HYMENOPTEROUS PARASITOIDS OF FILTH FLY (DIPTERA: MUSCIDAE) PUPAE IN CATTLE FEEDLOTS

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Abstract

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Results of a 2-year survey in Alberta, Canada, identified a parasitoid fauna of filth flies distinct from that generally reported for cattle confinements in the United States. Twenty-two feedlots were surveyed using freeze-killed sentinel house fly pupae. Parasitism averaged 0.25%. Ten species of hymenopterous parasitoids were recovered. As a percentage of the total number of pupae parasitized, these species were *Muscidifurax raptor* Girault & Saunders (37.4%), *Trichomalopsis sarcophagae* Gahan (23.9%), *Urolepis rufipes* (Ashmead) (18.5%), *Muscidifurax zaraptor* Kogan & Legner (6.9%), *Nasonia vitripennis* Walker (6.5%), *Trichomalopsis* sp. (3.7%) (Pteromalidae), *Phygadeuon* sp. (2.9%) (Ichneumonidae), *Dibrachys cavus* (Walker) (0.1%) (Pteromalidae), *Synacra* sp. (0.1%) (Diapriidae), and an unidentified Braconidae (0.1%). No differences were detected among natural regions of the province. Three categories of seasonal activity are identified which expand on previous groupings of species by their geographic distributions. The abundance of *T. sarcophagae* and rarity of species of *Spalangia* Latreille, 1805 are in marked contrast to results of surveys conducted in the United States. This difference suggests that species used to manage populations of pestiferous flies associated with livestock in the United States could be inappropriate for use in Canada.

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Résumé

Les résultats d'un inventaire d'une durée de 2 ans en Alberta, Canada, ont permis d'identifier une faune parasitoïde de Muscidae distincte de celle qui est généralement signalée dans les enclos d'alimentation de bétail aux États-unis. Vingt-deux enclos ont été inventoriés en y plaçant des pupes de Mouches domestiques tuées par congélation. Le parasitisme a été évalué en moyenne à 0,25%. Dix espèces d'hyménoptères parasitoïdes ont été recueillies: *Muscidifurax raptor* Girault et Saunders (parasitant 37,4% du nombre total de pupes parasitées), *Trichomalopsis sarcophagae* Gahan (23,9%), *Urolepis rufipes* (Ashmead) (18,5%), *Muscidifurax zaraptor* Kogan & Legner (6,9%), *Nasonia vitripennis* Walker (6,5%), *Trichomalopsis* sp. (3,7%) (Pteromalidae), *Phygadeuon* sp. (2,9%) (Ichneumonidae), *Dibrachys cavus* (Walker) (0,1%) (Pteromalidae), *Synacra* sp. (0,1% (Diapriidae) et une espèce

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non identifiée de Braconidae (0,1%). Aucune différence n'a été trouvée entre les diverses régions naturelles de la province. Trois catégories d'activité saisonnière se superposent aux catégories d'espèces déjà formées en fonction de leur répartition géographique. L'abondance de *T. sarcophagae* et la rareté des espèces de *Spalangia* Latreille, 1805 diffèrent des résultats enregistrés lors d'inventaires effectués aux États-Unis. Cette différence laisse à penser que les espèces utilisées pour lutter contre les populations de mouches nuisibles associées au bétail aux États-Unis pourraient s'avérer peu efficaces au Canada.

[Traduit par la Rédaction]

Introduction

The stable fly, *Stomoxys calcitrans* (L.) (Diptera: Muscidae), and house fly, *Musca domestica* L. (Diptera: Muscidae), are significant pests on feedlots and dairies in Alberta (Lysyk 1993). Stress induced by stable flies can reduce weight gain and feed conversion efficiency in feeder animals by up to 20% (Campbell *et al.* 1987) and reduce milk flow in dairy cattle by up to 0.7% per fly (Bruce and Decker 1958). House flies spread disease, reduce the aesthetics of livestock facilities, irritate employees, and generate lawsuits as urban developments expand into rural areas (Thomas and Skoda 1993).

Numerous surveys have identified parasitoids of these pestiferous flies (Legner 1994). Parasitoid complexes in confined livestock facilities in the United States are generally dominated by species of *Muscidifurax* Girault & Saunders, 1910 and *Spalangia* Latreille, 1805 (Hymenoptera: Pteromalidae) (Merchant *et al.* 1985, 1987; Mullens *et al.* 1986; Smith *et al.* 1987; Greene *et al.* 1989; King 1990; Henderson and Rutz 1991; Meyer *et al.* 1991; Seymour and Campbell 1993), whereas surveys in Canada suggest wasps of the genus *Spalangia* are rare (Lysyk 1995; McKay 1997). Several species of parasitoids are now available for commercial use as biological control agents [*e.g.*, *Muscidifurax raptor* Girault & Saunders, *Spalangia endius* Walker, and *Spalangia nigroaenea* Curtis (Cranshaw *et al.* 1996)].

The effectiveness of commercially available parasitoids for fly control has been variable. Some studies have shown their mass release to reduce populations of flies in poultry (Morgan *et al.* 1975; Rutz and Axtell 1979), swine (Weintraub 1984), and cattle operations (Morgan *et al.* 1976; Morgan and Patterson 1977; Miller *et al.* 1993). However, other studies suggest such releases have little, if any, effect on fly populations (Stage and Peterson 1981; Petersen *et al.* 1983; Meyer *et al.* 1990). One reason for these contradictory results may be the use of exotic species or geographic strains unsuited to local conditions (Legner and Olton 1971; Rutz and Axtell 1979; Greene 1990).

We report on results of a 2-year survey on parasitoids of filth flies in feedlots in Alberta, Canada. With approximately 1000 feedlots in 1991 (Canadian International Trade Tribunal 1993) and a provincial herd surpassing 5.5 million cattle in 1995 (Alberta Agriculture, Food and Rural Development 1995), methods of fly control are of considerable local importance. The specific objectives of the current study were to identify endemic species of parasitoids and their relative abundance and pattern of seasonal activity. The long-term objective of this research is to identify native strains or species of parasitoids for future study as biological control agents of the stable fly and house fly in Canada.

Materials and Methods

Twenty-two feedlots were sampled. None had previous releases of parasitoids for fly control and all had been operating for at least 3 years with a capacity of ≥1000 cattle

FIGURE 1. Distribution of feedlots surveyed across natural regions of Alberta, Canada. Distinguishing characters of each region are provided in Appendix 1.

per feedlot. Twelve feedlots were selected from the Grassland region, where the feedlot industry in Alberta is concentrated. Seven and three feedlots, respectively, were selected from the Parkland and Boreal Forest regions (Fig. 1). Features of climate, vegetation, and soil type which distinguish these regions, and the legal land descriptions for each feedlot sampled, are provided in Appendix 1. Feedlots spanned a west–east transect of about 200 km in the Grassland region of southern Alberta (Pincher Creek to Medicine Hat), and a west–east transect of about 400 km in the Parkland region of central Alberta (Fairview to Wainwright). Maximum distance between feedlots was about 700 km (Fairview to Medicine Hat). With the exception of a feedlot in the Parkland region near Fairview, each feedlot was sampled in 1996 and in 1997.

Daily maximum and minimum temperatures and precipitation were obtained for Lethbridge (49°42′N, 112°49′W), Lacombe (52°28′N, 113°44′W), and Athabasca (54°43′N, 113°17′W), representing Grassland, Parkland, and Boreal Forest regions, respectively.

Accumulated degree-days (°d) above 10°C from 1 May to 31 October were calculated from daily maximum and minimum temperatures using a sine wave function (Allen 1976). For rare instances of missing data, values were estimated as the average value for the five dates before and after the date in question.

Parasitoids were surveyed using sentinel house fly pupae (2–3 d old) killed by freezing and packaged in 10-cm^2 fibreglass screen bags (about 100 pupae per bag) with a mesh size of 1.7 mm. At biweekly intervals from mid-May to late October, pupae (10 bags per feedlot) were placed in moist, sheltered areas and covered with 2–4 cm of organic debris. These areas included silage pits, covered shelters, manure mounds, bedding or compost piles, and lagoons or settling ponds. One week after placement, bags were collected and each pupa was placed in a well (1 pupa per well) of a 96-well, ELISA microwell plates and held at 25°C for 6–8 weeks. Emergent parasitoids were identified to species using published keys (Rueda and Axtell 1985; Hoebeke and Rutz 1988) and reference to specimens in the Canadian National Collection of Insects and Arachnids in Ottawa, Ontario, Canada. Voucher specimens obtained in the current study were deposited in this same collection.

To compare the effects of freezing on parasitism of sentinel pupae, a bag of fresh pupae was placed immediately adjacent to each bag of freeze-killed pupae placed in two feedlots near Picture Butte and in a feedlot near Red Deer (Fig. 1). This was repeated for each sample interval throughout 1997.

Total percent parasitism of sentinel pupae (*i.e.*, the percentage of pupae placed in a feedlot during the season which were parasitized) was calculated for each feedlot and used in a two-way ANOVA (Wilkinson 1992) to test for differences ($P < 0.05$) between years and among regions. For each feedlot, total percent parasitism in 1996 was correlated with total percent parasitism in 1997 to examine the repeatability of results. Total percent parasitism of freeze-killed *versus* adjacent fresh sentinel pupae was compared using a modified χ^2 test with Yates correction factor for continuity ($P < 0.05$; Zar 1984, pp. 48–49).

The percentage of sentinel pupae parasitized by each species of parasitoid recovered (all feedlots combined) was compared between years, and for freeze-killed *versus* fresh pupae, using a χ^2 test ($P < 0.05$). Departures from 1:1 sex ratios were examined using a modified χ^2 test with Yates correction factor for continuity ($P < 0.05$).

Results and Discussion

Weather. Cumulative degree-days at Lethbridge from 1 May to 31 October were 950 in 1996 and 1067 in 1997. Average daily mean temperatures during these periods were 13.3 and 14.5°C, respectively. Cumulative degree-days at Lacombe from 1 May to 31 October were 620 in 1996 and 711 in 1997. Average daily mean temperatures during these periods were 10.5 and 11.4°C, respectively. Cumulative degree-days at Athabasca from 1 May to 31 October were 544 in 1996 and 657 in 1997. Average daily mean temperatures during these periods were 9.9 and 11.2°C, respectively. Differences between years reflected generally warmer temperatures in 1997 during May to June, in August, and in late September. This pattern was observed at each of the three weather stations (Fig. 2).

Cumulative precipitation at Lethbridge from 1 May to 31 October was 174 mm in 1996 and 279 mm in 1997. Cumulative precipitation at Lacombe during these periods was 451 and 581 mm, respectively. Cumulative precipitation at Athabasca was 436 mm in 1996 and 435 mm in 1997. The large difference in cumulative precipitation between Lethbridge *versus* Athabasca and Lacombe reflects both fewer and less intense periods of rain at the former location (Fig. 3).

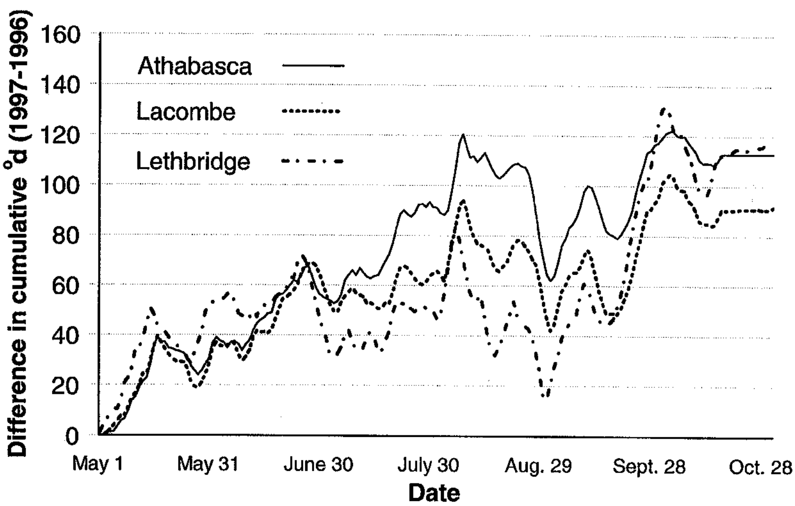

FIGURE 2. Differences in cumulative degree-days (°d) between years for three sites representing the natural regions of Alberta surveyed.

Relative differences in temperature and precipitation observed in the current study for these three regions (*i.e.*, Grassland, Parkland, and Boreal Forest) are consistent with previous reports (Strong and Leggat 1992).

Total Percent Parasitism. Total percent parasitism of sentinel pupae averaged 0.25% across all feedlots and years (Appendix 2). It averaged 0.31% in the Grassland region (SE = 0.08, n = 24 feedlots over 2 years), 0.18% in the Parkland region (SE = 0.05, n = 13 feedlots over 2 years), and 0.17% in the Boreal Forest region (SE = 0.08, n = 6 feedlots over 2 years). There was no effect of year ($F_{1,37}$ = 0.31, P = 0.58), region ($F_{2,37}$ = 0.83, P = 0.44), or year × region ($F_{2,37}$ = 0.39, P = 0.68). Total percent parasitism in a feedlot in 1996 predicted only 7% of the observed parasitism in the same feedlot in 1997 (r = 0.258, P = 0.25, n = 21 feedlots). If differences did occur among feedlots and (or) among regions, recovery of parasitoids was likely too low and sporadic to permit detection.

This level of parasitism was a magnitude lower than that previously reported for cattle confinements. Total percent parasitism of live sentinel house fly pupae has been reported to range from 1.5% to 9.5% on dairies (Rueda and Axtell 1985; Meyer *et al.* 1990; Miller *et al.* 1993; Lysyk 1995; McKay 1997), and from 0.8% to 3.5% on feedlots (Petersen *et al.* 1983; Rueda and Axtell 1985). Because some species may prefer live hosts (Roth *et al.* 1991; McKay 1997), our use of freeze-killed pupae may have underestimated levels of parasitism. However, we detected no significant difference in the current study between parasitism of fresh (0.10%, n = 28 080 pupae) *versus* freeze-killed (0.14%, n = 25 008 pupae) pupae (χ^2_1 = 1.47, P > 0.05).

For reasons unrelated to being fresh or freeze-killed, our use of sentinel pupae may have underestimated parasitism of pupae by wasps in the field. Parasitism of sentinel pupae has been reported to be 1.4- to 5-fold less than parasitism of naturally occurring pupae at the same locations (Meyer and Petersen 1982; Meyer *et al.* 1990; Petersen and Watson 1992; McKay 1997). When parasitism has been assessed only for field-collected pupae, parasitism during the season is typically higher (*e.g.*, 13–20%; Petersen *et al.* 1983; Meyer *et al.* 1990; Seymour and Campbell 1993; Jones and Weinzierl 1997) than that reported in other studies for sentinel pupae (see above).

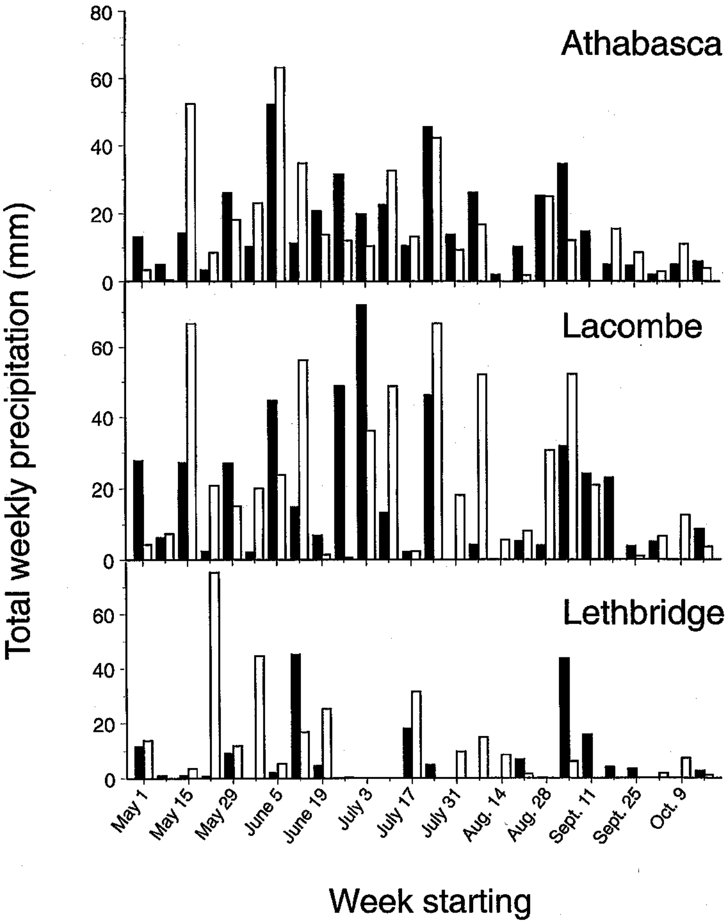

FIGURE 3. Total weekly precipitation in 1996 (solid bars) and 1997 (open bars) for three sites representing the natural regions of Alberta surveyed.

Species Composition. Ten species of Hymenoptera (n = 1929 individuals) emerged from 897 of the 361 023 sentinel pupae recovered during the 2-year study. As a percentage of these parasitized pupae, species of Pteromalidae (Chalcidoidea) were represented by *M. raptor* (37.4%), *Trichomalopsis sarcophagae* Gahan (23.9%), *Urolepis rufipes* (Ashmead) (18.5%), *Muscidifurax zaraptor* Kogan & Legner (6.9%), *Nasonia vitripennis* Walker (6.5%), a species of *Trichomalopsis* Crawford, 1913 (3.7%), and *Dibrachys cavus* (Walker) (0.1%). Other parasitoids included a species of *Phygadeuon* Gravenhorst, 1829 (Ichneumonidae) (2.9%), an unidentified Braconidae (0.1%), and a species of *Synacra* Foerster, 1856 (Diapriidae) (0.1%). Only one specimen of the latter two species and *D. cavus* were recovered. The relative abundance of species differed between years (χ^2_9 = 505.54, P < 0.001), primarily due to the higher numbers of *U. rufipes* and *M. raptor* and lower numbers of *N. vitripennis* collected in 1997 (Table 1).

We observed the emergence of more than one parasitoid per host only for *T. sarcophagae* and *N. vitripennis*. The former species produced fewer offspring per host ($\bar{x}$ = 4.5, SE = 0.21, range = 1–19, n = 214 pupae) than did *N. vitripennis* ($\bar{x}$ = 6.2, SE = 0.47, range = 1–15, n = 58 pupae) ($F_{1,270}$ = 12.63, P < 0.001). Averages of 4.5

TABLE 1. Number of parasitized sentinel pupae (freeze-killed and fresh) of *Musca domestica* by month in 1996 and in 1997, Alberta, Canada

Month	Mrap	Mzar	Nvit*	Psp	Tsar†	Tsp	Uruf	Total	No. of pupae	Parasitism (%)
					1996					
May	0	0	0	0	1	0	0	1	23 716	0.004
June	4	0	0	0	23	0	0	27	33 142	0.081
July	11	27	57	4	30	0	1	130	36 589	0.355
Aug.	82	18	0	5	81	15	27	229‡	31 928	0.717
Sept.	19	0	0	6	3	5	2	35	29 952	0.117
Oct.	0	0	0	0	0	1	0	1	18 432	0.005
Total	116	45	57	15	138	21	30	423	173 759	
					1997					
May	7	0	0	0	1	0	0	8	35 969	0.022
June	2	2	1	1	29	1	0	37§	39 367	0.094
July	0	4	0	1	4	0	0	10‖	29 444	0.034
Aug.	66	6	0	8	34	1	134	249	31 476	0.791
Sept.	104	2	0	1	8	10	2	127	26 208	0.485
Oct.	40	3	0	0	0	0	0	43	24 800	0.173
Total	219	17	1	11	76	12	136	474	187 264	

NOTE: Mrap, *Muscidifurax raptor*; Mzar, *Muscidifurax zaraptor*; Nvit, *Nasonia vitripennis*; Psp, *Phygadeuon* sp.; Tsar, *Trichomalopsis sarcophagae*; Tsp, *Trichomalopsis* sp.; Uruf, *Urolepis rufipes*.
*Average of 6.2 parasitoids per pupae.
†Average of 4.5 parasitoids per pupae.
‡Includes one specimen of *Dibrachys cavus*.
§Includes one specimen of Braconidae.
‖Includes one specimen of *Synacra* sp.

T. sarcophagae per host have been reported for house fly pupae parasitized in the field (Lysyk 1995) and 6.7–8.7 for house fly pupae parasitized in the laboratory (Dobesh *et al.* 1994; Lysyk 1998). An average of 7.2 *N. vitripennis* per host has been reported for house fly pupae parasitized in the field (Rutz and Scoles 1989).

Muscidifurax species (*M. raptor* and *M. zaraptor*) are common, cosmopolitan parasitoids of filth flies (Lysyk 1995; Jones and Weinzierl 1997). *Urolepis rufipes* is less frequently reported, but has been recovered from filth fly pupae in Alberta (Lysyk 1995), California (Meyer *et al.* 1991), Illinois (Jones and Weinzierl 1997), Nebraska (Petersen *et al.* 1985; Seymour and Campbell 1993), and New York (Smith and Rutz 1991). *Muscidifurax raptor* (Ables and Shepard 1976) and *U. rufipes* (Smith and Rutz 1985) have been identified as taxa adapted to cooler climates. Their abundance in the current study, at latitudes cooler than those of locations previously surveyed, supports this suggestion.

Nasonia vitripennis is occasionally abundant on poultry farms (Rutz and Scoles 1989; Henderson and Rutz 1991), but is typically rare or absent in cattle confinements (Petersen *et al.* 1983; Rueda and Axtell 1985; Smith and Rutz 1991; Meyer *et al.* 1990; Seymour and Campbell 1993; Lysyk 1995; Jones and Weinzierl 1997; McKay 1997). We do not discount its relatively high abundance in the current study (Table 1), but note that 56 of the 57 pupae parasitized by *N. vitripennis* in 1996 were from one feedlot during one sample period. Hence, its abundance in sentinel pupae may be skewed by the reproductive effort of relatively few individuals.

The absence of species of *Spalangia* differs markedly from studies in the United States, where species in this genus [*Spalangia cameroni* Perkins, *S. endius*, *S. nigroaenea*, and (or) *Spalangia nigra* Latreille] typically make up 10–90% of the parasitoids recovered from house fly pupae in feedlots and dairies (Petersen *et al.* 1983; Rueda and Axtell 1985; Miller and Rutz 1990; Meyer *et al.* 1991; Jones and Weinzierl 1997). Although the genus *Spalangia* may have been excluded by our use of freeze-killed pupae (Roth *et al.* 1991), it was not recovered when we used fresh pupae. Similarly, only 12 individuals of the genus *Spalangia* were recovered during a 2-year survey of dairies in southern Alberta using fresh sentinel pupae (Lysyk 1995). Thus, the use of sentinel pupae may have been inappropriate for the recovery of *Spalangia*. On dairies in Manitoba, 0.3% of parasitoids recovered from freeze-killed pupae belonged to the genus *Spalangia*, compared with 0.75% of parasitoids from fresh sentinel pupae and 15% of parasitoids from field-collected pupae (McKay 1997). On cattle confinements in Nebraska, higher numbers of specimens of *Spalangia* spp. also were reported from field-collected *versus* fresh sentinel pupae (Petersen and Watson 1992). Hence, collections of naturally occurring pupae may reveal a higher abundance of specimens of *Spalangia* spp. in southern Alberta than reported here.

The abundance of *T. sarcophagae* in the current study also differs markedly from results in the United States. Relatively common in both years, this species was recovered in 12 and 14 feedlots, respectively, in 1996 and 1997, and in each of four dairies surveyed in southern Alberta (Lysyk 1995). With the exception of feedlots in Nebraska, where the parasitoid was identified as a possible new species of *Trichomalopsis* near *americana* Gahan (Dobesh *et al.* 1994), we are unaware of any other reports for *T. sarcophagae* from filth fly pupae. Recent studies by Lysyk (1998) indicate that this species is better adapted than many other pteromalid species for cooler climates.

Trichomalopsis sp. is either *T. viridescens* (Walsh) or an undescribed species. The former was recovered from pupae of *Haematobia irritans* L. (Diptera: Muscidae) in Alberta and first identified as a species of *Habrocytus* Thomson, 1978 (Depner 1968), then later identified as *Eupteromalus* (= *Trichomalopsis*) *viridescens* (Peck 1974). Voucher specimens of this material are identical to our specimens of *Trichomalopsis* sp. However, *T. viridescens* is typically described as a gregarious hyperparasitoid of lepidopteran parasitoids (references in Krombein *et al.* 1979), whereas we recovered only one specimen of *Trichomalopsis* from each of 33 hosts. Because the type specimens of *T. viridescens* have been lost (Gahan 1921), verifying Peck's (1974) identification is impossible. *Trichomalopsis dubius* (Ashmead), the only other member of this genus reported from filth fly pupae (Hoebeke and Rutz 1988; Smith and Rutz 1991), is both gregarious and morphologically distinct from our specimens.

Species of *Phygadeuon* are described as internal larval parasitoids (Legner *et al.* 1976), but their recovery from pupae in the current study and elsewhere (Smith and Rutz 1991; McKay 1997) also identifies them as ectophagous pupal parasitoids. The species recovered here may be *Phygadeuon fumator* Gravenhorst, which has been recovered from filth fly pupae in New York (Smith and Rutz 1991) and was one of the main species recovered from house fly pupae in Manitoba (McKay 1997). Use of freeze-killed pupae has been reported to underestimate the relative abundance of *P. fumator* (McKay 1997). In addition, the relatively large size of this species and a mesh size of 1.7 mm used for bags of sentinel pupae may further have reduced parasitism (McKay 1997). Alone or in combination, these factors may explain the much lower parasitism of filth fly pupae by *Phygadeuon* in cattle confinements of Alberta (Lysyk 1995; this study) than that reported for dairies in Manitoba (McKay 1997).

Dibrachys cavus has been reported previously from house fly pupae on dairies in southern Alberta (Lysyk 1995). This species has an unusually broad host range (Krombein *et al.* 1979), but is rarely recovered from filth fly pupae (*e.g.*, Smith and Rutz 1991).

TABLE 2. Chi-square tests for departures of observed from hypothetical sex ratios of hymenopterous parasitoids of *Musca domestica*, Alberta, Canada

Species	No. of wasps	Observed sex ratio ♀:♂	χ^2 values for hypothetical ratios		
			2:1	3:1	4:1
M. raptor	335	4.9:1	25.77***	5.44*	0.02ns
M. zaraptor	62	4.6:1	4.07*	0.69ns	—
N. vitripennis	357	2.0:1	<0.01ns	—	—
Trichomalopsis sp.	33	15.5:1	6.57*	2.67ns	—
T. sarcophagae	957	3.8:1	44.77***	4.40*	0.13ns
U. rufipes	176	4.4:1	10.27**	1.61ns	—

NOTE: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P > 0.05$.

Without species determinations, little can be said about the specimens of braconid and *Synacra* recovered. The braconids *Apanteles carpatus* (Say) and *Aphaereta pallipes* (Say) have been recovered from house fly pupae in poultry facilities (Ables and Shepard 1974; Rutz and Scoles 1989). Species in the subfamily Belytinae have been identified as parasitoids of nematocerous, rather than cyclorrhaphous flies (Chambers 1971). Hence, the *Synacra* specimen recovered in the current study may have emerged from a nematoceran pupa that adhered to the outer surface of a sentinel pupa, rather than from the sentinel pupa.

Sex ratios. Sex ratios for all species were female biased (Table 2). Chi-square analyses suggested that, for the recovered specimens, ratios approximated 4♀♀:1♂ for *M. raptor* and *T. sarcophagae*, 3♀♀:1♂ for *M. zaraptor*, *Trichomalopsis* sp., and *U. rufipes*, and 2♀♀:1♂ for *N. vitripennis*. The single specimens of *D. cavus*, *Synacra* sp., and Braconidae recovered were female, as were the nine specimens of *Phygadeuon* sp. for which sex was determined.

Sex ratios of ~2–4♀♀:1♂ have been reported previously for *T. sarcophagae* (Lysyk 1998), ~3–8♀♀:1♂ for *M. raptor* and *M. zaraptor* (Coats 1976; Legner 1979; Seidl and King 1993), ~3♀♀:1♂ for *U. rufipes* (Smith and Rutz 1985), and ~3–8♀♀:1♂ for *N. vitripennis* (Wylie 1976; Fried and Pimentel 1986; Fried *et al.* 1990; McKay 1997).

Seasonal activity. Parasitoids were collected each month from May to October (Table 1). Peak parasitism occurred in August of both years. This overall pattern of parasitism differed between years ($\chi^2_5 = 1932.82$, $P < 0.001$), largely due to higher numbers of parasitoids collected in September and October of 1997, relative to the same period in 1996 (Table 1).

With the exception of *U. rufipes*, species exhibited a greater period of seasonal activity in 1997 than in 1996 (Fig. 4), which we attributed to warmer temperatures in 1997 (Fig. 2). In 1997, the difference was about 50°d by mid-June, explaining the earlier activity of parasitoids observed in the first three sampling intervals in 1997. By early October, this difference had increased to >100°d, which could explain the prolonged activity of *M. raptor*, *M. zaraptor*, and *T. sarcophagae* in 1997.

We suggest that parasitoids recovered in the current study can be placed in one of three arbitrary categories that are based on their seasonal activity (Fig. 4). Species in category 1 (*e.g.*, *M. raptor*, *M. zaraptor*, *Phygadeuon* sp., and *Trichomalopsis* sp.) are active from spring to fall, with peak activity in late summer. We interpret this pattern as a series of generations with populations peaking before the onset of colder temperatures. This pattern has been reported previously for the species of *Muscidifurax* (Rueda and Axtell 1985; Smith and Rutz 1991; Seymour and Campbell 1993; Lysyk 1995). In New York, *P. fumator* was recovered from June to October, depending upon the year

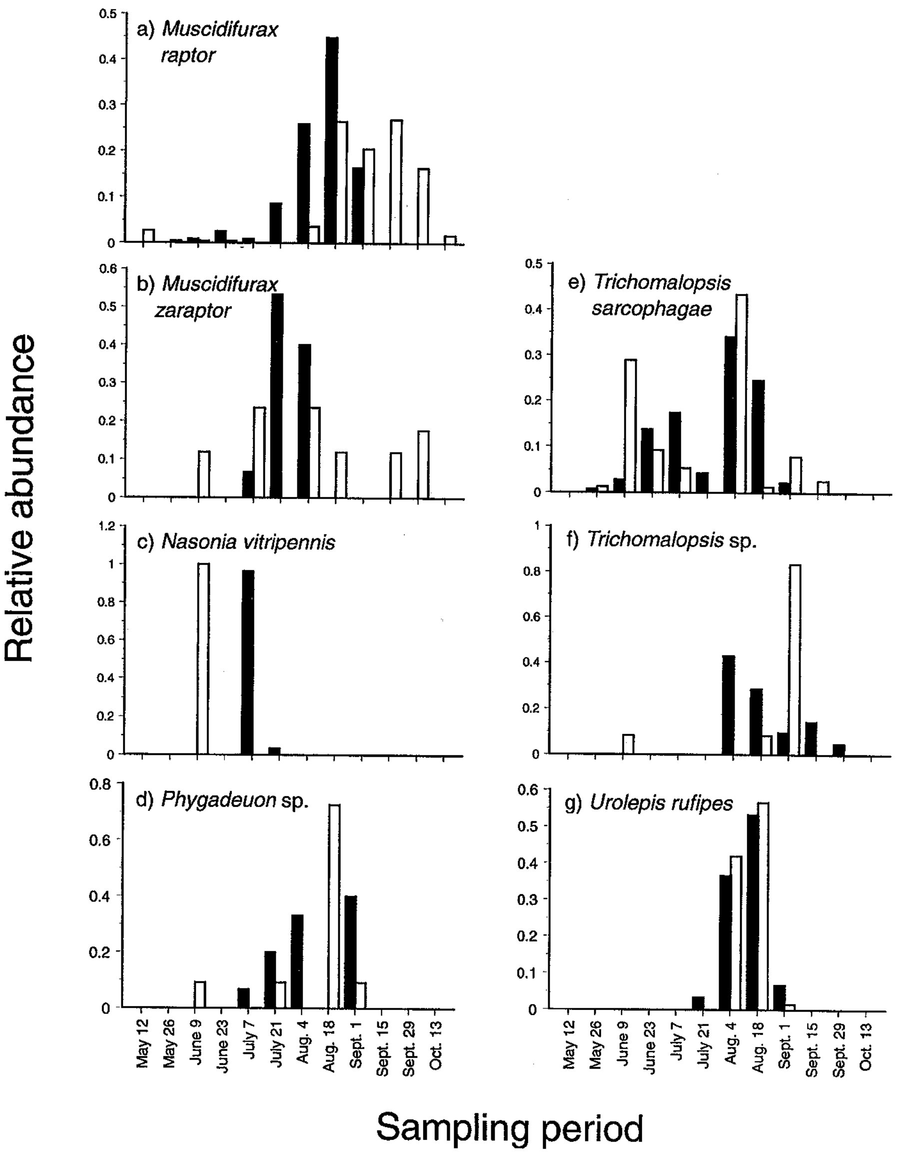

FIGURE 4. Seasonal activity of parasitoids (Hymenoptera) in 1996 (solid bars) and 1997 (open bars), based on the emergence of parasitoids from sentinel *Musca domestica* pupae exposed for a 1-week period at the start of each of the indicated dates.

(Smith and Rutz 1991), with peak activity in June. In Manitoba, peak activity of *P. fumator* was late June as determined by sentinel pupae, and late August to mid-September as determined by naturally occurring pupae (McKay 1997).

Species in category 2 (*e.g.*, *U. rufipes*) are active only from mid- to late summer. *Urolepis rufipes* exhibited this pattern in each year of the current study, and on dairies in southern Alberta (Lysyk 1995). On dairies in New York, specimens of *U. rufipes* were not recovered until mid-June (Smith and Rutz 1991). The reverse pattern was observed in California, with a single large peak of *U. rufipes* from April to June and infrequent collections in August and October (Meyer *et al.* 1991). Generally warmer temperatures explain the earlier emergence of *U. rufipes* in New York, and especially in southern California. Because *U. rufipes* appears to be adapted to cooler, wetter conditions (Smith and Rutz 1985), its pattern of emergence at the latter site would avoid hot dry conditions in mid- to late summer. *Urolepis rufipes* was relatively abundant on dairies in Manitoba, but its seasonal activity was not identified (McKay 1997).

Species in category 3 (*e.g.*, *T. sarcophagae*) are active from May to October, as are those in category 1. However, whereas species in the latter category exhibit one prominent peak of activity in late summer, the activity of species in category 3 is strongly bimodal, with activity peaking in mid-June to mid-July and again in mid- to late August. The difference between the two categories may reflect higher overwintering survivorship of species in category 3, favouring a large, first generation.

Because only one incidence of parasitism by *N. vitripennis* was observed in 1997, and because collections in 1996 were largely limited to one feedlot during one sample period, the data were inadequate to categorize this parasitoid. Similarly, because only single specimens were collected of *D. cavus*, *Synacra* sp., and Braconidae, we did not characterize the seasonal activities of these latter species.

The rigour of these categories remains to be determined. However, we note that our strongest data are for *M. raptor* (category 1), *U. rufipes* (category 2), and *T. sarcophagae* (category 3), and that the three different patterns of activity represented by these species were consistent between years.

Our classification of filth fly parasitoids expands, rather than changes, the geographical groupings proposed by Legner and Olton (1971). Their group III includes species "restricted to higher latitudes and colder winter climates," which would presumably include *U. rufipes* and *T. sarcophagae* (Lysyk 1998). Our further separation of these two species into categories 2 and 3, respectively, recognizes their very different seasonal patterns of activity in regions of co-occurrence.

Summary

In summary, the species complex of parasitoids attacking filth fly pupae in Alberta is distinct from that reported for filth flies in the United States. This is emphasized by the abundance of *T. sarcophagae* and the apparent rarity of *Spalangia* species. These combined results support a rationale to develop biological control programs for filth flies with consideration to regional differences.

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Appendix 1. Natural regions of Alberta summarized from Strong and Leggat (1992)

Grassland (ecoregions 1–3 in Strong and Leggat 1992). Characterized by needle grass (*Stipa* L. 1753), grama grass (*Bouteloua* Lagasca 1805), rough fescue (*Festuca scabrella* Torr.), and Parry oat grass (*Danthonia parryi* Scribn.). Brown, dark brown, and black Chernozem soils. Total precipitation of about 348 mm.

Mean summer (May–August) temperature of about 15.1°C. Mean minimum and mean maximum temperatures of about 7.7 and 22.4°C, respectively. Total summer precipitation of about 182 mm.

Mean winter (November–February) temperature of about –5.4°C. Mean minimum and mean maximum temperatures of about –11.1 and 0.4°C, respectively. Total winter precipitation of about 59 mm.

Legal land descriptions for feedlots surveyed in the Grassland region are as follows: Cactus Feeders (SE¼-05-12-06-W4), Haney Ranches (35-11-20-W4), Higginbothem feedlot (SW¼-14-07-30-W4), Hiltona Holdings Ltd. (SE¼-03-25-25-W4), Hi-Way 52 Feeders (1991) Ltd. (NW¼-08-06-19-W4), Keeler Feedlot (NW¼-03-06-21-W4), Nolan Cattle Company Ltd. (SW¼-10-11-20-W4), Reners feedlot (SE¼-04-06-30-W4), Tongue Creek Feeders Ltd. (SE¼-16-19-1-W5), Yanke feedlot (NE¼-34-11-05-W4), Western Feedlots Ltd. High River (SW¼-05-19-29-W5), Western Feedlots Ltd. Strathmore (SW¼-02-24-25-W4).

Parkland (ecoregion 4 in Strong and Leggat 1992). Characterized by aspen (*Populus tremuloides* Michaux) and rough fescue (*Festuca scabrella*). Dark brown and black Chernozem soils. Total precipitation of about 412 mm.

Mean summer (May–August) temperature of about 14.4°C. Mean minimum and mean maximum temperatures of about 7.7 and 20.9°C, respectively. Total summer precipitation of about 275 mm.

Mean winter (November–February) temperature of about –8.7°C. Mean minimum and mean maximum temperatures of about –14.0 and –3.7°C, respectively. Total winter precipitation of about 53 mm.

Legal land descriptions for feedlots surveyed in the Parkland region are as follows: Double R Ranches (SE¼-02-44-6-W4), Fairview College (SW¼-34-81-3-W6), Olson feedlot (SE¼-09-37-26-W4), Landmark feedlot (NW¼-04-40-25-W4), Triple 7 Ranch (SE¼-02-44-26-W4), Magneson feedlot (SW¼-09-50-17-W4), Voegtlin feedlot (SW¼-33-49-18-W4).

Boreal Forest (ecoregions 8, 11, and 12 in Strong and Leggat 1992). Characterized by aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera* L.), and white spruce [*Picea glauca* (Moench) Voss]. Gray luvisol and brunisol soils. Total precipitation of about 389 mm.

Mean summer (May–August) temperature of about 13.1°C. Mean minimum and mean maximum temperatures of about 7.1 and 19.0°C, respectively. Total summer precipitation of about 247 mm.

Mean winter (November–February) temperature of about –11.9°C. Mean minimum and mean maximum temperatures of about –17.2 and –6.5°C, respectively. Total winter precipitation of about 62.5 mm.

Legal land descriptions for feedlots surveyed in the Boreal region are as follows: Jesperson feedlot (SE¼-02-61-26-W4), Dargis feedlot (NW¼-07-60-8-W4), Stafford Feeders (NW¼-05-67-23-W4).

Appendix 2. Number of parasitized sentinel pupae of *Musca domestica* by feedlot in 1996 and in 1997

Feedlot	Mrap	Mzar	Nvit	Psp	Tsar	Tsp	Uruf	Total	No. of pupae	Parasitism (%)
					1996					
Athabasca	0	0	0	0	0	0	0	0	7 535	0.00
Fairview	0	3	0	1	0	3	0	7	9 133	0.08
High River 1	7	16	0	0	8	0	0	31	8 592	0.36
High River 2	1	0	0	1	0	2	0	4	8 592	0.05
Lacombe	0	0	0	0	0	0	0	0	4 787	0.00
Medicine Hat 1	0	0	0	0	26	0	0	26	7 149	0.36
Medicine Hat 2	24	17	0	0	7	0	0	48	7 149	0.67
Picture Butte 1	10	0	56	0	29	2	1	98	9 552	1.03
Picture Butte 2	19	8	1	0	7	0	0	35	9 552	0.37
Pincher Creek 1	0	0	0	1	2	0	0	3	8 271	0.04
Pincher Creek 2	17	0	0	5	27	10	1	60	8 271	0.73
Ponoka	0	1	0	0	0	0	0	1	2 934	0.03
Raymond 1	0	0	0	0	3	0	1	4	9 279	0.04
Raymond 2	18	0	0	7	3	0	0	28	9 279	0.30
Red Deer	0	0	0	0	23	1	0	24	4 896	0.49
Ryley	2	0	0	0	0	0	0	2	7 724	0.03
St. Paul	1	0	0	0	0	0	27	28	8 844	0.32
Strathmore 1	0	0	0	0	1	2	0	3	9 405	0.03
Strathmore 2	0	0	0	0	2	0	0	2	9 405	0.02
Tofield	3	0	0	0	0	0	0	4*	7 135	0.06
Wainright	14	0	0	0	0	1	0	15	7 395	0.20
Westlock	0	0	0	0	0	0	0	0	8 880	0.00
Total	116	45	57	15	138	21	30	423	173 759	$\bar{x}$ = 0.24

Feedlot	Mrap	Mzar	Nvit	Psp	Tsar	Tsp	Uruf	Total	No. of pupae	Parasitism (%)
					1997					
Athabasca	0	0	0	1	0	0	0	1	9 354	0.01
High River 1	8	0	0	0	3	0	33	44	7 536	0.58
High River 2	2	0	0	0	6	1	49	58	7 536	0.77
Lacombe	0	4	0	0	0	0	0	4	4 224	0.09
Medicine Hat 1	0	2	1	0	3	0	0	6	8 496	0.07
Medicine Hat 2	111	1	0	0	6	0	0	118	8 496	1.39
Picture Butte 1	7	0	0	0	26	0	0	33	19 440	0.17
Picture Butte 2	8	2	0	1	2	0	0	13	19 440	0.07
Pincher Creek 1	0	0	0	1	1	0	0	2	8 640	0.02
Pincher Creek 2	0	0	0	0	1	1	0	2	8 640	0.02
Ponoka	38	0	0	3	1	0	1	43	7 620	0.56
Raymond 1	0	0	0	0	0	0	1	1	8 160	0.01
Raymond 2	1	5	0	0	13	0	0	19	8 160	0.23
Red Deer	11	3	0	1	4	10	0	29	8 946	0.32
Ryley	0	0	0	0	6	0	0	7†	4 771	0.15
St. Paul	1	0	0	2	0	0	27	31‡	8 404	0.37
Strathmore 1	0	0	0	0	1	0	0	1	8 496	0.01
Strathmore 2	0	0	0	0	0	0	0	0	8 496	0.00
Tofield	0	0	0	0	0	0	0	0	3 461	0.00
Wainright	22	0	0	1	3	0	0	26	8 484	0.31
Westlock	10	0	0	1	0	0	25	36	10 464	0.34
Total	219	17	1	11	76	12	136	474	187 264	$\bar{x}$ = 0.26

NOTE: Mrap, *Muscidifurax raptor*; Mzar, *Muscidifurax zaraptor*; Nvit, *Nasonia vitripennis*; Psp, *Phygadeuon* sp.; Tsar, *Trichomalopsis sarcophagae*; Tsp, *Trichomalopsis* sp.; Uruf, *Urolepis rufipes*.

*Includes one specimen of *Dibrachys cavus*.

†Includes one specimen of *Synacra* sp.

‡Includes one specimen of Braconidae.