Reduced food consumption in the grasshopper *Melanoplus sanguinipes* (Orthoptera: Acrididae) parasitized by *Blaesoxipha atlanis* (Diptera: Sarcophagidae)[1]

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Abstract—*Blaesoxipha atlanis* (Aldrich) is a common parasite of *Melanoplus sanguinipes* (Fabr.) in western Canada. We tested the hypothesis that parasitism by *B. atlanis* reduces food consumption by adult *M. sanguinipes*. Unparasitized grasshoppers serving as controls and grasshoppers infected with a single parasite larva were fed known quantities of freshly cut wheat (*Triticum aestivum* L. 'Katepwa') (Poaceae) leaves in the laboratory. The median development time in hosts of larvae of both male and female *B. atlanis* was 5.5 days. Two thirds of parasitized grasshoppers died within 9 days of infection, but all control insects survived. The dry mass of leaves consumed each day did not differ between parasitized insects that died and insects that survived parasitism; both groups fed less than unparasitized controls. The influence of parasitism on food consumption differed between host sexes, with feeding being depressed earlier and more severely in female than in male grasshoppers. The reduction in food consumption was most pronounced on day 6 after infection, when parasitized males and females consumed only 10% and 7%, respectively, of the food consumed by unparasitized controls. Parasite sex did not influence food consumption. Grasshoppers that survived parasitism by *B. atlanis* resumed feeding, consuming as much as unparasitized counterparts. Reduced food consumption limited the ability of grasshoppers to compensate for the nutritional demands of developing parasite larvae. As a consequence, parasitized grasshoppers lost body mass during the interaction. We propose that the temporary reduction in feeding by grasshoppers parasitized by *B. atlanis* that survive parasitism is not evidence of host regulation, but is consistent with a stress-induced alteration in host behaviour.

Résumé—*Blaesoxipha atlanis* (Aldrich) est un parasite commun de *Melanoplus sanguinipes* (Fabr.) dans l'Ouest canadien. Nous avons vérifié l'hypothèse selon laquelle le parasitisme par *B. atlanis* réduit la consommation de nourriture chez les adultes de *M. sanguinipes*. En laboratoire, nous avons nourri de quantités connues de feuilles de blé (*Triticum aestivum* L. 'Katepwa') (Poaceae) fraîchement coupées des criquets témoins non parasités et des criquets porteurs d'une seule larve du parasite. La durée médiane du développement des larves mâles et femelles de *B. atlanis* dans leurs hôtes est de 5,5 jours. Deux tiers des criquets parasités sont morts en moins de 9 jours de l'infection, mais tous les criquets témoins ont survécu. La masse sèche des feuilles consommées chaque jour était la même chez les insectes parasités qui sont morts et chez ceux qui ont survécu au parasitisme; les deux groupes ont mangé moins que les témoins non parasités. L'influence du parasitisme sur la consommation de nourriture n'est pas la même chez les hôtes

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mâles et femelles : l'alimentation est réduite plus tôt et plus fortement chez les criquets femelles que chez les mâles. La réduction de la consommation de nourriture est maximale au jour 6 après l'infection; à ce moment, les mâles et les femelles parasités ne consomment respectivement que 10 % et 7 % de la nourriture ingérée par les témoins non parasités. Le sexe du parasite n'influence pas la consommation de nourriture. Les criquets qui survivent au parasitisme par *B. atlanis* se remettent à manger et consomment alors autant que les témoins non parasités. La réduction de la consommation de nourriture limite la capacité des criquets à compenser pour les besoins alimentaires des larves du parasite en développement. En conséquence, les criquets connaissent une réduction de leur masse corporelle pendant la durée du parasitisme. Nous croyons que la réduction temporaire de l'alimentation chez les criquets parasités par *B. atlanis* qui survivent au parasitisme n'est pas, de toute évidence, une régulation opérée par l'hôte, mais plutôt une altération du comportement de l'hôte causée par le stress.

[Traduit par la Rédaction]

Introduction

Infection with parasites or pathogens can influence the behaviour of insects. Parasitized insects, for example, may occupy different habitats and show altered responses to predators or disturbance (Horton and Moore 1993; Thompson and Kavaliers 1994). Commonly, feeding patterns and the amount of food consumed differ between infected and healthy individuals. Insects parasitized by hymenopteran parasitoids may consume less (Parker and Pinnell 1973; Beckage and Riddiford 1978; Couchman and King 1979; Duodu and Antoh 1984) or more food (Parker and Pinnell 1973; Slansky 1978; Cloutier and Mackauer 1979; Byers *et al.* 1993) than unparasitized counterparts, depending on the growth and developmental dynamics of the species involved (Mackauer and Sequeira 1993; Mackauer *et al.* 1997). For example, Slansky (1978) observed that food consumption generally increased in hosts parasitized by gregarious species, whereas consumption decreased in hosts parasitized by solitary species.

Compared with hymenopteran parasitoids, the nutritional ecology of Tachinidae and Sarcophagidae, the two main groups of dipteran parasites, is poorly understood. Tachinid parasites of Lepidoptera may cause a reduction in the amount of food consumed by their hosts (Soo Hoo and Seay 1972; Brewer and King 1978; Bourchier 1991), or parasitism may have no effect on the amount of time spent feeding by orthopteran hosts (Adamo *et al.* 1995). The effect of parasitism by sarcophagids on food consumption has been examined only in vertebrate hosts, which forage less and may experience reduced mass gain compared with unparasitized individuals (Crump and Pounds 1985; Michener 1993; Hall and Wall 1995; Dial and Roughgarden 1996).

This paper describes the effect of parasitism on food consumption in adults of the grasshopper *Melanoplus sanguinipes* (Fabr.) (Orthoptera: Acrididae), which were experimentally infected with a single larva of *Blaesoxipha atlanis* (Aldrich) (Diptera: Sarcophagidae). *Blaesoxipha atlanis* is a common parasite of several species of grasshoppers on the grasslands of Alberta (Rees 1973), including *M. sanguinipes*, a cyclical and significant pest of cereal crops (Johnson 1989). Adults of *B. atlanis* normally emerge from overwintering sites in June, and the species is potentially multivoltine in southern Alberta. Females deposit one or more first-instar larvae on a posterior area of the grasshopper abdomen. Larvae use their sickle-shaped mouthparts to enter the haemocoel of their host, where they develop as endoparasites. After 4–7 days, mature third-instar larvae exit hosts through a hole made in the dorsal area of the integumental membrane between head and thorax and then burrow into the soil to pupariate. Danyk *et al.* (2000) reported that more than one larva per host can develop successfully. Unlike parasitism by hymenopteran parasitoids, which generally kills the host, parasitism by sarcophagid larvae did not always result in host death. About 40% of singly parasitized males and females of *M. sanguinipes* survived and remained active for several days following parasitism, whereas no males and fewer than 25% of females parasitized by two or more sarcophagid larvae survived. Female *M. sanguinipes* are larger than males and, perhaps, contain more resources to sustain parasite development (Danyk *et al.* 2000).

The amount of food consumed by grasshoppers varies with both plant-specific (*e.g.*, quality, presence of antifeedant compounds, and water content of food plants) and individual insect specific attributes (*e.g.*, length of food deprivation, sex, instar, and volumetric changes in the gut) (Holmberg and Hardman 1984; Johnson and Mündel 1987; Chapman and Sword 1994; O'Neill *et al.* 1994). In addition, infection with entomopathogens has been found to reduce feeding by grasshoppers and locusts (Johnson and Pavlikova 1986; Olfert and Erlandson 1991; Moore *et al.* 1992; Sieglaff *et al.* 1997; Thomas *et al.* 1997). However, Ouedraogo *et al.* (2004) found that infection by the entomopathogen *Metarhizium anisopliae* (Metsch.) had no effect on the frequency of feeding events or the amount of food consumed by locusts. We tested the hypothesis that parasitism affects feeding by grasshoppers in a manner similar to infection with entomopathogens and results in reduced food consumption in hosts. We describe the dynamics of the changes in feeding and host body mass in healthy and parasitized males and females of *M. sanguinipes* and suggest a mechanism that may explain the effect of parasitism on feeding.

Materials and methods

Insect colonies

A laboratory colony of *B. atlanis* was established with insects collected near Lethbridge, Alberta, Canada (50°3′N, 112°38′W). Parasites were reared on a non-diapause strain of *M. sanguinipes* (Pickford and Randell 1969), which were fed a diet of wheat leaves, *Triticum aestivum* L. 'Katepwa' (Poaceae), commercially grown head lettuce, *Lactuca sativa* L. (Compositae), and wheat bran. Adult flies were provided with sucrose and water *ad libitum*. All insect colonies were maintained at 21 ± 1 °C and a 16L:8D photoperiod.

Host quality

Host quality was measured as dry mass. Dry mass is a more precise measure of body mass than wet mass; however, it requires destructive sampling. We therefore estimated the dry mass of grasshoppers at parasitism (DM_0) by measuring the wet mass (WM_0) of each insect and converting wet mass to dry mass. From a stock colony, 8- to 10-day-old adults of *M. sanguinipes* (n = 24 of each sex) were weighed individually (WM_0) on a Mettler AE50 microbalance to the nearest milligram, frozen for 24 h, dried in an oven at 55 °C for 24 h, and weighed again to determine DM_0. ANCOVA showed that the relationship between DM_0 and WM_0 did not differ between males and females in terms of slope ($F_{1,44}$ = 0.012, P = 0.91) and y intercept ($F_{1,44}$ < 0.001, P = 0.99), so data were pooled for one analysis ($F_{1,46}$ = 1928.21, P < 0.01, r^2 = 0.98, SE of the estimate = 5.976), yielding the following equation:

$$DM_0 = -38.959 + 0.424WM_0 \quad [1]$$

Influence of parasitism on host food consumption

Eight- to 10-day-old adults of *M. sanguinipes* (n = 48 of each sex) were weighed individually to obtain their initial WM_0. One half of the insects of each sex were manually parasitized with one larva each of *B. atlanis*, and the other half were left unparasitized and served as a control. Parasite larvae were obtained by dissection of the ovisacs of 11- to 13-day-old females (n = 12), which had been anaesthetized lightly with CO_2. To facilitate larval implantation, we removed the right fore and hind wings of each grasshopper with microscissors and inserted one larva through the mechanically ruptured tympanum using a camel's-hair brush moistened with deionized water. Larvae from one female fly were used to parasitize two male and two female grasshoppers. Grasshoppers in the control group also had the right fore and hind wings removed and the tympanum ruptured.

Parasitized and control grasshoppers were kept individually in 250-mL, clear plastic containers and maintained at 25 ± 0.5 °C and a 16L:8D photoperiod. Food consumption and any host mortality were recorded daily, at the same time, for 9 days. Larvae of *B. atlanis* normally complete development and emerge from their hosts within 9 days of parasitism (Danyk *et al.* 2000).

Grasshoppers were provided with freshly cut wheat leaves as food. Wheat plants were grown in vermiculite in a greenhouse until plants were in the two- to three-leaf stage. Each morning, wheat leaves were harvested and placed into one of 12 plastic bags, which were then sealed immediately to reduce the loss of wet mass due to water evaporation. From each of the bags, two samples of leaves were removed and weighed on a Mettler AE50 microbalance to the

nearest milligram to determine wet mass (WM_w), dried in an oven at 55 °C for 24 h, and reweighed to the nearest milligram to determine dry mass (DM_w). A mean DM_w/WM_w ratio was calculated, separately for each bag, and used to estimate the DM_w of leaves given to grasshoppers. Grasshoppers were fed once each day, at the same time, with 5–10 wheat leaves. To reduce loss of wet mass, leaves were dispensed from each of the bags during a period of 15–30 min only. Leaves given to individual grasshoppers daily were weighed (WM_w) on a Mettler AE50 microbalance to the nearest milligram immediately before placement of the leaves in the plastic containers. Leaves not consumed after 24 h were removed from containers and placed in paper bags, separately for each grasshopper, dried in an oven at 55 °C for 24 h, and weighed to the nearest milligram. The amount of biomass consumed daily by grasshoppers was determined as the difference between the estimated dry mass of leaves given to insects and the actual dry mass of leaves that remained in containers 1 day later; negative values were assigned a value of zero prior to analysis. 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 dry mass (DM_e). To correct for the loss in mass due to the amputation of the right fore and hind wings, we added to DM_e the mean dry mass of fore and hind wings, which was estimated from a sample of wings (n = 20 of each sex). Eggs laid by grasshoppers (n = 1 parasitized, n = 6 control) during the 9-day period of observation were collected, dried, and weighed as above; these values were added to the DM_e of grasshoppers that oviposited.

Data analysis

Only data from parasitized grasshoppers from which implanted larvae emerged were included in the analyses. Data were analysed using SAS (SAS Institute Inc. 1989) to determine the statistical significance among means or regression relationships (ANOVA, ANCOVA, t tests, pairwise t tests, Tukey's test) and median values (Wilcoxon 2-sample test). Probabilities from different tests of significance (ANOVA or pairwise t tests) were combined by Fisher's test (Sokal and Rohlf 1995, p. 794). For all tests, a value of $\alpha = 0.05$ was used to determine statistical significance.

To determine the effect of parasitism on food consumption, we analysed separately consumption before and after the median time of parasite emergence from hosts. Time of parasite emergence (males, median = 5.5 days, range = 4.5–6.5 days, n = 17; females, median = 5.5 days, range = 4.5–7.5 days, n = 14) did not differ between host sexes (Wilcoxon 2-sample test; $Z = 0.094$, $P = 0.93$). For each grasshopper, daily food consumption was regressed against time to produce individual-specific relationships. The parameter estimates (*i.e.*, linear and quadratic terms and intercepts) of these regression equations were then analysed by ANOVA to evaluate general differences in food consumption between male and female controls and parasitized grasshoppers over time. For control insects, we defined pre- and post-emergence periods as days 1–5 and days 6–9, respectively. The lengths of the pre- and post-emergence periods for individual parasitized insects varied depending on the day that parasites emerged from particular hosts. Only grasshoppers that survived parasitism for ≥2 days were included in the post-emergence analysis.

Results

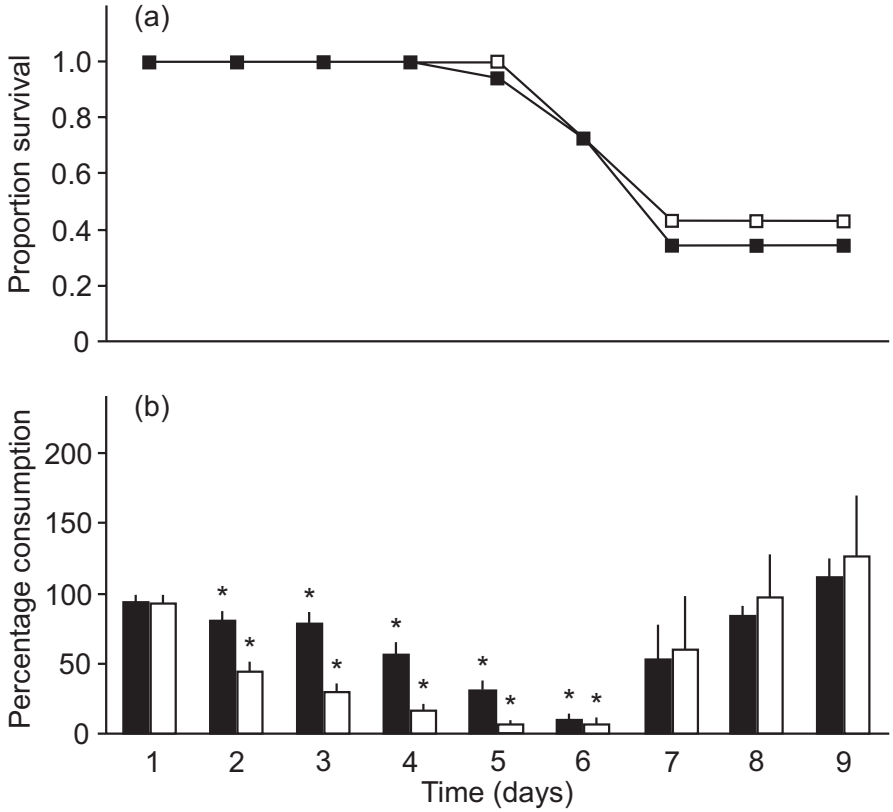
Females of *M. sanguinipes* had greater initial DM_0 than males (ANOVA; $F_{1,77} = 352.31$, $P < 0.01$), but mass did not differ between control and parasitized individuals within sexes (ANOVA; males, $F_{1,39} = 1.205$, $P = 0.28$; females, $F_{1,36} = 1.508$, $P = 0.23$) (Table 1). Unparasitized females consumed more dry mass in total than male counterparts during the experiment (ANOVA; $F_{1,46} = 8.450$, $P < 0.01$). However, total dry mass consumption was not related to initial DM_0 in either sex (ANOVA; male, $F_{1,22} = 0.035$, $P = 0.85$; female, $F_{1,22} = 0.401$, $P = 0.53$), and the slopes of the relationships did not differ between the sexes (ANCOVA; $F_{1,44} = 0.231$, $P = 0.63$). Within host sexes, sex of the parasite did not influence the amount of food consumed by grasshoppers prior to parasite emergence (Fisher's test; $\chi^2 = 5.197$, df = 8, $P = 0.74$) (Table 1). Also, there was no difference in mean food consumption (prior to the median time of parasite emergence) each day between grasshoppers that survived parasitism and those that died (Fisher's test; males, $\chi^2 = 7.316$, df = 10, $P = 0.70$; females, $\chi^2 = 13.73$, df = 10, $P = 0.19$). Therefore, we analysed food consumption separately by grasshopper sex (male *versus* female) and

Table 1. Body mass, survival, and food consumption of male and female adults of *Melanoplus sanguinipes* that were unparasitized or singly parasitized with *Blaesoxipha atlanis*.

				Pooled data[†]			Data classified by parasite sex[‡]			
Host sex	No. of larvae per host	Result of parasitism[§]	*n*	DM_0[‖] (mg, mean (SE))[¶]	Total dry mass consumed (mg, mean (SE))[¶]	Change in DM_0[‖] (mg, mean (SE))[¶]	Parasite sex	*n*	DM_0[‖] (mg, mean (SE))	Dry mass consumed during parasitism (mg, mean (SE))
Male	0		24	108.6 (2.1)*a*	118.0 (4.5)*a*	–0.7 (1.2)*a*				
	1	Died	11	111.6 (4.6)*a*	55.2 (4.9)*c*	–25.7 (1.8)*b*	Male	5	110.1 (9.1)	49.4 (7.8)
							Female	3	111.2 (3.8)	56.4 (8.6)
	1	Survived	6	114.6 (4.7)*a*	85.5 (7.1)*b*	–21.2 (2.7)*b*	Male	3	107.5 (3.7)	63.7 (9.1)
							Female	3	121.7 (6.8)	56.3 (5.4)
Female	0		24	179.1 (3.8)*a*	150.1 (10.1)*a*	+10.3 (5.2)*a*				
	1	Died	8	176.0 (8.2)*a*	48.9 (4.1)*c*	–39.0 (4.0)*b*	Male	3	193.7 (18.9)	48.1 (7.0)
							Female	3	167.5 (1.6)	54.6 (1.5)
	1	Survived	6	165.1 (3.7)*a*	96.5 (5.9)*b*	–26.1 (5.4)*b*	Male	3	167.8 (5.6)	63.7 (1.0)
							Female	2	157.1 (0.7)	75.0 (25.3)

[†]Unparasitized insects and hosts from which parasites emerged.
[‡]Hosts from which emerged parasites developed successfully into adults; see text for results of statistical analysis.
[§]Hosts that died during, or survived until the end of, the 9-day observation period.
[‖]DM_0, initial dry mass of grasshoppers at parasitism.
[¶]For each host sex, values within a column followed by different letters are significantly different (Tukey's test; $P < 0.05$).

Fig. 1. Influence of parasitism by *Blaesoxipha atlanis* on survival and feeding of *Melanoplus sanguinipes*. Grasshoppers were infected with a single larva each and monitored daily for 9 days for mortality and food consumption. (*a*) Proportion of grasshoppers surviving parasitism; (*b*) mean (+SE) daily amounts of food consumed (measured as dry mass) by parasitized grasshoppers relative to unparasitized controls (= 100%). Solid and open points or bars correspond to male (n = 17) and female (n = 14) grasshoppers, respectively. Asterisks indicate significant differences in mean food consumption between control and parasitized grasshoppers (t test; $P < 0.05$).



treatment (control *versus* parasitized), pooling between parasite sexes and between hosts that died and those that survived parasitism.

Among parasitized *M. sanguinipes* (n = 24 of each sex), parasites developed beyond the first-instar stage in 21 male and 17 female grasshoppers, but egressed from only 17 male and 14 female hosts. In contrast to insects in the control group, which were all alive at the end of the 9-day observation period, only six grasshoppers of each sex survived parasitism (Fig. 1*a*). Parasitism influenced the amount of dry mass consumed by grasshoppers during and after parasitism, as demonstrated by the significance of treatment in the analysis of individual-specific feeding relationships (Table 2). On each of days 2 through 6, parasitized grasshoppers consumed less (t test; $P < 0.05$) food than control insects of the same sex, in both absolute and relative terms (Fig. 1*b*). The patterns of food consumption differed between host sexes prior to parasite emergence, as indicated by significant sex and sex × treatment interaction terms (Table 2). Female hosts consumed more dry mass initially and experienced a greater rate of decline in food consumption than male counterparts (Fig. 1*b*, Table 3). Following parasite emergence, food consumption did not differ between host sexes, and differences in the amount of food consumed were apparent between control and parasitized insects only (Fig. 1*b*, Tables 2–3). Because survivors resumed feeding after parasite emergence, the total mass of food consumed by insects that survived parasitism exceeded that of insects that did not survive parasitism (ANOVA; males, $F_{1,15} = 12.92$, $P <$

Table 2. Results of ANOVA of relationships that describe food consumption over time by individual male and female *Melanoplus sanguinipes* that were unparasitized or singly parasitized with *Blaesoxipha atlanis*.

		F values of terms in ANOVA model[†]		
Source of variance	df	Linear	Quadratic	Intercept
Before parasite emergence[‡]				
Sex	1,75	45.75*	27.64*	59.78*
Treatment[§]	1,75	4.346*	1.292	0.004
Sex × treatment[§]	1,75	9.917*	11.92*	1.051
After parasite emergence[‖]				
Sex	1,55	0.017	0.030	0.179
Treatment[§]	1,55	27.89*	22.86*	33.26*
Sex × treatment[§]	1,55	3.479	2.875	3.977

[†]Only data from hosts from which parasites emerged were included. Significance: *, $P < 0.05$.
[‡]For unparasitized insects, data are from days 1–5, inclusive; for parasitized insects, data are from all days prior to parasite emergence.
[§]Treatments consist of unparasitized and parasitized insects.
[‖]For unparasitized insects, data are from days 6–9, inclusive; for parasitized insects, data are from hosts that lived ≥2 days after parasite emergence.

Table 3. Least square (LS) mean values associated with terms in ANOVA model that describe food consumption over time by individual male and female *Melanoplus sanguinipes* singly parasitized with *Blaesoxipha atlanis*.

	LS mean (SE) values for terms in ANOVA model		
Host sex	Linear	Quadratic	Intercept
Before parasite emergence			
Male	–5.34 (1.84)*b*	0.12 (0.28)*b*	25.71 (3.15)*b*
Female	–22.71 (2.03)*a*	2.45 (0.31)*a*	51.95 (3.47)*a*
After parasite emergence			
Male	58.01 (13.24)*a*	–3.58 (0.86)*a*	–223.76 (50.93)*a*
Female	79.71 (14.50)*a*	–4.65 (0.94)*a*	–324.94 (55.80)*a*

Note: Only data from hosts from which parasites emerged were included. For the period before parasite emergence, data are from all days preceding egression. For the period after parasite emergence, data are from hosts that lived ≥2 days. All measurements are in milligrams. In each emergence period, values within a column followed by different letters are significantly different (*t* test; $P < 0.05$).

0.01; females, $F_{1,12} = 46.47$, $P < 0.01$) (Table 1).

There was no significant difference between initial DM_0 and final DM_e in unparasitized insects (pairwise *t* test; male, $t = -0.596$, $P = 0.56$; female, $t = 1.959$, $P = 0.06$); however, parasitized grasshoppers lost dry mass (pairwise *t* test; male, $t = -15.33$, $P < 0.01$; female, $t = -9.340$, $P < 0.01$) (Table 1). During the period of observation, there was no significant difference in the amount of dry mass lost between grasshoppers that died and those that survived (Tukey's test; $P > 0.05$).

Discussion

Our results show that *M. sanguinipes* parasitized by *B. atlanis* fed less than unparasitized counterparts that were maintained under similar conditions (Fig. 1*b*). A common consequence of parasitism in insects is a change in the amount of food consumed (Slansky 1978; Cloutier and Mackauer 1979; Thompson 1993). In Orthoptera, reduced food consumption is a frequent response to infection with a parasite larva or pathogens. For example, first-instar larvae of *M. sanguinipes* infected with an

entomopoxvirus (Olfert and Erlandson 1991) and fourth-instar larvae infected by the microsporidian *Nosema locustae* Canning (Johnson and Pavlikova 1986) fed less than uninfected individuals. Reduced food consumption was observed also in *Melanoplus differentialis* (Thompson) infected with *N. locustae* (Oma and Hewitt 1984), and in *Schistocerca americana* (Drury) (Orthoptera: Acrididae) (Sieglaff *et al.* 1997), *Schistocerca gregaria* (Forskal) (Moore *et al.* 1992), and *Zonocerus variegatus* (L.) (Orthoptera: Pyrgomorphidae) (Thomas *et al.* 1997) infected with *Metarhizium flavoviride* Gams *et* Rozsypal.

A loss of host body mass as a result of reduced food consumption during parasitism was not unexpected in our experiment (Table 1). Danyk *et al.* (2000) suggested that larvae of *B. atlanis* act as a metabolic sink for host nutrients, and the acquisition of biomass by the larval parasite would prevent the host from using these resources for growth and maintenance (Grenier *et al.* 1986). In addition, because of the reduction in the amount of food hosts consume during parasitism, individuals of *M. sanguinipes* are unable to compensate for any resources that are required for their own metabolism but are sequestered by larvae of *B. atlanis*. A similar reduction in host biomass during parasitism has been observed in Lepidoptera larvae parasitized by tachinids (Soo Hoo and Seay 1972; Brewer and King 1978; Bourchier 1991) and in insects parasitized by hymenopterous parasitoids (Beckage and Riddiford 1978; Duodu and Antoh 1984).

In the first 5 days following parasitism, females of *M. sanguinipes* experienced a greater rate of decline in food consumption than observed in male counterparts. Similarly, Oma and Hewitt (1984) reported that the amount of food consumed by females of *M. differentialis* was less than that consumed by males when insects were infected with *N. locustae*. Female grasshoppers and other Orthoptera females normally are expected to consume more food than male counterparts because of the greater requirement for resources in females for gonadal development (Elliott and Gillott 1977; Miranpuri *et al.* 1991; Simmons 1994). In our experiment, control female grasshoppers consumed more dry mass daily than males. If larvae of *B. atlanis* act solely as a metabolic sink for host nutrients, then it is reasonable to predict not only that female grasshoppers may respond to the metabolic demands of a parasite in a manner similar to that of gonadal tissue during oogenesis but also that females may be better adapted than males to meet the demands of a metabolic sink. However, we observed a decline, rather than an increase, in food consumption by parasitized females of *M. sanguinipes*, which suggests that neither sex compensated well for the loss of resources to parasites during parasitism, and females appeared to be more sensitive to the effects of parasitism than males.

The relationship between parasite and host is intimate, and parasites are expected to exploit the host to their advantage (Slansky 1986; Thompson and Kavaliers 1994; Poulin 1995). Parasitic Hymenoptera have been shown to modify host biology; examples include interference by parasitoid larvae with the host's endocrine system (Beckage 1985) and disruption of host immune systems by polydnavirus placed in hosts by ovipositing females (Jones *et al.* 1986; Vinson 1990). The influence that dipteran larvae have on their hosts may be attained by less sophisticated means. In contrast to the closed hind gut of larvae of parasitic Hymenoptera, the hind gut of parasitic Diptera is open during larval development (Askew 1971), and therefore dipteran larvae can excrete into the haemocoel of hosts metabolic wastes, digestive enzymes, and additional enteric components. Excretion of larva-specific materials has been shown to modify the environment in which dipteran larvae develop (Pavillard and Wright 1957; Nogge 1972; Casu *et al.* 1996). Similarly, there is evidence that larvae of *B. atlanis* may alter the environment in which they live. *Beauveria bassiana* (Balsamo) Vuillemin does not sporulate as readily on cadavers of adults of *M. sanguinipes* previously infected with the fungal pathogen and parasitized with *B. atlanis* in comparison with sporulation observed on unparasitized grasshoppers (T. Danyk, unpublished data). Sarcophagid parasites of grasshoppers feed on haemolymph and fat body and usually do not injure host tissue (Rees 1973; Baker 1995). The effect that *B. atlanis* larvae have on hosts may therefore be restricted primarily to the response of hosts to excretory products of larval parasites. If the presence of larva-specific materials in hosts influences host food consumption, then it would be reasonable to expect that in the absence of parasites, the effect on food consumption would diminish. Indeed, we observed an initial decline in feeding

by parasitized *M. sanguinipes*, a near complete suppression of food consumption prior to parasite emergence, and then an increase in feeding following parasite egression. Catabolic enzymes are known to be active in the haemolymph of *M. sanguinipes* (Gillespie *et al.* 1991; Vincent *et al.* 1993), and excretion and (or) detoxification of larva-specific materials by the host following parasite egression may explain the temporary effect that *B. atlanis* has on grasshoppers that survive parasitism.

Survival of parasitized adult insects is rare (Godfray 1994); however, about one third of male and female *M. sanguinipes* survived parasitism by *B. atlanis*. Prior to parasite emergence, the total amount of food consumed by parasitized *M. sanguinipes* did not differ between grasshoppers that survived parasitism and those that died, so survival was not dependent on the amount of food consumed prior to parasite egression. Rather, Danyk *et al.* (2000) reported that survival and longevity of *M. sanguinipes* parasitized by *B. atlanis* were related to host dry mass at parasitism.

Unlike the sex-specific differences in food consumption observed prior to parasite emergence, food consumption did not differ between formerly parasitized males and females of *M. sanguinipes* following parasite egression. Because of the resumption of feeding, survivors of parasitism consumed more dry mass than individuals that died, but less food than unparasitized counterparts, over the course of the 9-day observation period. We did not extend the experiment to assess the degree to which hosts recovered from parasitism. However, Rees (1986) reported that *M. sanguinipes* that survived parasitism by various dipteran species had lower lifetime fecundity but produced the same number of eggs per pod, in comparison with unparasitized individuals.

We propose that a reduction in the amount of food consumed by parasitized *M. sanguinipes* results in temporary starvation, which in turn may limit the quantity of resources that the host can assimilate to sustain itself and to compensate for losses to the developing parasite. Chapman and Sword (1994) showed that in *S. americana*, a decrease in the daily food ration resulted in reduced growth and survival, which is similar to our observations. Although we cannot exclude the possibility that reduced feeding by *M. sanguinipes* is due to host regulation by *B. atlanis*, it is not clear how a parasite might gain in fitness by limiting resource accumulation in its host (Slansky 1986; Poulin 1995). However, one possibility is that decreased food consumption may reduce foraging and thereby limit the host's exposure to mortality factors such as parasites, predators, and food-borne pathogens. Unlike true parasitoids, which normally kill their host, *B. atlanis* is similar to a parasite in that the larva does not necessarily kill the host. Under these circumstances, an indirect stress effect of parasitism (Thompson 1993) provides a more general and therefore more likely correct explanation of a temporary reduction in feeding by hosts.

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