Effects of a parasite mite on life-history variation in two grasshopper species

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ABSTRACT

Parasites often have large effects on the life-history patterns of their hosts. There is a need to examine how observed life-history patterns of parasitized organisms under field conditions fit theoretical predictions. I conducted a field experiment to examine the effects of an ectoparasitic grasshopper mite on survival and reproductive allocation in two grasshoppers with different life-history characteristics, *Melanoplus sanguinipes* and *Ageneotettix deorum*. Proportional survival was lower in mite-parasitized *A. deorum* during the period of mite parasitism, but not in *M. sanguinipes*. As predicted in response to a short-lived parasite, females in both species had reduced initial and total reproduction. Egg production declined by 39–44% with mite parasitism in the two species of grasshoppers studied. Parasitized females of both species completed development of a lower percentage of ovarioles initiating development. Future reproduction of *A. deorum* females was unaffected by parasitism. However, future reproduction of parasitized *M. sanguinipes* remained lower at the end of the experiment, indicating parasitism had an effect on reproduction up to 40 days after mite parasites left *M. sanguinipes* females. There were no interactions between population density and mite parasitism on reproductive allocation or survival in *M. sanguinipes*. Parasitized females of both species appeared to differentially allocate resources in response to parasitism. The reduced reproduction in parasitized individuals probably resulted from the inability of grasshoppers to increase resource intake to compensate for the direct or indirect costs of parasitism.

Keywords: *Eutrombidium locustorum*, *Melanoplus sanguinipes*, parasitism, reproductive allocation.

INTRODUCTION

Parasites can have large effects on the life-history patterns of organisms (Jokela *et al.*, 1999a). Reduced survival or reproduction in parasitized hosts can occur from the direct detrimental effects of the parasite on a host, reduced resource availability resulting from parasitism or, indirectly, through the costs of immune system activation (Moret and Schmid-Hempel, 2000; Hurd, 2001). Parasitized organisms commonly exhibit reduced

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reproduction (Hurd, 2001) or an increased cost of reproduction (Sorci *et al.*, 1996). Several models have been developed that predict life-history characteristics of parasitized organisms based on the type of parasite involved or the effect of the parasite on the host (Hochberg *et al.*, 1992; Forbes, 1993, 1996; Michalakis and Hochberg, 1994; Perrin and Christe, 1996; Sorci *et al.*, 1996). Reduced fecundity in parasitized hosts can be a constrained non-adaptive by-product of parasitism or an adaptive strategy by a host in response to the parasite (Hurd, 2001). However, both increases and decreases in the reproductive allocation of parasitized organisms can be adaptive (Forbes, 1993).

Resource availability can play an important role in the effect parasites have on reproductive allocation and survival, since organisms often exhibit trade-offs in the allocation of resources to reproduction and maintenance or growth (Jokela *et al.*, 1999b). When resources are limiting, resources consumed by a parasite or required by defence responses reduce available resources for maintenance and reproduction. Moret and Schmid-Hempel (2000) and Polak (1996) found that reductions in survival and/or reproduction under parasitism or simulated parasitism were noticeable only when resources were limiting.

In this study, I conducted a field experiment to examine the effects of ectoparasitic grasshopper mites on survival and reproductive allocation of two common grasshopper species in western Montana, USA, with differing life-history characteristics. The study was designed to examine the within-generation effects of a mite parasite on survival and reproductive allocation of grasshoppers, not the inherited environmental effects resulting from parasitism (Rossiter, 1996). The importance of mites on grasshopper life-history variation under natural abiotic and resource availability conditions has not been examined to date. In addition, there is a need for more studies examining how changes in reproductive allocation in response to parasitism fit theoretical predictions (Forbes, 1993).

The *Eutrombidium locustorum*–grasshopper (Orthoptera: Acrididae) system

Little is known about the impacts of ectoparasitic larval mites on grasshopper life-history variation (Rees, 1973; Belovsky *et al.*, 1997). Parasitic mites have been assumed to have small detrimental effects on grasshopper survival and reproduction and to convey no known diseases (Severin, 1944; Campbell, 1964). Ectoparasitic larval mites attach to grasshoppers by piercing either the integument or a wing vein, often during moulting (Rees, 1973). Attempts to artificially parasitize grasshoppers with larval mites have typically failed (Huggans and Blickenstaff, 1966). Given the nature of larval mite attachment to grasshoppers, genetic or behavioural differences between parasitized and unparasitized grasshoppers are unlikely to have a significant effect on the probability of parasitism (Leonard *et al.*, 1999). The mites feed on hemolymph and remain attached for 5–14 days (Severin, 1944; Rees, 1973). *Eutrombidium locustorum* (Walsh), the mite used in this experiment, is widely distributed throughout the western United States (Huggans and Blickenstaff, 1966; Rees, 1973).

The effects of parasitic mites on life-history variation were examined using two common grasshopper species with different life-history characteristics: *Melanoplus sanguinipes* (Fabricius) (Acrididae: Melanoplinae) is polyphagous, eating both grasses and forbs (Pfadt, 1994); *Ageneotettix deorum* (Scudder) (Acrididae: Gomphocerinae) feeds primarily on grasses (Pfadt, 1994). *Ageneotettix deorum* female dry mass averages 40% less than that of

M. sanguinipes females. *Melanoplus sanguinipes* females average 32 ovarioles, whereas *A. deorum* females average 6 ovarioles. Grasshopper ovaries consist of a series of ovarian follicles, or ovarioles, which are capable of developing and producing eggs (Bellinger *et al.*, 1987). The number of ovarioles is equivalent to the largest egg pod that can be produced, although egg pods produced under field conditions are typically smaller (Bellinger and Pienkowski, 1985). Vitellogenesis occurs when an ovarian follicle initiates development (Chapman, 1998). Grasshoppers can reduce reproductive allocation in response to a stressor or reduced resource availability by reducing vitellogenesis or increasing resorption of ovarian follicles (Joern and Klucas, 1993; Chapman, 1998), leaving a greater percentage of available resources to be used for survival and maintenance (Papaj, 2000). Allocation of resources to a given ovarian follicle may become fixed after a given developmental stage of vitellogenesis in grasshoppers (Moerhlin and Juliano, 1998). Since the smaller bodied *A. deorum* lays up to 10 small egg pods while *M. sanguinipes* typically lays 1–3 larger egg pods under field conditions (Branson, 2001), a short-lived mite parasite could have differential effects on life-history variation in these two species.

Objectives and predictions

The main objective of the experiments was to examine the effects of mite parasitism on reproductive allocation and survival of *M. sanguinipes* and *A. deorum* and to examine how the responses fit theoretical predictions. An additional objective, addressed with *M. sanguinipes*, was to examine if the effects of mite parasitism changed with grasshopper population density. Increased environmental stress at higher grasshopper population densities could increase the impact of a mite parasite (Oppliger *et al.*, 1998). Mite parasitism would be expected to have an increased impact on reproduction and/or survival as resource limitation increases with population density, as a grasshopper would be unable to increase resource intake to compensate for the effects of parasitism (Moret and Schmid-Hempel, 2000). Belovsky and Slade (1995), in a study at the same location, found the main effect of increased intraspecific grasshopper densities on survival resulted from reduced resource availability leading to increased exploitative scramble competition for resources.

Forbes (1993) developed an optimal reproductive effort model for parasitized organisms that assumes limited resources are available for reproduction and trade-off curves are convex. Predictions of optimal reproductive effort for current and future reproduction differ for each of three categories of parasites (Forbes, 1993). In cases in which the parasite is short-lived on the host, as is the case with ectoparasitic mites, a host should reduce reproductive effort during the period of parasitism (initial reproduction) compared with unparasitized hosts (Forbes, 1993). This results from fewer resources being available for reproduction during the period of parasitism (Forbes, 1993). The reduction in initial reproduction should lead to reduced total reproduction in parasitized individuals (Forbes, 1993). Mites were not predicted to have large effects on future reproduction of grasshoppers (Forbes, 1993), since they remain on host grasshoppers for only 5–14 days and their presence would not be expected to have long-term effects on resource availability for the host. If mites repeatedly parasitized grasshoppers over a season, this prediction would change. However, repeated parasitism was not detected during the experiment. Specific experimental predictions are shown in Table 1.

Table 1. Specific predicted experimental life-history responses of grasshoppers and experimental outcomes

General prediction with parasitism	Specific experimental prediction	Outcome with parasitism
1. Reduced total reproduction (Forbes, 1993)	Reduction in number of follicular relicts (eggs) in parasitized females as assessed by univariate ANOVA	Reduced egg production in both species ($P < 0.01$)
2. Reduced reproductive allocation during the period of parasitism (Forbes, 1993)	Decreased ratio of eggs laid to vitellogenesis or a reduction in vitellogenesis in parasitized females as assessed by univariate ANOVAs	Decreased ratio of eggs laid to vitellogenesis in both species ($P < 0.01$) No differences in vitellogenesis in both species ($P > 0.5$)
3. No effect on future reproductive allocation (Forbes, 1993)	No differences in functional ovariole number in parasitized females as assessed by univariate ANOVA	*A. deorum*: no differences ($P > 0.6$) *M. sanguinipes*: reduced functional ovariole number ($P < 0.001$)
4. Stronger effects of mite parasitism as resource limitation increases (Moret and Schmid-Hempel, 2000)	Interaction between density and parasitism treatments on reproductive allocation or survival as assessed by a multivariate ANOVA on reproductive characteristics	No significant interactions affecting reproductive characteristics ($P > 0.2$) or proportional survival ($P > 0.8$)

MATERIALS AND METHODS

General methods

I conducted the experiments at the National Bison Range in northwestern Montana, USA, at an elevation of 800 m. The study site is a Palouse prairie where biomass is dominated by C_3 grasses (Belovsky and Slade, 1995). I placed 0.1 m^2 basal area cages, with a height of 0.9 m, over similar patches of natural vegetation. The square cages were constructed of aluminium screening fastened to aluminium garden edging at the base, which was buried in the ground and closed with binder clips. Similar cages have been used in a variety of studies with grasshoppers (Joern and Klucas, 1993; Schmitz, 1993; Belovsky and Slade, 1995). Cage effects on microclimate are minimal (Belovsky and Slade, 1993). Treatments were randomly assigned to cages with five replicate cages for each treatment.

I caught newly eclosed mite-parasitized and unparasitized adult grasshoppers of *M. sanguinipes* and *A. deorum* at the same field site. Parasitized grasshoppers had an average of three larval mite ectoparasites attached. I used newly eclosed adults to minimize the likelihood of previous parasitism of adults. Both the *M. sanguinipes* and *A. deorum* experiments had mite-parasitized and control (no mite) treatments stocked at 10 grasshoppers per cage. In addition, the *M. sanguinipes* experiment had a lower population

density treatment of four grasshoppers per cage for both parasitized and control treatments. The lower density treatment was at or below historical field densities at the site when corrected for the proportion of bare ground in the environment (Belovsky and Slade, 1995). Only one *A. deorum* density treatment was initiated due to limited numbers of parasitized grasshoppers. All cages were initiated at an even sex ratio of grasshoppers. Grasshoppers were counted throughout the experiment to monitor survival in each cage. At the end of the experiment, all surviving females were frozen for reproductive analysis.

Reproductive analysis

I examined the ovaries of female grasshoppers to assess egg production, future reproduction, oosorption and vitellogenesis (Launois-Luong, 1978). Ovary analysis is particularly informative, as grasshopper egg pods are difficult to recover in the field. When an egg is released into the oviduct, the covering of the egg compresses into a narrow visible band called the follicular relict. When an ovarian follicle is resorbed, a brightly coloured resorption body is evident. I determined the number of functional, or developing, ovarioles, which is a measure of future reproduction (Uvarov, 1966).

Statistical analysis

The experiment was designed to use repeated-measures analysis of variance (ANOVA) models to examine treatment effects on proportional survival (Joern and Klucas, 1993; von Ende, 2001). Following the methods of Joern and Klucas (1993), I analysed proportional survival both to 8 days and to the end of the experiment to assess initial and longer-term effects of parasitism on survival. Proportion survival measures were arcsine transformed as necessary to normalize values (Lentner and Bishop, 1986). Survival curve analyses were not considered, as each replicate cage was initiated with multiple unmarked individuals (Moret and Schmid-Hempel, 2000; Fox, 2001). I used a multivariate analysis of variance (MANOVA) to assess overall treatment effects on egg production, future reproduction, vitellogenesis and the ratio of egg production to vitellogenesis, since multiple reproductive characteristics were measured on individual grasshoppers (Zar, 1999). If the MANOVA model was significant, univariate analyses of variance were used to examine treatment differences in individual reproductive characteristics (Zar, 1999). I used cage means as replicate values for all analyses and used SYSTAT 10 (SPSS Inc., 2000) for all statistical analyses.

RESULTS

Reproductive allocation

Melanoplus sanguinipes

Based on a multivariate analysis, mite parasitism significantly affected reproductive characteristics (Table 2). Parasitism negatively affected total reproduction, as measured by follicular relicts (Tables 2, 3). Vitellogenesis was not affected by mite parasitism, while the ratio of eggs laid relative to vitellogenesis was lower in mite-parasitized females (Tables 2, 3). Therefore, vitellogenesis was initiated equally in parasitized and unparasitized grass-

Table 2. Statistical results for *M. sanguinipes* and *A. deorum* reproductive characteristics

MANOVA of reproductive characteristics	Source	d.f.	Wilks' lambda	F	P
M. sanguinipes	Density	4,8	0.135	12.830	0.001
	Mite	4,8	0.331	4.051	0.04
	Interaction	4,8	0.515	1.883	0.21
A. deorum	Mite	4,4	0.091	9.953	0.023

Univariate tests	Source	d.f.	Mean square	F	P
M. sanguinipes					
Functional ovarioles	Mite	1	290.956	11.320	0.006
	Density	1	7.488	0.291	0.600
Follicular relicts	Mite	1	728.665	20.103	0.001
	Density	1	1059.212	29.222	0.000
Vitellogenesis	Mite	1	7.793	0.172	0.686
	Density	1	2139.923	47.326	0.000
Proportional reproduction	Mite	1	1.336	13.947	0.003
(follicular relicts/vitellogenesis)	Density	1	0.083	0.865	0.372
A. deorum					
Functional ovarioles	Mite	1	0.050	0.179	0.685
Follicular relicts	Mite	1	92.450	14.860	0.006
Vitellogenesis	Mite	1	3.335	0.482	0.510
Proportional reproduction (follicular relicts/vitellogenesis)	Mite	1	0.222	42.175	< 0.001

Note: All analyses are based on per capita cage averages.

Table 3. Estimates of reproductive allocation parameters of *M. sanguinipes* and *A. deorum* for each treatment (mean ± 1 standard error)

Species	Treatment	Functional ovarioles	Follicular relicts	Vitellogenesis	Proportional egg production
M. sanguinipes	Mite/higher	11.9 ± 2.5	11.9 ± 3.0	32.8 ± 3.4	0.38 ± 0.07
	Mite/lower	12.3 ± 2.9	24.3 ± 3.5	56.7 ± 3.9	0.43 ± 0.08
	Control/higher	19.9 ± 2.3	21.4 ± 2.7	33.7 ± 3.0	0.65 ± 0.06
	Control/lower	22.3 ± 2.9	43.3 ± 3.5	58.7 ± 3.9	0.74 ± 0.08
A. deorum	Mite	3.1 ± 0.2	9.8 ± 1.3	23.6 ± 1.5	0.41 ± 0.04
	Control	3.2 ± 0.3	16.2 ± 0.8	22.4 ± 0.5	0.73 ± 0.03

Note: Unparasitized treatments are represented as control, while parasitized treatments are indicated as mite. *Melanoplus sanguinipes* density treatments are represented as higher and lower.

hoppers, but egg production was completed less frequently in mite-parasitized individuals (Tables 2, 3). Functional ovariole number, an indication of future reproduction, was lower in mite-parasitized females (Tables 2, 3).

Both per capita egg production and vitellogenesis were lower in the *M. sanguinipes* higher-density treatment (Tables 2, 3). More ovarioles were resorbed in the higher-density treatment (Tables 2, 3). Functional ovariole number and the proportion of eggs laid relative to vitellogenesis were not affected by the density treatments (Tables 2, 3). No significant interactions occurred between population density and parasitism, based on a multivariate analysis of reproductive characteristics (Table 2).

Ageneotettix deorum

For most reproductive characteristics, the effects of mite parasitism in *A. deorum* were similar to those in *M. sanguinipes* (Table 2). Parasitized *A. deorum* females had fewer follicular relicts and a lower ratio of eggs laid relative to vitellogenesis (Tabes 2, 3); vitellogenesis was unchanged compared with unparasitized females (Tables 2, 3). In contrast to *M. sanguinipes*, functional ovariole number was not affected by mite parasitism (Tables 2, 3).

Survival

Melanoplus sanguinipes

Average proportional survival in each treatment throughout the experiment is shown in Fig. 1. The proportion of grasshoppers surviving to the end of the experiment or surviving at 8 days did not differ between treatments (Table 4) when analysed by a repeated-measures ANOVA. Most ectoparasitic mites dropped off the host grasshoppers within the first 12 days of the experiment.

Proportional survival in the lower density treatment was higher both at 8 days and at the end of the experiment (Table 4). The number of *M. sanguinipes* surviving in the higher-density treatment declined to levels similar to the lower-density cages by the end of the experiment. The mite parasitism and density treatments did not interact in their effects on proportional survival (Table 4).

Ageneotettix deorum

Changes in the average proportional survival in each treatment throughout the experiment are shown in Fig. 1. Proportional survival to the end of the experiment was not affected by mite parasitism (Table 4). However, proportional survival at 8 days was lower in the mite-parasitized treatment (Table 4).

DISCUSSION

Total and initial reproduction

Mite parasitism led to a 39–44% reduction in egg production in *M. sanguinipes* and *A. deorum*, indicating that mites had a large negative impact on total reproduction in both species (Tables 2, 3). Although there were no differences in vitellogenesis, the ratio of eggs laid relative to vitellogenesis was lower in parasitized females of both species (Tables 2, 3). This indicates that parasitized females initiated ovariole development at similar rates to unparasitized females, but completed development of ovarioles less frequently. As a result, mite parasitism appeared to have a negative effect on reproductive allocation during the
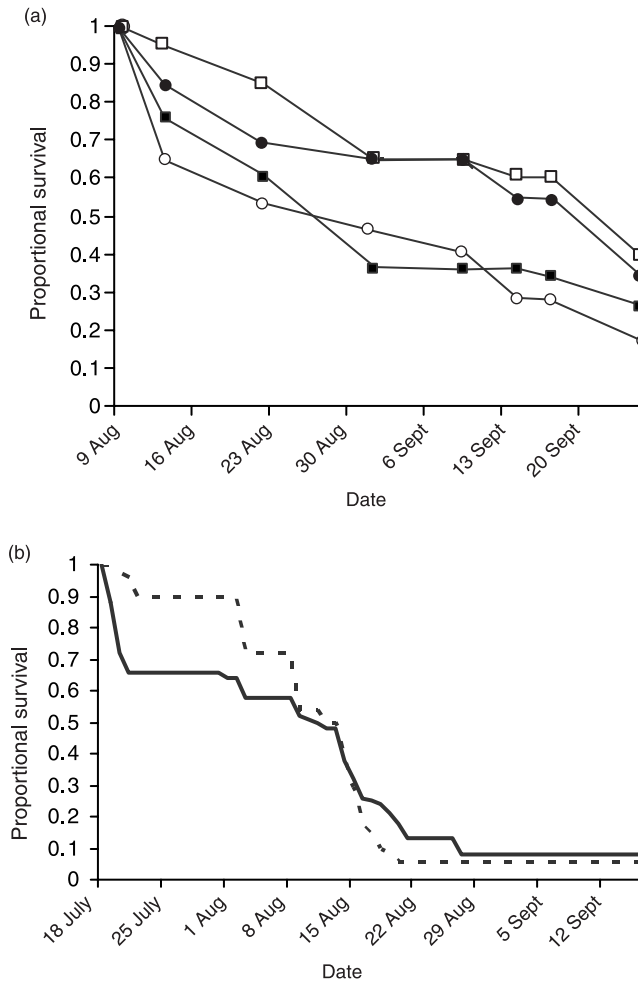
Fig. 1. Mean proportional survival over the course of the experiment for (a) *M. sanguinipes* and (b) *A. deorum*. Unparasitized treatments are represented as control, while parasitized treatments are indicated as mite. *Melanoplus sanguinipes* population density treatments are represented as higher and lower. Treatment mean proportional survival was calculated from the mean proportion survival in each replicate cage. (a) ○, mite/higher; ■, control/higher; ●, mite/lower; □, control/lower. (b) dashed line = control; solid line = mite.

period of parasitism (initial reproduction). The observed reduction in initial and total reproduction in response to parasitism in both species is in agreement with the predictions of Forbes' model (Table 1). Although there was no effect of parasitism on vitellogenesis in female *M. sanguinipes* or *A. deorum*, the ratio of eggs laid relative to vitellogenesis was significantly lower in parasitized individuals in both species (Tables 2, 3). This finding indicates that the effects of mite parasitism did not have large enough detrimental effects to lead to reductions in the rate at which ovarioles, and thus egg pods, were initiated. Since fewer of the ovarioles initiating development completed development in parasitized

Table 4. Statistical results for *M. sanguinipes* and *A. deorum* survival using repeated-measures ANOVA for proportion of grasshoppers surviving through the experiment (Proportional survival) and proportional survival of grasshoppers at 8 days after stocking (Proportional survival at 8 days)

Source	d.f.	Mean square	F	P
M. sanguinipes				
Proportional survival at 8 days				
Mite	1	0.118	1.705	0.210
Density	1	0.405	5.838	0.028
Interaction	1	0.001	0.002	0.965
Proportional survival				
Mite	1	0.078	0.597	0.451
Density	1	1.806	13.857	0.002
Interaction	1	0.003	0.027	0.872
A. deorum				
Proportional survival at 8 days				
Mite	1	0.961	5.373	0.049
Proportional survival				
Mite	1	0.464	0.945	0.359

individuals of both species, parasitized females diverted resources from reproduction as predicted.

Future reproduction

No differences in future reproduction, as measured by functional ovariole number, were expected between parasitized and unparasitized individuals at the end of the experiment (Table 1; Forbes, 1993). In contrast to this prediction, mite-parasitized *M. sanguinipes* had lower numbers of functional ovarioles (Table 3). This indicates mite parasitism had an effect on reproductive allocation for up to 40 days after the mites left *M. sanguinipes* females, impacting much of the typical egg production period in the field (Pfadt and Smith, 1972). As predicted, no differences in future reproduction were observed between mite-parasitized and unparasitized *A. deorum*. This finding indicates that the detrimental effects of mite parasitism did not persist to the end of the experiment. *Ageneotettix deorum* has a maximum of seven ovarioles, limiting potential variation in functional ovariole number. Since *M. sanguinipes* typically lays an average of two egg pods in the area of the study site (Branson, 2001), it may have less reproductive flexibility to increase the size of egg pods following the period of parasitism than *A. deorum*.

Mite parasitism and survival

Increased mortality from parasitism could occur either during the initial 5–10 days of parasitism or with a delay if parasitized grasshoppers are weakened and unable to

recover fully. Parasitized *A. deorum* had reduced survival during the initial period of parasitism, as proportional survival at 8 days was lower in the mite parasitism treatment than in the unparasitized treatment (Table 4). There was no effect of parasitism on survival to 8 days in *M. sanguinipes*. The average of three ectoparasitic mites on each parasitized *A. deorum* and *M. sanguinipes* could have a larger effect on the smaller-bodied *A. deorum* than *M. sanguinipes*. Mite parasitism did not affect proportional survival to the end of the experiment in either *M. sanguinipes* or *A. deorum* (Table 4). If a parasitized female has the potential for future reproduction and resources are limited, she would be predicted to devote a higher proportion of resources to survival during the period of parasitism (Hurd, 2001). Parasitized grasshoppers of both species initiated egg production at the same rate as unparasitized females, but laid fewer eggs (Tables 2, 3), indicating that mite-parasitized *M. sanguinipes* and *A. deorum* could have selectively allocated resources to survival. Since resource intake cannot be measured directly in field cages, additional laboratory experiments are required to quantify the amount of resources allocated to survival by parasitized and unparasitized females.

Effects of population density and parasitism in *M. sanguinipes*

Both population density and parasitism affected reproductive allocation of *M. sanguinipes*. Proportional survival both at 8 days and at the end of the experiment was lower in the higher-density treatment (Tables 2, 3), which is indicative of density-dependent mortality (Joern and Klucas, 1993). Density dependence in egg production was also evident (Tables 2, 3). The density dependence in survival and reproduction observed here was expected, as the higher-density cages were stocked above the average long-term carrying capacity for *M. sanguinipes* at the site (Belovsky and Slade, 1995). The detrimental effect of mite parasitism on total egg production was similar in magnitude to the effects of density dependence (Table 3). Although *M. sanguinipes* females modified reproductive allocation in response to both the density and parasitism treatments, the treatments affected reproductive allocation in different ways (Table 2). Females at higher densities had reduced vitellogenesis, but had similar future reproduction and completed development of ovarioles initiating vitellogenesis in similar proportions to females at the lower population density (Tables 2, 3). The negative effect of density, but not of parasitism, on vitellogenesis indicates that the increased density treatment led to stronger resource limitation than that resulting from mite parasitism (Stauffer and Whitman, 1997). Differences in the timing and extent of resource limitation between the density and parasitism treatments could have contributed to the treatment differences in reproductive allocation (Hurd, 2001).

There were no significant interactions between parasitism and density on either reproductive characteristics or survival (Tables 2, 4). In addition, population densities declined to similar levels in both density treatments by the end of the experiment and future reproduction did not differ between density treatments (Table 3). These findings indicate grasshoppers in both density treatments were probably resource-limited, with similar resource availabilities by the end of the experiment (Joern and Klucas, 1993; Belovsky and Slade, 1995). Therefore, the effects of mite parasitism and population density appeared to act largely in an additive fashion.

CONCLUSION

This study has shown that two grasshopper species with different life-history characteristics respond similarly to mite parasitism. As predicted, total and initial reproduction decreased in parasitized individuals. Parasitized females of both species appeared to differentially allocate resources in response to parasitism. However, there were differences in the effects of parasitism on both survival and future reproduction. Under field conditions, reduced reproduction in parasitized individuals may have resulted from the inability of grasshoppers to increase resource intake to compensate for the direct or indirect costs of parasitism. However, additional experimentation would be required to determine if the two species differ in their ability to overcome the effects of mite parasitism with additional resources. These results have implications for grasshopper population dynamics and possibly the implementation of biocontrol strategies, as smaller effects of mite parasitism on grasshopper population dynamics are predicted when only considering differences in survival. The effect of parasitism on reproduction could have a large impact on grasshopper population dynamics.

ACKNOWLEDGEMENTS

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