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GRASSHOPPER CONTROL: IMPLICATIONS OF INVESTIGATIONS INTO POPULATION/COMMUNITY ECOLOGY

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Introduction.

The studies of experimental populations initiated in 1992 (Belovsky 1992) were continued to address: 1) whether a previously proposed population model (Belovsky 1991) could be experimentally validated so that pest managers could be confident of its predictions for the design of control strategies? 2) whether the model's parameters and predictions could be simplified and made operational so OICs could employ it in implementing grasshopper control in a more timely and economical fashion? I report here the results from the first full year of studies with the experimental populations (hatchlings produced in one year through hatchlings produced in the next year) and preliminary results from a second year (hatchlings produced in the current year and their survival).

These grasshopper population/community ecology studies supported by GHIPM have indicated a shifting importance of density independent abiotic-induced mortality, food limitation, interspecific competition, parasitism and predation in determining grasshopper abundances in different habitats and years (Belovsky 1986a, b, 1989, 1990a, b, 1992, 1993, Belovsky and Slade 1993, 1994, Chase and Belovsky 1994, Belovsky *et al.* 1990). These processes have been integrated into a model of grasshopper population regulation (Fig. 1: Belovsky 1991). The model indicates that grasshopper populations that cause economic damage are food-limited, either chronically or periodically, and it may be possible for pest managers to shift populations into a natural enemy- and abiotic mortality-limited state, where economic damage is less likely, through limited control efforts.

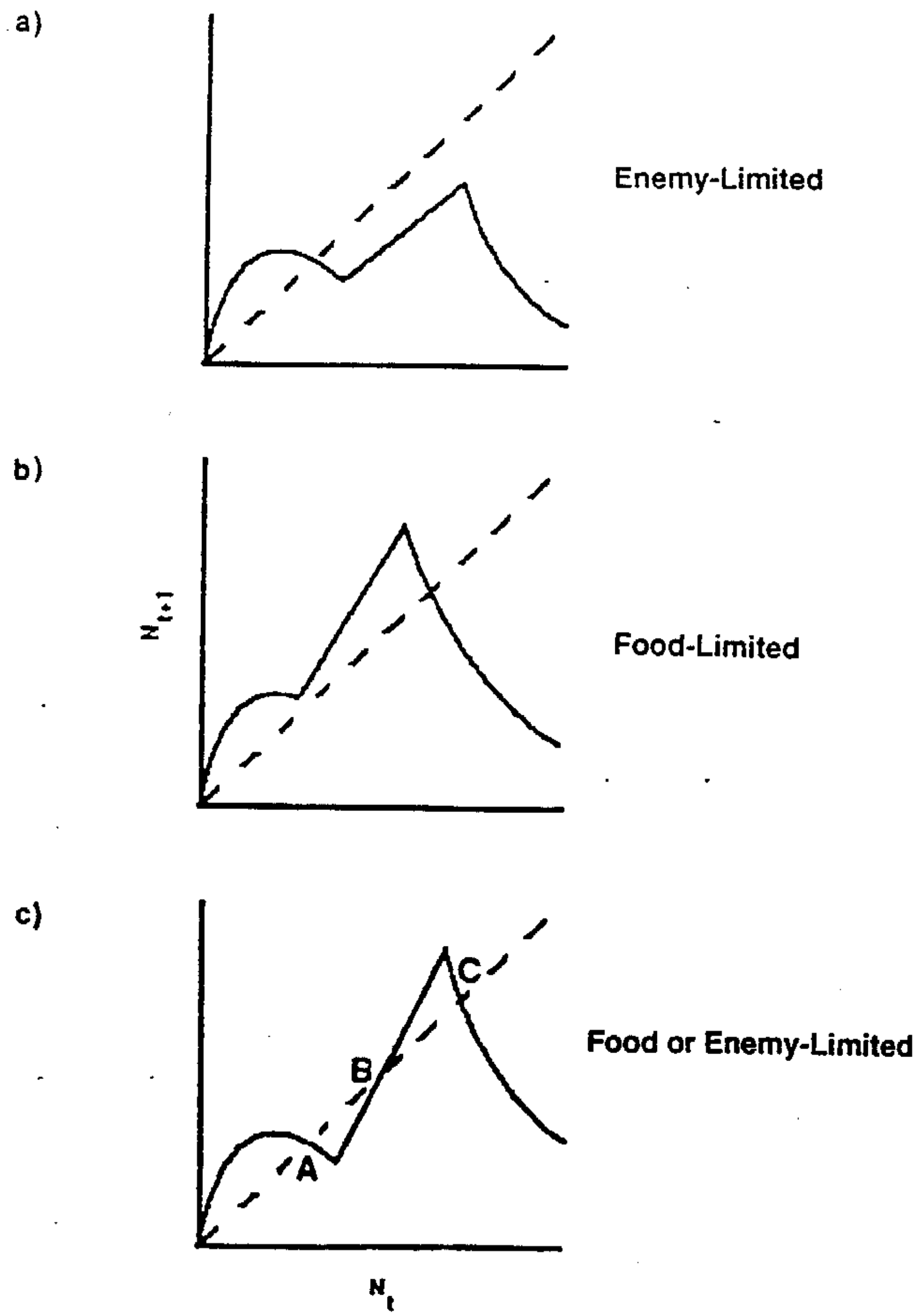
Materials and Methods.

The construction, treatments and methods employed with the experimental populations of *Melanoplus sanguinipes* at the National Bison Range, Montana were described in Belovsky (1992). The treatments include (3 replicates of each $9m^2$ enclosed populations, and 10 replicates of small cages):

1) field plots of $9m^2$;
2) control - $9m^2$ enclosed populations with predation and initiated with the observed field densities of hatchlings;
3) decreased density - $9m^2$ enclosed populations with predation and initiated with 50% of the average observed field densities of hatchlings;
4) increased density - $9m^2$ enclosed populations with predation and initiated with 125% of the average observed field densities of hatchlings;
5) control with no predation (only 1993) - $9m^2$ enclosed populations initiated with the observed field densities of hatchlings;
6) control with supplemental food - $9m^2$ enclosed populations with predation and initiated with the observed field densities of hatchlings, where food is supplemented by providing water every 2 days, so that an additional 3.5 cm of water/month (June 20 - Sept. 1) is available;

Figure 1.

The Ricker curve model of grasshopper population-community dynamics emerging from our 15 years of studies with grasshoppers at two semiarid grassland sites. The first "hump" in the curve is driven by natural enemy and abiotic induced mortality. The second "hump" in the curve is driven by increased mortality and reduced reproduction due to competition for food plants. As depicted, the grasshoppers can be natural enemy limited if the reference line ($N_t = N_{t+1}$) intersects the first or only "hump" (a or point A in c), and food-limited if the reference line intersects the second "hump" (b or point C in c). In c the grasshoppers can be either natural enemy- or food-limited depending upon whether the population is initiated to the left or right of point B, an unstable equilibrium, "saddle point".



7) high density and no predation - $0.01m^2$ enclosed population initiated with 10 hatchlings.

All methods for these experimental populations were described earlier (Belovsky 1992); the only new measure is that the emergence of hatchlings from the experimental populations established in the previous year were censused from early-June through June 20, when the densities in the experimental populations were once again manipulated to begin the experiment anew. This was done by counting the number of nymphs at 3 times during a day on 3 different days in 6 $0.01m^2$ rings located in each experimental population (9 m^2).

As described earlier (Belovsky 1992) in conjunction with the above experimental populations, 3 replicate $100m^2$ areas excluded birds for comparison with 3 replicate $100m^2$ control areas. The grasshopper numbers measured in these areas can be compared to assess whether avian predators limit grasshopper numbers.

Table 1 presents the expected experimental results that enable identification of the different population regulating states predicted (Belovsky 1991) and portrayed in Fig. 1.

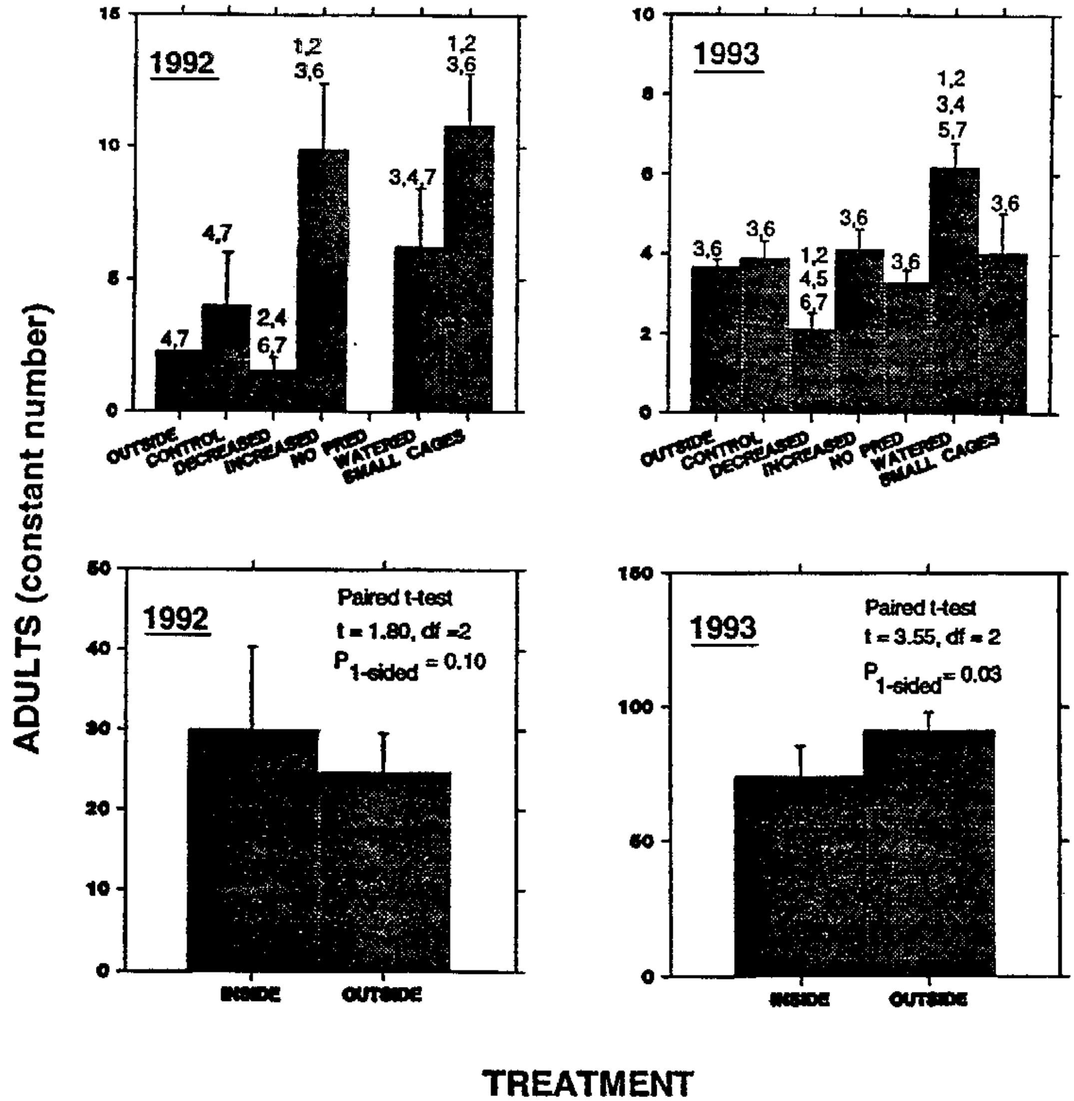
TABLE 1. Experimental results compared with control measures for adult density, eggs produced per female and total hatchlings emerging in the next year. A + means greater than field, - means less than control, and 0 means no difference with control. The control and field measures should not differ, and there should be no differences between the increased density populations and the small cages, if there are no experimental artifacts.

	MEANS OF REGULATION			
TREATMENT	ENEMIES (FIG. 1a)	FOOD (FIG. 1b)	EITHER (FIG. 1c) ENEMIES	EITHER (FIG. 1c) FOOD
DECREASED DENSITY	0/0/0 -/+/-		0/0/0 -/+/-	
INCREASED DENSITY	0/0/0 0/-/-		+/-/+ 0/-/-	
SUPPLEMENTAL FOOD/ CONTROL DENSITY	0/0/0 +/+/+	0/0/0 +/+/+		
NO PREDATION/ INCREASED DENSITY	+/-/+ 0/-/-		+/-/+ 0/-/-	

Results.

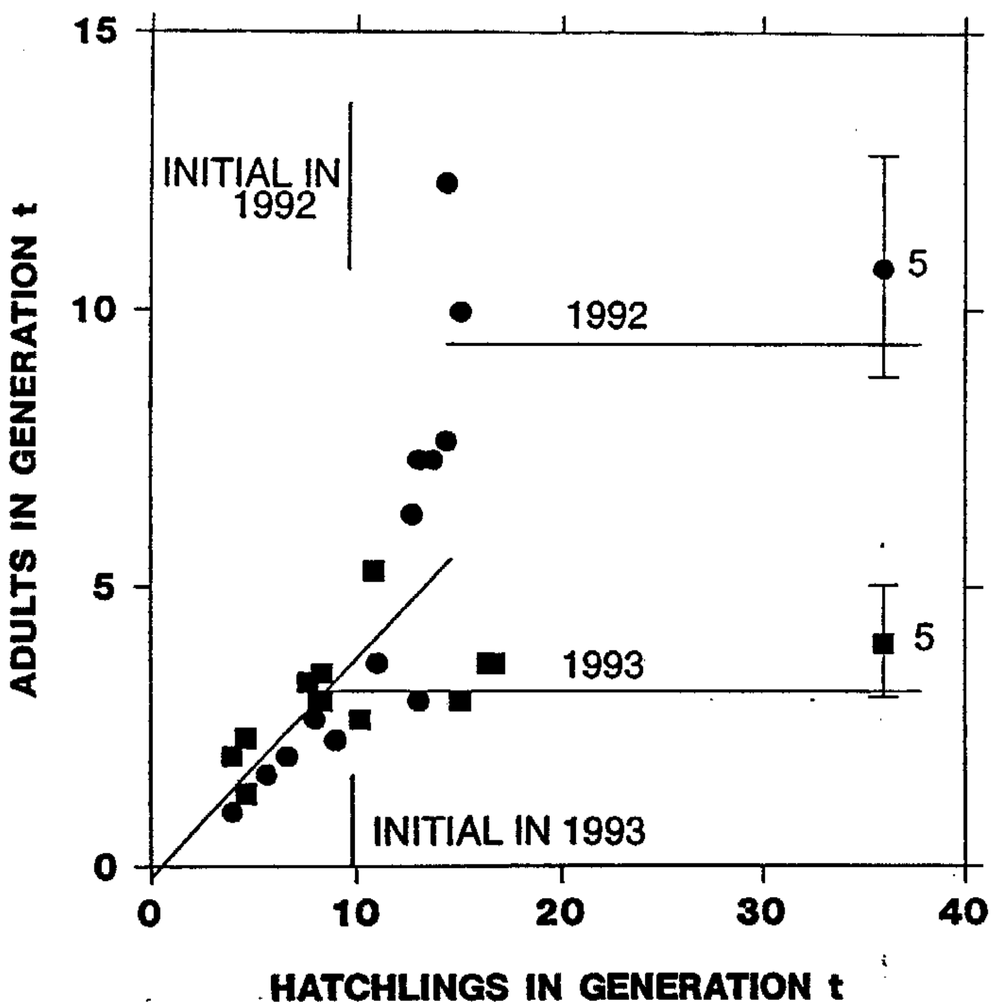
1) Alternating regulating effects on adults in different years. Belovsky and Slade (1993, 1994) reported that predation did not limit adult densities over 10 years (1981 - 1991, 1988 not measured) in this study area. However, in 1992, the experimental population and avian exclosure results indicated that birds appeared to limit adult densities for the first time at this site (Fig. 2). In contrast, in 1993 the same experimental results indicated that the population had returned to a state where adult density was not limited by predation (Fig. 2).

FIGURE 2. Comparison of adult numbers in the experimental populations and avian exclosures in 1992 and 1993.



To better evaluate these shifting states of limitation, adult density was plotted against hatchling density for the 2 years, indicating that the number of hatchlings needed to provide the food-limited adult density was lower in 1993, than in 1992 (Fig. 3). The striking difference between the 2 years is that the constant food-limited adult density was greater in 1992; however, in both years the probability of surviving from a hatchling to the adult stage, when hatchling densities were less the food-limited level, were similar in both years (same slope, Fig. 3). This means that density-independent abiotic and natural enemy mortality did not substantially differ between years, but food availability did vary. Therefore, given food availability, there exists a minimum number of hatchlings required to start the population, above which the population can escape the mortality imposed by natural enemies, so the population attains a constant density limited by food, and below which the natural enemies determine adult density.

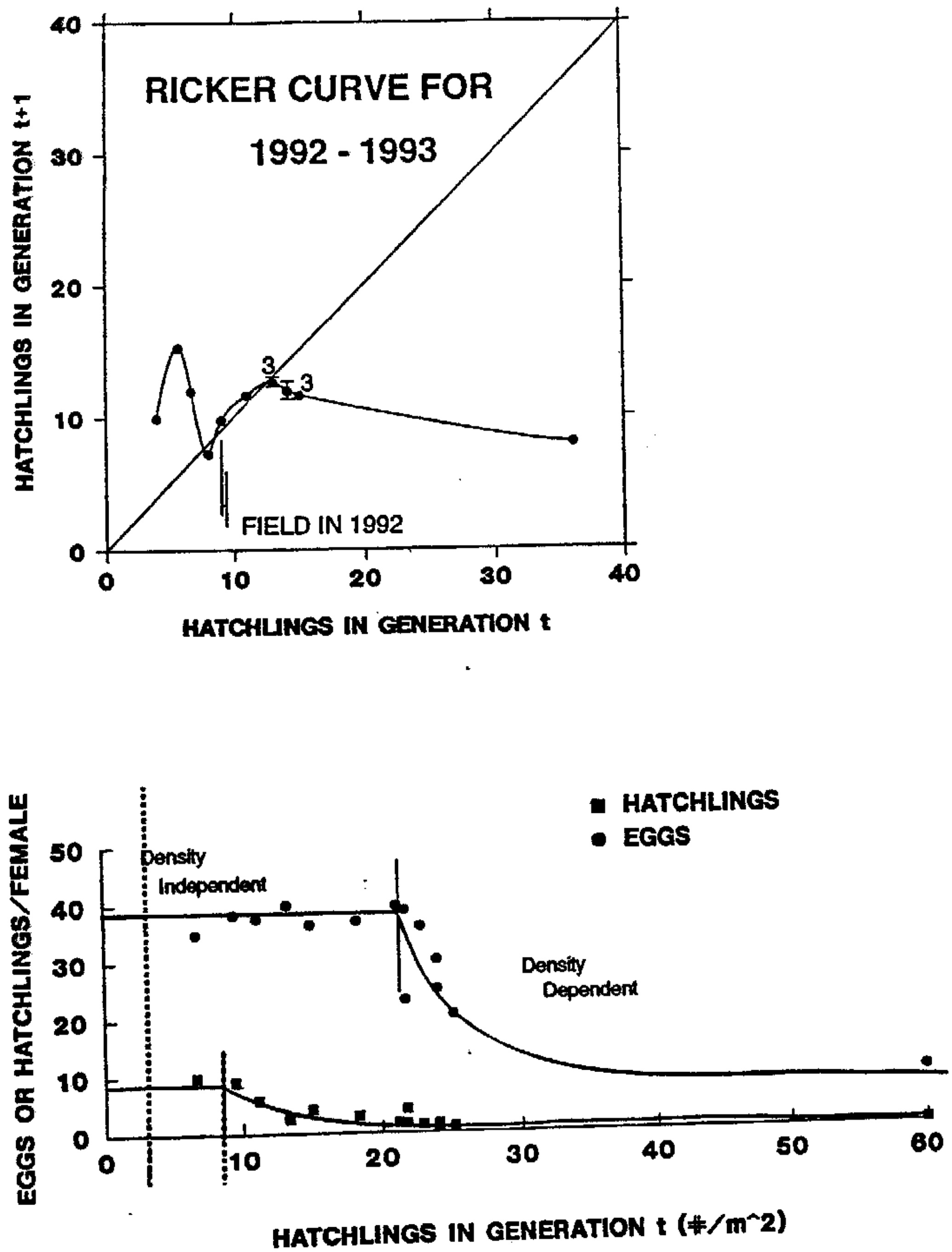
Figure 3. The initial density of hatchlings versus the density attained by adults is plotted. The results of piece-wise linear regression indicate the constant food-limited densities in 1992 (circles) and 1993 (squares), while the line with positive slope indicates the approach to these densities which did not differ between years.



2) <u>What limits adult numbers does not mean that the grasshopper population is limited by the same factor</u>. Survival to the adult stage is but one element of population regulation depicted in Figure 1. In addition, reproduction per female and total hatchling production are important considerations. The reproductive data is currently only available for 1992 in the experimental populations. Rather than presenting the detailed reproductive data for each of the

experimental treatments, the data will be used to plot the Ricker Curve (hatchlings initiating the population versus the number of hatchlings produced to start the population in the next year, Fig. 4a) to compare with the hypothesized Ricker Curves for grasshoppers (Fig. 1).

FIGURE 4. a) The Ricker Curve plotted for the population in 1992. b) The reproductive output per female (eggs and hatchlings) plotted against initial hatchling density in 1992.



In 1992, the grasshopper population exhibited a Ricker Curve (Fig. 4a) consistent with a population that could be regulated by either natural enemies or food, depending upon the number of hatchlings initiating the population (Fig. 1c). However, even though the adults in 1992 were limited in the field by natural enemies, the reproduction per female was still limited by food availability (Fig. 4b). This can be concluded, because the hatchling density at which reproduction per female begins to decline due to food-limitation was less than the density of hatchlings required to produce food-limited survival to the adult stage. Furthermore, given the initial density of hatchlings in the field in 1992, there were too few to produce the food-limited equilibrium, but too many for the population to be limited by natural enemies (initial density greater than point B in Fig. 1c). Therefore, the grasshopper's population dynamics in 1992 were still food-limited, not natural enemy-limited, even though survival to the adult stage was affected by natural enemies and the population did not approach a food-limited equilibrium.

Discussion.

The idea that initial hatchling density is important to grasshopper populations and important to know for pest managers in developing strategies for the monitoring and control of grasshoppers is not new. However, there is no set threshold for initial hatchling density, instead this threshold will vary between sites and years at the same site. Variation in food abundance, natural enemy effects and density-independent abiotic mortality as integrated in the Ricker Curve models (Fig. 1) set the threshold values. If an OIC could identify that a particular population never or seldom escapes limitation by natural enemies, that population would not have to be monitored or considered for control. On the other hand, if an OIC could identify that a particular population frequently or always escapes limitation by natural enemies, that population would have to be monitored closely and considered for control.

The above findings have very subtle, but important, implications. First, the results instruct us that identifying that adult densities are lower in the presence of predators than in their absence (*e.g.*, Fowler *et al.* 1991) is necessary, but not sufficient, to imply natural enemy limitation for the grasshopper population. Second, based upon preliminary results, I (Belovsky 1992) claimed that grasshopper populations in 1992 might be shifted from food-limitation to natural enemy-limitation by as little as ~20% reduction in the number of initial hatchlings. This conclusion is based upon the assumption that in 1992 the population was limited by natural enemies, but given the measured Ricker Curve (Fig. 4a), this was found not to be the case and the population would have to be reduced by ~42%, not ~20%. While the ~20% reduction would diminish the damage by grasshoppers in that year, these benefits would be short-lived because the population is still food-limited; the ~42% could provide greater benefits because it would produce a natural enemy-limited population.

Summary.

As indicated in the *GHIPM USER HANDBOOK* sections that I have provided (5 sections for which I was principally responsible), understanding grasshopper population regulation is critical for developing better grasshopper management strategies, including reduced levels of pesticide application, habitat manipulations, grazing and biocontrol. Ways to identify the alternate states of population regulation for grasshoppers so that OICs can take advantage of them in designing better monitoring and control strategies are being developed. Furthermore, a set of computer models based upon the notions developed here are being constructed with A. Joern, J. Onsager, W. Kemp and J. Berry to provide a more advanced tool than *Hopper* for the future.

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