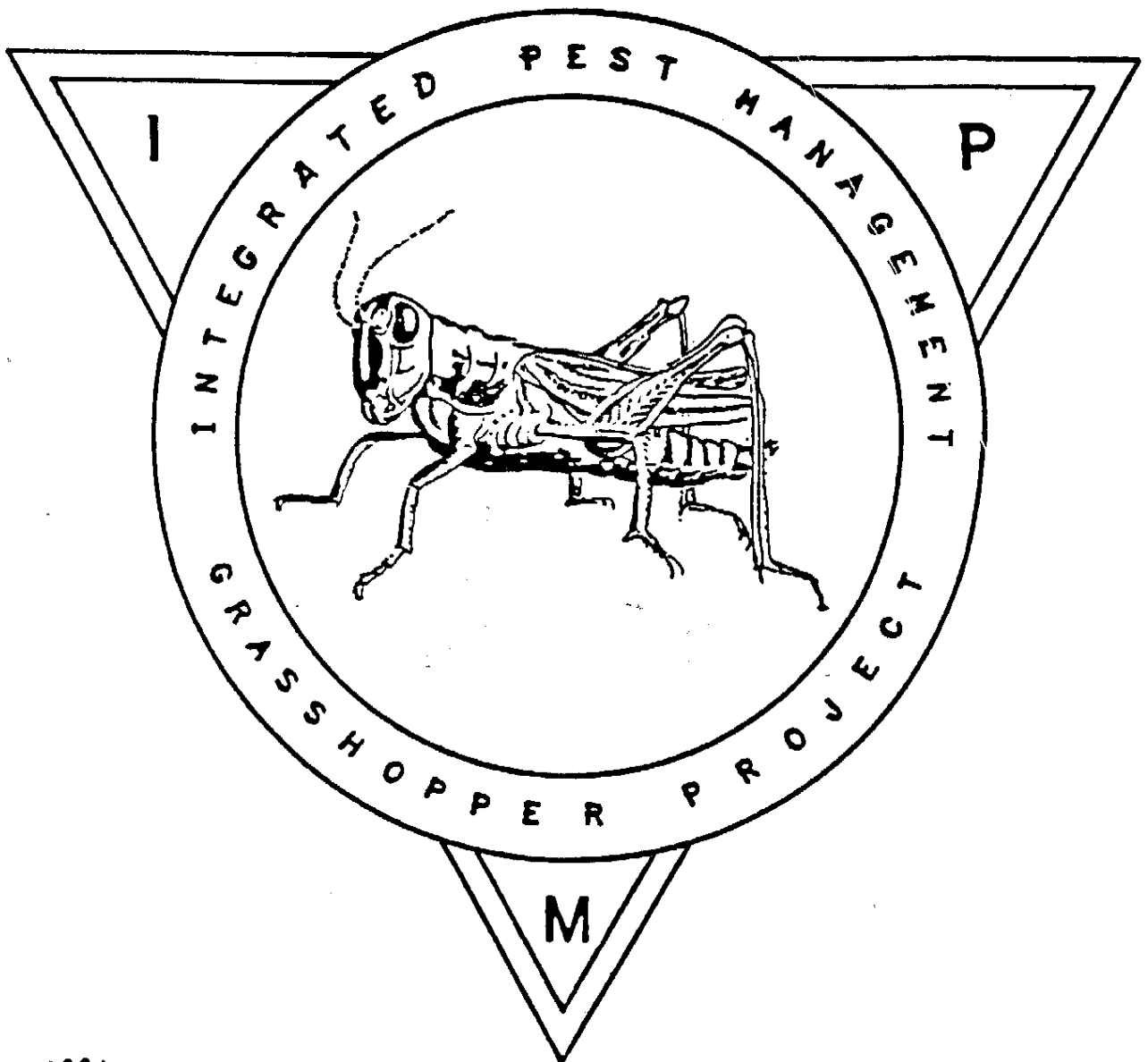# COOPERATIVE
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GRASSHOPPER COMPETITION AND PREDATION:
BIOLOGICAL CONTROL OPTIONS

Gary E. Belovsky
Department of Biology and School of Natural Resources
University of Michigan
Ann Arbor, MI 48109

INTRODUCTION

In this paper, I will attempt to use a summary of the findings on grasshopper population studies being conducted at the National Bison Range in Montana to address the feasibility of some potential elements of an IPM program for grasshopper control. Potential population control mechanisms (*e.g.* predators, parasitioids, competitors, and food resources) are being studied. These findings from my studies of basic population ecology provide insights into which mechanisms might be used in an IPM program and provide information about the conditions at other sites that might modify the possibilities.

Basic population studies of grasshoppers may not seem to have immediate relevance to biological control strategies. However, basic studies provide important insights into which mechanisms might be manipulated to control grasshopper populations, and perhaps more important, the conditions when a particular control measure will be successful. We should not expect a single control measure to be useful over the diverse rangeland habitats plagued by grasshoppers, or even at the same site in different years. A wildlife manager (Keppie 1990) argues that previous management studies have generally dealt exclusively with management methods *per se* without addressing the basic ecological conditions under which the method was employed, thereby making it impossible to extrapolate to other situations. The entomologist, Paul Ehrlich (1989), in a recent review of the importance of basic ecological information in solving environmental problems, documents the waste of billions of dollars each year because basic ecological studies are either not incorporated into management programs or the findings of basic studies are ignored.

How relevant are studies of basic grasshopper population ecology at the National Bison Range? The Bison Range is a native Palouse prairie at elevations comparable to most rangelands included in the IPM project (700-1400 m). The habitats at this site are dominated by grasses (70-90% of plant biomass), receive comparable precipitation to most North American rangelands (< 40 cm/yr), and have standing crop biomasses of vegetation ranging from 15 to 120 g-dry/m². The grasshoppers inhabiting this site and included in the study are some of the most important pest species: *Melanoplus sanguinipes, M. femurrubrum, M. bivittatus, Camnula pellucida,* and *Ageneottetix deorum.* Grasshoppers at this site consistently achieve high densities: adult densities in late August-early September are 2-20/m², and densities of 3rd-5th instars consistently exceed APHIS pest status (12-70/m²). Therefore, this site is not atypical of the rangelands being studied by the IPM project and the grasshoppers consistently approach outbreak conditions.

My studies of basic grasshopper population ecology at the Bison Range (Belovsky 1986, 1990a, b, in press, Belovsky *et al.* 1990, Belovsky and Slade a, b, c, d, e, f) can be summarized by the following points:

1) Grasshopper densities are limited by food abundance.
2) Grasshoppers compete for food intra- and interspecifically.
3) Large-bodied grasshoppers are superior competitors for food.
4) Birds are the principal predators of grasshoppers.
5) Birds are size-selective predators, preferentially preying upon large-bodied grasshoppers.
6) Avian predation reduces the abundance of large-bodied grasshoppers, but this reduces competition for the smaller species and they increase in abundance.

With these results in mind, the efficacy of predators/parasitoids, competitors, and food resources as potential control mechanisms in an IPM program will be addressed.
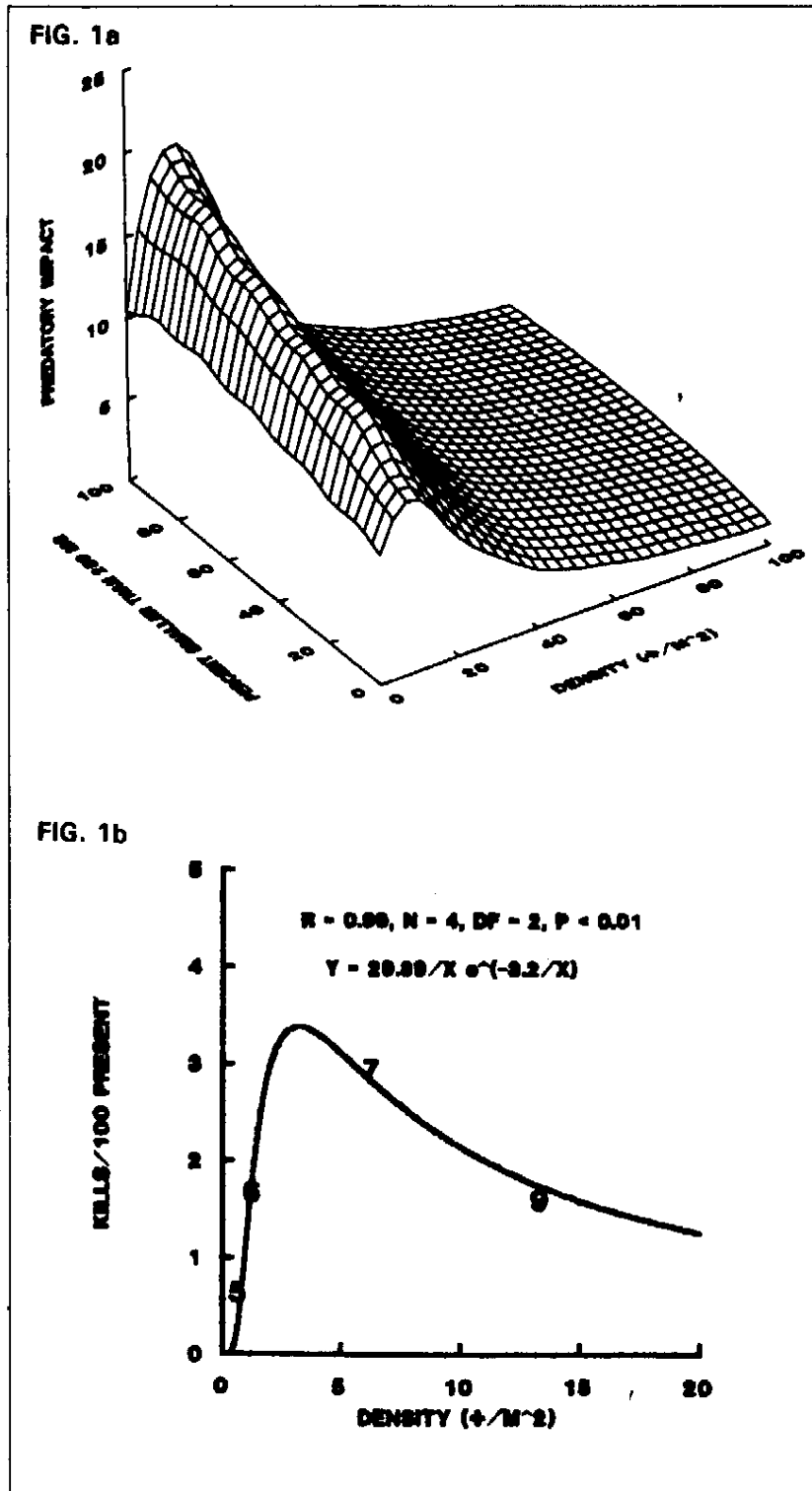
PREDATORS/PARASITOIDS:

Figure 1. A) The predation intensity plotted against grasshopper density and relative abundance of grasshoppers of different body sizes. B) The observed predation intensity versus grasshopper density at the Bison Range: equivalent to a cross-section through a given relative abundance value in A).

One of the most commonly held concepts about grasshopper population ecology is that natural enemies (predators, parasitoids, parasites, disease) frequently limit densities (Dempster 1963, Joern and Gaines 1990) with predators and parasites considered most important. Except for the large-bodied grasshoppers, my studies indicate that predators are not important for grasshopper populations at the Bison Range (Belovsky in press, Belovsky et al. 1990, Belovsky and Slade submitted e). Birds and other predators (e.g. spiders: Belovsky and Slade submitted e; O. J. Schmitz, pers. comm.) are abundant in this native prairie. Therefore, predation is not unimportant because of a low density of predators.

Using feeding behavior experiments with captive cowbirds (*Molothrus ater*), one of the most important avian predators of grasshoppers (Belovsky 1990a), the intensity of avian predation at different grasshopper densities and distributions of grasshopper body-sizes can be predicted (Belovsky in press). The results indicate that predation is most intense when grasshoppers are at densities below outbreak levels (approx. 5/m²) and when small-bodied grasshoppers are relatively more abundant in the habitat (Fig. 1a). Using western meadowlarks (*Sturnella neglecta*), the same feeding behavior patterns and predictions emerge (T. Tompkins, pers. comm.).

The observed change in predation intensity at the Bison Range with different annual grasshopper densities (Belovsky and Slade submitted e) is in
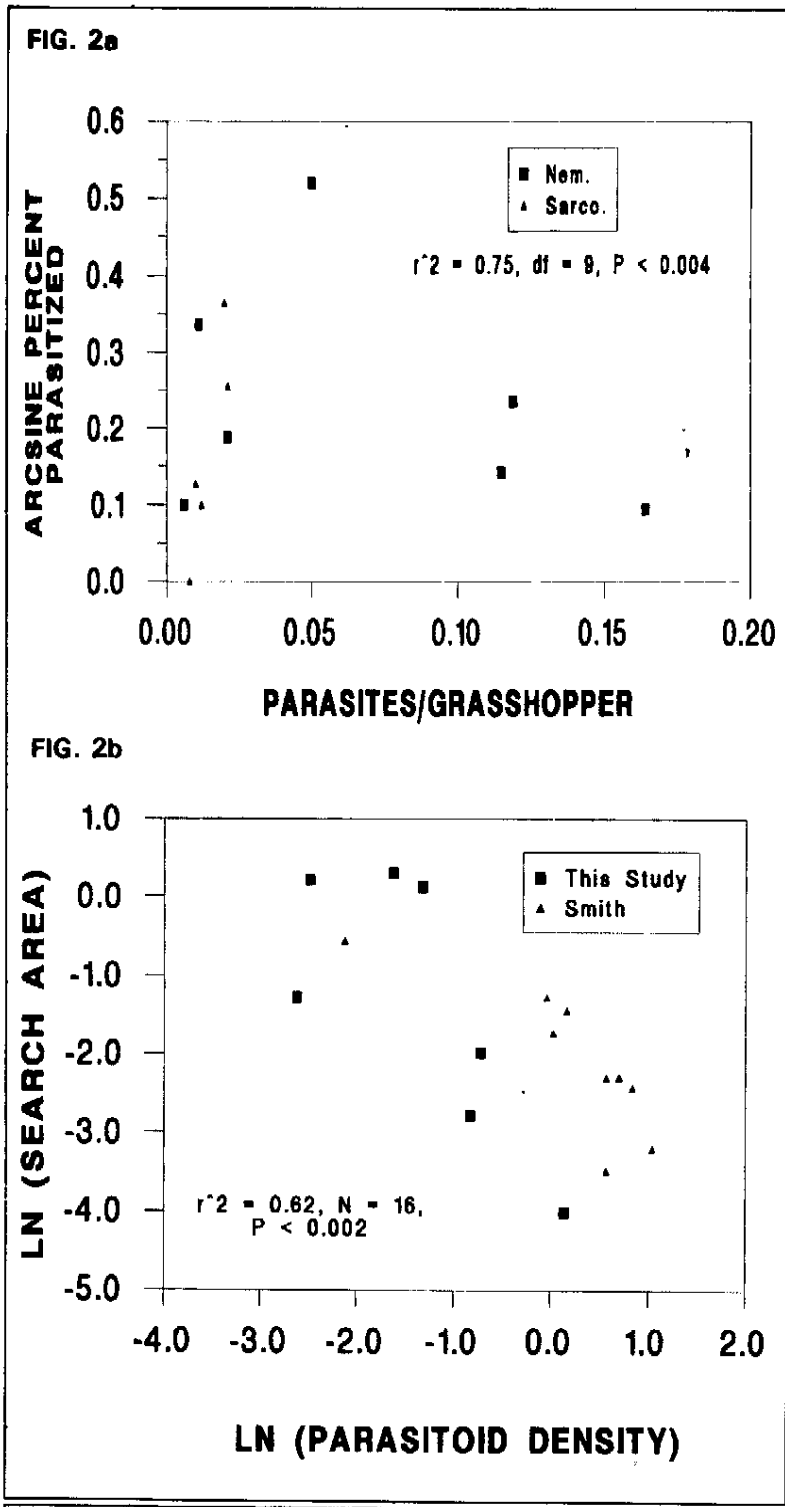
FIG. 2a

FIG. 2b

Figure 2. A) The effect of parasitoid density and grasshopper density on the percentage of grasshoppers being parasitized. The regression values are for a parabola fit to the data. B) The relationship between parasitoid effectiveness (search area *sensu* Hassell 1985, and parasitoid density is plotted. Values are also plotted from Smith's 1965 Ontario study.

accord with the experimental predictions (Fig. 1b). Predation intensity is measured as predation rate (% killed/day); whether a given predation level is adequate to control grasshopper densities will depend upon the number of eggs hatching in a year. Nonetheless, if predation is to be important in controlling grasshopper densities, the grasshoppers will have to be at low densities. Therefore, using predation to control grasshopper outbreaks in an IPM program would require some other method to reduce grasshoppers to low densities whenever grasshopper densities increase.

Parasitoid infestations of *Melanoplus sanguinipes* populations have been monitored in a number of habitats at the Bison Range for as long as 5 consecutive years (Lietti de Guibert *et al.* submitted). *Melanoplus sanguinipes* is the most common grasshopper (48-82%). Nemestrinid, Sarcophagid and Tachinid larvae were identified with Nemestrinids most abundant (70% of parasitized grasshoppers). The intensity of this parasitism varied between 0-28% in different years and habitats.

The parasitoids at the Bison Range demonstrate very strong density dependence in response to grasshopper density and parasitoid densities. This can be shown by plotting the percentage of grasshoppers (hosts) parasitized in the current year versus the density of parasitoid pupae produced in the previous year relative to grasshopper density (hosts) in the current year (Fig. 2a). Initially, as parasitoid density relative to grasshopper (host) abundance increases, the parasitoids attack more of the grasshoppers, but as this ratio continues to increase the attacks diminish. The attacks decline because the parasitoids interfere with each other in finding grasshoppers to parasitize.

Based upon insect parasitoid-host models (Hassell and May 1973, Comins and Hassell 1979), Hassell (1985) provides a measure of parasitoid efficacy in controlling host density called "search area". Plotting the logarithm of parasitoid density from the previous year versus the logarithm of the "search area" in the current year, the slope of the line defines the ability of the parasitoid to control host numbers. A slope of -1 or smaller indicates that the host cannot be controlled by the parasitoid. The data from the Bison Range (Fig. 2b) provide a slope of -1.2, indicating that parasitoids cannot limit the grasshoppers at this site.

Using data on parasitoid infestations of *M. sanguinipes* in Ontario (Smith 1965), the same analysis can be conducted (Fig. 2b). The resulting slope is smaller than -1 and not different from that measured at the Bison Range. The Ontario site is an old field that receives four-fold more precipitation and is very different from the Bison Range. These results suggest that parasitoids are unlikely to limit grasshopper populations at any site. This arises because the parasitoids cannot achieve great enough attack rates on the grasshoppers since the parasitoids inhibit their attacks at high densities (Fig. 2a). Therefore, even enhancing parasitoid densities will be ineffective in an IPM program because of their own inhibition of attacks.

The Bison Range results suggest that native predators/parasitoids do not offer much hope for successful control of grasshoppers in an IPM program.

FOOD RESOURCES:

Total grasshopper density at the Bison Range appears to be limited by food abundance (Belovsky and Slade submitted a, b, e, Lietti de Guibert *et al.* submitted). Also, the most common species appear to have populations limited by food abundance (Belovsky 1986, Belovsky and Slade submitted a, b, e). Food abundance is not a simple measure of plant biomass, but depends upon biomass and its digestibility to the grasshoppers.

Managing food availability to control grasshopper density might be one of the most simple control measures (habitat control *sensu* Pfadt 1962). However, this may not be practical for the IPM project. Since the goal of the IPM project is to control grasshoppers to increase forage for livestock on rangelands, management methods that reduce grasshopper food resources also might reduce livestock forage.

Management methods that reduce grasshopper food resources might be practical for an IPM strategy in two situations. First, if grasshopper outbreaks develop and spread from localized "hot spots", these local areas might be identified and the vegetation within them might be managed to prevent outbreaks. Second, if management methods could be developed to control grasshopper food resources selectively without affecting livestock forages, grasshopper control through managing their food resources over large areas would become practical. This would require a better basic knowledge of how grasshoppers and livestock select food plants which define their food resources at each site and what food resources are shared (Belovsky 1986).

COMPETITORS:

The grasshoppers at the Bison Range appear to compete intra- and interspecifically for food (Belovsky 1986, Belovsky and Slade submitted c, d, e). Competitors would not seem to be a likely control measure in a grasshopper IPM project. The IPM's goal is to reduce livestock forage losses and using competitors to reduce populations of abundant grasshoppers implies the substitution of one agent reducing livestock forage for another. Therefore, while a competitor might reduce one grasshopper population, another grasshopper or herbivore would increase in abundance and use the livestock forage. However, my studies of basic grasshopper population ecology indicate the potential utility of certain competitors for controlling grasshopper population outbreaks.

The use of competitors to control grasshopper outbreaks relies upon an observation emerging from my continued studies at the Bison Range. Some habitats have abundant early season (late-May to early-July) assemblages of grasshoppers, but the pest grasshoppers belong to late season assemblages (mid-June to October). The early season assemblage's adult grasshoppers overlap phenologically with the late season assemblage's newly emerging nymphs. These adults by definition are larger than the nymphs, and my results have indicated that large-bodied grasshoppers are competitively superior. Therefore, the early season adults have the potential to limit the

FIG. 3a

Legend:
- ALONE
- W/OR
- W/ST

Y-axis: NUMBER/CAGE (0–6)
X-axis: YEAR (89, 90)

FIG. 3b

Legend:
- ALONE
- W/CON
- W/AUL
- W/CONSP
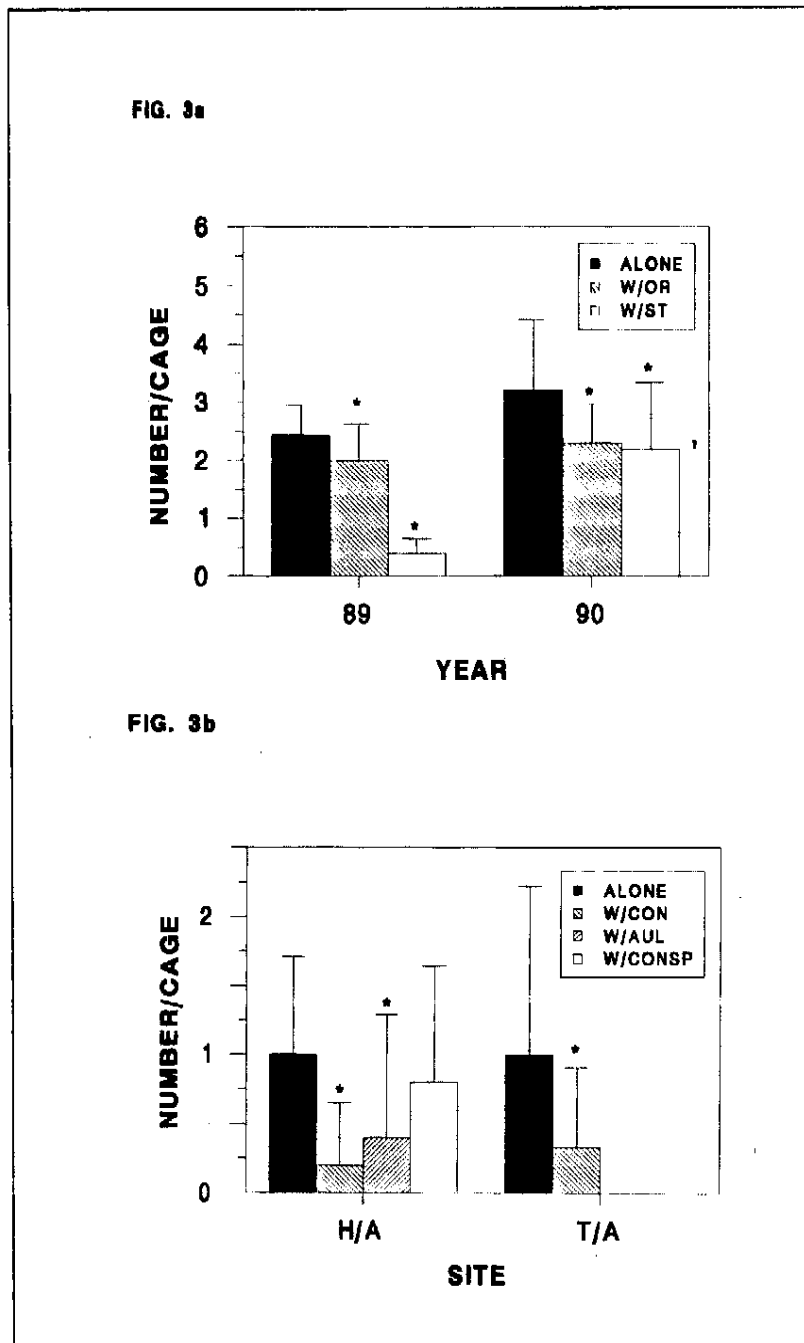
Y-axis: NUMBER/CAGE (0–2)
X-axis: SITE (H/A, T/A)

Figure 3. A) The effects of early season orthoptera on *Melanoplus sanguinipes* in experimental populations (N = 15) at a 1400 m prairie site (OR = *M. oregonensis*; ST = *Steiroxys* sp.) are presented for two years. This site has an abundant early season assemblage. *'s represent a significant difference (t-test). B) The effects of early season grasshoppers on *M. sanguinipes* in experimental populations (N = 15) during 1990 at a 700 m (H) and 1200 m (T) site (CON = *M. confusus*; AUL = *Aulocara ellioti*; CONSP = *Arphia conspersa*). These sites do not have abundant early season assemblages. *'s represent a significant difference (t-test).

abundance of late season grasshoppers.

Population experiments, conducted like those reported elsewhere (Belovsky 1986, Belovsky 1990b, Belovsky and Slade submitted a, b, c, d), indicate that the early season adults can reduce the densities of late season adults by reducing the survival of late season nymphs (Fig. 3). This was examined by pairing adults of one of the early season species (*Melanoplus confusus*, *M. oregonensis*, *Arphia conspersa*, *Aulocara ellioti*, and an un-named new species of decticid, *Steiroxys* sp.: Belovsky and Slade in press), with nymphs of the most abundant late season pest species (*M. sanguinipes*).

What makes competition by early season species a potential control measure in an IPM program? First, the early season adults die in the habitats no later than mid-July. Experiments using methods to study predation intensity (Belovsky *et al*. 1990) indicate that predation is not eliminating them. Furthermore, these adults in caged populations die at the same time as observed in the field. The causes of these die-offs are being investigated at present. Second, the vegetation recovers after early season consumption. This can be seen by stocking experimental populations first with early season grasshoppers, and then after their die-off, restocking the cages with late season grasshopper nymphs. These late season grasshoppers attain the same density which they attain in experimental populations where early season grasshoppers have been excluded (Fig. 4a).

The recovery of the vegetation occurs because there still is sufficient precipitation during and after the early season grasshopper die-off to permit regrowth. The
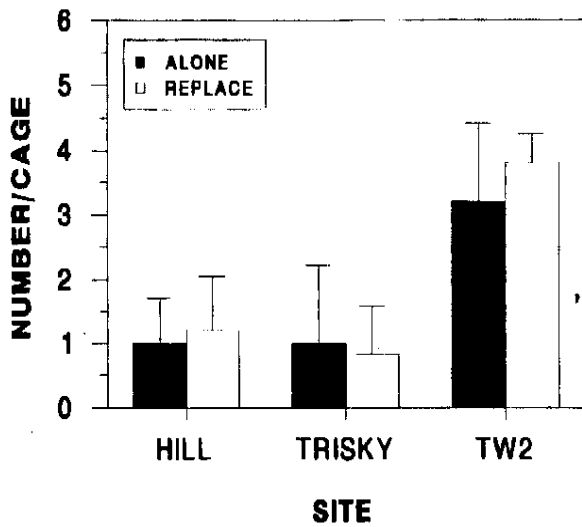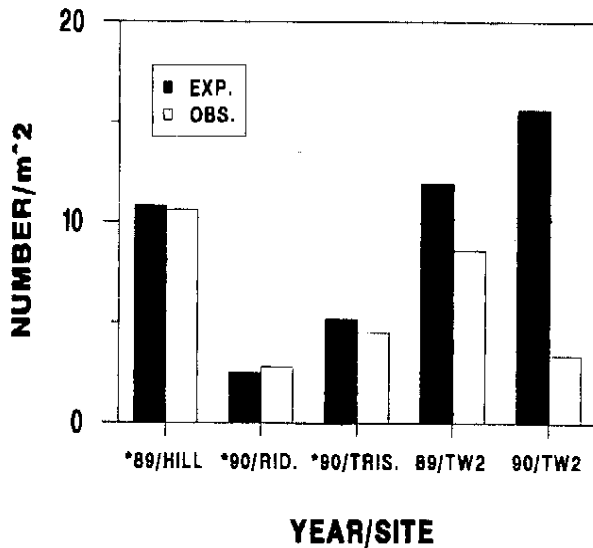
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FIG. 4a

FIG. 4b

Figure 4. A) Densities of *Melanoplus sanguinipes* in 1990 are compared for experimental populations (N = 10) when stocked alone and when the population previously contained early season grasshoppers (replace). There are no significant differences. B) Densities attained in experimental populations without early season grasshoppers are compared with observed field densities at different sites and years. The * indicates sites without abundant early season assemblages.

late season grasshoppers cannot completely utilize the recovered food resources because the early season grasshoppers have caused sufficient mortality among their nymphs so there are too few to consume all the available food.

Do early season grasshoppers limit late season grasshopper densities in the field? The answer is "yes" for some habitats at the Bison Range where early season grasshoppers attain high densities, and "no" in habitats where early season grasshoppers do not attain high densities (Fig. 4b). The early season grasshoppers reduce late season densities by as much as 76% without decreasing plant biomass at the end of the summer. Experimental studies of predation (Belovsky 1990) indicate that none of these differences are due to predation. Therefore, early season grasshoppers are a likely control measure in an IPM program.

But why do early season grasshoppers attain high densities and reduce late season grasshopper densities in some habitats, but not others? This is being studied at the Bison Range at present with experimental populations, and must be understood if early season densities are to be enhanced to control late season grasshoppers in an IPM program.

GENERALITY OF THESE FINDINGS:

The diversity of rangeland habitats at the Bison Range span the plant biomasses and grass/forb relative abundances found over most North American rangelands. In all the Bison Range habitats studied, late season grasshopper populations consistently have been found to be limited by survival, not reproduction. This distinction means that more than adequate numbers of eggs are

deposited and hatch than are needed for the populations to utilize all available food resources (Belovsky and Slade submitted a, b) in the subsequent year. In the worst possible year (lowest food resources), the grasshoppers were able to produce more hatchlings than could be supported by the most abundant food resources observed. Grasshopper mortality either brings densities into balance with food resources or to levels less than supportable by food resources through competition with early season grasshoppers. If predators/parasitoids were important, they also would reduce densities to levels less than those supported by food resources. Therefore, mechanisms of mortality (food abundance, intra- and interspecific competition) limit population densities.

In many habitats at the Bison Range, early season grasshopper populations may be reproduction limited, *i.e.* insufficient eggs are deposited and hatch to provide adequate densities to utilize the available food resources. Studies at other sites have suggested that late season grasshoppers can be reproduction limited (Sanchez and Onsager 1988, Sanchez *et al.* 1988). Different control mechanisms will have to be employed in IPM programs for reproduction-limited versus survival-limited grasshopper populations. Therefore, ascertaining the conditions that lead to reproduction versus survival limited grasshopper populations will enable us to better understand the methods needed to construct IPM programs at different sites and years.

From studies of different habitats at the Bison Range, some patterns relevant to reproduction versus survival limited grasshopper populations are emerging. Reproductive limitation appears to apply to species composing the Gomphocerinae which are most abundant at the Bison Range in habitats where the vegetation desiccates early in the summer. Members of the Melanoplinae and Oedopodinae, which are most abundant at the Bison Range in habitats where the vegetation desiccates less quickly, appear to be survival limited. The Gomphocerinae mature more rapidly and deposit fewer eggs per pod, but the time between consecutive pod depositions is shorter than for Melanoplinae and Oedopodinae.

The above distinctions would suggest that Gomphocerinae are typical of "r-selected" species, while Oedopodinae and Gomphocerinae are typical of "K-selected" species (Begon *et al.* 1986). The Gomphocerinae should predominate in habitats where food resources are ephemeral (*e.g.* desiccate rapidly) and their densities are limited by the number of eggs deposited in the previous year. The Melanoplinae/Oedopodinae should predominate in habitats where food resources persist and their densities will not be limited by reproduction because eggs can be deposited over an extended period.

The scenario suggested above would lead IPM projects to be structured differently for Gomphocerinae versus Melanoplinae/Oedopodinae dominated habitats. However, these important distinctions must be better understood to develop adequate IPM projects.

CONCLUSION:

The preliminary results indicate the need to understand basic grasshopper population ecology to construct successful and efficient IPM programs. At the Bison Range, native predators/parasitoids do not appear to provide much potential as biological control agents for an IPM program. Results of predation experiments indicate the limited conditions under which predators might effectively control grasshopper densities. However, the experiments also demonstrate that predation cannot be a successful control agent by itself without assistance from other management methods: pesticides or other biological control agents (*e.g. Nosema locustae, Entomophaga grylli,* or viral infections) (Belovsky in press).

At the Bison Range, the pest grasshopper populations appear to be limited by food abundance and the competition for food. These findings suggest that habitat manipulations to reduce grasshopper food supplies may be a useful control measure. Furthermore, competition from early season grasshoppers on the nymphs of late season pest species may be fostered as an unexpected control measure.

The choice of population mechanisms as control measures in an IPM program depend upon whether the grasshopper populations are limited by reproduction or survival. This distinction is shown to be important for designing effective and efficient control strategies. However, this distinction requires a better basic understanding of the conditions that lead to either reproduction or survival, as the controlling agents of grasshopper populations at different sites, and as in any

research program raises more new questions. Regardless, answers to these questions are essential to the design of better IPM programs that are cost effective (Ehrlich 1989, Keppie 1990).

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