Reproductive Allocation and Survival in Grasshoppers: Effects of Resource Availability, Grasshopper Density, and Parasitism

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REPRODUCTIVE ALLOCATION AND SURVIVAL IN GRASSHOPPERS:
EFFECTS OF RESOURCE AVAILABILITY, GRASSHOPPER
DENSITY, AND PARASITISM

by

David Heath Branson

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
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in
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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Reproductive Allocation and Survival in Grasshoppers:
Effects of Resource Availability, Grasshopper Density, and Parasitism

by

David Heath Branson, Doctor of Philosophy
Utah State University, 2001

Major Professor: Dr. Gary E. Belovsky
Department: Fisheries and Wildlife

A major challenge in ecology is to understand intraspecific variation in life histories. Variation in resource availability can lead to differences in reproductive allocation and life histories. Grasshoppers are a good organism for the study of variation in life histories, since they exhibit life history plasticity in response to biotic and environmental factors. An optimality model for grasshoppers was developed that predicts optimal total allocation to reproduction and optimal effort-per-offspring as functions of resource availability and mortality. Relative allocation to reproduction is predicted to increase with resource availability, while relative allocation to survival declines. A resource-based trade-off between egg size and number does not exist, as optimal egg size is predicted to be independent of resource intake. I examined if changes in reproductive allocation and survival of Melanoplus sanguinipes (Fabricus)
under a range of resource availabilities fit the predictions of the model. The patterns of reproductive allocation and survival in the field were in qualitative agreement with the predictions.

I examined the importance of density, resources, and parasitism on the life history patterns of grasshoppers. I conducted an experiment to examine if differences in reproductive allocation of *M. sanguinipes* are primarily explained by exploitative competition. Per capita resource availability explained a significant amount of the variation in reproduction, as expected with exploitative competition. *M. sanguinipes* grasshoppers appeared to trade off resource allocation to reproduction for that of allocation to survival, because per capita resource availability did not affect survival.

Careful examinations of changes in life history characteristics in response to parasitism are lacking, despite the fact that parasites often influence resource availability for the host. I investigated the effects of a grasshopper ectoparasitic mite on grasshopper reproduction and survival. Mites had small effects on grasshopper survival. As predicted, both species had reduced initial and total reproduction, and completed development of a lower percentage of ovarioles initiated when parasitized. These experiments act to expand our knowledge of life history theory and further our understanding of grasshopper life history variation and population fluctuations.
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David Heath Branson
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CHAPTER 1
INTRODUCTION

Literature Review

A major challenge in evolutionary ecology is understanding both intra- and interspecific variation in life histories (Roff 1992, Stearns 1992). Theoretical developments in life history evolution have far outpaced empirical tests of these theories (Roff 1992, Stearns 1992), partially because the mathematical complexity of many theoretical models makes empirical tests difficult. Theories of reproductive allocation, a subset of life history theory, predict how an organism should allocate resources between reproduction, survival, growth, storage and maintenance in order to maximize fitness (Roff 1992, Stearns 1992). Many of these reproductive allocation models have dealt with timing or frequency of reproduction (Cole 1954, Murphy 1968, Sibly and Calow 1986), effort devoted to reproduction (Lack 1948, Sibly 1991, Roff 1992) and effort devoted to each offspring (Smith and Fretwell 1974, McGinley et al. 1987, Shine 1989).

One of the main challenges an organism faces when resources or nutrients are limiting is how much to expend on reproduction. Life history theory assumes that allocation of resources to reproduction leads to a reduction in allocation of resources to other activities when resources are limiting (Roff 1992, Nylin and Gotthard 1998). In particular, the amount of resources devoted to current reproduction should depend on the prospects for future reproduction. If an individual female has little chance to survive after breeding, she has no reason to conserve resources.
Models of resource allocation for reproduction have addressed optimal total allocation to reproduction, optimal clutch size and optimal effort-per-offspring. Optimal effort-per-offspring models typically assume that the total reproductive allocation must be divided among a limited number of offspring, resulting in a trade-off between effort-per-offspring and number of offspring produced (McGinley et al. 1987). Theoretical models of both optimal total allocation to reproduction and optimal effort-per-offspring have been developed for constant environments (Smith and Fretwell 1974, Kozlowski and Wiegert 1986, Sibly and Calow 1986), environments varying in resource abundance (Sibly and Calow 1986, van Noordwijk and de Jong 1986) and environments varying abiotically (Schaffer 1974, McGinley et al. 1987). However, optimal effort-per-offspring and total reproductive allocations are seldom considered simultaneously (Winkler and Wallin 1987).

Life history optimization approaches, the primary focus of this review, assume evolution acts to maximize fitness and are ideal for studying the ecological significance of life history plasticity in varying environments (Roff 1992). An optimal life history is one that maximizes an individual’s reproductive value, the average number of offspring an organism can expect to produce over the remainder of its life. An optimal life history is one that maximizes fitness; however, an organism’s reproductive value is difficult to measure and surrogate correlates of fitness are often used (Roff 1992, Stearns 1992). These complications are more pronounced when dealing with organisms whose populations exhibit age structure (Charlesworth 1994). Simple, yet realistic, life history models can be developed for univoltine organisms
with determinate growth. The importance of resource availability for reproduction and survival of organisms has been shown both theoretically (Sibly and Calow 1986, van Noordwijk and de Jong 1986) and empirically (Begon et al. 1990, Roff 1992). The theory reviewed provides an important framework for the model and experiments presented in this dissertation. In addition, this review allows an examination of areas where theoretical approaches have been lacking.

**Optimal Allocation to Reproduction**

Since the total amount of resources available for allocation is limited, the relative resource allocation to reproduction and survival has important implications for fitness (Sibly and Calow 1986, van Noordwijk and de Jong 1986, Winkler and Wallin 1987, Kozlowski 1991). According to the “principle of allocation” (Cody 1966, Williams 1966a, Gadgil and Bossert 1970), a trade-off is made in the allocation of resources to growth, metabolism, reproduction, and other functions. Two critical assumptions of the principle of allocation exist. First, there is a direct relationship between the amount of resources allocated to reproduction and fitness of an organism (Calow 1981). Second, the benefit of increased reproduction is assumed to be offset by decreased survival, unless fitness is zero at all levels (Johansson and Tuomi 1994). Williams (1966a, b) argued that an organism should increase reproduction as long as current benefits outweigh future costs. In addition, reproductive effort should increase with age if there is a cost to future survival (Williams 1966a).
Environmental variability

The theory discussed above assumes a stable abiotic environment; however, environmental variation is common in nature and may differentially affect adults or juveniles. Murphy (1968) conducted the first examination of environmental variation by analyzing the effect of uncertain juvenile survival on life history strategies. When juvenile mortality is high, the reproductive effort per clutch should decline. However, when adult mortality is high, the preferred strategy is to increase early reproductive effort to ensure reproduction before death. Schaffer (1974) considered uncertain juvenile and adult environments and found the life history strategy of adults in a population is largely determined by whether mortality affects juveniles or adults (Schaffer 1974). There have been few attempts to test these ideas (Roff 1981, 1992) and the importance of environmental uncertainty on intraspecific reproductive effort remains unclear.

Resource availability

How resource availability and acquisition affect fitness is frequently overlooked in life history theory. Resource availability considerations can lead to a number of complications in the analysis of life history trade-offs, since it acts as a constraint on the potential life history response of organisms. van Noordwijk and de Jong (1986) developed a model examining variation in resource acquisition and resource allocation in organisms. If individual variation in resource acquisition occurs, individuals with high acquisition may be able to allocate more resources to all life history traits, resulting in positive correlations between life history traits. Variation in resource
allocation should be studied by minimizing variation in resource acquisition between individuals being compared, since differential performance of individuals may explain the positive correlations between life history traits observed between populations (van Noordwijk and de Jong 1986). The consideration of different resource levels complicates the determination of optimal reproductive allocation. Trade-offs should exist at each resource level, although each resource level may have different optimal trade-offs (Sibly and Calow 1986). In addition, the level of resource availability can constrain potential life history responses of organisms rather than causing adaptive changes in resource allocation (Nylin and Gotthard 1998). Therefore, changes in resource availability may lead to life history plasticity, but those plastic responses are not always adaptive (Nylin and Gotthard 1998).

**Parasite effects**

Although parasites can regulate arthropod host population dynamics (May 1983), relatively little is known about parasitic arthropods’ effects on population dynamics and host fitness (Polak 1996). Parasitized individuals often have reduced growth, reproduction, or survival as compared to unparasitized individuals, presumably in response to the parasites’ use of limited resources. Parasitized organisms often exhibit different life history patterns than unparasitized ones; in addition, life history responses often differ with the type of parasite involved (Minchella 1985, Moller 1993). Thus, parasites potentially have large effects on the reproductive strategies of organisms (Forbes 1993).

Although both reduced (Forbes and Baker 1991) and increased initial
reproductive efforts (Minchella and LoVerde 1981) have been observed in parasitized organisms, the examination of changes in reproductive allocation in response to parasitism has been limited (Forbes 1993, Moller 1993). Parasites are assumed to either increase the cost of reproduction or reduce overall reproduction in their hosts by reducing resource availability for the host (Moller 1993). The cost of parasitism may also be due to a defense or immune response to the parasite instead of a direct resource drain, as Moret and Schmid-Hempel (2000) found reduced survival associated with immune system activation. Changes in reproductive allocation under parasitism can be nonadaptive or adaptive (Forbes 1993, Michalakis and Hochberg 1994, Sorci et al. 1996). Since evidence for adaptive changes in reproductive allocation under parasitism is lacking, it is important to examine if observed patterns of reproduction and survival fit theoretical predictions (Forbes 1993).

Resource availability can also play an important role in the effect parasites have on reproductive allocation and survival. The presence of ad libitum food often acts to obscure life history trade-offs (Roff 1992). For example, Simmons (1987) found that male bushcrickets fed a rich diet were able to overcome the effect of parasitism on reproduction. When resources are limiting, however, allocation of resources to a parasite or defense reduces resources available for other functions. Both Moret and Schmid-Hempel (2000) and Polak (1996) found that reductions in survival and or reproduction with parasitism or simulated parasitism were noticeable only when resources were limiting.

In order to investigate the relationship between parasitism and life history traits,
it is important to determine the amount of resources not taken by the parasite, derive
predictions of life history characteristics and then determine if the patterns fit with the
predictions of life history theory (Sorci et al. 1996). A number of models predict life
history characteristics based on the type of parasite involved or the effect of a parasite
on a host (Hochberg et al. 1992, Michalakis and Hochberg 1994, Sorci et al. 1996,
Forbes 1993, Perrin and Christe 1996). A host that reproduces at an earlier age may
have a selective advantage when parasitized by virulent parasites (Hochberg et al.
1992), while less virulent parasites should lead to evolution of a longer-lived host
(Hochberg et al. 1992).

Forbes (1993) developed a reproductive effort model for parasitized organisms,
which assumes limited resources are available for reproduction. Adaptive increases
and decreases in reproductive effort by parasitized hosts can be explained depending
on the type of parasite involved (Forbes 1993, 1996). Forbes categorized parasites into
three types differing in their effects on resources available for an organism. Type I
parasites, such as ectoparasitic mites, are on the host for a relatively short period of
time before leaving the host. Thus, Type I parasites should reduce current
reproduction but have minimal effects on future reproduction. Type II parasites, such
as castrating trematodes, have small effects on current reproduction but large effects
on future reproduction. Type III parasites, such as multi-season infections by worms,
significantly reduce resources available for both current and future reproduction.

Predictions for current and future reproduction differ for each type of parasite
(Forbes 1993). In cases where the parasite is either short-lived on the host (Type I) or
uses a large amount of the total available resources (Type III), parasites should lead to a reduction in current reproductive effort (Forbes 1993). Type III parasites should lead to reduced future reproduction while future reproduction should not be affected by Type I parasites (Forbes 1993). When the parasite has little effect on current reproduction but a large effect on future reproduction (Type II), organisms should increase initial reproductive effort, as there is little reason to conserve resources (Forbes 1993). Since reproductive allocation of parasitized organisms may not change as expected, this model has implications for evaluating the efficacy of potential parasitic biological control agents (Forbes 1996).

Perrin and Christe (1996) extended the model of Forbes (1993) to consider situations where offspring condition and survival are related, as is often the case in birds (Sorci and Clobert 1995, Forbes 1996). With parental care or maternal effects, which was not considered in Forbes' (1993) model, an increase in initial reproductive effort is possible even when hosts are parasitized by short-lived (Type I) parasites. The differences in predictions between the models of Forbes (1993) and Perrin and Christe (1996) illustrate the importance of understanding both the life history of an organism and the biology of a host-parasite system before applying a given model.

Sorci et al. (1996) developed a graphical model that predicts the relationship between reproduction and survival for infected and uninfected individuals. Their model considers the amount of resource reduction resulting from the parasite and also how resource allocation changes with parasitism. If an organism adaptively changes its allocation patterns when parasitized, there can be a positive correlation between
reproduction and parasite load. If the allocation pattern does not change with parasitism, there should be a positive correlation between survival and reproduction but a negative correlation between parasitism and both survival and reproduction. To date, little empirical evidence exists to examine if parasite-induced changes in reproductive effort fit with these theoretical predictions.

**Effort-Per-Offspring**

An area of theory largely separate from optimal allocation to reproduction is optimal effort-per-offspring. When more than one offspring can be produced, an organism’s total reproductive allocation must be divided up among offspring (Fox and Czesak 2000). Smith and Fretwell (1974) pioneered the mathematical analysis of effort-per-offspring by examining what size offspring a female should produce to maximize parental fitness. When resources are limiting, Smith and Fretwell (1974) assumed increasing effort-per-offspring results in offspring with higher potential fitness. Since resources available for reproductive allocation are limited, increased offspring size results in decreased fecundity. Therefore, a trade-off exists between the size and number of offspring and parental fitness is maximized at an intermediate offspring size (Smith and Fretwell 1974).

A second contribution of their model that has shaped much subsequent theory is the prediction of a single optimal offspring size in constant environments. Their model assumes progeny fitness is affected only by offspring size; however, factors such as parental care and sibling competition can change offspring fitness separate from offspring size (Fox and Czesak 2000). Most models examining variation in
effort-per-offspring developed since Smith and Fretwell (1974) make the same basic assumptions (Fox and Czesak 2000).

In a departure from optimality models, Geritz (1998) developed an Evolutionary Stable Strategy (ESS) model examining the effect of resource availability on effort-per-offspring variation in plants. In contrast to Smith and Fretwell (1974), Geritz (1998) argued that variable-sized offspring should be produced when competition between individuals is high, when juvenile mortality is low and when resource availability is high. However, under low resource availability a single optimal offspring size should result, since resources are too low to permit strong competition (Geritz 1998).

*Abiotic environmental variability*

McGinley et al. (1987) incorporated environmental variation into the optimality model of Smith and Fretwell (1974) and predicted that optimal effort-per-offspring should remain constant under most conditions. However, if the environment varies predictably during the season, variable-sized offspring will maximize the parents' fitness, which is in agreement with bet hedging proposals (McGinley et al. 1987).

*Resource variation*

The effect of variation in resources on development times and optimal effort-per-offspring has been examined by Sibly and Calow (1986). They combined adult and juvenile fitness variables and assumed no age structure or environmental variation and a trade-off between egg number and development time. Larger offspring should
be produced in poorer growth environments, since larger offspring will take less time to develop to maturity than smaller offspring.

**Total Effort and Effort-Per-Offspring**

Despite the number of models considering optimal total reproductive effort and effort-per-offspring individually, few studies have linked these ideas. One of the few that has (Winkler and Wallin 1987) predicts that increasing clutch size should lead to a lower rate of increase in the total reproductive effort, because egg size can only be increased to a point when resources are limiting. Because optimal total effort responds to several variables as well as the variables affecting effort-per-offspring, Winkler and Wallin (1987) predicted more variability should exist in measurements of total reproductive effort than in effort per offspring. Their model does not examine the effects of resource availability on optimal life histories, indicating that this would be a fruitful approach to the study of life histories.

**A Review of Grasshopper Life Histories**

*Introduction*

Many species of grasshoppers have variability in their reproductive characteristics (Joern and Gaines 1990), a crucial characteristic to examine life history theory dealing with plasticity or variation in life cycles. Grasshoppers are small enough to allow manipulations of density, resource availability, predation and abiotic conditions in the field, all of which have been shown to be important in the field (Joern and Gaines 1990, Belovsky and Joern 1995). An understanding of how biotic
and abiotic environmental factors affect life histories is crucial if we are to further our understanding of population fluctuations of grasshoppers (Joern and Gaines 1990).

Field studies of grasshopper life histories have primarily focused on traits at a single site where resource availability is typically not controlled (Sanchez et al. 1988, Sanchez and Onsager 1988), or along an environmental gradient where the importance of environmental variation has not been carefully examined (Dearn 1977, Bellinger and Pienkowski 1985b, Dingle et al. 1990, Dingle and Mousseau 1994). Few studies have examined variation in reproductive allocation within a single field population by manipulating resource availability. Therefore, the importance of resource availability for reproduction and population responses under natural conditions has not been fully examined, despite evidence that resource availability and grasshopper density are important to reproductive output (Belovsky and Slade 1995).

Low levels of resource availability can simply act to constrain the potential life history responses of organisms rather than leading to adaptive changes in resource allocation (Nylin and Gotthard 1998), while high resource availabilities can obscure life history trade-offs (Roff 1992, Moret and Schmid-Hempel 2000). A large amount of research on grasshopper reproduction and survival has been done under laboratory conditions with \textit{ad libitum} food and often ideal abiotic conditions (Pfadt 1949, Pickford 1958, Riegert 1965, Smith 1970, 1972, Dean 1981, Atkinson and Begon 1987, Wall and Begon 1987).

\textit{Grasshopper reproductive allocation}

Grasshoppers have determinate growth and only allocate significant resources to
Grasshoppers can reduce resource allocation to reproduction in at least two ways when resources are limiting, which allow a higher percentage of the available resources to be used for functions other than reproduction. The first way for grasshoppers to reallocate nutrients is by decreasing vitellogenesis. Vitellogenesis, the number of ovarian follicles initiating development, occurs when yolk is deposited into an ovarian follicle and determines the interval between egg pods (Chapman 1982). Vitellogenesis appears largely controlled by adult experience of grasshoppers (Chapman 1982) and increases with resource consumption and resource quality (Pfadt and Smith 1972, Hewitt 1985). A second way for grasshoppers to reallocate nutrients to survival during periods of resource shortage is by increasing oosorption, when the nutrients are resorbed from a developing ovarian follicle (Chapman 1982, Joern and

Analysis of ovariole scars on ovarioles allows a determination of eggs laid and the amount of oosorption of ovarioles (Launois-Luong 1978, Bellinger and Pienkowski 1985b, Joern and Klucas 1993). Ovariole analysis is particularly informative because egg pods of many grasshopper species are difficult to recover in the field and even if they can be found, egg pods cannot be attributed to individual females.

*Environmental variation*

*Comparative studies.* Comparative studies between grasshopper species often detect reproductive patterns consistent with life history models. However, careful experimentation is necessary to determine the causes of these allocation patterns. It is likely that a combination of factors drives these patterns, including resource availability changes over environmental or altitudinal gradients. For example, Dearn (1977) studied three species of grasshoppers in Australia and found that numbers of ovarioles per female and number of eggs per pod increased with increasing altitude. However, Dearn’s results contrast with those of Bellinger and Pienkowski (1985a), who found a decrease in ovariole number with increasing altitude in a variety of grasshopper species in the U.S.

Season length differences mediated through environmental gradients appear important in understanding variation in grasshopper life history traits. Bellinger et al. (1987) found variation in the length of the growing season, as determined by degree-
days, explained 99.8% of the variation in ovariole number between populations of *Melanoplus femurrubrum* (DeGeer). However, year-to-year variation within a population was not addressed by this study.

**Evidence for allocation trade-offs.** Sibly and Monk (1987) analyzed life cycle variation in egg size and clutch size for one grasshopper species along a gradient and predicted the optimal effort-per-offspring to maximize fitness. Using data from Monk (1985), Sibly and Monk (1987) developed an optimality analysis for the trade-off between clutch size and development time as mediated by egg size, which follows the predictions of Sibly and Calow (1986) regarding optimal egg sizes. They assumed that larger eggs develop faster than smaller eggs. Optimal development led to adults who matured at the beginning of the reproductive window in order to maximize egg production. Nymphal mortality and the length of the egg laying period were the two parameters that were critical to the predictions and both had large confidence intervals. Sibly and Monk (1987) concluded that season length was the key constraint for the grasshoppers, although the large confidence intervals of the parameters limited generalizations.

Grant et al. (1993) used a larger data set to modify the model of Sibly and Monk (1987). In contrast to Sibly and Monk (1987), they argued that season length is seldom the critical constraint, but juvenile development time and mortality rates are the most important constraints. They concluded that shortened season length is not of great selective value in temperate univoltine organisms except at extremes, as most adults are dead before the season ends (Grant et al. 1993). Season length may act to
constrain grasshoppers to one generation per year in temperate climates, but juvenile mortality rates and development times likely limit the northern range of a species. Their predictions fit observations of grasshopper development time and reproduction during cold rainy seasons and have important implications in the analysis of season length manipulations with grasshoppers.

*Seasonal changes.* Changing patterns of reproductive allocation within a season have been studied with nymph overwintering grasshoppers. Landa (1992) found that *Chortophaga viridifasciata* hatchling size increased over the course of the growing season, as predicted by optimal offspring effort models when there is size-dependent mortality (Begon and Parker 1986, Sibly and Monk 1987). In egg overwintering grasshoppers, diapause may act as an equilibrating factor on egg size. Therefore, it is possible that egg over-wintering grasshoppers would not exhibit similar changes in egg size, as egg over-wintering mortality may not be as size dependent.

*Resource availability*

*Cost of reproduction.* A trade-off inherent to much life history work is the potential cost that reproduction can have on survival, as an increase in reproduction often leads to a corresponding decrease in survival or longevity (Reznick 1985, Bell 1986, Roff 1992). Laboratory studies investigating the cost of reproduction in grasshoppers have been inconclusive, although this may be due to a failure to control food availability (Pickford and Gillot 1972, Dean 1981, Stearns 1992). Food availability is crucial in the identification of trade-offs, as *ad libitum* food availability may obscure trade-offs (Sibly and Calow 1986, Roff 1992).
de Souza Santos and Begon (1987) studied the cost of reproduction on survival in *Chorthippus brunneus*. Reproductive effort was reduced with low food levels, as predicted. There was also a negative correlation between reproductive effort and survival for individuals at a given food level. Since females at high food levels reproduced more, differences in resource intake obscured the correlation of reproductive effort and survival between food levels. These findings agree with Sibly and Calow (1986), who argued that the slope of the negative correlation between survival and reproduction should vary with resource availability, leading to different optimal allocation strategies in different environments.

*Structural size or adult mass.* Various studies have attempted to correlate ovarirole number with structural size or adult body mass. There is a strong correlation between structural size, measured as femur length and ovarirole number in interspecific comparisons of grasshoppers (Bellinger and Pienkowski 1985b), but intraspecific studies have found only weak correlations (Dearn 1977, Bellinger et al. 1987, Sanchez et al. 1988).

Atkinson and Begon (1987) examined the effect of body size on reproductive allocation and effort-per-offspring through a comparative study of egg size and clutch size. Mature adult mass was used as a measure of the adult environment, since this is largely a function of resource intake after reaching adulthood (Atkinson and Begon 1987). Structural size of the grasshopper (femur length) was used as a measure of resource availability and growth in the nymphal environment. Femur length was not correlated with clutch size, while body mass was correlated with clutch size. Thus, it
appears that the current adult environment is more important than the nymphal environment in determining clutch size in grasshoppers (Atkinson and Begon 1987).

**Adult resource availability.** Early studies of grasshopper reproduction found that survival, development and fecundity varied both with the species of plant used (Pfadt 1949, Smith et al. 1952, Pickford 1958, 1962) and the nitrogen content of vegetation (Smith 1960). Smith (1966) found that grasshoppers fed every other day lived twice as long as grasshoppers given unlimited food every day, but had a large reduction in the rate of egg production. Resource addition in a field experiment increased both grasshopper survival and number of functional ovarioles (Belovsky and Slade 1995).

**Nymphal resource availability.** In determinate growth organisms that acquire and primarily allocate resources to reproduction as adults (Stauffer and Whitman 1997, Papaj 2000), the effects of nymphal resource availability on adult reproduction and survival are often assumed minor. In some cases low nymphal resources apparently lead to a higher percentage of undeveloped ovarioles (MacFarlane and Thorsteinson 1980). Additionally, structural size or body mass and adult reproduction have been highly correlated (Atkinson and Begon 1987, Wall and Begon 1987) and not correlated (Sanchez et al. 1988).

**Density effects**

Densities of grasshoppers in the field can have large effects on observed life history patterns (Joern and Klucas 1993, Belovsky and Slade 1995, Belovsky and Joern 1995). However, most studies examining the effects of intraspecific grasshopper
density on life history variation fail to separate the potential effects of density per se from the effects of changing per-capita resource availability. Although the effects of grasshopper density on survival, behavior, or physical characteristics have been examined in the field (Evans 1992, Ritchie and Tilman 1992, Schmitz 1993, Chase and Belovsky 1994, Applebaum and Heifetz 1999), variation in reproductive allocation in response to grasshopper density has received less attention (Joern and Klucas 1993, Belovsky and Slade 1995). Research by Belovsky and Slade (1995) indicates the primary effects of rangeland grasshopper densities in western Montana are due to exploitative competition for resources. Increasing grasshopper densities results in reduced per-capita resource availabilities above a threshold density when food limitation begins.

There is little evidence of interference competition or antagonistic behavior in grasshoppers in the Palouse prairie (Belovsky and Slade 1995), although some desert grasshoppers exhibit territoriality (Greenfield et al. 1987). However, grasshoppers can exhibit other less obvious plastic life history responses to density that could be important in grasshopper population dynamics (Applebaum and Heifetz 1999). Depending on the grasshopper species examined, the effects of intraspecific density can lead to changes in development rate, behavior and physiology (Smith 1972, Hewitt 1985, Stauffer and Whitman 1997, Applebaum and Heifetz 1999, Simpson et al. 2001). Even nonmigratory grasshoppers can exhibit changes in melanism, behavior and phase shifts in response to intra- and inter-specific densities (Applebaum and Heifetz 1999).
When individual grasshoppers differ in their exploitative competitive ability, individuals with lower fitness acquire fewer resources than individuals with higher competitive abilities (Lomnicki 1980, Belovsky et al. 1996). Individual differences can lead to reduced survival of less competitive individuals (Belovsky et al. 1996) and increased variance around the mean value of reproductive characteristics due to individual differences in reproductive output (Crowl et al. 1997, Richardson and Verheyen 1999).

Although a variety of laboratory experiments with grasshoppers have examined the importance of density on reproduction, they have not yielded consistent results. For example, Pickford (1958) found no effect of adult grasshopper density on reproduction when females were provided with *ad libitum* food. However, Smith (1970) found density-dependent reproduction in *M. sanguinipes*. Since resources were unregulated, he was unable to determine the manner in which increased densities led to changes in reproductive characteristics. Interestingly, increased density of adults led to increased survival and fecundity of the offspring (Smith 1972). Wall and Begon (1987) conducted a controlled laboratory experiment examining the effects of late nymph and adult density on total reproductive effort in *Chorthippus brunneus*. They found significantly lower reproductive output at higher densities. Since all densities were given the same amount of food, it is likely that the results are simply due to resource limitation and exploitative competition. Therefore, although indicative that density affects reproduction and survival, laboratory studies have failed to clearly separate the roles of density dependence and resource availability.
Mite parasitism effects

Very little is known about the macroparasites of grasshoppers such as nematodes and mites (Rees 1973). In many cases, these natural enemies of grasshoppers have not been carefully studied for their impacts on grasshopper populations. Mites, in particular, have complex life cycles and are poorly understood (Huggans and Blickenstaff 1966). *Eutrombidium locustorum*, the mite most commonly found on grasshoppers in the field in Montana, is widely distributed throughout North America (Huggans 1962, Campbell 1964, Huggans and Blickenstaff 1966). In its larval state it is parasitic on grasshoppers and in its nymphal and adult stages it preys on grasshopper eggs (Huggans and Blickenstaff 1966). The larval mites attach around the wing pads of nymphal grasshoppers and on the wings of adult grasshoppers. The mites remain attached for approximately 7-14 days, feeding on hemolymph from the grasshopper (Huggans and Blickenstaff 1966).

Since mites spend a relatively short period of time on the host grasshopper and transmit no known diseases, they presumably have smaller detrimental effects on grasshoppers than many other parasites (Severin 1944). Huggans and Blickenstaff (1966) conducted a laboratory study, which indicated that mites were not important for survival and reproduction of grasshoppers. This result might be expected, however, since the grasshoppers were provided *ad libitum* high-quality food and were maintained at near optimum temperatures and humidities. Therefore, the importance of mites under realistic field conditions and food availability has not been determined.
Conclusion

To examine life history variation in an organism, it is important to understand the relationships between resource level, density, reproductive effort and survival. The effect of resource availability on both reproductive effort and effort-per-offspring has not been fully examined theoretically. In addition, the importance of resource availability has been largely ignored in grasshopper life history experiments. As discussed in the literature review, research on environmental factors that may lead to changes in allocation patterns has not been adequately examined with grasshoppers. The effects that resource availability, grasshopper density and parasitism have on grasshopper life history variation have not been fully examined and have important implications for our understanding of grasshopper population dynamics.

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CHAPTER 2

VARIATION IN REPRODUCTIVE ALLOCATION AND SURVIVAL IN

*MELANOPPLUS SANGUINIPES* IN RESPONSE TO RESOURCE
AVAILABILITY AND GRASSHOPPER STOCKING DENSITY

Abstract

Given the large fluctuations in grasshopper densities that occur periodically in the
western United States, an increased understanding of how both grasshopper survival and
reproduction vary with changes in both grasshopper density and resource availability is
critical. The relative importance of exploitative competition on reproductive allocation
has not been fully examined with grasshoppers. This experiment was designed to examine
if differences in reproductive allocation of *Melanoplus sanguinipes* with resource
availability and grasshopper density treatments are primarily explained by exploitative
competition. In addition, I examined if individual differences in competitive ability
played a large role in observed mean egg production values.

Stocking density and resource treatments did not affect grasshopper survival during
the experiment. However, per capita resource availability explained a significant amount
of the variation in all reproductive characteristics examined, as expected with exploitative
competition for resources. The effects of per capita resource availability were evident at
the end of the experiment, as functional ovariole number increased with per capita
resource availability. *M. sanguinipes* grasshoppers allocated resources to reproduction in
response to per capita resource availability as predicted by a resource allocation model.
Therefore, *M. sanguinpes* grasshoppers appeared to trade off resource allocation to
reproduction for that of allocation to survival, because there was no effect of per capita resource availability on survival.

Residuals for the regressions of egg production and vitellogenesis with per capita resource availability did not differ for resource or density treatments, indicating exploitative competition for resources played the most important role in determining reproductive allocation in *M. sanguinipes*. There was higher variation around the mean of egg production at the highest stocking density and with natural resource availability, indicating individual differences between grasshoppers have important implications for our understanding of life history variation. Therefore, both individual and population level responses are important to fully understand the reproductive responses of grasshoppers to resource availability.

**Introduction**

Life history variation of grasshoppers can occur in response to factors such as grasshopper density (Smith 1972, Joern and Klucas 1993, Belovsky and Joern 1995), resource availability (Belovsky and Slade 1995), and thermal conditions (Willot and Hassall 1998). Resource availability is an important factor to consider when trying to understand life history variation, although the effect of adult per capita resource availability on grasshopper reproductive allocation and survival has received limited attention (Belovsky and Slade 1995). Differences in resource availability can lead to large differences in life history patterns of reproduction and survival (Roff 1992, Monson et al. 2000), although low levels of resource availability can constrain potential life history responses rather than causing adaptive changes in resource allocation (Nylin and Gotthard
Reproductive allocation by grasshoppers varies with resource availability (de Souza Santos and Begon 1987, Belovsky and Slade 1995, Joern and Behmer 1997, 1998) and grasshoppers appear capable of adaptive resource allocation (de Souza Santos and Begon 1987). Few field studies have examined how *Melanoplus sanguinipes* responds to reduced per capita resource availability by changing patterns of oosorption and vitellogenesis.

Most studies examining the effects of intraspecific grasshopper density on life history variation fail to distinguish between interference competition and exploitative competition for resources (Applebaum and Heifetz 1999). Although the effects of intraspecific and interspecific grasshopper density on grasshopper survival have been examined in the field (Belovsky 1986, Evans 1992, Ritchie and Tilman 1992, Schmitz 1993, Chase and Belovsky 1994), variation in reproductive allocation in response to grasshopper density has received less attention (Joern and Klucas 1993, Belovsky and Slade 1995). Density-dependent food limitation and exploitative competition for food have been documented in grasshopper populations in western Montana (Belovsky and Slade 1995).

When the effects of grasshopper densities are primarily due to exploitative competition for resources, increased stocking densities should result in reduced per capita food availability for grasshoppers beyond densities where food limitation occurs (Belovsky and Slade 1995). However, food limitation can occur simply as a result of digestive processing constraints separate from resource availability (Stephens and Krebs 1986). When individual grasshoppers differ in their ability to exploit resources,
individuals with lower competitive abilities acquire fewer resources than more competitive individuals (Lomnicki 1980, Belovsky et al. 1996). Individual differences can lead to increased mortality rates of less competitive individuals (Belovsky et al. 1996) and increased variance around the mean value of reproductive characteristics (Forbes and Depledge 1996, Richardson and Verheye 1999, Callaghan and Holloway 1999).

Grasshoppers can exhibit a variety of other density-dependent life history responses, and these responses can have important implications for grasshopper population dynamics (Applebaum and Heifetz 1999). High intraspecific grasshopper densities can lead to modified behavior and physiology of grasshoppers and locusts (Smith 1972, Hewitt 1985, Stauffer and Whitman 1997, Applebaum and Heifetz 1999, Simpson et al. 2001). Although there is little evidence of interference competition or antagonistic behavior in grasshoppers in the Palouse prairie (Belovsky and Slade 1995), some desert grasshoppers exhibit territoriality (Greenfield et al. 1987).

The experiment was designed to examine the effects of per capita resource availability and the importance of exploitative competition on *M. sanguinipes* survival and reproductive allocation. I also examined the importance of other density or resource based differences resulting from the experimental treatments. A consideration of changing vegetation quality components (Joern and Behmer 1997, 1998), individual differences in competitive ability (Belovsky et al. 1996), or interference competition (Greenfield et al. 1987, Applebaum and Heifetz 1999) might be necessary to explain the variation in reproductive allocation. An understanding of how both grasshopper reproduction and survival respond to changing per capita resource availability is important for...
understanding the population dynamics of grasshoppers (Joern and Behmer 1998).

Materials and Methods

Study site

I conducted the experiments at the National Bison Range in northwestern Montana, USA, at an elevation of 800 m. The study site consisted of a Palouse prairie whose biomass is dominated by grasses (Belovsky and Slade 1995). Grass biomass averaged 96% of total vegetative biomass remaining in cages at the end of the experiment. The dominant grass species were *Poa pratensis*, *Elymus spicatum*, and *Elymus smithii*; and the dominant forbs were *Achillea macrofolia*, *Aster falcatus*, and *Erigeron* sp. The most common grasshoppers at the site were *Melanoplus sanguinipes* (Fabricius), *Melanoplus femurrubrum* (DeGeer), and *Ageneotettix deorum* (Scudder). Grasshopper densities in the area of the site range from less than 2 to 70, 4th and 5th instar grasshoppers per m² (G. E. Belovsky, pers. comm.). In 1993, when the experiment was conducted, adult grasshopper densities averaged 18 per m². The summer of 1993 had above average rainfall of 13.5 cm in July and August, compared to the long-term mean of 5.8 cm. In addition, average maximum temperature during July 1993 was 21.2 °C, 8 °C cooler than the long-term average.

*Melanoplus sanguinipes* (Fabricius) (Subfamily Melanoplinae), the grasshopper used in this experiment, is the most common species of rangeland grasshopper in much of the Western United States (Pfadt 1994). *M. sanguinipes* is polyphagous and exhibits reproductive plasticity (Dean 1982, Dingle et al. 1990). In Montana, *M. sanguinipes* is a univoltine, egg overwintering grasshopper, and lays egg pods averaging 18-24 eggs (Pfadt
Experimental procedures

I studied grasshopper responses to density and resource availability using 0.36-m$^2$ cages placed over similar patches of natural vegetation. The square cages were constructed of aluminum screening fastened to aluminum garden edging at the base, which was buried in the ground. The cages were attached to support stakes and closed with binder clips at the top. Similar cages have been used in a variety of studies with grasshoppers (Belovsky 1986, Belovsky and Slade 1993, 1995, Joern and Klucas 1993, Schmitz 1993). Cage effects on microclimate are minimal (Belovsky and Slade 1993), although cages affect some plant characteristics (Joern and Klucas 1993).

The increased resource treatment received 1000 ml of water with 0.04% N by volume every other day, to increase resource availability for grasshoppers (Table 2.1). Natural treatment cages were not modified (Table 2.1). I initiated resource treatments one week prior to stocking. I collected grasshoppers at the site and held them in terrariums for 24 hours to minimize post-stocking mortality from grasshoppers injured during collection. I stocked cages in early July with five densities of 4th instar grasshoppers (6, 10, 16, 22, 32 per cage) at an even sex ratio (Table 2.1). I also established vegetation control cages without grasshoppers for each resource treatment. Treatments were randomly assigned to cages. Four cage counts were conducted over the eight weeks of the experiment to assess grasshopper survival.
Table 2.1. Grasshopper stocking density (Density) and resource treatments (Resource) used in the experiment.

<table>
<thead>
<tr>
<th>Treatment name</th>
<th>Resource</th>
<th>Density</th>
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<tr>
<td>N-C</td>
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<tr>
<td>N-6</td>
<td>Natural</td>
<td>6</td>
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<tr>
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<td>32</td>
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<tr>
<td>I-C</td>
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<tr>
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<td>6</td>
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</tr>
<tr>
<td>I-32</td>
<td>Increased</td>
<td>32</td>
</tr>
</tbody>
</table>

Reproduction

At the end of the experiment (late September), all surviving adults were frozen. Female reproductive characteristics were measured through ovary analysis, because *M. sanguinipes* egg pods are difficult to recover in the field (Launois-Luong 1978, Bellinger and Pienkowski 1985, Joern and Klucas 1993). Grasshopper ovaries consist of a series of ovarian follicles, which are typically not all functional (Uvarov 1977, Bellinger et al. 1987, Joern and Gaines 1990). When an egg is released into the oviduct, the egg covering compresses into a narrow band called the follicular remnant, which is visible under a dissecting microscope.

When grasshoppers are resource limited, they can reduce resource allocation to reproduction in at least two ways, by reducing vitellogenesis or increasing oosorption (Chapman 1982). Reduced reproductive allocation when resources are in short supply allows a higher percentage of available resources to be used for continued survival.
Vitellogenesis occurs when yolk is deposited into an ovarian follicle, initiating development of the follicle. Vitellogenesis appears to be controlled by adult experience and can increase with the quantity and quality of vegetation consumed (Pfadt and Smith 1972, Chapman 1982, Hewitt 1985). Reproductive allocation to a given ovarian follicle may not be continuously flexible, but may become fixed after a given developmental stage of vitellogenesis (Moerhlin and Juliano 1998). Grasshoppers can also reallocate nutrients by resorbing developing ovarian follicles, called oosorption (Chapman 1982, Joern and Gaines 1990, Joern and Klucas 1993, Papaj 2000). Oosorption results in a brightly colored resorption body, which is visible under a dissecting microscope. The percentage of oosorption is negatively related to resource intake and quality (McCaffery 1975, Chapman 1982). In addition, I calculated the ratio of oogenesis to vitellogenesis (eggs laid/vitellogenesis). Ovary analysis allows a determination of reproductive allocation and can attribute egg production to individual females.

Vegetation

At the end of the experiment, I clipped green vegetation in each treatment and control cage and separated it between grass and forb, to examine treatment effects on vegetation. I dried, weighed, and ground vegetation samples following the methods of Belovsky and Slade (1995). I assessed plant nutritional quality by acid-pepsin digestion of grasses and forbs (Terry and Tilley 1964). Acid-pepsin digestion is correlated with in vivo digestibility of vegetation by grasshoppers and serves as a measure of plant nutritional quality (Bailey and Mukerji 1976, Belovsky and Slade 1995). I calculated total digestible biomass by combining the products of grass biomass and its percent digestibility with
forb biomass and its percent digestibility (Belovsky and Slade 1995). Per capita resource availability was calculated by dividing the total digestible biomass in a cage by the initial stocking density.

Analysis

I used ANOVA models to examine density and resource treatment effects on egg production and average number of grasshoppers surviving the experiment. If exploitative competition for food is playing an important role, per capita resource availability should explain a significant amount of the variation in survival and reproductive characteristics. With high per capita resource availability, both vitellogenesis and the ratio of eggs laid to vitellogenesis should increase, because resources can be allocated to all necessary functions (Branson Chapter 4). At very low levels of per capita resource availability, vitellogenesis, survival, and the ratio of oogenesis to vitellogenesis should be lower, as few resources can be selectively allocated (Branson Chapter 4, Chapman 1982). The relationship between per capita resource availability measurements and reproductive characteristics was assessed by linear regression (Zar 1999). Resulting residuals were analyzed as dependent variables in ANOVA models with resource and density treatments (Draper 1981).

If density-dependent factors other than exploitative competition are contributing to the results, the regression residuals should differ between density treatments. Differences in residuals would indicate that exploitative competition for resources is only partly responsible and that interference competition is contributing to the results. If the resource treatment changed resource availability in ways not detected by acid-pepsin digestibility
(Belovsky and Slade 1995), the residuals from the regressions on reproductive characteristics should differ between resource treatments. If the residuals differ, factors such as carbohydrate, mineral, secondary compound, structural, and fatty acid composition of plants may be changing in ways not detected by the acid-pepsin digestibility quality assessment, and in ways that are important for grasshopper reproductive allocation (Chapman 1990, Simpson and Raubenheimer 1993, Muralirangan et al. 1997, Joern and Behmer 1998).

If individual variation plays an important role in exploitative competition in *M. sanguinipes*, competitively superior individuals should have higher reproduction than expected from treatment means. These differences would not be evident from comparisons of the treatment means, but only by investigating the variance around the mean (Crowl et al. 1997). The coefficient of variation (CV) is a scale free measure of variability that scales the variance by the value of the sample mean (McCadle et al. 1990, Crowl et al. 1997). However, the use of small sample sizes can result in a bias toward larger CV values (McCadle et al. 1990). The CV was used to compare the variability in egg production between experimental treatments (Crowl et al. 1997, Richardson and Verheyen 1999), and should increase with stocking density if individual differences are significant. ANOVA tests with the CVs as the dependent variable were used to compare density and resource treatments (Sokal and Braumann 1980, Crowl et al. 1997). Pairwise post-hoc comparisons were made with Tukey's HSD (p level protected). SYSTAT 10 (SPSS Inc., ©2000) was used for all statistical analyses.
Results

Resource availability

Fig. 2.1 illustrates the total digestible vegetation in cages at the end of the experiment. The resource and density treatments appeared to change available resources in cages, although there was a significant interaction (Table 2.2 Part A). The interaction results from a larger biomass reduction at higher stocking densities in the increased resource treatment (Fig. 2.1). Vegetation biomass in 1993 was at the upper end of the range of vegetation biomass documented in the site area (Belovsky and Slade 1995).

![Fig. 2.1. Total digestible vegetation biomass (g dry/m²) for each treatment at the end of the experiment. Vegetation control cages are designated with a stocking density of zero. Values are mean ± SE.](image-url)
Table 2.2. (A) Statistical results for digestible vegetation, average survival, follicular remnants (eggs laid) and CV of follicular relics for females alive at the end of the experiment based on per capita cage averages. (B) Selected pairwise comparison probability (p) values for follicular relics and CV of follicular relics. All p values are based on Tukey’s HSD.

<table>
<thead>
<tr>
<th>A</th>
<th>ANOVA tables for:</th>
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<th>Mean square</th>
<th>F</th>
<th>P</th>
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<tr>
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<td>Interaction</td>
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<td>0.999</td>
<td>0.433</td>
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</table>

<table>
<thead>
<tr>
<th>B</th>
<th>Selected pairwise contrasts</th>
<th>CV of follicular remnants</th>
</tr>
</thead>
<tbody>
<tr>
<td>N-6 vs. N-32</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>N-6 vs. N-24</td>
<td>&gt;0.9</td>
<td></td>
</tr>
<tr>
<td>N-10 vs. N-32</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>I-6 vs. I-32</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>I-6 vs. I-24</td>
<td>&gt;0.9</td>
<td></td>
</tr>
<tr>
<td>I-6 vs. I-16</td>
<td>&gt;0.9</td>
<td></td>
</tr>
<tr>
<td>I-10 vs. I-32</td>
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<td></td>
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<tr>
<td>I-10 vs. I-24</td>
<td>0.75</td>
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</tr>
</tbody>
</table>

**Grasshopper survival**

Changes in the number of individual *M. sanguinipes* surviving in each treatment are indicated in Fig. 2.2. The nearly linear relationship between initial stocking densities and average cage densities indicates a lack of strong density dependence (Fig. 2.2). Final
Fig. 2.2. Average number of grasshoppers alive during the experiment in each treatment over the experiment in relation to stocking density. Values are mean ± SE.

densities did not converge to similar levels in the highest density treatments by the end of the experiment as found in previous studies (Joern and Klucas 1993, Belovsky and Slade 1995). The significant relationship between stocking density and number surviving indicates the initial stocking differences remained to the end of the experiment (Table 2.2 Part A). The number of grasshoppers surviving was not affected by the resource treatments (Table 2.2 Part A).

Reproductive allocation

Variation in per capita digestible biomass explained over 60% of the variation in
egg production, with per capita digestible biomass and egg production positively correlated (Fig. 2.3A). Vitellogenesis was positively related to per capita resource availability, with per capita digestible biomass explaining 47% of the variation in vitellogenesis (Fig. 2.4A). The percentage of initiated follicles that completed egg development increased with per capita digestible biomass (Fig. 2.4B). Functional ovariole number was positively associated with per capita digestible biomass (Fig. 2.3B), indicating grasshoppers with higher per capita resource availability would have laid larger egg pods if the experiment had not been terminated. Because both vitellogenesis and the ratio of eggs laid relative to vitellogenesis increased with per capita digestible biomass, the reduced egg production with lower per capita resource availability results from both a lower rate of ovariole initiation and a lower percent of initiated ovarioles completing development (Figs. 2.4A, B). Increased grasshopper stocking density and reduced resource availability negatively affected the number of eggs laid, as measured by numbers of follicular relicts (Fig. 2.5A, Table 2.2 Part A).

The residuals from the regressions of egg production and vitellogenesis did not differ between resource or density treatments (Table 2.3). Because the residuals did not differ, the principal difference between the effects of stocking density and resource availability on reproductive allocation was the variation in per capita resource availability resulting from the experimental treatments (Table 2.3).

*Individual differences*

The CV of the number of eggs laid (follicular relicts) was significantly higher in females in the natural resource treatment (Fig. 2.5B, Table 2.2 Part A) and was
Fig. 2.3. Eggs laid versus digestible vegetation biomass (g dry/m²) in cages at termination of the experiment. Line and equation are from regression analysis.
Fig. 2.4. (A) Vitellogenesis versus digestible vegetation biomass (g dry/m²) in cages at the end of the experiment. Line and equation are from regression analysis. (B) Percent of initiated follicles completing egg development versus digestible vegetation biomass (g dry/m²) in cages at the end of the experiment. Line and equation are from regression analysis.
Fig. 2.5. (A) Average number of eggs laid (follicular relicts) by individuals in relation to stocking density and resource treatments. (B) Coefficient of variation for numbers of eggs laid in relation to stocking density and resource treatments. Values are mean ± SE.
negatively affected by stocking density (Fig. 2.5B, Table 2.2 Part A). Among females in the natural resource treatment, the CV of follicular remnants in the highest density treatment was significantly higher than in the lowest density treatment (Fig. 2.5B, Table 2.2 Part B). Therefore, higher variation around the mean for egg production existed both at higher densities and with natural resource availability (Table 2.2 Part A).

**Discussion**

**Survival**

With strong density dependence in the form of non-egalitarian scramble competition, final densities would be expected to converge to similar levels in the higher density treatments as found by Joern and Klucas (1993) and Belovsky and Slade (1995). However, grasshopper numbers in higher stocking density cages did not converge (Table 2.3. Statistical results for ANOVA models comparing regression residuals with density and resource treatments.

<table>
<thead>
<tr>
<th>Source</th>
<th>ANOVA tables for:</th>
<th>DF</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
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<td>Follicular Remnants residuals</td>
<td>Resource</td>
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<td>24.202</td>
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<td>0.528</td>
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<td>0.440</td>
<td>0.513</td>
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<tr>
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<td>Density</td>
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<td>89.699</td>
<td>1.716</td>
<td>0.181</td>
</tr>
<tr>
<td>Vitellogenesis regression residuals</td>
<td>Density</td>
<td>4</td>
<td>110.182</td>
<td>1.345</td>
<td>0.284</td>
</tr>
</tbody>
</table>
2.2 Part A, Fig. 2.2). The highest grasshopper stocking densities used in this experiment, approaching 90 grasshoppers per m$^2$, did not create strong density dependent survival (Fig. 2.2). In addition, survival was not affected by the resource treatment (Table 2.2 Part A). Therefore, there was no indication of food-limited survival in either density or resource treatments (Fig. 2.2, Table 2.2 Part A). In agreement with the experimental results, resource allocation models (Branson Chapter 4) predict an organism should devote a higher proportion of available resources to survival when resources are in short supply as long as an organism has a chance at future reproduction. Additionally, small survival differences are predicted over a range of resource availabilities when food is not highly limiting (Branson Chapter 4).

The combination of abundant food in the environment and lowered metabolic demands due to cool temperatures likely contributed to the higher survival rates in this study. Grasshoppers can actively thermoregulate and increase their body temperatures to develop and process food (Willott 1997). However, the cool abiotic conditions during the study, and shade from the abundant vegetation, likely reduced grasshopper metabolic requirements (Willott and Hassall 1998). Even though there was no relationship between resource availability and survival, resources could still be limiting for grasshoppers. Grasshoppers could be selectively allocating resources to survival instead of reproduction, which would minimize survival differences between treatments (Branson Chapter 4).

Reproductive allocation

As predicted if exploitative competition for food is playing an important role, per capita resource availability explained a significant amount of the variation in egg
production (Fig. 2.3A, Branson Chapter 4). Vitellogenesis also increased with per capita resource availability, indicating females with lower per capita resource availability initiated fewer ovarioles (Fig. 2.4A) (Branson Chapter 4). Females responded to reduced per capita resource availability by still reproducing, but producing fewer eggs, and completing development in a lower proportion of ovarioles that initiated development (Figs. 2.3A, 2.4B). The results support predictions that grasshoppers should decrease either vitellogenesis or the proportion of oocytes initiated that complete development with low resource availability (Branson Chapter 4, Chapman 1982). The increasing ratio of eggs laid relative to vitellogenesis with per capita resource availability (Fig. 2.4B) fits predictions that organisms should increase allocation to survival when resource availability is low (Branson Chapter 4, Roff 1992), and has also been found in locusts (McCaffery 1975). Even if the amount of energy recovered by resorbing oocytes is small, future resource demands for reproductive allocation would be significantly reduced.

Functional ovariole number was positively associated with per capita resource availability, indicating the effects of per capita resource availability were evident at the end of the experiment (Fig. 2.3B). Females with higher per capita resource availability would have produced larger egg pods had the experiment not been terminated. Therefore, per capita resource availability explained a significant amount of the variation in all reproductive characteristics examined, as expected with exploitative competition for resources.

*Resource limitation*

Significant amounts of digestible biomass remained in cages at the end of the
experiment (Fig. 2.1). Grasshoppers often appear to have abundant food in their environment; however, much of this vegetation has very low nitrogen levels that limit grasshopper survival or reproduction (Smith and Northcott 1951, Smith 1960, Joern and Behmer 1998). When biomass is abundant, grasshoppers may selectively forage on the highest quality portions of the available biomass (Chapman 1990, Bernays and Chapman 1994), resulting in small biomass reductions. Under cool abiotic conditions grasshoppers may be constrained by their ability to process food (Stephens and Krebs 1986), however, resource acquisition rates would differ if vegetation quality varies. Therefore, grasshoppers can be resource limited even though vegetation is abundant.

In a study at the same site, Belovsky and Slade (1995) found the effectiveness of increased resources declined in years with greater precipitation and also found the strength of food limitation varied by year. Although they found stronger density-dependent effects on grasshopper survival than in this study, Belovsky and Slade (1995) conducted their experiment during years with lower vegetative biomass and warmer abiotic conditions than 1993, which could increase food limitation. The results of this experiment agree with Belovsky and Slade (1995), as resource availability played an important role in reproductive allocation. Ritchie and Tilman (1992) also found that stocking grasshoppers at high densities did not always lead to competition, but found competition occurred more commonly on low biomass unfertilized plots.

Since resource availability affects reproductive allocation while not affecting survival, is food truly limiting for grasshoppers? Grasshoppers were food limited, because reproduction of grasshoppers increased with increasing resource availability. Therefore,
M. sanguinipes females allocated resources to reproduction in response to per capita resource availability, even in a year with high natural resource availability and cool temperatures. The level of food limitation was not extreme enough to create large survival differences, however, with stronger food limitation both survival and reproduction would likely decrease (Branson Chapter 4). An organism should devote a higher proportion of resources to survival when resources are limiting as long as it has a chance at future reproduction (Branson Chapter 4, Roff 1992, Forbes 1993), trading off reproduction for continued survival. Because grasshoppers increased reproductive allocation with per capita resource availability, while survival was not affected, M. sanguinipes grasshoppers appeared to trade off resource allocation to reproduction for that of allocation to survival. Therefore, M. sanguinipes grasshoppers allocated resources to reproduction in response to per capita resource availability as predicted by a resource allocation model (Branson Chapter 4).

Residual analysis of reproductive allocation

If other density-dependent factors such as interference competition are important in determining grasshopper reproductive allocation, the regression residuals should differ between stocking density treatments. The regression residuals for egg production and vitellogenesis did not differ by density treatment (Table 2.3), indicating interference competition did not have a large effect on reproductive allocation (Applebaum and Heifetz 1999). Therefore, exploitative competition for resources apparently played the most important role in determining the reproductive allocation of M. sanguinipes. The regression residuals for egg production and vitellogenesis did not differ by resource
treatment, despite the cool wet period of the study and the addition of both water and nitrogen to cages. The lack of a difference between resource treatments indicates acid-pepsin digestibility accurately assessed the quality of resources available for grasshoppers (Table 2.3).

**Individual differences**

Although exploitative competition appears most important in determining the average values of egg production within a cage, individual differences in exploitative competitive ability could also be playing an important role (Lomnicki 1980). Because the CV was higher in the natural resource treatment, higher variation existed in egg production with lower resource availability (Table 2.2 Part A). It appears individual differences in the exploitative competitive ability of grasshoppers led to increased variance in reproductive characteristics (Forbes and Depledge 1996, Callaghan and Holloway 1999, Richardson and Verheye 1999), because at the highest stocking density more competitive individuals had higher reproduction than expected from treatment means (Table 2.2 Part B). Although the treatment means for egg production declined with density, much of the decrease in mean egg production with density is likely due to a few individuals being stronger exploitative competitors (Table 2.2 Part A, Fig 2.3A). Small sample sizes can create a bias for larger CV’s (McCardle et al. 1990); however, the results for the density treatment are in the opposite direction of this potential bias.

**Conclusion**

The highest stocking densities of 90 grasshoppers per m² did not lead to density-
dependent survival, as the cool, wet conditions during the study increased vegetative biomass and reduced metabolic requirements. The changes in mean reproductive allocation with per capita resource availability were consistent with exploitative competition for resources (Belovsky and Slade 1995, Branson Chapter 4). Grasshoppers were food limited, because reproduction increased with resource availability. Therefore, *M. sanguinipes* grasshoppers allocated resources to reproduction in response to per capita resource availability, even in a year with high natural resource availability and cool temperatures. Grasshoppers should devote a higher proportion of resources to survival when resources are limiting, as long as they have a chance of future reproduction. Because grasshoppers had increased reproductive allocation with per capita resource availability, while survival was not affected, *M. sanguinipes* grasshoppers appeared to trade off resource allocation to reproduction for that of allocation to survival. Therefore, *M. sanguinipes* grasshoppers allocated resources to reproduction in response to per capita resource availability as predicted.

Individual differences in exploitative competitive ability appear to be important in determining egg production of individual grasshoppers, because the coefficient of variation increased both with lower resource availability and at the highest stocking density. Both individual and population level responses appear important for a full understanding of reproductive allocation responses to resource availability. Individual variation in reproduction allocation has important implications for our understanding of life history variation (Roff 1992), while mean responses of reproductive allocation are important for predictions of population dynamics (Joern and Gaines 1990).
References


CHAPTER 3
EFFECTS OF A PARASITIC MITE ON LIFE HISTORY VARIATION IN TWO GRASSHOPPER SPECIES

Abstract

Careful examinations of changes in life history characteristics in response to parasitism are lacking, despite the fact that parasites often influence resource availability for the host. A number of life history models incorporating parasitism have been developed and predict life history characteristics based on the nature of the host-parasite interaction. I investigated the effects of a grasshopper mite ectoparasite, *Eutrombidium locustorum*, on reproductive allocation and survival in two grasshopper species, *Melanoplus sanguinipes* and *Ageneotettix deorum*. Mites had small effects on grasshopper survival, but both mite parasitism and grasshopper stocking density affected reproductive characteristics. As predicted, both species had reduced initial and total reproduction, and completed development of a lower percentage of ovarioles initiated when parasitized. However, in contrast to predictions for short-lived parasites, future reproduction of parasitized *M. sanguinipes* was lower at the end of the experiment. Since there were no interactions between grasshopper density and parasitism, mites did not have stronger effects at high densities. Although the effects of mite parasitism could be due to either a direct resource drain or an immune response, mite parasitism clearly had large effects on grasshopper population dynamics in the field.
**Introduction**

Although it is known that parasites can regulate arthropod host population dynamics (May 1983), relatively little is known about parasitic arthropods’ effects on population dynamics and host fitness (Polak 1996). Parasitized individuals can exhibit changes in growth, reproduction or survival compared to unparasitized individuals, presumably in response to the parasites’ use of limited resources. In addition, life history responses of organisms can differ with the type of parasite involved (Minchella 1985, Thornhill et al. 1986, Forbes 1991, Lafferty 1993, Moller 1993). Thus, parasites potentially have large effects on the reproductive strategies of organisms (Jokela et al. 1999a, Forbes 1993).

Although both reduced (Forbes and Baker 1991) and increased (Minchella and LoVerde 1981) initial reproductive effort have been observed in parasitized organisms, the examination of changes in reproductive allocation in response to parasitism has been limited (Forbes 1993, Moller 1993). Parasites are assumed to either increase the cost of reproduction or reduce overall reproduction in their hosts by reducing resource availability for the host (Moller 1993). The cost of parasitism may also be due to a defense or immune response to the parasite instead of a direct resource drain, as Moret and Schmid-Hempel (2000) found reduced survival associated with immune system activation. Changes in reproductive allocation under parasitism could be nonadaptive or adaptive (Forbes 1993, Michalakis and Hochberg 1994, Sorci et al. 1996). Evidence for adaptive changes in reproductive allocation under parasitism is lacking, and it is important to examine if observed patterns of reproduction and survival fit theoretical predictions (Forbes 1993).
Resource availability can also play an important role in the effect parasites have on reproductive allocation and survival (Jokela et al. 1999b), as \textit{ad libitum} food often acts to obscure life history trade-offs (Roff 1992). For example, Simmons (1987) found that male bushcrickets fed a rich diet were able to overcome the effect of parasites on reproduction. When resources are limiting, however, allocation of resources to a parasite or defense reduces resources available for other functions such as reproduction. Both Moret and Schmid-Hempel (2000) and Polak (1996) found that reductions in survival and or reproduction with parasitism or simulated parasitism were noticeable only when resources were limiting.

When resources are limiting, a parasitized organism will be unable to fully compensate for the effects of the parasite by increasing resource intake. If an organism can increase consumption to partially compensate for resource demands of parasitism, allocation to reproduction will decrease and any increases in mortality will depend on the strength of resource limitation (Jokela et al. 1999b, Moret and Schmid-Hempel 2000). Nonlethal parasites should have a larger negative impact on a host’s survival and reproduction in years when reproduction is already reduced because of low resource input, unless the parasite is negatively affected by the same conditions.

A number of models predict life history characteristics based on the type of parasite involved or the effect of the parasite on the host (Hochberg et al. 1992, Forbes 1993, Michalakis and Hochberg 1994, Sorci et al. 1996, Perrin and Christe 1996). Forbes (1993) developed an optimal reproductive effort model for parasitized organisms, which assumes limited resources are available for reproduction. Adaptive increases and decreases in
reproductive effort by parasitized hosts can be explained depending on the type of parasite involved (Forbes 1993, 1996). Forbes categorized parasites into three types, differing in their effects on resources available for current reproduction and/or future reproduction. Type I parasites, such as ectoparasitic mites, are short-lived on the host, negatively affecting current reproduction of a host with minimal effects on future reproduction. Type II parasites, such as slow developing digenetic trematode parasites, have small effects on current reproduction but potentially large effects on future reproduction. Type III parasites, such as worm infections lasting multiple seasons, significantly reduce resources available for both current and future reproduction.

Predictions of optimal reproductive effort for current and future reproduction differ for each type of parasite, assuming convex trade-off curves (Forbes 1993). In cases where the parasite is short-lived on the host (Type I), a host should reduce initial reproductive effort compared to unparasitized hosts (Forbes 1993). When the parasite has little effect on current reproduction but a large effect on future reproduction (Type II), a parasitized organism should increase initial reproductive effort relative to unparasitized hosts (Forbes 1993). When the parasite uses a large amount of the total available resources (Type III), a parasitized host should reduce both current and future reproductive effort compared to unparasitized hosts (Forbes 1993). On average, hosts with Type III parasites should have smaller reductions in initial reproductive effort than hosts with Type I parasites. Since reproductive allocation of parasitized organisms may not change as expected, this model has implications for evaluating the efficacy of potential parasitic biological control agents (Forbes 1996).
Perrin and Christe (1996) extended the model of Forbes (1993) to consider situations where offspring condition and survival are related both in parasitized and unparasitized hosts, as is often the case in birds (Sorci and Clobert 1995, Forbes 1996). With parental care or maternal effects, which was not considered in Forbes' (1993) model, an increase in initial reproductive effort is possible even when hosts are parasitized by short-lived (Type I) parasites. The differences in predictions between the models of Forbes (1993) and Perrin and Christe (1996) illustrate the importance of understanding both the life history of an organism and the biology of a host-parasite system before applying a model.

*Study organisms*

Very little is known about macroparasites of grasshoppers, such as nematodes and mites, and their impacts on grasshopper populations (Rees 1973). Parasitic mites of grasshoppers have complex life cycles that are poorly understood (Huggans and Blickenstaff 1966), and could provide an unexploited source of native biocontrol agents that might be fostered to help control grasshoppers (Belovsky et al. 1996).

Eutrombidium locustorum, the mite used in this experiment, is widely distributed through the western United States (Huggans and Blickenstaff 1966, Rees 1973). In its larval state it is parasitic on grasshoppers, and in its nymphal and adult stages it preys on grasshopper eggs (Severin 1944). The larval mites attach by piercing the body integument around the wing pads of nymphal grasshoppers and on the wings of adult grasshoppers. The mites remain attached for approximately 7-14 days feeding on hemolymph from the grasshopper (Huggans and Blickenstaff 1966, Rees 1973).
Since larval ectoparasitic mites spend a short period of time on the host grasshopper, mites have been assumed to have only small detrimental effects on grasshoppers (Severin 1944, Huggans 1962, Campbell 1964, Huggans and Blickenstaff 1966). These mites transmit no known diseases, although the frequency and importance of multiple parasitism events throughout a season have not been examined. A laboratory study by Huggans and Blickenstaff (1966) found mites were not important for grasshopper survival and reproduction. However, the grasshoppers were provided high quality *ad libitum* food and maintained near optimum temperatures and humidities during the experiment. Therefore, the importance of mites on grasshopper life history variation under field conditions, and with limited resources, has not been determined.

In this study, two grasshopper species in different subfamilies with different life history characteristics were used to examine the importance of mite parasitism. *Melanoplus sanguinipes* (Fabricius) (subfamily Melanopinae) is the most common species of rangeland grasshopper in much of the western United States (Pfadt 1994). *M. sanguinipes* is polyphagous, eating both grasses and forbs, and is reproductively plastic (Dean 1982, Scott and Dingle 1990). In Montana, *M. sanguinipes* is a univoltine, egg overwintering grasshopper. *M. sanguinipes* lays egg pods averaging 18-24 eggs, although pods can range from one to 36 eggs. The second grasshopper studied, *Ageneotettix deorum* (Scudder) (subfamily Gomphocerinae), is also a univoltine egg overwintering grasshopper. *A. deorum* male dry mass averages 73% less than *M. sanguinipes* males, while *A. deorum* female dry mass averages 40% less than *M. sanguinipes*. *A. deorum* is widely distributed, often a common species in grasshopper outbreaks, feeds primarily on
grasses, and lays egg pods of two to seven eggs (Pfadt 1994). In addition, *A. deorum* can produce over 10 egg pods under field conditions while many other species, including *M. sanguinipes*, often produce less than three egg pods in the field (Pfadt 1994).

**Objectives and predictions**

The primary objective was to determine the effects of mite parasitism on reproductive allocation and survival of *M. sanguinipes* and *A. deorum* and to examine how reproductive allocation and survival fit with *a priori* predictions. Few studies have tested whether parasitized individuals change their reproductive allocation in ways predicted by life history theory (Forbes 1996). Mite parasites on grasshoppers appear to meet the characteristics of a Type I parasite described by Forbes (1993) since they are short lived on the host. Since parental care is not important in grasshoppers and maternal effects cannot be distinguished in a single generation study, the model predictions of Perrin and Christe (1996) were not examined. Predictions from general life history theory were also examined. An additional objective with *M. sanguinipes* was to examine whether effects of parasitism and grasshopper density on survival and reproduction interacted or were additive, since per capita resource availability should decrease with increased stocking density (Belovsky and Slade 1993, 1995).

I generated a number of specific predictions for grasshopper survival and reproductive allocation characteristics (Table 3.1). First, I predicted total reproduction should be reduced for parasites that are short-lived on the host, such as mites on grasshoppers (Type I) (Forbes 1993). Second, mite parasites should reduce the amount of resources available for a grasshopper while parasitizing a grasshopper, thus reducing
Table 3.1: *A priori* experimental predictions of life history characteristics with specific predicted experimental reproductive allocation and survival responses of grasshoppers.

<table>
<thead>
<tr>
<th>Prediction with mite parasitism</th>
<th>Specific predicted experimental observation</th>
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</thead>
<tbody>
<tr>
<td>1. Reduced total reproduction with parasitism</td>
<td>Reduction in number of follicular relicts (eggs) in parasitized females</td>
</tr>
<tr>
<td>2. Reduced initial reproduction with mite parasitism</td>
<td>No differences in vitellogenesis</td>
</tr>
<tr>
<td>3. Little effect of parasitism on future reproduction</td>
<td>Decreased ratio of eggs/vitellogenesis with parasitism</td>
</tr>
<tr>
<td>4. Smaller effect of mite parasitism on survival</td>
<td>No differences in functional ovariole number in parasitized females</td>
</tr>
<tr>
<td>5. Interactive effects of mite parasitism with exploitative competition</td>
<td>Interaction between density and parasitism on reproduction, or both reproduction and survival, when resources are only limiting in the high-density treatment.</td>
</tr>
</tbody>
</table>

initial reproductive allocation (Forbes 1993). Third, since mites only stay on the grasshoppers for 7-14 days, they should not have large effects on future reproduction of grasshoppers (Forbes 1993). If mites repeatedly parasitized grasshoppers over a season the effect of mites could resemble a Type III parasite and affect future reproduction; however, repeated parasitism was not detected during the experiment. Fourth, general life history models (Roff 1992) predict an organism should devote a higher proportion of resources to survival when resources are in short supply as long as an organism has a chance at future reproduction and proportionally less to reproduction. Fifth, assuming resources are not limiting at low densities and exploitative resource competition exists (Belovsky and Slade 1993, 1995), there should be an increased impact of mite parasitism at high density due to increased resource limitation (Moret and Schmid-Hempel 2000).
With either unlimited resource availability in all treatments or resource limitation in all treatments, no interaction would be expected (Moret and Schmid-Hempel 2000). I examined these predictions by manipulating parasitism and grasshopper density in field experiments.

**Materials and Methods**

*Experimental procedures*

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 was dominated by C3 grasses (Belovsky and Slade 1993, 1995). The dominant grass species were *Poa pratensis*, *Elymus spicatum*, and *Elymus smithii*; and the dominant forbs are *Achillea macrofolia*, *Aster falcatus* and *Erigeron* sp. The most common grasshoppers at the site were *Melanoplus sanguinipes* (Fabricius), *Melanoplus femurrubrum* (DeGeer), and *Ageneotettix deorum* (Scudder).

I placed 0.1-m² cages over similar patches of natural vegetation. The square cages were constructed of aluminum screening fastened to aluminum garden edging at the base, which is buried in the ground. The cages were attached to support stakes and closed with binder clips. Similar cages have been used in a variety of studies with grasshoppers (Belovsky 1986, Belovsky and Slade 1993, Joern and Klucas 1993, Schmitz 1993). Cage effects on microclimate are minimal (Belovsky and Slade 1993).

Newly eclosed adult grasshoppers of *M. sanguinipes* and *A. deorum*, either parasitized by a minimum of three mites or with no mites present, were caught at the
same field site. The *M. sanguinipes* experiment consisted of a 2x2 factorial design with high and low grasshopper density, as well as mite and control (no mites) treatments. Stocking densities were four and 10 *M. sanguinipes* per 0.1111 m² cage. The lower-density treatment was stocked at or below field densities when corrected for proportion of bare ground in the environment while higher-density treatment was stocked well above field densities. The experiment with *A. deorum* consisted of mite and control (no mite) treatments stocked at a density of 10 individuals per cage. Cages were stocked at an even sex ratio with five replicates; treatments were randomly assigned to cages. Experiments ran for six to eight weeks and cages were counted twice weekly to monitor development and survival. Following the experiment vegetation in each cage was clipped and weighed.

**Reproductive analysis**

I measured reproductive characteristics through an analysis of ovaries of female grasshoppers (Launois-Luong 1978, Bellinger and Pienkowski 1985, Joern and Klucas 1993). Grasshopper ovaries consist of a series of ovarian follicles, or ovarioles, each of which is capable of developing and producing an egg. The number of ovarioles determines the maximum number of eggs that a grasshopper can produce in a given egg pod; however, typically not all ovarioles are functional at a given time (Uvarov 1977, Bellinger et al. 1987). Intraspecific variation in functional ovariole number results from a combination of genetic and environmental factors, with functional ovariole number determining the size of the next egg pod laid (Joern and Gaines 1990).

When an egg is released into the oviduct, the covering of the egg compresses into a narrow band (the follicular remnant) visible under a dissecting microscope. If an ovarian
follicle stops development of an egg, the nutrients and ovarian follicle are resorbed, leaving a brightly colored resorption body. Vitellogenesis, the number of ovarian follicles initiating development, was calculated by combining the numbers of follicular remnants and resorption bodies. In addition, the proportion of eggs produced relative to vitellogenesis was calculated. Ovary analysis allows a determination of reproductive allocation, can attribute egg production to individual females, and is highly correlated with actual egg production. It is particularly informative since *M. sanguinipes* egg pods are difficult to recover in the field.

**Statistics**

I used ANOVA models to examine grasshopper survival. A MANOVA was used to assess overall treatment effects and interactions on multiple reproductive characteristics, since multiple reproductive characteristics were measured on individual grasshoppers (Zar 1999). If the MANOVA model was significant, univariate ANOVAs were used (Zar 1999). Repeated measures analyses were used when experimental units were sampled multiple times. Cage means were used as replicate values for all analyses. Proportion survival measures were transformed as necessary to normalize values. SYSTAT 10 (SPSS Inc., ©2000) was used for all statistical analyses.

**Results**

*Parasitism and reproductive allocation*

*M. sanguinipes*. Mite parasitism significantly affected reproductive characteristics based on a multivariate analysis (Table 3.2). Parasitism negatively affected eggs laid, or
Table 3.2. Statistical results for *M. sanguinipes* and *A. deorum* reproductive characteristics. All analyses are based on per capita cage averages.

<table>
<thead>
<tr>
<th>MANOVA of reproductive characteristics</th>
<th>Source</th>
<th>df</th>
<th>Wilks' lambda</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. sanguinipes</em></td>
<td>Density</td>
<td>4,8</td>
<td>0.135</td>
<td>12.830</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Mite</td>
<td>4,8</td>
<td>0.331</td>
<td>4.051</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>4,8</td>
<td>0.515</td>
<td>1.883</td>
<td>0.21</td>
</tr>
<tr>
<td><em>A. deorum</em></td>
<td>Mite</td>
<td>4,4</td>
<td>0.091</td>
<td>9.953</td>
<td>0.023</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Univariate tests</th>
<th>Source</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. sanguinipes</em></td>
<td>Functional ovarioles</td>
<td>Mite</td>
<td>1</td>
<td>290.956</td>
<td>11.320</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Density</td>
<td>1</td>
<td>7.488</td>
<td>0.291</td>
</tr>
<tr>
<td></td>
<td>Follicular relics</td>
<td>Mite</td>
<td>1</td>
<td>728.665</td>
<td>20.103</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Density</td>
<td>1</td>
<td>1059.212</td>
<td>29.222</td>
</tr>
<tr>
<td></td>
<td>Resorption bodies</td>
<td>Mite</td>
<td>1</td>
<td>585.744</td>
<td>8.633</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Density</td>
<td>1</td>
<td>188.067</td>
<td>2.772</td>
</tr>
<tr>
<td></td>
<td>Vitellogenesis</td>
<td>Mite</td>
<td>1</td>
<td>7.793</td>
<td>0.172</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Density</td>
<td>1</td>
<td>2139.923</td>
<td>47.326</td>
</tr>
<tr>
<td></td>
<td>Proportional reproduction</td>
<td>Mite</td>
<td>1</td>
<td>1.336</td>
<td>13.947</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Density</td>
<td>1</td>
<td>0.083</td>
<td>0.865</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Univariate tests</th>
<th>Source</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. deorum</em></td>
<td>Functional ovarioles</td>
<td>Mite</td>
<td>1</td>
<td>0.050</td>
<td>0.179</td>
</tr>
<tr>
<td></td>
<td>Follicular relics</td>
<td>Mite</td>
<td>1</td>
<td>92.450</td>
<td>14.860</td>
</tr>
<tr>
<td></td>
<td>Vitellogenesis</td>
<td>Mite</td>
<td>1</td>
<td>3.335</td>
<td>0.482</td>
</tr>
<tr>
<td></td>
<td>Proportional reproduction</td>
<td>Mite</td>
<td>1</td>
<td>0.222</td>
<td>42.175</td>
</tr>
</tbody>
</table>
total reproduction, as measured by follicular relics (Tables 3.2, 3.3). Number of resorption bodies, a measure of ovarioles that initiated but stopped development, was higher with parasitism (Tables 3.2, 3.3). Vitellogenesis, the number of follicles initiating development, was not affected by mite parasitism, while the ratio of eggs laid relative to vitellogenesis was lower in mite-parasitized females (Tables 3.2, 3.3). Therefore, although vitellogenesis was initiated equally in parasitized and unparasitized grasshoppers, egg production was completed less frequently in mite parasitized individuals (Tables 3.2, 3.3). Functional ovariole number, an indication of future reproduction, was significantly lower in mite parasitized females (Tables 3.2, 3.3).

_A. deorum._ Effects of mite parasitism on reproductive characteristics of _A. deorum_ were similar to _M. sanguinipes_ for most reproductive characteristics (Table 3.2). Parasitized _A. deorum_ females had fewer follicular relics and more resorption bodies (Tables 3.2, 3.3). As was the case with _M. sanguinipes_, vitellogenesis was not affected by mite parasitism (Tables 3.2, 3.3). However, in contrast to _M. sanguinipes_, functional ovariole number was not affected by mite parasitism (Tables 3.2, 3.3).

**Density and reproductive allocation**

Increased _M. sanguinipes_ density resulted in lower per capita egg production and higher numbers of resorption bodies (Tables 3.2, 3.3), responses similar to that of mite-parasitized grasshoppers. Functional ovariole number, a measure of future reproduction, was not affected by grasshopper density (Tables 3.2, 3.3). In contrast to the effects of mite parasitism, vitellogenesis was lower at high density, while the proportion of eggs
Table 3.3. Mean (1 SE) estimates of reproductive allocation parameters of *M. sanguinipes* and *A. deorum* for each treatment. Unparasitized treatments are represented as control while parasitized treatments are indicated as mite. Density treatments are represented as high and low.

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Functional ovarioles</th>
<th>Follicular relics</th>
<th>Resorption bodies</th>
<th>Vitellogenesis</th>
<th>Proportional egg production</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. sanguinipes</em></td>
<td>Mite-high</td>
<td>11.9 (2.5)</td>
<td>11.9 (3.0)</td>
<td>20.9 (4.1)</td>
<td>32.8 (3.4)</td>
<td>0.38 (0.07)</td>
</tr>
<tr>
<td></td>
<td>Mite-low</td>
<td>12.3 (2.9)</td>
<td>24.3 (3.5)</td>
<td>32.3 (4.8)</td>
<td>56.7 (3.9)</td>
<td>0.43 (0.08)</td>
</tr>
<tr>
<td></td>
<td>Control-high</td>
<td>19.9 (2.3)</td>
<td>21.4 (2.7)</td>
<td>12.3 (3.7)</td>
<td>33.7 (3.0)</td>
<td>0.65 (0.06)</td>
</tr>
<tr>
<td></td>
<td>Control-low</td>
<td>22.3 (2.9)</td>
<td>43.3 (3.5)</td>
<td>15.3 (4.8)</td>
<td>58.7 (3.9)</td>
<td>0.74 (0.08)</td>
</tr>
<tr>
<td><em>A. deorum</em></td>
<td>Mite</td>
<td>3.1 (0.2)</td>
<td>9.8 (1.3)</td>
<td>13.8 (0.7)</td>
<td>23.6 (1.5)</td>
<td>0.41 (0.04)</td>
</tr>
<tr>
<td></td>
<td>Control</td>
<td>3.2 (0.3)</td>
<td>16.2 (0.8)</td>
<td>6.1 (0.7)</td>
<td>22.4 (0.5)</td>
<td>0.73 (0.03)</td>
</tr>
</tbody>
</table>

Produced relative to vitellogenesis was not affected (Tables 3.2, 3.3). Therefore, although increased density led to reduced vitellogenesis, egg production was completed in similar proportions in both densities. No significant interactions occurred between density and parasitism based on a multivariate analysis of reproductive characteristics (Table 3.2).

**Parasitism and survival**

*M. sanguinipes.* I predicted mite parasites would not have statistically significant effects on grasshopper survival (Table 3.1), since any reductions in survival should be too small to detect with the replication used in this experiment. Survival reductions due to parasitism could happen either while grasshoppers are parasitized or with a delay if parasitized grasshoppers are able to initially compensate for the effects of the parasite. *M. sanguinipes* survival curves for each treatment are indicated in Fig. 3.1. No significant differences existed between mite treatments in either numbers surviving the study, the proportion of grasshoppers alive at the end of the experiment, or the proportion of
Fig. 3.1. Treatment average numbers of grasshoppers for each treatment surviving 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. Density treatments are represented as high and low.
grasshoppers surviving at 14 days (Table 3.4). Most mite parasites left the host grasshoppers within the first 14 days of the experiment.

*A. deorum.* Changes in the number of individuals surviving in each treatment throughout the experiment are indicated in Fig. 3.1. Mite parasitism did not affect the numbers of grasshoppers surviving (Table 3.4) or the proportion of grasshoppers surviving the study (Table 3.4). Proportional survival to 14 days was marginally lower in mite-parasitized grasshoppers (Table 3.4, p = 0.062).

*Density and survival*

The number of *M. sanguinipes* surviving in the high-density treatment converged to similar levels as low density cages by the end of the experiment (Fig. 3.1), as would be expected with density dependent survival. Repeated measures analysis of proportional survival to 14 days and to the end of the experiment indicated reduced survival in the high-density treatment (Table 3.4). Mite parasitism and density treatments did not interact in their effects on proportional survival (Table 3.4).

*Discussion*

*Predictions 1 and 2: Total and initial reproduction*

Forbes’ (1993) predictions indicate total reproduction should be reduced under mite parasitism. In this experiment, mite parasitism led to a 39 to 44% reduction in egg production, indicating that mites had a large impact on grasshopper reproduction. The observed reduction in total reproduction in response to parasitism fits with Forbes’
Table 3.4. Statistical results for *M. sanguinipes* and *A. deorum* survival data using repeated measures ANOVA for (A) numbers of grasshoppers surviving over time (Grasshopper Numbers), (B) proportion of grasshoppers surviving through the experiment (Proportional Survival), (C) proportional survival of grasshoppers to 14 days after stocking (Proportional Survival to 14 days).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. sanguinipes</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grasshopper numbers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mite</td>
<td>1</td>
<td>3.150</td>
<td>0.568</td>
<td>0.462</td>
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<td>Density</td>
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</tr>
<tr>
<td>Interaction</td>
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<td>0.179</td>
<td>0.032</td>
<td>0.860</td>
</tr>
<tr>
<td>Proportional survival to end of study</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mite</td>
<td>1</td>
<td>0.078</td>
<td>0.597</td>
<td>0.451</td>
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<tr>
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<td>13.857</td>
<td>0.002</td>
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<td>Interaction</td>
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<td>0.027</td>
<td>0.872</td>
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<tr>
<td>Proportional survival to 14 days</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mite</td>
<td>1</td>
<td>0.116</td>
<td>1.689</td>
<td>0.212</td>
</tr>
<tr>
<td>Density</td>
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<td>0.410</td>
<td>5.992</td>
<td>0.026</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>0.003</td>
<td>0.045</td>
<td>0.835</td>
</tr>
<tr>
<td><em>A. deorum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grasshopper numbers</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mite</td>
<td>1</td>
<td>83.33</td>
<td>1.807</td>
<td>0.216</td>
</tr>
<tr>
<td>Proportional survival to end of study</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mite</td>
<td>1</td>
<td>0.464</td>
<td>0.945</td>
<td>0.359</td>
</tr>
<tr>
<td>Proportional survival to 14 days</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mite</td>
<td>1</td>
<td>1.740</td>
<td>4.690</td>
<td>0.062</td>
</tr>
</tbody>
</table>
predictions (1993). Although there was no effect of mites on the number of eggs initiated by *M. sanguinipes* or *A. deorum*, the ratio of eggs laid relative to vitellogenesis was significantly lower in parasitized individuals. This indicates parasitized *M. sanguinipes* and *A. deorum* females reduced initial reproduction while parasitized. Since fewer ovarioles initiating development completed development in parasitized individuals, grasshoppers diverted resources from reproduction. Therefore, it appears that parasitized grasshoppers are selectively allocating resources in response to parasitism and that both initial and total reproduction was reduced as predicted.

**Prediction 3: Future reproduction**

Forbes (1993) predicted that mite parasitism should not affect future reproduction since the mites are short-lived on the host grasshopper. As a result, no differences in functional ovariole number are predicted between parasitized and unparasitized individuals based on his model (Table 3.1). In contrast to this prediction, *M. sanguinipes* mite-parasitized grasshoppers had reduced future reproduction, indicated by lower numbers of functional ovarioles, at the end of the experiment (Table 3.3). Since mites remain on the grasshopper for only 7-14 days, this reduction indicates mite parasitism had an effect on *M. sanguinipes* for up to 40 days after the mites left the grasshopper, impacting much of the egg production period (Pfadt and Smith 1972). Allocation of resources to a given ovarian follicle may become fixed after a given developmental stage of vitellogenesis (Moehrlin and Juliano 1998). Since *A. deorum* has few ovarioles and lays many egg pods, the two species may differ in their reproductive allocation flexibility. As predicted, and in contrast to *M. sanguinipes*, no differences in functional ovariole
number occurred in mite-parasitized *A. deorum*. The effects of mite parasitism did not persist to the end of the experiment; however, since *A. deorum* has a maximum of seven ovarioles versus 36 in *M. sanguinipes*, potential variation in functional ovariole number is limited.

*Prediction 4: Mite parasitism and survival*

Relatively small survival differences were predicted from life history models (Table 3.1), since adult grasshoppers should devote more resources to survival when resources are in short supply (i.e., when mites are on grasshoppers) and less to reproduction. The effect of parasitism on survival appeared to be smaller than the effects on reproduction as predicted. Parasitism did not affect either numbers of grasshoppers surviving or proportional survival to the end of the experiment in either *M. sanguinipes* or *A. deorum* (Table 3.4). In addition, since parasitized grasshoppers initiated egg production at the same rate, but laid fewer eggs (Tables 3.2, 3.3), it appears that mite-parasitized *M. sanguinipes* and *A. deorum* selectively allocated resources to survival. However, survival to 14 days of parasitized *A. deorum* was lower (Table 3.4), possibly indicating reduced survival during the period of parasitism. Due to limited replication, statistical power was relatively low for parasitism effects on survival (power < 0.5). Thus, although strong generalizations on effects of mite parasitism on survival are potentially complicated by low power, as predicted the survival differences due to parasitism were small.
Prediction 5: Interactive or additive effects of parasitism

There were no significant interactions between parasitism and density on either reproductive characteristics or survival (Tables 3.2, 3.4), indicating mites did not have larger effects on grasshoppers at higher densities. The results of the experiment indicate that the effect of parasitism and grasshopper stocking density were largely additive in nature, and that the effect of grasshopper stocking density was primarily to reduce per capita resource availability. Given the limited amount of vegetation remaining at the end of the study, food availability was likely limited in all cages. Additional studies would be required to determine if the two species differ in their ability to overcome the effects of mite parasitism with additional resources.

Effects of density

Density-dependent mortality in *M. sanguinipes* was evident from the decreased proportional survival at high density (Table 3.4). The reduced survival at high density occurred early during the experiment, as there were differences in the proportional survival at 14 days (Table 3.4, Fig. 3.1). I expected to find density-dependent mortality, since the high-density cages were stocked above carrying capacity (Belovsky and Slade 1993).

Reproductive density dependence was also evident in the high-density treatment (Table 3.2), likely resulting from resource limitation and exploitative competition (Belovsky and Slade 1993). Females in high-density cages initiated development in fewer ovarioles and produced fewer eggs (Tables 3.2, 3.3), indicating density-dependent effects
on reproduction. If both increased density and parasitism simply decrease resource availability, similar responses to both treatments might be expected. Although grasshoppers at high density completed development of a similar percentage of initiated ovarioles, individuals at high densities had greatly reduced vitellogenesis (Table 3.3). These results are opposite those seen with parasitism. The effects of stocking density did not persist to the end of the experiment, since future reproduction was not affected by stocking density (Tables 3.2, 3.3). Females in both density treatments may have had similar resource availability at the end of the experiment, as densities converged to similar levels (Fig. 3.1) (Belovsky and Slade 1993).

**Conclusion**

The effect of mites on total reproduction was similar in magnitude to the effects of density dependence (Table 3.3). Although both density and parasitism led to modification of reproductive allocation, they affected reproductive allocation in different ways. Mite parasitism led to a reduction in the proportion of initiated eggs that were laid (Tables 3.2, 3.3), while females at high densities reduced vitellogenesis and modified the rate of ovariole initiation. The differences in allocation patterns between the two treatments could result from differences in the timing and strength of resource limitation between the two treatments, or through selective allocation of resources (Nylin and Gotthard 1998).

Two grasshopper species with different life histories responded in a largely similar fashion to mite parasitism, as there was decreased total and initial reproduction in parasitized individuals. I was unable to determine whether the effect of mites was due to a simple resource drain or another factor. Moret and Schmid-Hempel (2000) found that
there was a cost associated with immune system activation even when there was no resource drain due to a parasite. With the low physiological stress and high resource availability for parasitized grasshoppers in the study by Huggans and Blickenstaff (1966), grasshoppers were likely able to overcome the effects of the mite parasites. Under field conditions, reduced reproduction in parasitized individuals could result from the inability of grasshoppers to increase resource intake to compensate for the direct or indirect costs of parasitism. Mite parasitism of grasshoppers had a large impact on grasshopper reproduction, and had effects on reproductive allocation well after the ectoparasite left the grasshopper. It appears that mite-parasitized grasshoppers are allocating resources to survival to overcome the direct or indirect effects of mite parasitism.

Due to the complex life cycle of mites, experimental manipulations of parasitism were not feasible. Therefore, genetic or behavioral differences could exist between parasitized and unparasitized grasshoppers at a given location (Leonard et al. 1999). Large genetic or behavioral differences seem unlikely given the nature of parasitism in the field, although maternal effects could play a role (Rossiter 1996). These results have implications for the implementation of biocontrol strategies, as small impacts of mite parasitism would be predicted by only analyzing survival differences. However, mite-parasitism reduced grasshopper reproduction by as much as 40%, which could have a large impact on grasshopper population dynamics.

References


Lafferty, K. D. 1993. The marine snail, Cerithidea californica, matures at smaller sizes where parasitism is high. — Oikos 68: 3-11.


CHAPTER 4

REPRODUCTIVE ALLOCATION IN GRASSHOPPERS AS A FUNCTION OF RESOURCE AVAILABILITIES: A MODEL

Abstract

An optimality model was developed to predict optimal total reproductive effort and effort-per-offspring as functions of resource availability, maintenance requirements, and survival. The model was developed for univoltine organisms with non-overlapping generations, determinate growth, and no adult age structure. The model assumes that allocation of resources by adults is divided into reproduction and survival after maintenance requirements are met. To maximize fitness, a female should allocate resources to reproduction as a function of available resources and expected survivorship. Increased resource availability is predicted to lead to an optimal allocation pattern that increases both reproductive and survival allocation, resulting in a positive correlation. With either increasing resource intake or density-independent mortality, individuals should increase the proportional allocation of resources to reproduction. Exploitative competition should lead to increased proportional allocation to survival. The effects of nonlethal parasitism are predicted to differ based on the strength of resource limitation. A resource-based trade-off between egg size and number does not exist, as optimal egg size is predicted to be independent of resource intake.

We examined the model’s assumptions that reproductive allocation increases with resource intake and that survival asymptotes as resource intake exceeds metabolic

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1 Co-authored by David Branson and Gary E. Belovsky.
requirements. The laboratory parameter measurements were in the form predicted, supporting the model's assumptions and construction. The patterns of reproductive allocation and survival of *Melanoplus sanguinipes* in the field were in qualitative agreement with the model's predictions. Two additional field experiments supported the qualitative predictions of the model, as grasshoppers appeared to trade off resource allocation to reproduction for that of allocation to survival. Although we did not determine if the changes in grasshopper reproductive allocation in the adult resource treatments were adaptive, reproductive allocation of grasshoppers in field experiments was consistent with predictions from the model.

**Introduction**

A major focus of evolutionary ecology has been the development of life history theory explaining intraspecific variation in life histories (Roff 1992, Stearns 1992). Theoretical examinations of resource allocation to reproduction, a subset of life history theory, have primarily focused on optimal total allocation to reproduction, optimal clutch size, and optimal effort-per-offspring. Reproductive allocation models assume that allocation of resources to reproduction leads to reduced resource allocation to other traits when resources are limiting (Roff 1992). In addition, the amount of resources allocated to current reproduction should depend on the prospects for future reproduction (Williams 1966a, b), as there is little reason to conserve resources if a female will not survive (Forbes 1993). The relative allocation of resources to reproduction or survival ultimately controls fitness (Sibly and Calow 1986, van Noordwijk and de Jong 1986, Winkler and Wallin 1987, Kozlowski 1991).
Theoretical models of both optimal allocation to reproduction and optimal effort-per-offspring have been developed for environments that are constant (Smith and Fretwell 1974, Kozlowski and Wiegert 1986, Sibly and Calow 1986, Geritz 1998), environments with abiotic variation (Schaffer 1974, McGinley et al. 1987), and environments with resource variation (Sibly and Calow 1986, van Noordwijk and de Jong 1986, Geritz 1998). However, few models have simultaneously examined effort-per-offspring and total reproductive effort when resource availability varies (Sibly and Calow 1986, Winkler and Wallin 1987). The importance of resource availability for reproduction and survival of organisms has been shown theoretically (Sibly and Calow 1986, van Noordwijk and de Jong 1986,) and empirically (Roff 1992, Belovsky and Slade 1995). However, life history responses to resource availability are not always adaptive (Nylin and Gotthard 1998).

When more than one offspring can be produced, an organism's total reproductive allocation must be divided up among offspring (Fox and Czesak 2000). Theoretical approaches to effort-per-offspring have typically been considered separately from optimal allocation to reproduction. Smith and Fretwell (1974) pioneered the mathematical analysis of effort-per-offspring by examining the optimal-sized offspring that a female should produce to maximize parental fitness. Smith and Fretwell (1974) assumed increased effort-per-offspring, or offspring size, results in offspring with higher potential fitness. When resources available for reproductive allocation are limited, increasing offspring size decreases the number of offspring that can be produced. Due to this trade-off between the size and number of offspring, parental fitness is maximized at an intermediate offspring size (Smith and Fretwell 1974). A second contribution of their
model that has shaped much subsequent theory is the prediction of a single optimal offspring size in constant environments.

Most models that examine variation in effort-per-offspring make the same basic assumptions as Smith and Fretwell (Fox and Czesak 2000). McGinley et al. (1987) incorporated environmental variation into the model of Smith and Fretwell (1974) and predicted variable-sized offspring should be produced only when environmental variation is predictable. The effects of variation in resource availability on optimal effort-per-offspring were examined by Sibly and Calow (1986). Sibly and Calow predicted larger offspring should be produced in environments with lower resource availability, since larger offspring have reduced nymphal development times.

Theoretical developments in the area of optimal reproductive allocation and effort-per-offspring have outpaced empirical tests of these theories (Fox and Czesak 2000). Life history optimization approaches, the focus of this model, assume evolution acts to maximize fitness and are ideal for studying the ecological significance of life history plasticity in varying environments (Roff 1992). An optimal life history is one that maximizes fitness; however, an organism’s reproductive value is difficult to measure and surrogate correlates of fitness are often used (Roff 1992, Stearns 1992).

In this paper, we develop a reproductive allocation model examining the effects of resource availability on both optimal total reproductive effort and effort-per-offspring in grasshoppers. Few models have predicted optimal allocation over a range of resource intakes, despite the demonstrated importance of resource availability in empirical studies. Although total reproductive allocation and effort-per-offspring are often examined
separately (Roff 1992, Fox and Czesak 2000), few models explicitly combine optimal
total reproductive allocation with optimal effort-per-offspring to determine how resource
availability affects optimal offspring size.

The model is developed for univoltine organisms with non-overlapping generations,
which allows simple, yet realistic, life history models to be developed and tested. The
model predicts optimal total reproductive effort and effort-per-offspring as functions of
maintenance requirements, resource availability, adult survival, and juvenile survival.
Since grasshoppers have determinate growth, we make the simplifying assumption that
resource allocation by females is divided into either reproduction or survival. Survival
allocation includes all demands other than reproduction, such as maintenance and somatic
investment (Nylin and Gotthard 1998). An explicit testable hypothesis emerges from the
model that can be used to design meaningful experiments.

**Grasshopper Resource Allocation**

Since grasshoppers exhibit life history variation in response to environmental factors,
they are suitable for testing life history predictions related to resource allocation (Joern
and Gaines 1990). Most grasshoppers in temperate climates are univoltine, which acts to
minimize age structure (Joern and Gaines 1990). Nymphal resource availability has been
assumed to have minor effect on adult reproductive allocation in grasshoppers and other
organisms that both acquire and allocate resources to reproduction primarily as adults
(Stauffer and Whitman 1997, Papaj 2000).

Ovarian development in insects allows insects to deal with changes in resource
availability (Papaj 2000). Grasshopper ovaries consist of a series of ovarian follicles, or
ovarioles, each of which is capable of developing and producing an egg. When resources are limiting, grasshoppers can reduce resource allocation to reproduction by modifying vitellogenesis or oosorption, allowing a higher percentage of resources to be used for other functions. Vitellogenesis, the number of ovarian follicles initiating development, occurs when yolk is deposited into an ovarian follicle (Chapman 1982). A second way for grasshoppers to reallocate nutrients during periods of resource shortage is oosorption, when the nutrients are resorbed from a developing ovarian follicle (Chapman 1982, Joern and Gaines 1990, Joern and Klucas 1993, Papaj 2000). Allocation of resources to a given ovarian follicle is not always continuously flexible in grasshoppers, but may become fixed after a given developmental stage of vitellogenesis (Moerhlin and Juliano 1998).


Model Description

Expected survivorship

The relationship between resource availability and individual survival can be written as a function for the rate of mortality. The function of mortality rate ($D$) is expressed analytically in eq. (1).
\[
\begin{aligned}
D &= A + \frac{k}{(M - B)} \\
\end{aligned}
\]

The function in eq. (1) represents mortality based on both resource availability and resource allocation to survival: \(A\) is the environment specific density-independent mortality including field predation rates, \(k\) represents a function of the environment-specific slope of the curve converting resource availability to adult mortality (mortality/time/resource), \(M\) represents the total resources devoted to survival (resources/time), and \(B\) represents basal metabolism (minimum resources required for survival/time). As a simplifying assumption, basal metabolism is assumed to be a species-specific constant independent of size. Since body mass is correlated with metabolism in grasshoppers (Ashby 1998), parameter measurements could have larger confidence intervals when the body mass of grasshoppers varies significantly. We assume that increases in resource allocation to survival \((M)\) over basal metabolic requirements \((B)\) result in increased survival, and that resource allocation to survival \((M)\) less than basal metabolism results in death. As resource intake \((I)\) increases above \((B)\), \(\{k/(M-B)\}\) becomes small and mortality approaches the density independent mortality level in the environment \((A)\) (Fig. 4.1).

The model does not incorporate mortality based on season length, since Grant et al. (1993) concluded that shortened season length is not a strong selective force in temperate univoltine grasshoppers. Typical adult mortality rates result in univoltine grasshopper populations in temperate climates reaching very low densities before environmental conditions terminate the season (Scharff 1961, Grant et al. 1993, Joern and Klucas 1993).
Fig. 4.1. Hypothesized relationship between mortality rate (D) and resource intake (I). Mortality decreases with increasing resource intake above basal metabolic requirements (B) and asymptotes at the background mortality rate (A).

Because mortality is a rate, we computed expected survivorship as the area under the mortality function curve. Since average survival is equal to half of the area under a mortality curve, the integral of eq. (1) was set at 0.5 to allow a determination of the expected average survival (eq. 2).

$$0.5 = \int_{0}^{\infty} \frac{-t \left( A + \frac{k}{(M-B)} \right)}{e} dt$$

Equation 2 was then solved for expected survivorship (q) (eq. 3).
Optimal allocation to reproduction

To maximize fitness, a female is assumed to allocate resources to reproduction as a function of both available resources ($I$) and expected survivorship ($q$) (eq. 3), resulting in an optimal total reproductive allocation or fitness ($W$) (eq. 4).

$$W = q(I-M)$$ (4)

$I$ is the total resource intake of an organism per unit time. $(I-M)$ is the amount of resources devoted to reproduction per unit time. Although grasshoppers lay egg pods in a discrete fashion, allocation to reproduction and survival occurs continuously (Stauffer and Whitman 1997) and is assumed to approximate a continuous function. In addition, modeling discrete events based on continuous allocation results in complex models that must be solved at multiple time periods (Hilborn and Mangel 1997).

To calculate the optima, the derivative with respect to $M$, of eq. (4), is set equal to zero and solved for $M$ (eq. 5, eq. 6).

$$0 = \frac{dW}{dM} = -AM^2 + M(2AB - 2k) + kI - AB^2 + kB$$ (5)

$$M = B - \frac{k}{A} + \left[ \frac{\sqrt{k} \sqrt{A(I-B)} \pm k}{A} \right]$$ (6)

The effect of variation in both annual resource availability and annual density-
independent mortality on optimal reproductive allocation can be examined by varying resource intake $(I)$ and density-independent mortality $(A)$. Increased resource availability is predicted to lead to an optimal allocation pattern that not only increases reproductive allocation $(I-M)$, but also increases allocation to survival (Fig. 4.2). Proportional resource allocation to reproduction should increase with resource intake (Fig. 4.3). Increasing density-independent adult background mortality $(A)$ leads to increased reproductive allocation across a wide range of resource intakes (Fig. 4.4).

*Effort-per-offspring*

The second part of the model develops a trade-off between egg size and egg number.
Fig. 4.3. Predicted percent reproductive resource allocation (---) and percent survival resource allocation (—) as functions of resource intake (I).

Fig 4.4. Predicted absolute resource allocation to reproduction as a function of resource intake (I) at low background density-independent mortality rates (—) and high background density-independent mortality rates (---).
to examine how the optimal total reproductive allocation is divided among offspring. Egg size is used as a measure of effort-per-offspring (Roff 1992, Fox and Czesak 2000) since the dry mass of eggs is representative of variation in effort-per-offspring in some grasshopper species (Landa 1992). Effort-per-offspring analyses with arthropods typically examine egg size, although eggs can differ in other characteristics (Fox and Czesak 2000).

Offspring survival ($L$) equals maximum survival of an egg ($a$), minus the reduction in survival with a smaller egg sizes ($b/s$) (eq. 7) (Smith and Fretwell 1974).

$$L = a - \frac{b}{s}$$  \hspace{1cm} (7)

$b$ is a function converting egg size into mortality and $s$ represents egg size, or egg dry mass. When egg size ($s$) is large, offspring survival approaches the maximum survival as $b/s$ approaches zero. The number of eggs ($N$) that can be produced declines asymptotically to zero with increasing egg size ($s$), since resources are finite (Smith and Fretwell 1974) (eq. 8). The number of eggs produced asymptotes to a maximum, based on a minimum egg size.

$$N = \frac{1 - M}{s}$$  \hspace{1cm} (8)

**Optimal total reproductive allocation and effort-per-offspring**

Although total reproductive allocation and effort-per-offspring are often examined separately (Roff 1992, Fox and Czesak 2000), few models explicitly combine optimal
total reproductive effort with optimal effort-per-offspring to determine the effects of resource availability on optimal offspring size. To determine total reproductive success ($W$), the optimal total reproductive effort ($I-M$) is placed into the equation for egg size (eq. 9).

$$W = \left( a - \frac{b}{s} \right) \left( \frac{I-M}{s} \right)$$  \hspace{1cm} (9)$$

To calculate the optimum egg size that maximizes fitness ($W$) as a function of resource availability, the derivative is set equal to zero and solved for egg size ($s$) (eq. 10, eq. 11).

$$\text{Max. } \frac{dW}{ds} = 0 = \left[ \frac{(I-M)b}{s^3} \right] - \left[ \frac{(I-M)\left( a - \frac{b}{s} \right)}{s^2} \right]$$  \hspace{1cm} (10)$$

$$0 = b(I-M) - (I-M)\left( a - \frac{b}{s} \right)s$$

$$\left\{ \begin{array}{l}
s = \frac{2b}{a} \\
\end{array} \right.$$  \hspace{1cm} (12)$$

Optimal effort-per-offspring ($s$) is not related to resource intake ($I$) and is constant for a given maximum survival rate ($a$) (eq. 12). Consequently, egg number increases linearly with reproductive allocation. As resource availability increases, an organism should produce more eggs of the same size. Decreasing maximum survival rates ($a$), which is equivalent to increasing juvenile mortality, is predicted to result in larger offspring sizes. Due to the mathematical complexity required to generate predictions of egg size variation within egg pods (Roff 1992), this is not addressed by the model.
Validity of Model Assumptions

To examine if the construction of the model appears appropriate, we examined the validity of the assumptions that influence the model’s predictions (Hilborn and Mangel 1997). The parameter tests and field experiments were conducted at the National Bison Range in northwestern Montana, in a Palouse prairie dominated by grasses (Belovsky and Slade 1995). *Melanoplus sanguinipes* (Fabricius), the species of grasshopper used to examine the assumptions and qualitatively test the model, is reproductively plastic and univoltine in Montana (Dean 1982, Dingle et al. 1990, Pfadt 1994). We evaluated the assumption that nymphal resource availability does not affect adult survival or reproduction (Stauffer and Whitman 1997). In a field test of this assumption, nymphal resource availability did not affect average adult survival or egg production of female *M. sanguinipes* (Table 4.1). We also conducted outdoor laboratory experiments to qualitatively examine the assumptions that survival rapidly approaches the maximum survival rate as resource intake exceeds metabolic requirements (Fig. 4.1) and reproductive allocation would increase continuously with resource intake (Fig. 4.2). The

Table 4.1. Statistical results for ANOVA model for eggs laid and mean survival time of females in the experiment.

<table>
<thead>
<tr>
<th>ANOVA table for:</th>
<th>Factor</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs laid</td>
<td>Nymphal resources</td>
<td>1</td>
<td>108.021</td>
<td>0.995</td>
<td>0.326</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>33</td>
<td>108.562</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average survival</td>
<td>Nymphal resources</td>
<td>1</td>
<td>54.450</td>
<td>0.443</td>
<td>0.510</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>34</td>
<td>123.024</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
four resource treatments used in the experiments spanned a wide range of resource availabilities.

To examine the hypothesized relationship between mortality rate and resource intake (Fig. 4.1), we measured metabolic requirements of grasshoppers ($B$) and the conversion of resource availability into survival rates ($k$). We placed individual female grasshoppers on various food levels and measured survival (number of days alive), to assess the influence of resource availability on survival (Roff 1992). We performed a nonlinear regression to determine metabolic requirements and the relationship between resource availability and survival (Fig. 4.5). Since all females in a given food level received the same amount of food, differences in the body mass of grasshoppers likely increased the variation in the data (Fig. 4.5) (Ashby 1998). The nonlinear regression explained two thirds of the

\[ y = 60.36 - 0.0839/x \]

\[ R^2 = 0.65, P < 0.0001 \]

Fig. 4.5. Lifespan in days of individual females as a function of available digestible vegetation per day (g dry). Line and equation are from nonlinear regression analysis.
variation in grasshopper lifespan (Fig. 4.5). As a result, the hypothesized relationship between mortality rate and resource intake used in the model appears appropriate (Figs. 4.1, 4.5).

To examine the validity of the assumption that reproduction allocation increases continuously and linearly with resource intake (Fig. 4.2), we measured allocation to reproduction (I-M). To determine the resource input necessary to produce a given number of eggs, a male and female grasshopper were placed on one of four resource availability levels. Egg production was significantly related to the amount of digestible food provided to grasshoppers (Fig. 4.6), with resource availability explaining over half of the variation in egg production. Egg production increased linearly with resource availability over the range of resources used in the experiment (Fig. 4.6), fitting the form of the model's

![Graph](image)

Fig. 4.6. Egg production of individual females as a function of available digestible vegetation per day (g dry). Line and equation are from regression analysis.
prediction (Fig. 4.2). Therefore, measurements of parameters in laboratory studies were in the form predicted by the model, supporting the model's assumptions and construction.

**Field Examination of Predictions**

Since development of theory without experimental tests of models is of limited utility (Hilborn and Mangel 1997), we conducted a field experiment to examine if reproductive allocation varies with resource availability as predicted by the model. Grasshoppers were stocked below their carrying capacity; therefore, the experiment allowed an examination of reproductive allocation responses when food was not strongly limiting. The results can be used to examine whether increased food quality or quantity changes the intercepts of reproduction or survival as predicted by the model (Fig. 4.2).

We placed 0.1-m² screen cages over similar patches of natural vegetation (Joern and Klucas 1993, Belovsky and Slade 1995). To achieve a range of resource availabilities, cages received either 250 ml of water every two days, 250 ml of water plus 0.4% N by volume fertilizer every two days, or no additions. Two female and two male *M. sanguinipes* grasshoppers were randomly stocked in each cage. Stocking densities were below the average carrying capacity at the site when adjusted for vegetative cover (Belovsky and Slade 1995). At the end of the experiment, all surviving individuals were frozen for reproductive analysis.

We clipped all green vegetation in cages at the end of the experiment to determine vegetation quantity and quality, following the methods of Belovsky and Slade (1995). When stocked below their carrying capacity, grasshoppers only remove a small portion of the available biomass, because they are selective foragers (Chapman 1990, Simpson
1990, Bernays and Chapman 1994). Although clipping vegetation in cages at the end of the experiment cannot assess resource intake for grasshoppers, it can assess differences in resource availability. The samples were divided into grasses and forbs, and plant nutritional quality was assessed by acid-pepsin digestion (Terry and Tilley 1964). Acid-pepsin digestion is highly correlated with in vivo digestibility of grasshoppers and provides a measure of nutritional quality (Belovsky and Slade 1995). Total digestible biomass was calculated by combining the products of grass biomass and its percent digestibility with forb biomass and its percent digestibility (Belovsky and Slade 1995).

We measured reproductive characteristics by analyzing the ovaries of female grasshoppers (Launois-Luong 1978, Bellinger and Pienkowski 1985, Joern and Klucas 1993). The relationship between resource availability measurements and reproductive characteristics was assessed by linear regression (Zar 1999). SYSTAT 10 (SPSS Inc., ©2000) was used for all statistical analyses.

Field experiment

Vegetation characteristics and survival of female grasshoppers were not related ($r^2 < 0.01$, $p > 0.5$). Additionally, survival of females receiving ad libitum high-quality food in field cages did not differ from that of females with field vegetation ($p > 0.5$). When resource availability significantly exceeds basal metabolic requirements ($B$), differences in resource availability should have small effects on survival because mortality remains fairly constant (Fig. 4.1). Therefore, the results support the model’s predictions when food is plentiful in the environment (Fig. 4.1).
As predicted by the model, egg production increased with the amount of total digestible vegetation in a cage (Figs. 4.2, 4.7A). Although the amount of digestible vegetation explained only 25% of the variation in egg production, reproductive allocation increased with increasing resource availability (Fig. 4.7A). While cages averaged 83% grass by biomass, egg production was unaffected by the amount of digestible grass biomass (Fig. 4.7B), indicating females responded to the presence of forbs. Grasshoppers did not decrease the initiation rate of follicles (vitellogenesis) with decreasing resource availability (Fig 4.8B), but completed development of a lower percentage of ovarioles that initiated development (Fig. 4.8B). As predicted by the model, grasshoppers responded to increased quantity or quality of food by increasing reproductive allocation even when resources were not strongly limiting.

Qualitative tests

To examine if the model appears predictive, it is important to determine if the predictions of the model are consistent with the results from field experiments. Two experiments were used to examine the validity of the model’s predictions (Branson Chapters 2, 3). An experiment was conducted to determine if differences in reproductive allocation of Melanoplus sanguinipes with changing per capita resource availability fit the predictions of the model (Branson Chapter 2). The experiment consisted of five grasshopper density treatments in both increased and natural resource treatments. The variation in grasshopper stocking density ensured a range of per capita resource availabilities and allowed an examination of the model’s predictions (Fig. 4.2). The
Fig. 4.7. (A) Eggs laid versus digestible vegetation biomass (g dry) in cages at termination of the experiment. Line and equation are from regression analysis. (B) Eggs laid versus digestible grass biomass (g dry) in cages at termination of the experiment. Equation is from regression analysis.
Fig. 4.8. (A) Vitellogenesis versus digestible vegetation biomass (g dry) in cages at the end of the experiment. Equation is from regression analysis. (B) Percent of initiated follicles completing egg development versus digestible vegetation biomass (g dry) in cages at the end of the experiment. Line and equation are from regression analysis.
experiment was conducted during a year with cool temperatures and high biomass production. Survival did not differ over a range of per capita resource availabilities, fitting predictions when food is not strongly limiting (Fig. 2.2, Branson Chapter 2).

As predicted by the model when resources are limiting, egg production increased linearly with per capita resource availability (Fig. 2.2, Branson Chapter 2). The increasing percentage of initiated ovarioles completing development with per capita resource availability fits predictions that organisms should increase proportional allocation to survival when resource availability is low (Fig. 2.3, Branson Chapter 2). *M. sanguinipes* females appeared to trade off resource allocation to reproduction for that of allocation to survival, since there was no effect of per capita resource availability on survival. Therefore, female *M. sanguinipes* allocated resources to reproduction in response to per capita resource availability as predicted.

A second experiment examined if a mite ectoparasite affected grasshopper reproductive allocation as predicted by the model (Branson Chapter 3). Mites are short-lived parasites on grasshoppers and should reduce the resources available for allocation, resulting in lower reproductive allocation (Fig. 4.2). Since proportional allocation to survival should increase with reduced resource availability (Fig. 4.3), parasitism was predicted to lead to small survival differences. As predicted, mites had small effects on grasshopper survival, while reducing reproduction (Branson Chapter 3). Grasshoppers appeared to divert resources from reproduction, since fewer ovarioles initiating development completed development in parasitized individuals (Branson Chapter 3).
Therefore, it appears that parasitized grasshoppers selectively allocated resources to survival and reproduction as predicted.

**Discussion**

**Total reproductive allocation**

*Resource effects.* Since mortality is predicted to decline rapidly as resource intake exceeds metabolic requirements, organisms should shift proportional allocation of resources to reproduction with increasing resource intake (Fig. 4.3). It is intuitive that allocation to survival increases continually with resource intake (Fig. 4.2, Eq. 6), since a large number of biological functions are included in survival allocation \( M \). However, absolute increases in survival allocation appear small compared to increases in reproductive allocation (Fig. 4.2). Since allocation to survival and reproduction both increase with resource availability, a positive correlation between reproduction and survival should exist over a range of resource availabilities (Fig. 4.2). van Noordwijk and de Jong (1986) predicted individuals with high acquisition rates may be able to allocate more resources to all life history traits when individual variation exists, resulting in positive correlations between life history traits. Although Sibly and Calow (1986) examined resource effects on optimal allocation, they did not predict optimal allocation over a range of resource intakes as predicted by this model (Fig. 4.2).

*Adult mortality effects.* In agreement with previous predictions of Gadgil and Bossert (1970), Schaffer (1974), and Murphy (1968), the model predicts resources should be preferentially allocated to reproduction with high density-independent mortality (Fig. 4.1).
4.4). When an organism has a high chance of dying, it is intuitive that it would attempt to reproduce and reduce allocation to survival (Fig. 4.4) (Nylin and Gotthard 1998). When predation acts in a density-independent fashion, increased predation rates would lead to similar results. However, increased density-independent background mortality ($A$) is predicted to lead to smaller absolute increases in reproductive allocation than increases in resource availability (Fig. 4.4).

Predation and resource intake. Grasshoppers appear able to be capable of adaptive changes in both behavior and diet in response to predation risk (Schmitz 1998). Organisms with low resource availability can potentially increase their fitness by moving to a habitat with higher resource availability and higher predation rates (Gilliam 1982, Werner and Gilliam 1984). Based on the model’s assumptions, increases in resource availability should lead to larger increases in reproductive allocation than increases in predation risk (Fig. 4.4). An organism moving to a resource-rich environment with increased predation rates should increase allocation to reproduction at a greater rate than that predicted by considering the factors separately (Fig. 4.4). In contrast, if an organism moves to an environment with reduced resource availability to reduce predation risk, resource allocation to survival should increase at a higher rate than would be predicted by considering either factor separately (Fig. 4.4).

Exploitative competition effects. Density-dependent exploitative competition for food should lead to reduced per capita food availability (Lomnicki 1980). The model considers the effects of adult resource availability and mortality, not that of nymphs (Schaffer 1974). In addition, interference competition was not considered, since there is
little evidence of interference competition in rangeland grasshoppers (Belovsky and Slade 1995). Adult exploitative competition should decrease per capita food intake ($I$), increasing mortality (Fig. 4.1, eq. 1), and changing the pattern of optimal resource allocation (Fig. 4.2). Since resource intake is incorporated into the mortality rate predictions (Fig. 4.1, eq. 1), increased exploitative competition is predicted to lead to a higher proportional allocation to survival (Fig. 4.3), opposite the predictions with increasing density-independent mortality (Fig. 4). The predictions would change if individual differences in resource acquisition ability lead to increased per capita resource intake of some individuals (Lomnicki 1980). In a field experiment examining reproductive allocation of *M. sanguinipes* females in relation to per capita resource availability, females allocated resources to reproduction as predicted by the model (Branson Chapter 2).

**Parasite effects.** Impacts of nonlethal parasitism (Forbes 1993) may be due to a direct resource drain or a defense response (Moret and Schmid-Hempel 2000). The effect of parasites on optimal allocation depends largely on the biology of the host parasite system and the nature of the resource demand from parasitism (Forbes 1993). When the main effect of parasitism is to directly reduce resource availability for the host, the effects can be modeled by increasing the maintenance requirements for survival ($B$) to reflect the additional resource requirements from parasitism (Figs. 4.1, 4.2). This should be realistic for nonlethal grasshopper parasites such as ectoparasitic mites (Huggans and Blickenstaff 1966).

When resources are not limiting and a parasitized organism can increase resource
intake to entirely compensate for resource losses due to the parasite (Moret and Schmid-Hempel 2000), resource allocation above maintenance requirements ($B$) would not change (Fig. 4.2). However, actual allocation to survival and reproduction would be lower for a given level of resource intake. When a parasite removes a large amount of the available resources, reproduction would be significantly reduced even with unlimited resource availability.

When resources are limiting, a parasitized organism will be unable to, or only partially compensate for, the increased resource requirements by increasing resource intake. This would result in increased proportional allocation to survival (Fig. 4.3). Any reductions in survival would depend on the strength of resource limitation (Schoener 1974). When resource intake just exceeds the metabolic requirements with parasitism, or when the effects of parasitism require a high percentage of available resources, both survival and reproductive allocation should decline (Fig. 4.2). In an experimental examination of the effects of a mite parasite, parasitized grasshoppers allocated resources in response to parasitism as predicted (Branson Chapter 3).

Therefore, the effects of parasitism are dependent on food availability in the environment and should differ in their impact on grasshopper population dynamics as a consequence of naturally occurring fluctuations in resource availability. Nonlethal grasshopper parasites should have a larger impact on grasshopper population dynamics in years when reproduction is already reduced because of low resource input (I) (Fig. 4.2), unless the parasite does poorly under similar conditions. These predictions are in agreement with Moret and Schmid-Hempel (2000), who found reductions in survival due
to immune responses were noticeable only when resources were limiting.

When a parasite results in direct mortality separate from the effects of reduced resource availability, the effects can be modeled by increasing density-independent mortality \((A)\) (Fig. 4.4). This should result in higher allocation to reproduction than would occur if the parasite had no direct mortality effects (Fig. 4.4). The timing of mortality from the parasite could change these predictions, as expected survivorship would change (Eq. 3).

**Effort-per-offspring**

Since the effort-per-offspring subcomponent of the model incorporates the same assumptions as Smith and Fretwell (1974), the basic model predictions are the same. However, the intent of the model was to expand the model of Smith and Fretwell (1974) to examine changes in optimal effort per offspring under varying resource inputs. As predicted by Williams (1966a) and Winkler and Wallin (1987), larger offspring should be produced in an environment where juvenile survival is low. However, a single optimal egg size should result at any given juvenile mortality level. Interestingly, when optimal total allocation is combined with effort-per-offspring, the solution for optimal egg size simplifies to a constant (Eq. 12). Therefore, in contrast to the predictions of both Geritz (1998) and Sibly and Calow (1986), optimal egg size is independent of variation in resource intake. Since egg number is related to resource availability, while egg size is not, a resource-based trade-off for optimal egg size does not exist. Although many models predict a trade-off between offspring size and number (Roff 1992), empirical support is not strong among iteroparous organisms that use adult resource intake for reproduction.
(Carriere and Roff 1995, Fox and Czesak 2000). The prediction is empirically supported, as Moerhlin and Juliano (1998) examined grasshopper egg pods under a range of resource availabilities and found egg size did not vary with resource availability.

**Conclusion**

This model predicts optimal total reproductive allocation over a range of resource intakes, which is not commonly examined. Allocation to reproduction and survival are both predicted to increase with resource intake, although resource allocation to reproduction increases at a faster rate. When resource availability is low, organisms should allocate a higher proportion of available resources to survival. Although many models have examined reproductive allocation and effort-per-offspring separately, few models have explicitly combined optimal reproductive allocation with optimal effort-per-offspring to determine how resource availability affects optimal offspring size. Interestingly, optimal egg size is predicted to be independent of variation in resource intake. Since egg number is related to resource availability, while egg size is not, no resource-based trade off exists for optimal egg size. The unexpected lack of a resource-based trade off for optimal egg size warrants further empirical investigations with egg-overwintering grasshoppers.

Although a quantitative parameterization of the model was not conducted, the parameter measurements in laboratory studies were in the form predicted by the model. In addition, the patterns of field reproductive allocation and survival of *M. sanguinipes* were in qualitative agreement with the predictions of the model. As predicted by the model, grasshoppers increased resource allocation to reproduction with increasing
resource availability. Two additional field experiments with grasshoppers were used to qualitatively examine the predictions of the model. Reproductive allocation of grasshoppers over a range of per capita resource availabilities was consistent with model's predictions. Additionally, grasshoppers parasitized by mite ectoparasites appeared to allocate resources to survival and reproduction as predicted. Although we are unable to determine if the changes in grasshopper reproductive allocation were adaptive, reproductive allocation of grasshopper in field experiments was consistent with predictions from the model. Therefore, the model appears to generate predictions that are consistent with field observations, supporting the model's assumptions and construction.

References


A major challenge in ecology is to understand intraspecific variation in life histories. Variation in resource availability can lead to differences in reproductive allocation and life histories. I developed an optimality model for univoltine grasshoppers to predict optimal total reproductive effort and effort-per-offspring as functions of resource availability, maintenance requirements, and survival. The model was developed for organisms with non-overlapping generations, determinate growth, and no adult age structure. In addition, I examined the effects of both adult and offspring mortality on reproduction. The model suggests increased resource availability leads to an optimal allocation pattern that increases both reproductive and survival allocation resulting in a positive correlation. Individuals should increase the proportional allocation of resources to reproduction with increasing resource intake and increased density-independent mortality. Exploitative competition should lead to increased proportional resource allocation to survival. The effects of non-lethal parasitism are predicted to differ based on the strength of resource limitation.

I examined the model's assumptions that reproductive allocation increases with resource intake and that survival asymptotes as resource intake exceeds metabolic requirements. The laboratory parameter measurements were in the form predicted, supporting the model's assumptions and construction. I examined if changes in reproductive allocation and survival of *Melanoplus sanguinipes* (Fabricus) under a range of resource availabilities fit the predictions of the model. The patterns of reproductive
allocation and survival of *M. sanguinipes* in the field were in qualitative agreement with the predictions.

An organism’s life history response to varying resource availability and stocking density is often plastic and varies between species; however, little research has examined this plasticity with grasshoppers in the field. In addition, natural variation in both grasshopper density and resource quality has important implications for predicting population responses following a year of high densities or resource availability. I examined if differences in reproductive allocation of *M. sanguinipes* with resource availability and grasshopper density treatments are primarily explained by exploitative competition. I also examined if individual differences in competitive ability played a large role in observed mean egg production values. Grasshoppers responded to low adult resource availability and high grasshopper stocking densities by reducing egg production. The effects of per capita resource availability were evident at the end of the experiment since functional ovariole number increased with per capita resource availability. Residuals for the regressions of egg production and vitellogenesis with per capita resource availability did not differ for either resource or density treatments, indicating exploitative competition for resources played the most important role in determining changes in reproductive allocation in *M. sanguinipes*. There was higher variation around the mean of egg production at the highest density and with natural resources, indicating individual differences between grasshoppers may play an important role in understanding patterns of reproductive allocation.

Careful examinations of changes in life history characteristics in response to parasitism are lacking, despite the fact that parasites often influence resource availability
for the host. I investigated the effects of a grasshopper mite ectoparasite, *Eutrombidium locustorum*, on reproductive allocation and survival in two grasshopper species, *M. sanguinipes* and *Ageneotettix deorum*. Mites had small effects on grasshopper survival, but both mite parasitism and grasshopper stocking density affected reproductive characteristics. As predicted, both species had reduced initial and total reproduction, and completed development of a lower percentage of ovarioles initiated when parasitized. However, in contrast to predictions for short-lived parasites, future reproduction of parasitized *M. sanguinipes* was lower at the end of the experiment. Since there were no interactions between grasshopper density and parasitism, mites did not have stronger effects at high densities. Mite parasitism clearly had large effects on grasshopper population dynamics in the field.

These experiments act to expand our knowledge of life history theory and also to further our understanding of grasshopper life history variation and population fluctuations. An understanding of how both biotic and abiotic environmental factors affect grasshopper life histories is crucial if we are to further our understanding of population fluctuations of grasshoppers. Therefore, this research has important implications not only for life history theory, but also for our understanding of grasshopper population dynamics.
CURRICULUM VITAE

David H. Branson

EDUCATION:


Dissertation: Reproductive Allocation and Survival in Grasshoppers: Effects of Resource Availability, Grasshopper Density, and Parasitism

Major Professor: Dr. Gary E. Belovsky


EXPERIENCE:

Planned and conducted research investigating how grazing management can be used to reduce grasshopper outbreaks, the effects of rangeland fire and livestock grazing on grasshoppers, and the influence of grasshopper herbivory on nutrient cycling and rangeland productivity. Developed and edited a grasshopper management CD-ROM.

Conducted Ph.D. field work on the reproductive ecology of grasshoppers on the National Bison Range in western Montana. Assisted in the design, field work, and analysis of community ecology experiments funded by NSF and experiments examining the influence of grasshoppers on ecosystem dynamics. Supervised field and laboratory technicians.

GRADUATE INSTRUCTOR IN ECOLOGY. Utah State University, Logan, Utah. 1997.
Taught General Ecology (FW/RR 284) to 90 non-major undergraduate students. Taught principles of population ecology, community ecology, ecosystem ecology, biodiversity, and ecosystem management. Used active learning techniques and small group discussions to facilitate
student learning. Responsible for preparing lectures and tests, assigning grades, and supervising teaching assistant.

GRADUATE INSTRUCTOR. Utah State University, Logan, Utah. 1997. Lab Coordinator and Graduate Instructor for Natural Resource Quantitative Methods (NR 370). Taught statistical methods, statistical programming using SAS, and statistical interpretation to undergraduate natural resource majors. Responsible for preparing lectures, practice sets, and assigning grades.

PUBLICATIONS:


AWARDS RECEIVED:

Sigma Xi Grant in Aid of Research
University of Michigan Block Grant Research Award
Presidential Fellowship, Utah State University