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Article *in* Bulletin of Entomological Research · January 2006

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Bulletin of Entomological Research (2005) **95**, 571–578 DOI: 10.1079/BER2005388

The influence of host suitability on the range of grasshopper species utilized by *Blaesoxipha atlanis* (Diptera: Sarcophagidae) in the field

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Abstract

Blaesoxipha atlanis (Aldrich) is a common parasitic fly of agriculturally important grasshoppers in Canada. The suitability of *Camnula pellucida* (Scudder), *Melanoplus bivittatus* (Say), *Melanoplus packardii* Scudder, and *Melanoplus sanguinipes* (Fabricius) as hosts was studied in the laboratory. Grasshoppers were singly-parasitized or left unparasitized and reared for 9 days. *Melanoplus bivittatus* and *M. packardii* did not support parasite development, i.e. were non-permissive hosts. In both species, parasite larvae were melanized and encapsulated, but development proceeded further in *M. packardii*. *Melanoplus sanguinipes* and *C. pellucida* were permissive host species with, respectively, 70% and 35% of the implanted larvae emerging from their hosts of which 86% and 50% developed into adults. Parasite development time was longer in *C. pellucida*. Adult *B. atlanis* dry mass varied with host species and host mass at parasitism, but not with host sex. Parasites developing in *M. sanguinipes* were larger in terms of dry mass than counterparts developing in *C. pellucida*. In permissive species, unparasitized grasshoppers gained in body mass while parasitized insects lost mass during the 9-day observation period. In non-permissive species, all insects gained in body mass, but parasitized females gained less mass than unparasitized conspecifics. All unparasitized grasshoppers survived while 75–95% of permissive and 30–40% of non-permissive hosts died. Variation in the intensity of field parasitism among grasshopper species may be explained, at least in part, by qualitative differences in suitability between potential host species. Novel pest management strategies emphasize preservation of a small proportion of the pest population for natural enemies. Consideration of the outcome of specific host–parasite interactions should improve the understanding of grasshopper population dynamics and increase the predictive value of models that assess potential crop losses.

Keywords: Acrididae, *Blaesoxipha atlanis*, host suitability, host range, parasitoid

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Introduction

Grasshoppers (Orthoptera: Acrididae) are the most destructive herbivorous rangeland insects found on the Canadian prairies (Johnson *et al.*, 1986). They can cause a significant reduction in the yield of cereal crops and in the grazing potential of grasslands (Hardman & Smoliak, 1982; Johnson, 1989; Olfert *et al.*, 1990; Quinn *et al.*, 1993). Acridid populations are presently managed with chemical insecticides when densities warrant action. However, these pesticides are costly and have broad environmental effects, including toxicity to non-target organisms (Martin *et al.*, 2000). Alternate pest-management strategies that utilize biological control agents or integration of conventional and biocontrol components have therefore been investigated (Streett & McGuire, 1990; Lomer *et al.*, 2001).

Non-microbial natural enemies of grasshoppers, which include invertebrates (Rees, 1973) and vertebrates (Martin *et al.*, 2000), are expected to benefit the most from a reduction in the use of insecticides (Lomer *et al.*, 2001). Natural populations of parasitic organisms have been shown to have a significant, but variable, effect on grasshopper numbers (Joern & Gaines, 1990; Greathead, 1992). For example, Smith (1965) determined that during a ten-year period parasitic flies (principally in the family Sarcophagidae) and nematodes (Mermithidae) reduced end-of-season abundance of the grasshopper, *Melanoplus sanguinipes* (Fabricius) by 6–33%. He (Smith, 1958) demonstrated also that the prevalence of parasitism by sarcophagids differed among four species of agriculturally important grasshoppers in western Canada. Sarcophagids were recovered from 33% of the collections of *M. sanguinipes*, but less often from collections of *Melanoplus packardii* Scudder (20%), *Melanoplus bivittatus* (Say) (10%), and *Camnula pellucida* (Scudder) (9%). Similarly, T. Danyk (unpublished data) monitored parasitism of grasshoppers by species in the dipteran families of Anthomyiidae, Sarcophagidae and Tachinidae in southern Alberta, Canada, between 1993 and 1998. He found that parasitism (measured as the number of emerged parasites divided by the number of hosts collected) was highest in *M. sanguinipes* (0.077), followed by *M. packardii* (0.005), *M. bivittatus* (0.002), and *C. pellucida* (0). Over 80% of the sarcophagids recovered were identified as *Blaesoxipha atlanis* (Aldrich), with the remaining specimens belonging to *Acridiophaga angustifrons* (Aldrich), *Acridiophaga reversa* (Aldrich), *Kellymyia kellyi* (Aldrich), and *Sarcotachinella sinuata* (Meigen).

Sarcophagid parasites appear to have relatively broad host ranges (Clausen, 1940). In contrast to hymenopteran parasitoids (Godfray, 1994) and, to a lesser extent, tachinids (Stireman, 2002; Stireman & Singer, 2003), the factors determining host use by sarcophagids are only poorly understood. In general, a female parasitoid is expected to select hosts for her offspring that maximize her own fitness and to avoid hosts in which offspring are at risk of mortality or do poorly (Charnov & Skinner, 1985; Poulin, 1995). Differences in the intensity of successful parasitism among host species may be due to differences between female parasitoids in host selection behaviour prior to attack, or may be due to variations in host suitability following ovi- or larviposition, or both. An experiment was conducted to test the hypothesis that observed differences in the intensity of parasitism among economically important grasshopper species can be explained by differences in their host suitability and/or quality. A host is considered suitable for a parasitoid if the latter can develop successfully to the adult stage; in contrast, the rate of parasitoid development and growth are functions of host quality (Mackauer & Sequeira, 1993). *Blaesoxipha atlanis* was selected as a candidate parasite. The species is potentially multivoltine. Adults emerge from puparia in overwintering sites in June and are active until September. Females are larviparous. The number of first-instar larvae present in a gravid female is a function of her body size (Danyk *et al.*, 2000). In the laboratory, females of *B. atlanis* typically approach a potential host from behind, spending a brief period in close proximity to the posterior end of the latter. An attack takes only a fraction of a second, during which time the female may place one or more larvae on the host's integument. Smith (1958) noted that both late-instar and adult grasshoppers are used as hosts in the field. After cutting a hole with its sickle-shaped mandibles in the grasshopper's integument, the larva enters the haemocoel where it develops, feeding primarily on haemolymph and fat body (Rees, 1973). Unlike hymenopteran parasitoids, which generally kill their hosts, successful larval development of sarcophagid parasites does not always result in host death (Danyk *et al.*, 2000, 2005).

Danyk *et al.* (2000) reported that the growth and survival of immature *B. atlanis* developing in adults of *M. sanguinipes* varies with the sex and the body size of hosts at parasitism. Therefore, development of *B. atlanis* was examined in males and females of *M. bivittatus*, *M. sanguinipes*, *M. packardii* and *C. pellucida* maintained under controlled laboratory conditions. The reciprocal effects of the parasite on host growth and survival were also examined.

Materials and methods

Insect colonies

A laboratory colony of *B. atlanis* was established from flies collected from a field site (50°3′ N, 112°38′ W) adjacent to cereal crops near Lethbridge, Alberta, Canada. The parasite colony was propagated using as hosts a non-diapause strain of *M. sanguinipes* (Pickford & Randell, 1969) fed wheat leaves, *Triticum aestivum* L. cv. 'Katepwa' (Poaceae), commercially grown head lettuce, *Lactuca sativa* L. (Compositae), and wheat bran. Adult flies were provided with sucrose and water *ad libitum*. Adult parasites and non-diapause grasshoppers were maintained at 21 ± 1°C and a 16L : 8D photoperiod. The grasshoppers used to assess host suitability were F_1 individuals that developed from eggs laid in the laboratory by adults captured in the field.

Estimating host quality

Body size of grasshoppers at parasitism, in terms of dry mass, was used as a proxy of host quality, which is the potential amount of resources available to immature parasites (Mackauer *et al.*, 1997). Because dry mass can be determined only by destructive sampling, the relationship between initial wet mass (WM_0) and dry mass (DM_0) was determined separately for each grasshopper species and sex. Adult grasshoppers ($n = 19$–40 each of males and females) were weighed individually on a Mettler AE50 electrobalance to the nearest mg to obtain their initial wet mass. Next, the insects were frozen for 24 h, dried in an oven at 55°C for 24 h, and weighed again to determine dry mass.

ANCOVA showed that the y-intercepts (a) and slopes (b) of the dry mass versus wet mass relationships did not differ between the sexes in *C. pellucida* (a, $F_{1,37} = 0.428$, $P = 0.52$; b, $F_{1,37} = 4.089$, $P = 0.05$), *M. bivittatus* (a, $F_{1,76} = 1.189$, $P = 0.28$; b, $F_{1,76} = 0.145$, $P = 0.71$), *M. packardii* (a, $F_{1,76} = 1.103$, $P = 0.30$; b, $F_{1,76} = 0.065$, $P = 0.80$), and *M. sanguinipes* (a, $F_{1,75} < 0.001$, $P = 0.98$; b, $F_{1,75} = 0.152$, $P = 0.70$), so data were pooled between sexes to obtain species-specific equations:

C. pellucida ($F_{1,39} = 287.64$, $P < 0.01$; $r^2 = 0.878$; SE of $b = 0.017$)

$$DM_0 = -2.956 + 0.295\,WM_0 \quad (1)$$

M. bivittatus ($F_{1,78} = 1102.31$, $P < 0.01$; $r^2 = 0.933$; SE of $b = 0.010$)

$$DM_0 = -28.084 + 0.335\,WM_0 \quad (2)$$

M. packardii ($F_{1,78} = 1156.40$, $P < 0.01$; $r^2 = 0.936$; SE of $b = 0.012$)

$$DM_0 = -45.325 + 0.407\,WM_0 \quad (3)$$

M. sanguinipes ($F_{1,77} = 670.17$, $P < 0.01$; $r^2 = 0.896$; SE of $b = 0.017$)

$$DM_0 = -31.454 + 0.439\,WM_0 \quad (4)$$

Host suitability

Six- to 10-day-old adults of *C. pellucida*, *M. bivittatus*, *M. packardii* and *M. sanguinipes* were used as hosts ($n = 40$ in each sex and species), for a total of eight kinds of hosts. Grasshoppers were weighed individually to obtain their initial wet mass. To facilitate parasitism, the right fore and hind wings of each insect were removed with microscissors, and the right tympanum was ruptured with a pin. For each species, one half of the grasshoppers ($n = 20$ in each sex) were parasitized manually with one larva each of *B. atlanis*, with the remaining insects serving as unparasitized controls. First-instar larvae used to parasitize hosts were obtained from 11- to 13-day-old females of *B. atlanis* ($n = 10$) that had been lightly anaesthetized with CO_2. Ovisacs containing larvae were removed from flies and ruptured on filter paper moistened with deionized water to release the larvae. Individual larvae were transferred with a camel's hair brush into the ruptured tympanum of each grasshopper. Larvae of *B. atlanis* normally complete development and emerge from hosts within 9 days after parasitism (Danyk *et al.*, 2000). Grasshoppers were maintained individually in 250-ml clear plastic containers at 25 ± 0.5°C and a 16L : 8D photoperiod. They were fed freshly cut wheat leaves once daily for up to 9 days or until death. After 9 days or at host death following parasite emergence, whichever came first, grasshoppers were frozen, dried in an oven, and weighed individually to the nearest milligram to determine their final dry mass. To the final dry mass of each grasshopper was added the mean dry mass of a fore and hind wing, obtained from a sample of wings ($n = 20$ in each sex and species) to adjust for the loss in mass following removal of wings prior to parasitism.

Parasites that emerged from hosts were placed individually in 20-ml glass shell vials containing sand moistened with deionized water and maintained under the same conditions as above. Flies that emerged from puparia were similarly maintained for 1 day, and then were frozen for 24 h, dried at 55°C for 24 h, sexed and weighed individually on a Cahn 29 automatic electro-balance to the nearest μg to determine the dry mass of parasites. The total dry mass of individual parasites that developed successfully into flies included the mass of the puparium. Grasshoppers from which parasites did not emerge were dissected to recover larvae. Puparia containing dead parasites, dead larvae that remained in the sand, and dead parasites dissected from grasshoppers were also dried, and weighed individually.

Host immune responses

In a separate trial, parasite development was evaluated in relation to possible host immune responses. Larvae were assessed in terms of size and appearance. Larvae retained in the ovisacs of two females of *B. atlanis* were compared with larvae developing in the different host species ($n = 5$ in each sex). Grasshoppers were parasitized with one larva each of *B. atlanis* and maintained for 3 days under the same conditions as described above. Hosts were dissected and any parasite larvae found were placed in 0.8% $NaCl_{(aq)}$ in a Petri dish and examined using a dissecting microscope with a back-light apparatus. Specimens were photographed through the microscope at a magnification of 25× with a 35 mm single lens reflex camera.

Data analysis

Events such as host death and egression of parasites from hosts were assumed to have occurred at the midpoint between two successive observation periods. SAS (SAS Institute, 1989) was used to test the significance of differences between treatment means (ANCOVA, ANOVA, Tukey's test, t-test) and median values (Wilcoxon 2-sample test). Percentages were analysed using z-tests (Johnson, 1980). For all tests a value of $\alpha = 0.05$ was used to determine statistical significance. For the analysis of host survival, median times after parasitism were transformed into values of 'lifeloss', which is defined as the amount of time that a parasitized host is expected to die earlier than unparasitized counterparts. All but three control insects survived to the age of 225 h after parasitism. Therefore, lifeloss was estimated by subtracting from 225 h the observed survival time of individual parasitized grasshoppers and then multiplying this value by -1 to obtain a positive number. The final survival time of unparasitized grasshoppers was not determined, which was much longer than the 9-day period of observation.

Results

Host quality

Mean initial dry mass of grasshoppers differed among the four host species ($F_{3,313} = 121.64$, $P < 0.01$). Individuals of *M. bivittatus* and *M. packardii* were approximately twice as large in terms of initial dry mass as *C. pellucida* and *M. sanguinipes* (table 1). Males and females differed in mass, with females being significantly larger than males except in *M. sanguinipes*. Initial host dry mass did not differ between unparasitized and parasitized groups of grasshoppers within each sex.

Table 1. Change in initial host dry mass and survival of individuals in four species of grasshoppers experimentally parasitized with one larva each of *Blaesoxipha atlanis* relative to unparasitized controls.

Host species	Host sex	Number of larvae per host[a]	Host dry mass at parasitism (mg, mean ± SE)	Change in host dry mass[b,c] (mg, mean ± SE)	Host lifeloss[b,d] (h, mean ± SE)	Host mortality[b] (%)
Camnula pellucida	♂	0	63.4 ± 1.9b	+12.2 ± 1.2b		
		1	58.1 ± 2.5b	−6.0 ± 1.5c	98.4 ± 11.1	90.0a
	♀	0	87.3 ± 4.6a	+45.8 ± 3.7a		
		1	98.0 ± 6.7a	−7.9 ± 3.3c		75.0a
Melanoplus bivittatus	♂	0*	128.4 ± 4.2b	+28.7 ± 3.3bc		
		1	106.9 ± 4.8b	+15.7 ± 6.3c	48.0 ± 11.1	35.0a
	♀	0	200.9 ± 11.6a	+121.0 ± 8.1a		
		1	185.9 ± 6.6a	+62.0 ± 16.9b		40.0a
M. packardii	♂	0*	149.3 ± 8.0b	+23.1 ± 4.4b		
		1	144.9 ± 5.3b	+8.7 ± 4.9b	58.2 ± 13.7	30.0a
	♀	0	173.9 ± 10.0ab	+59.6 ± 3.4a		
		1	181.5 ± 9.7a	+13.5 ± 9.5b		35.0a
M. sanguinipes	♂	0	85.8 ± 4.2a	+12.6 ± 3.0b		
		1	87.5 ± 4.4a	−16.4 ± 1.4c	93.0 ± 10.2	95.0a
	♀	0*	88.7 ± 5.1a	+45.8 ± 3.6a		
		1	83.5 ± 5.8a	−6.6 ± 2.9c		75.0b

[a]In each host species and sex combination: $n = 20$, $*n = 19$.
[b]Within host species, numbers in columns followed by different letters are significantly different ($P < 0.05$); Tukey's test for means; z-test for percentages.
[c]Mean values with positive and negative signs indicate that during the 9-day period of observation insects, respectively, gained or lost dry mass relative to dry mass at parasitism.
[d]Reduction in survival time of parasitized insects in comparison to surviving unparasitized controls; data from male and female hosts pooled.

Table 2. Survival and dry mass of *Blaesoxipha atlanis* larvae in singly-parasitized grasshoppers.

Parasite stage at death	Mean ± SE dry mass, mg, of parasites in each host species			
	Camnula pellucida	*Melanoplus bivittatus*	*M. packardii*	*M. sanguinipes*
L1	–	0.015 ± 0.004 (5)	0.011 (1)	–
L2	0.034 ± 0.011 (2)	0.019 (1)	0.046 ± 0.011 (7)	–
L3	2.101 ± 0.478 (10)	–	–	5.336 ± 2.334 (3)
Pupa	4.919 ± 0.381 (7)	–	–	6.268 ± 0.574 (4)
Adult	5.302 ± 0.514 (7)	–	–	7.129 ± 0.251 (24)

Abbreviations: L1, L2, L3 refer to first-, second- and third-instar stage, respectively. Number of parasites recovered is noted in round brackets. Male and female host data pooled. In each host species, $n = 20$ grasshoppers of each sex were parasitized.

Parasite growth and development

Because dry mass of parasites that emerged from *C. pellucida* and *M. sanguinipes* was independent of host sex ($F_{1,1} = 3.544$, $P = 0.31$) (see Danyk *et al.*, 2000) and smaller than expected sample sizes (15–78% of implanted parasites emerged from hosts or were recovered during host dissections; table 2), data were pooled within each host species across sexes for the analysis of parasite growth and development.

Blaesoxipha atlanis developed successfully in *C. pellucida* and *M. sanguinipes* (table 2). In *C. pellucida*, 35% of the implanted parasites emerged from hosts as mature third-instar larvae, of which one half completed development to adults; the remainder died in the pupal stage. Ten of 12 dead parasites found during host dissections were in the third-instar stage while two larvae died in the second-instar stage. In *M. sanguinipes*, 70% of implanted parasites emerged from hosts, and of these 86% completed development to the adult stage. Only three third-instar larvae were recovered during host dissections. Parasites needed less time for development in *M. sanguinipes* (median = 129 h, range = 105–177 h) than in *C. pellucida* (median = 153 h, range = 129–177 h) (Wilcoxon 2-sample test; $Z = 3.339$, $P < 0.01$).

No parasites emerged from either *M. bivittatus* or *M. packardii*; however, immature parasites appeared to survive longer in *M. packardii* (table 2). In *M. bivittatus*, five of six implanted parasites found in dissected hosts

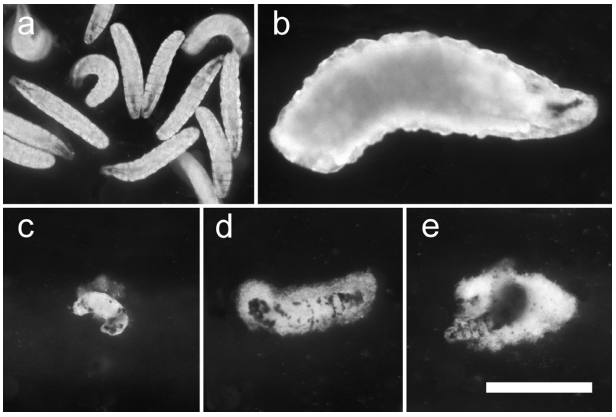

Fig. 1. Larvae of *Blaesoxipha atlanis*: (a) live first-instar larvae dissected from an ovisac of an adult female fly; (b) live third-instar larva dissected from an adult of *Melanoplus sanguinipes* three days after parasite implantation; (c), (d), (e) dead larvae dissected from adults of *Melanoplus bivittatus* three days after parasite implantation, and showing encapsulation, melanization and reduced growth. Bar = 1 mm.

developed no further than the first-instar stage and the remaining individual died as a second-instar larva. By contrast, only one of 18 larvae implanted in *M. packardii* ceased development in the first instar while the remaining 17 died in the second instar.

In *M. bivittatus* and *M. packardii* (but not in *C. pellucida* and *M. sanguinipes*), dead parasite larvae were partially or completely encapsulated and melanized. In a separate group of *M. bivittatus* dissected 3 days after parasite implantation, all *B. atlanis* larvae that were completely encapsulated were dead, whereas larvae that were only partially encapsulated were alive, as indicated by their movement following a slight prod with a dissection needle (fig. 1).

The influence of host species and initial host dry mass on the development of *B. atlanis* was examined using only the data from parasites that emerged from grasshoppers and then survived to the pupal or adult stage. Because the difference in the mean (±SE) dry mass between male and female parasites developing in *C. pellucida* ($t = 0.821$, $P = 0.45$; male, 5.48 ± 0.57 mg, $n = 6$; female, 4.24 mg, $n = 1$) and *M. sanguinipes* ($t = -1.45$, $P = 0.16$; male, 6.67 ± 0.50 mg, $n = 9$; female, 7.41 ± 0.26 mg, $n = 15$) were not significant, data were pooled between sexes. ANCOVA showed that parasite dry mass was influenced by the co-variate of initial host dry mass ($F_{1,39} = 5.584$, $P = 0.02$) and the effect of host species ($F_{1,39} = 8.437$, $P < 0.01$). Parasites that developed in *M. sanguinipes* were larger in terms of their dry mass (mean ± SE) (7.01 ± 0.23 mg, $n = 28$) than counterparts that developed in *C. pellucida* (5.11 ± 0.31 mg, $n = 14$) ($t = -4.766$, $P < 0.01$).

Host growth and survival

Unparasitized grasshoppers continued to grow during the 9-day trial, and females gained relatively more in dry mass than males (table 1). Compared with unparasitized counterparts, parasitized individuals of *C. pellucida* and *M. sanguinipes* lost dry mass (table 1). Grasshoppers in which parasites completed development lost an average (±SE) of 13.7 ± 1.1 mg ($n = 42$) in dry mass, which was independent of host species ($F_{1,1} = 0.066$, $P = 0.84$) and host sex ($F_{1,1} = 0.001$, $P = 0.98$). In contrast to *C. pellucida* and *M. sanguinipes*, parasitized *M. bivittatus* and *M. packardii* gained dry mass; however, parasitized females but not males gained less mass than unparasitized counterparts (table 1).

All control insects survived the 9-day period of observation, while 30–95% of parasitized grasshoppers died, depending on the species (table 1). Percentage mortality in parasitized *C. pellucida* and *M. sanguinipes* exceeded that observed in parasitized *M. bivittatus* and *M. packardii* (*z*-test, $P < 0.05$). Percentage mortality did not vary with host sex, except that more females than males died in *M. sanguinipes* (table 1).

Lifeloss, the reduction in survival time of parasitized hosts, varied with host species ($F_{3,156} = 4.673$, $P < 0.01$), but was independent of host sex ($F_{1,3} = 0.746$, $P = 0.45$) and initial host dry mass ($F_{1,151} = 0.813$, $P = 0.37$) (table 1). There was no difference in lifeloss between *C. pellucida* and *M. sanguinipes*, and hosts in both species survived for a shorter period after parasitism than did hosts in *M. bivittatus*, but not *M. packardii* (Tukey's test); survival time did not differ between hosts in the latter two species. In *C. pellucida* and *M. sanguinipes*, grasshoppers from which parasite larvae emerged (mean ± SE lifeloss, 77.7 ± 5.8 h, $n = 42$) died earlier than counterparts from which larvae did not egress (35.2 ± 11.9 h, $n = 15$) ($F_{1,55} = 12.60$, $P < 0.01$).

Discussion

Blaesoxipha atlanis developed successfully in adults of *C. pellucida* and *M. sanguinipes*. In *M. sanguinipes*, 60% of parasites implanted in grasshoppers completed development and metamorphosed into adults. By contrast, only 18% of parasite larvae placed in *C. pellucida* survived to the adult stage. Smith (1958) reported that *B. atlanis* is a 'relatively persistent' parasite of *M. sanguinipes* in the field. It was also one of very few parasites attacking *C. pellucida*; however, the intensity of parasitism in *C. pellucida* varied geographically. T. Danyk (unpublished data) obtained similar results in his grasshopper surveys in southern Alberta which, however, failed to yield any sarcophagid parasites from field-collected *C. pellucida*. Whereas *M. sanguinipes* can be classified as a permissive host of *B. atlanis* under most conditions (Danyk *et al*., 2000), the suitability of *C. pellucida* in the field is relative, possibly being influenced by the state and physiological condition of individual insects (Cioli *et al*., 1977; Mackauer *et al*., 1997; Beckage & Tan, 2002) and by environmental factors that may increase pre-emergence parasite mortality (Vinson & Iwasntsch, 1980). Host discrimination, which is common among parasitic Hymenoptera (Mackauer, 1990) and was demonstrated in some Tachinidae (Lopez *et al*., 1995; Stireman, 2002), cannot be safely excluded as a factor influencing the intensity of parasitism in the field. For example, Przybyszewski & Capinera (1991) reported disproportionately high rates of parasitism by Sarcophagidae and Tachinidae in comparison to relative host availability in field populations of *Melanoplus* species. Most larvae of *B. atlanis* implanted in adults of *M. bivittatus* and *M. packardii* developed no further than, respectively, the first- or second-instar stage, which is consistent with the low incidence of parasitism in field-captured grasshoppers (T. Danyk, unpublished data).

Host quality, as measured by dry mass at parasitism, was comparable in *C. pellucida* and *M. sanguinipes* (table 1) and hence the amount of resources available to implanted *B. atlanis* larvae theoretically would have been similar. In these hosts, the dry mass of parasites was influenced by initial host dry mass at parasitism and, as well, by host species, independent of initial host dry mass. In many hymenopteran parasitoids, adult size is a positive function of host size and/or age (Mackauer & Sequeira, 1993), as was shown also by Danyk *et al*. (2000) for *B. atlanis* developing in *M. sanguinipes*. It is noteworthy that parasites that developed in *M. sanguinipes* were, on average, 37% larger as adults than parasites that emerged from *C. pellucida*. These results suggest that initial host dry mass alone is not a sufficient predictor of host quality and that there may be additional qualitative differences between *M. sanguinipes* and *C. pellucida* not accounted for by variation in initial host dry mass (Nicol & Mackauer, 1999).

Successful development of parasites in hosts suggests adaptation of parasites to host-related constraints, including defence reactions, toxins, and nutritional adequacy (Vinson & Iwantsch, 1980). Such adaptations can be identified by rearing parasites under one or more developmental constraints. In some species of non-parasitic Sarcophagidae, larval developmental time declined in response to reduced resource availability due to competition for food (Baxter & Morrison, 1983; So & Dudgeon, 1989). In contrast, larvae of some parasitic Diptera reared on artificial diets responded to declining nutritional quality by developing more slowly (Taylor & Mangan, 1987; Gross *et al*., 1996). Analysis of parasite developmental time, therefore, may reveal differences in the suitability for parasite development of seemingly similar hosts (Beckage & Riddiford 1978, 1983; Taylor, 1988; Sequeira & Mackauer, 1992; Mackauer *et al*., 1997). Results in the present paper concerning the larval developmental time of *B. atlanis* in *M. sanguinipes* did not differ from those of Danyk *et al*. (2000) for solitary larvae; however, parasite developmental time was reduced if larvae developed gregariously and competed for nutrients (Danyk *et al*., 2000) or were constrained by small host size (T. Danyk, unpublished data). Larval developmental time was longer in *C. pellucida* than in *M. sanguinipes*. This disparity, however, may not be the result of a difference in the quantity of available nutritional resources between individuals in the two host species but, rather, indicate that *C. pellucida* is nutritionally less suitable for *B. atlanis* than is *M. sanguinipes*.

Parasites can effect changes in host behaviour and physiology, which in turn may influence the amount and quality of resources available for their own development (Parker & Pinnell, 1973; Beckage & Riddiford, 1978; Cloutier & Mackauer, 1979; Thompson, 1993). Parasitized individuals of *C. pellucida* and *M. sanguinipes* lost dry mass while unparasitized individuals gained dry mass during the 9-day trial period (table 1). The reduction in biomass of parasitized *C. pellucida* and *M. sanguinipes* may result from the assimilation of host resources by the parasite, a reduction in food consumption by the host limiting its ability to replenish reserves lost to the parasite, or both. For example, in *M. sanguinipes*, individuals infected by Protozoa (Johnson & Pavlikova, 1986) or parasitized by *B. atlanis* (Danyk *et al*., 2005) fed less than unparasitized counterparts.

With rare exceptions (King *et al*., 1976), insects attacked by parasitoids do not recover from parasitism but die once the immature parasitoid has completed development. Up to 25% of *C. pellucida* and *M. sanguinipes* survived emergence of the parasite larva, which confirms the results of Danyk *et al*. (2000) for *M. sanguinipes*. There was no difference in mortality or lifeloss between parasitized *M. bivittatus* and *M. packardii*, but parasitized individuals did not survive as long as unparasitized counterparts despite the failure of *B. atlanis* larvae to develop beyond the second-instar stage. Early-instar larvae of *B. atlanis* feed primarily on host haemolymph (Rees, 1973) and are relatively small compared with the much larger host so it is unlikely that the parasite's nutritional demands or physical damage of host tissues would have contributed significantly to grasshopper mortality. Anti-microbial metabolites, proteases and other digestive excreta produced by dipteran larvae during development (Pavillard & Wright, 1957; Nogge, 1972; Casu *et al*., 1996) may account for increased mortality and decreased survival time, especially in non-permissive hosts such as *M. bivittatus* and *M. packardii*.

The failure of *B. atlanis* to develop fully in *M. bivittatus* and *M. packardii* cannot be explained by any of the host variables measured. Dead parasite larvae found 9 days after implantation in these grasshoppers generally were smaller than counterparts found dead in *C. pellucida* and *M. sanguinipes*. Grasshoppers have evolved a number of defence reactions against parasites including phagocytosis, encapsulation and serum-mediated responses (Streett & McGuire, 1990) as well as melanization (Przybyszewski & Capinera, 1991). The appearance of dead and moribund parasite larvae in non-permissive, but not in permissive, hosts suggests the presence of host immune reactions. Differences among host species in the intensity of parasite-elicited immune reactions may reflect innate interspecific variability in quality of host defences, diversity in the ability of parasites to regulate or tolerate the host defence reactions, or both (Vinson & Iwantsch, 1980; Boulétreau, 1986). Przybyszewski & Capinera (1991) also observed differences among grasshopper species in the percentage of dipterous parasites found melanized in hosts collected in the field.

In conclusion, only *M. sanguinipes* and, to a lesser degree, *C. pellucida* can be classified as suitable hosts for *B. atlanis*. Parasites failed to develop successfully in *M. bivittatus* and *M. packardii* although parasitized grasshoppers did not survive as long as unparasitized counterparts. The results of this experiment, together with information from field surveys of parasitism, suggest that variation in the intensity of parasitism in the field may be explained, at least in part, by qualitative differences in the suitability of potential host species for the development of immature *B. atlanis*.

Grasshopper populations are regulated by a set of abiotic and biotic factors. A greater understanding of these factors may help to elucidate the processes that influence populations of these agriculturally important herbivores (Joern & Gaines, 1990). Lomer *et al*. (2001) suggested that natural enemies may not provide a reliable check to grasshopper populations that are in a state of rapid growth. However, in non-outbreak years, the overall population dynamics of grasshoppers appears to be influenced significantly by a suite of natural enemies attacking successive developmental stages. Models that estimate the economic damage resulting from grasshopper infestations generally include host parameters such as grasshopper density and species composition (Hewitt & Onsager, 1982) but ignore the role of natural enemies. It will be important to consider natural enemy

activity should biorational pest management strategies become more widespread because such approaches advocate preservation of a small proportion of the targeted pest population to encourage maintenance of natural enemies (Lockwood *et al*., 2000; Martin *et al*., 2000; Lomer *et al*., 2001). Results described in the present paper suggest that the potential effect of parasites on pest numbers in a particular agro-ecosystem may depend on the species- and age-structure of the grasshopper and parasite species present.

Acknowledgements

Technical assistance was provided by Craig Andrews, Toby Entz, Linda Harrison, Francine May, and Dan Watson. This project was funded, in part, by the Western Grains Research Foundation, the Natural Sciences and Engineering Council of Canada, and Agriculture and Agri-Food Canada. This is contribution No. (387) 04065 of the Agriculture and Agri-Food Canada, Lethbridge Research Centre, Lethbridge.

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(Accepted 26 July 2005)