia found in accumulated manure were also sampled for parasitoids. Five locations at each farm were sampled twice weekly from 13 May to 17 October. Each location within a barn was searched for 10 minutes or until at least 50 puparia were collected. Pupae were taken to the lab and placed in the tissue culture plates and incubated as described above. The species, sex and prevalence of parasitoids that emerged from each pupa was recorded. *Phygadeuon fumator* adults were added into the colony as described above. After a minimum of six weeks, all intact puparia were dissected. Data on parasitoid species, sex, prevalence and stage of development were recorded. A ^{2} statistical test was used to determine if the proportions of *P. fumator* in the various developmental stages were the same for both locations. This test was also used to determine if the proportions of *P. fumator* in various developmental stages were the same for naturally occurring and sentinel pupae.

Choice experiment. A choice experiment was conducted to determine if *P. fumator* prefers to oviposit in house fly pupae or larvae. Individual females were placed in

each of two clear plastic cages (16.5 x 16.5 x 16.5 cm) and each was offered 10 one-day-old house fly pupae and 10 third instar house fly larvae. Two dishes, one for pupae and one for larvae, were placed on opposite sides of the cage. Cages were placed side by side and an incandescent light (100 watts) was positioned 10 cm behind the cages allowing light to be equally dispersed. The location of the female wasp in each cage was recorded every 60 seconds (one observation) for one hour. Observations on the location of female wasps (in pupal dish, in larval dish or in neither) were recorded. Since two cages were monitored at the same time, the recording of activity was alternated between cages every 30 seconds. After 30 minutes, the positions of the cages were reversed, allowing each cage to have the same light exposure. At the end of the experiment, pupae were removed from the cages and placed in tissue culture plates and incubated as described above. Larvae were allowed to pupate before placing them in the plates. If nothing had emerged after approximately three months, they were dissected to see if they had been parasitized. Twenty-seven females were used in this experiment. Of the 27 females, 16 females were field-collected (unknown age) and 11 were lab-reared (one day old) with no previous exposure to pupae or larvae. All females had been caged with males and were assumed to have mated. A ^{2} statistical test was used to determine if there was a difference between females from the field and colony and if there was a preference for larvae or pupae. A Mann-Whitney test was performed to determine if there were differences in oviposition between the two categories of females.

Laboratory Colonization. A colony of *P. fumator* was established by combining adults found in containers of sentinel pupae, and those that emerged from live sentinel and naturally occurring pupae. Since it appeared that females were affected by light, the colony was covered with black cloth and kept at 22 ± 1 C with a photoperiod of 18L:6D. One-day-old house fly pupae were mixed with 250-300 ml of fly-medium retained after larvae had pupated, and exposed to female *P. fumator* for 3 d. After exposure, the pupae were removed and placed in plastic cages (16.5 x 16.5 x 16.5 cm) to allow flies to emerge from unparasitized pupae. After the flies had emerged and died, the tray containing the remaining parasitized pupae was placed into a new cage to allow *P. fumator* to emerge. The puparia were incubated for 60 days at 22 ± 1 C (18L:6D) during which time any emerging adult wasps were recorded, removed and sexed. After 60 days, remaining puparia were dissected and the developmental stage of all *P. fumator* was recorded. Development times for males and females were compared using a two-sample t-test.

RESULTS

Sentinel pupae and larvae. At the Staerk farm, 22,075 live sentinel pupae were recovered. Of the 633 that were parasitized, *P. fumator* parasitized 597 (94.3%). *Phygadeuon fumator* was first collected from sentinel pupae placed in the field from 13-17 June and last collected from 5-9 September, 1996 (Fig. 1A). At the Stengel dairy, 28,767 sentinel pupae were recovered. Of the 1,419 pupae that were parasitized, *P. fumator* emerged from 1,401 (98.7%). *Phygadeuon fumator* was first collected from sentinel pupae placed in the field from 3-10 June and last collected from 2-5

September, 1996. No *P. fumator* parasitized pupae in October on either farm (Fig. 1A). For a list of other parasitoids collected, see McKay and Galloway (1999). None of the 5,426 and 6,950 sentinel larvae recovered from Staerk's and Stengel's, respectively, were parasitized.

Of the total 1,998 sentinel pupae parasitized by *P. fumator*, 298 adults emerged. The remaining 1,700 sentinel pupae were dissected. Most (75.8%) of *P. fumator* were in the larval stage (Fig. 1A). Since these larvae were alive after being incubated for a minimum of 60 d, it is presumed that they had entered a state of diapause. Emerged adults and pupae accounted for 14.9% and 9.3%, of the stages of *P. fumator*, respectively. It is not known whether pupae would have continued to develop into adults in the next several days, or whether there is a pupal diapause as well. At the Staerk farm, 92.1% of *P. fumator* were in the larval stage after 60 d, with pupal and adult stages accounting for 5.9% and 2.0%. At the Stengel farm, only 68.9% *P. fumator* were in the larval stage and more *P. fumator* emerged as adults (20.4%) than were in the pupal stage (10.7%). The proportion of individuals in each stage of development for live sentinel pupae varied between farms ($x^2 = 135.5$, $P < 0.001$).

Naturally occurring pupae. At the Staerk farm, adult house flies were first seen on 10 June, but house and stable fly pupae were not collected until 13 June and 15 July, 1996, respectively. *Phygadeuon fumator* first emerged from naturally occurring pupae collected on 8 July (Fig. 1B). Pupae were collected until 17 October when no fly larvae or adults could be found. At the Stengel farm, adult house flies were first seen 30 May. Two adult *P. fumator* were first collected on 17 June. The first stable fly pupa was collected on 8 July, while house fly pupae were not found until 22 July. *Phygadeuon fumator* first emerged from naturally occurring pupae collected on 22 July. Pupae were collected at the Stengel dairy until 17 October after which no larvae, pupae or adult flies could be found (Fig. 1B). Of the 2,753 fly pupae collected at the Staerk farm, 332 (12.1%) were parasitized by *P. fumator* (Table 1). Of the 1,938 fly pupae collected at Stengel's, 110 (5.7%) were parasitized (Table 1).

The proportion of individuals in each stage of development for naturally occurring pupae was similar for both farms ($x^2 = 5.44$, $P = 0.07$). More *P. fumator* emerged as adults (64.6%) than remained in the larval (29.5%) and pupal (5.9%) stages (Fig. 1B). The proportion of individuals in each stage of development varied among naturally occurring and sentinel pupae ($x^2 = 428.3$, $P < 0.001$). For sentinel pupae, more *P. fumator* were in the larval stage after 60 d.

Choice experiment. *Phygadeuon fumator* spent more time in containers with pupae than with larvae, but females from the colony and the field differed in their responses ($x^2 = 189.32$, $P<0.001$). For females from the colony, of the 660 observations, 401 (60.8%) were made when females were away from either the larval or pupal dishes. Two hundred and fifty-seven (38.9%) observations were taken while females were in the pupal dishes, and only 2 (0.3%) were made when females were in the larval dishes. For females collected from the field, of the 957 observations, 587 (61.3%) were taken when females were in contact with the pupal dishes. Two hundred and seventy-eight (29.1%) observations were made when females were away from both dishes, while 92 (9.6%) observations were taken from females in the larval dishes. For both categories of females, of the 1,617 observations made,

844 (52.2%) were taken when females were in contact with the pupal dishes, 679 (42.0%) away from both dishes and 94 (5.8%) in the larval dishes.

Fifty-two pupae were examined by the 16 females from the field, of which 24 were accepted and drilled. Twenty-one pupae were examined by the 11 females from the colony, but only 5 were drilled. No significant difference in oviposition behaviour was observed between females with known and unknown histories (Mann-Whitney U test = 53.0, $P<0.08$). Of all the pupae which were drilled, only three were parasitized and had been drilled by two females with unknown histories. All three *P. fumator* died in the larval stage.

Laboratory Colonization. At 22 ± 1 C, males of *P. fumator* have significantly shorter development times ($t=7.03, P< 0.001, =0.05$) than females. Mean $\pm$ SE development time was 24.8 ± 0.1 days (14.0 to 35.0 days; $n=615$) for males and 26.5 ± 0.2 days (18.0 to 35.0 days; $n=147$) for females, a difference of 1.7 days. Of the 1,256 parasitized house fly puparia examined, adult *P. fumator* emerged from 44.8%, while 50.2% and 4.9% remained in the larval and pupal stages, respectively.

DISCUSSION

In assessing the potential of *P. fumator* as a biological control agent of house flies and stable flies, it is essential that the stage or stages of the hosts attacked be clearly determined. Legner *et al.* (1976) and Rueda and Axtell (1985) considered *Phygadeuon* spp. attacking house flies and stable flies to be larval parasitoids, while Blanchot (1988) and Floate *et al.* (1999) reported *Phygadeuon* spp. attacking house fly pupae. In Manitoba in 1995, *P. fumator* did not parasitize freeze-killed sentinel pupae (McKay and Galloway 1999), therefore it was a consideration that *P. fumator* might be a larval parasitoid. However, in the present study, *P. fumator* was found to attack only live pupae in the field. Of all the live sentinel larvae recovered, none were parasitized by *P. fumator* or by any other parasitoid. In a choice experiment in the laboratory, female *P. fumator* clearly spent more time investigating pupae. For all observations, females were in contact with the pupal and larval dishes 52.2% and 5.8% of the time, respectively. No larvae were attacked during the choice experiment. We conclude that *P. fumator* is a pupal parasitoid of house and stable flies in Manitoba.

Having determined the stage of host attacked, it is also important to understand the dynamics of *P. fumator* in the field. In previous studies, *Phygadeuon* spp. accounted for 11.0% of the parasitism of house flies in central New York (Smith and Rutz 1991*c*), 6.1% and 2.9% of parasitoids reared from fly pupae in Alberta (Lysyk 1995; Floate *et al.* 1999) and 1.0% in Denmark (Mourier 1972). Results from the current study are the first in which *P. fumator* was the most abundant parasitoid. Smith and Rutz (1991*a*) examined microhabitat associations of parasitoids and found that *P. fumator* preferred sheltered sites primarily in moist bedding and feed. Legner and Olton (1968) concluded that the activity of *Phygadeuon* sp. was higher when other parasitoids are scarce or absent. Small populations of pteromalids and a suitable microhabitat in this study might have contributed to the greater prevalence of *P. fumator*.

Smith and Rutz (1991*c*) found that *P. fumator* was most abundant in June in New

York, while Floate *et al.* (1999) found that *Phygadeuon* sp. was present from spring through until fall, but was most abundant in late summer in Alberta. In Manitoba, the majority of *P. fumator* attacked sentinel pupae from 6 June to 15 July (Fig. 1A) and naturally occurring pupae from 19 August to 17 October (Fig. 1B). Naturally occurring hosts were unavailable in early June, thus sentinel pupae were the only hosts available inside the barns. After 15 July, when naturally occurring fly pupae became available, parasitism by *P. fumator* was lower in the sentinels and increased in naturally occurring pupae. When given the choice, *P. fumator* may prefer to parasitize naturally occurring pupae in moist areas to dry sentinel pupae in plastic containers.

Phygadeuon fumator is a major parasitoid of house flies and stable flies in some Manitoba dairy operations. It is important to know whether this species could be cultured for detailed study and perhaps for innoculative or inundative releases. Blanchot (1988) determined that *P. fumator* males and females developed in 21 and 22 days, respectively at 22 C (14L:10D). Differences in development times from Blanchot's study were 3.8 and 4.5 days for males and females. Photoperiod was longer in our study which may have contributed to the difference in development times, but there maybe differences in host factors, or even inherent differences between populations of parasitoids. Of all pupae parasitized from the colony and dissected after 60 days, the majority of *P. fumator* were in the larval and pupal stages. We assumed that these individuals were in diapause, as observed by Smith and Rutz (1991*a*).

In most instances, extrinsic factors such as temperature and photoperiod induce diapause and affect the generation entering diapause (Schneiderman and Horwitz 1958). However, factors which influenced diapause of *P. fumator* in this study were not determined. Like *Nasonia vitripennis* (Hymenoptera: Pteromalidae) and the egg parasitoid, *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae), diapause might be maternally influenced (Godfray 1994). Most sentinel pupae in our study were parasitized by *P. fumator* from June to July. When intact sentinel pupae were dissected, the majority of *P. fumator* were in the larval stage (Fig. 1A). However, for naturally occurring pupae, most were parasitized by *P. fumator* from August to October with the majority emerging as adults (Fig. 1B). Schneiderman and Horwitz (1958) found a correlation between host deprivation and the incidence of diapause for *N. vitripennis*. Per cent diapause increases from 0 to 97.3% when *N. vitripennis* experienced 1 to 5 days of host deprivation, respectively. Blanchot (1988) stated that *P. fumator* overwinters in fly puparia. We hypothesize that when female *P. fumator* emerged, there was a low probability of finding live pupae in the field since there was no substantial house fly or stable reproduction observed until July. The parasitoids may have eventually moved inside the facilities where there were sentinel pupae. Having been deprived of hosts, females parasitized sentinel pupae and produced a greater proportion of diapausing offspring. When naturally occurring hosts became available, females were no longer deprived of hosts, and the majority of the offspring developed to maturity and emerged as adults.

Temperature and photoperiod regimes were unlikely to have had an affect on developing parasitoids since there were differences in the proportion of individuals in each stage of development between naturally occurring and sentinel pupae. The pro-

portions of larvae that developed through to adult were similar for the colony. However, it is not known if temperature and photoperiod triggered the female to illicit a diapause response in her offspring or if these factors influenced the developing larva. Research is required to determine if *P. fumator* larvae may enter a true diapause at any time in the season, or if some larvae have a period of extended development which might be unique to this species. More information is needed on the factors that induce and terminate diapause.

A colony of *P. fumator* was difficult to establish in the laboratory. Female production was low, so the colony slowly declined to the point where it consisted of predominantly males. Since the factors that affect sex ratios of *P. fumator* have never been examined, it is not known why the colony became predominantly male. However, if the factors that affect sex ratios of *P. fumator* are similar to other parasitoids that attack house and stable flies (e.g. Pteromalidae), a number of variables could have contributed. The proportion of *P. fumator* to hosts might have influenced sex ratio. Female *N. vitripennis* produce a smaller percentage of female progeny at high parasitoid:host ratios (Wylie 1966). The pupae exposed in the lab might not have been suitable for parasitism. King (1994) reported females of *Spalangia cameroni* Perkins (Hymenoptera: Pteromalidae) lay a greater proportion of daughters than sons in large hosts rather than small hosts. Before this parasitoid can be mass produced for biological control, the factors which affect sex ratios must be understood.

Though there was a preference for pupae, females from the colony versus females collected in the field were different. Females from the colony spent less time investigating containers of pupae and larvae. However, these females were only one day old, and may not have been mated and it is unlikely that they were ready to lay eggs. There were no differences in oviposition behaviour between the two categories of females. To understand factors which effect oviposition behaviour, host seeking strategies should first be addressed with more research conducted with regards to the mating system and reproductive development of *P. fumator*.

Phygadeuon fumator was relatively abundant in barns included in our study. It appears that *P. fumator* may have potential as a biological control agent in some parts of Canada. However, there are several important fundamental aspects of its life history and interaction with other parasitoids that must be determined. In addition, before *P. fumator* can be mass reared and its full potential assessed, factors regulating larval diapause and sex determination must be examined.

ACKNOWLEDGEMENTS

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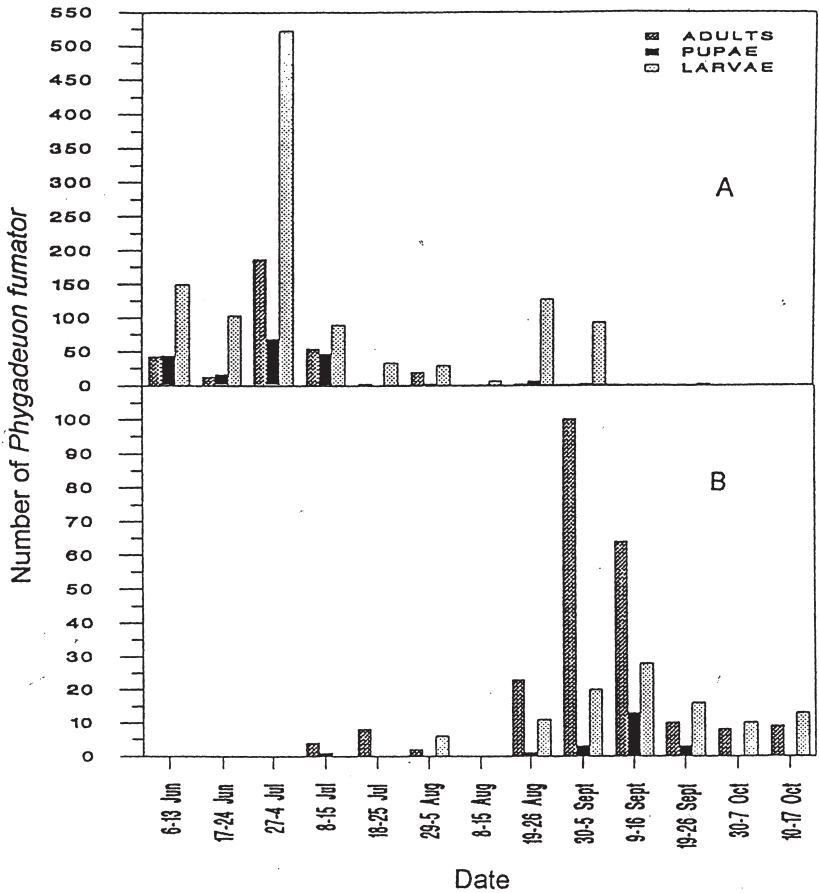

Figure 1. Numbers of *Phygadeuon fumator* Gravenhörst that developed through to larval, pupal and adult stages collected from two Manitoba farms from 6 June to 17 October, 1996. (A) Sentinel house fly pupae. (B) Naturally occurring house fly pupae.

Table 1. Proportions of house fly and stable fly pupae parasitized by *Phygadeuon fumator* in collections from two Manitoba dairy farms from 13 May to 17 October, 1996.

Farm	House fly pupae	Parasitized house fly pupae		Stable fly pupae	Parasitized stable fly pupae		Total fly pupae	Total parasitized pupae	
		No.	%		No.	%		No.	%
Staerk	2,431	284	11.7	322	48	14.9	2,753	332	12.1
Stengel	1,707	108	6.3	231	2	0.9	1,938	110	5.7
Total	4,138	392	9.5	553	50	9.0	4,691	442	9.4