# COOPERATIVE GRASSHOPPER INTEGRATED PEST MANAGEMENT PROJECT

# 1991 ANNUAL REPORT

COMPILED BY:

UNITED STATES DEPARTMENT OF AGRICULTURE
ANIMAL AND PLANT HEALTH INSPECTION SERVICE
PLANT PROTECTION AND QUARANTINE
GRASSHOPPER IPM PROJECT
BOISE, IDAHO

# ALTERNATE POPULATION DYNAMICS FOR GRASSHOPPERS: IMPLICATIONS FOR PEST CONTROL

Gary E. Belovsky

Department of Fisheries and Wildlife and Agricultural Experiment Station
Utah State University
Logan, Utah 84322-5210

## INTRODUCTION:

For 11 years, I have been studying factors influencing grasshopper densities in western Montana (Belovsky and Slade in press a, b; Belovsky *et al.* 1990, Belovsky 1990, 1992). For 3 years as part of GHIPM, experimental investigations of grasshopper populations have been conducted at a series of prairie sites in western Montana (Belovsky 1990b, 1991). This resulted in identifying alternative conditions that lead to differences in how grasshopper populations are limited; *i.e.*, food and competition for food, natural enemies and abiotic factors, or both sets of conditions operating in different years for the same population. Different limits to populations have implications for assessing when populations will attain pest status and how they might be controlled over the long term at the least cost and effort.

## MATERIALS AND METHODS:

Experimental studies were conducted at the National Bison Range (Sanders and Lake Counties), Montana, a 9000 ha area composed primarily of native Palouse prairie. Data on *Melanoplus sanguinipes* populations are presented here because this data currently is most extensive and best analyzed, but similar data on 18 other species (including the pests: *Aulocara ellioti*, *Ageneotettix deorum*, *Amphitornus coloradus*, *Camnula pellucida*, *Melanoplus femurrubrum*, *M. bivittatus* and *M. confusus*) are being collected. Data on 3 *M. sanguinipes* populations are reported on: 1) entrance to the Bison Range (Hill: a level area at 799 m); 2) Tower 2, a west facing slope at 1366 m; 3) Trisky Creek, an east facing slope at 1097 m.

Grasshopper population parameters were obtained using 0.1 $m^2$ cages containing natural vegetation and grasshopper populations at varying densities and species combinations (Belovsky and Slade in press a, b, Belovsky 1990b, 1991). Over each summer, these measures were related to bi-weekly densities in the area that were measured using a catch-effort technique (Belovsky and Slade in press a, b). Whether or not avian predation reduced grasshopper densities was determined using 100 $m^2$ avian exclosures and control areas at each site/year (Joern 1986, Belovsky 1990b, 1991), and avian predation rates were measured using grasshoppers tethered in the environment (Belovsky *et al.* 1990, Belovsky 1990a, 1992).

The population parameters measured in the experimental cages included food-based carrying capacity in the absence of predation, abiotic-induced mortality, maximum *per capita* reproductive output when food is not limiting, *per capita* reproductive output per unit of available food, and intensity of interspecific competition. These values change between sites and years; however, food-based carrying capacity, abiotic factors, and expected adult lifespan which influences *per capita* reproductive output, seem to vary most. While these parameters for *M. sanguinipes* are still being collected and refined, current data can be used in population models to assess what mechanisms are limiting at each site and year.

A graphical population model can be used to summarize the results of my studies. The model uses a technique common to applied entomological studies of univoltine species, *i.e.*, Ricker Curves (Varley *et al.* 1973). Three basic population mechanisms have been identified in the study, and their equations and variables are presented and defined in Table 1.

**Factor 1) Density dependence – competition for food.** Reproductive output is constant at a maximum value and then declines as density increases (Fig. 1a). This is caused by both reduced survivorship from hatchling to adult, reduced adult longevity, and reduced reproductive rate as an adult. In my studies, this density dependence was found to arise principally from competition for food affecting survival (Belovsky and Slade in press a, b).

**Factor 2) Natural enemies.** Predation on grasshoppers (*per capita* predation rate) increased as density increased, and then decreased as density increased further (Fig. 1b).

**Factor 3) Abiotic factors.** Grasshopper populations demonstrated strong density dependence and very weak density independent mortality that might be attributed to abiotic factors, <7% of the variance in mortality within and between summers. However, there was one way that the grasshoppers did not respond to changing food abundance in a density dependent fashion; at certain sites as the summer progressed, food abruptly disappeared due to desiccation, reducing adult lifespan and reproductive output.

Combining the equations for the 3 processes, a Ricker Curve can be constructed (plot of $N_{t+1}$ versus $N_t$, where N is the number of hatchlings in a year) (Fig. 1c). Two distinct Ricker Curves (Cases) are obtained:

**Case A)** In Fig. 1.c.1, $N_{t+1}$ rises as $N_t$ increases, but then natural enemies/abiotic factors quickly lead to a decline in $N_{t+1}$, as $N_t$ increases further. Natural enemies and/or abiotic factors prevent the population from attaining its food-limited potential.

**Case B)** In Fig. 1.c.2, the curve representing $N_{t+1}$ versus $N_t$ has twin peaks. The first peak represents the conditions in Case A. The second peak represents the population released from natural enemies/abiotic factors, and limitation from food resources.

Population growth trajectories and the resulting stability conditions cannot be addressed with the current data. But, the equilibrium population(s) can be predicted, where a reference line ($N_{t+1} = N_t$) intersects the Ricker Curve. For Case B, equilibria can arise in three ways.

**Condition 1)** The reference line intersects only the first peak, so the population is maintained at low densities by natural enemies and/or abiotic factors (Fig. 2a).

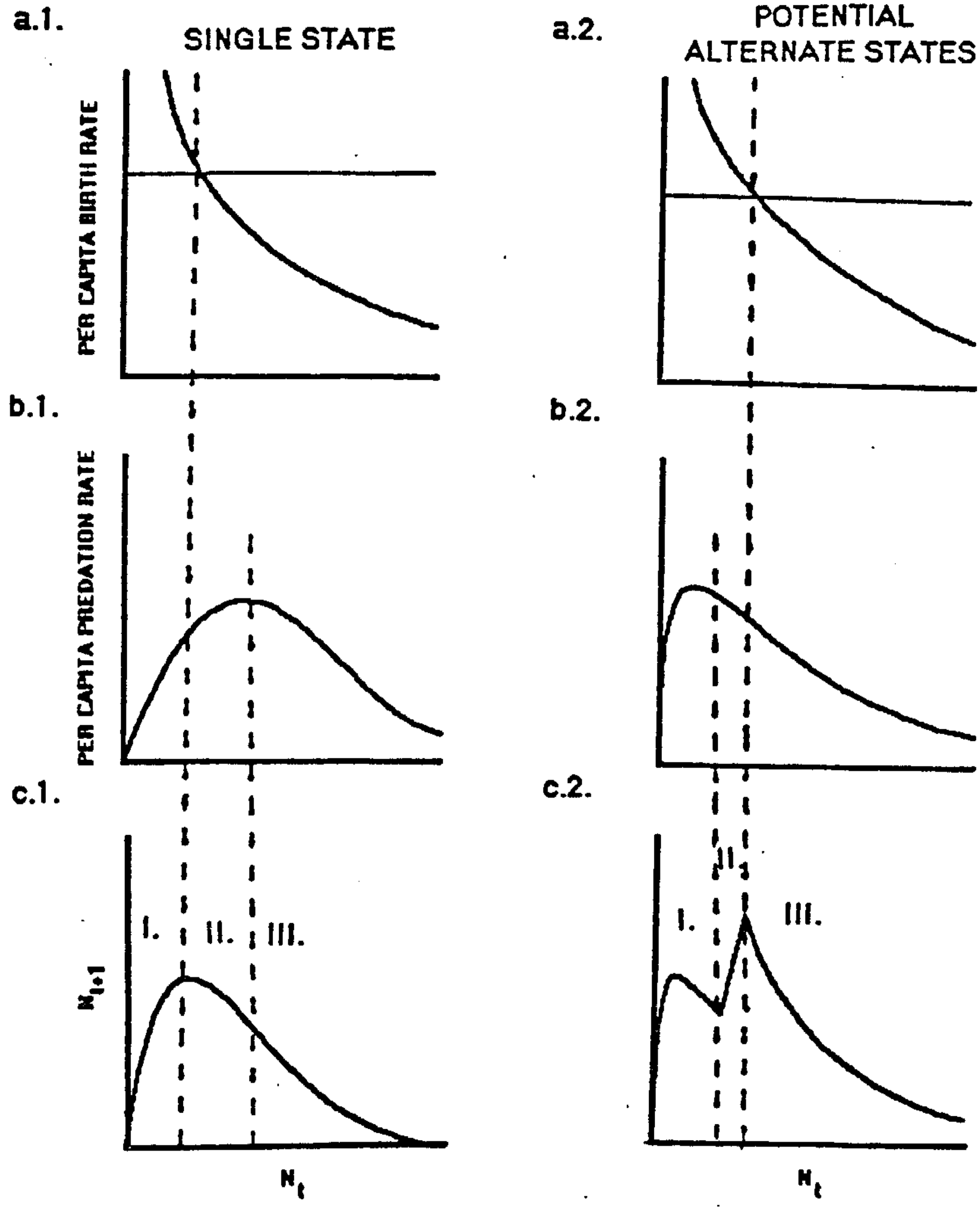
## TABLE 1.

A mathematical development of the Ricker Curve model depicted in Fig. 1 and 2 is presented. The parameters are defined as: density independent *per capita* reproductive rate (R); abiotic-induced *per capita* mortality rate (i); the aspect of natural enemy caused mortality rate that increases with density (a); the availability of food (I); the food-based (density dependent) *per capita* reproductive rate; the *per capita* maintenance food requirement (C); the aspect of natural enemy induced *per capita* mortality that decreases to an asymptotic value (b, c).

|  | **ONE STABLE STATE** | **TWO POSSIBLE STABLE STATES** |
|---|---|---|
| **REGION IN FIG. 4** | **EQUATION** | **EQUATION** |
| I. | $N_{t+1} = N_t R[1 - i - aN_t]$ | $N_{t+1} = N_t R[1 - i - aN_t]$ |
| II. | $N_{t+1} = N_t R'[(I/N_t - C) - i - aN_t]$ | $N_{t+1} = N_t R[1 - i - b/N_t - c]$ |
| III. | $N_{t+1} = N_t R'[(I/N_t - C) - i - b/N_t - c]$ | $N_{t+1} = N_t R'[(I/N_t - C) - i - b/N_t - c]$ |
| **LABELLED POINTS IN FIG. 5** |  |  |
| A |  | $N_t = (1 - i)/2a$ |
| B |  | $N_t = N_{t+1} = (R - iR - 1)/aR$ |
| C |  | $N_t = [c + (c^2 + 4ab)^{1/2}]/2a$ |
| D |  | $N_t = N_{t+1} = bR/(R - iR - cR - 1)$ |
| E |  | $N_t = [IR' + b(R - R')]/(R - iR - cR + CR' + iR' + cR')$ |
| F |  | $N_t = N_{t+1} = (R'I - bR')/(1 + R'C + iR' + cR')$ |
| **STABLE POINT CONDITIONS** |  |  |
| ONE POINT - PREDATION |  | $N_{t+1}$ at $C > N_t$ at C, and $N_{t+1}$ at $E < N_t$ at E |
| ONE POINT - COMPETITION |  | $N_{t+1}$ at $C > N_t$ at C, and $N_{t+1}$ at $E > N_t$ at E |
| TWO POINTS - PREDATION AND COMPETITION |  | $N_t$ at $C > N_t$ at B; $N_{t+1}$ at $E > N_t$ at E; |

FIG. 1.

Graphical development of a mechanistic model of grasshopper population dynamics is presented (see text). a) Birth rate is presented as a constant density independent value which declines as density increases (competition for food). b) Predation rates increase and then decline as the predator's functional and numerical responses saturate. c) Combining the above two responses with abiotic mortality factors, a Ricker Curve model (plot of population density at time t vs. time t+1) can be constructed.



**Condition 2)** The reference line intersects only the second peak, so the population is maintained at high densities and experiences food/competition limitation (Fig. 2b).

**Condition 3)** The reference line intersects both the first and second peak. In this case, the population can be limited as in Condition 1 or 2; the particular equilibrium attained depends upon initial densities, $N_t$ (Fig. 2c), and can annually vary between the Conditions.

The depiction of grasshopper populations using Ricker Curves, however, is not as simple as the two Cases and three Conditions presented above, because the Ricker Curves are not constant for a population, but vary between years with changing food abundance, adult lifespan, and abiotic factors. The various combinations of Cases and Conditions can produce three Domains in which the populations can fluctuate over time.

**Domain A.** If Case A and/or Case B-Condition 1 are met in all years, then the populations are predominantly limited by natural enemies and/or abiotic factors (Fig. 3a).

**Domain B.** If Case B-Condition 2 is met in all years, then the populations are always food/competition limited (Fig. 3b).

**Domain C.** If in some years Case B-Conditions 2 or 3 (high food abundance - low natural enemies/abiotic factors) occur, and in other years, Case A or Case B-Condition 1 or 3 occur (intense effects of natural enemies/abiotic factors - low food abundance), then the populations can vary between being attracted towards states controlled by food/competition and natural enemies/abiotic factors (Fig. 3c).

The Ricker Curve positions that define the Cases/Conditions in any year are presented in Fig. 2c, and are mathematically defined in Table 1, along with the needed relationships to produce each Case/Condition. An important value defining the Case/Condition in any year is the ratio of $N_{t+1}$ to $N_t$ at the greatest production of hatchlings ($N_{t+1}$) for a given initial population ($N_t$), when food is limiting (Point E, Fig. 2c). If the ratio is less than or equal to 1, then the population will be limited by natural enemies/abiotic factors; if the ratio is greater than 1, then the population might be food-limited, depending upon $N_t$. Furthermore, as the ratio increases above 1, natural enemy effects decrease and food-limitation always occurs.

Statistics comparing experimental results with model predictions require the following:

1) The Ricker Curve shapes (major points: Table 1) are computed using the population parameters that were experimentally attained (cages).

2) The Ricker Curve predictions of the mechanism limiting the population can be compared with experiments indicating the presence/absence of predator-limitation (exclosures).

3) Each population from a site/year was treated as an independent observation, so the ratios of $N_{t+1}$ to $N_t$ at point E on each population's Ricker Curve were correlated with the ratios of grasshopper population numbers from the controls and exclosures at each site/year.

FIG. 2.

In a Ricker Curve model equilibria occur where $N_t = N_{t+1}$. The number of stable equilibria predicted by the Ricker Curve model can be one, set by either natural enemies/abiotic factors (a) or food/competition (b), or two, one set by natural enemies/abiotic factors and the other by food/competition (c) (a third equilibrium between the two stable equilibria is a "saddle" point). The letters in c represent critical points that define the Ricker Curve's shape.

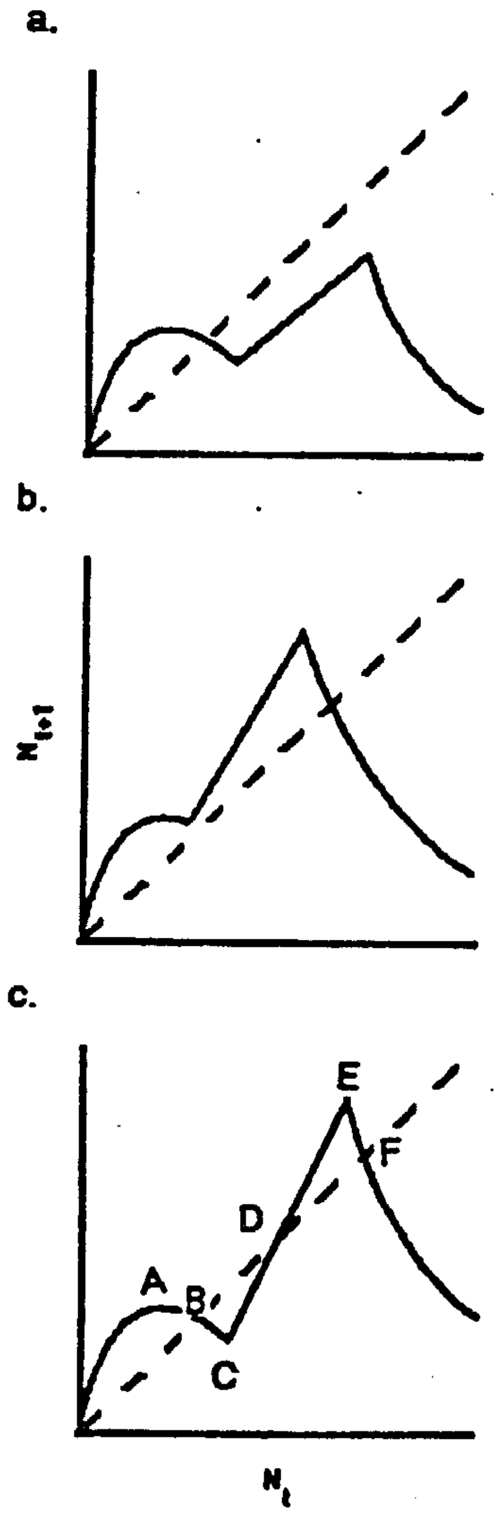
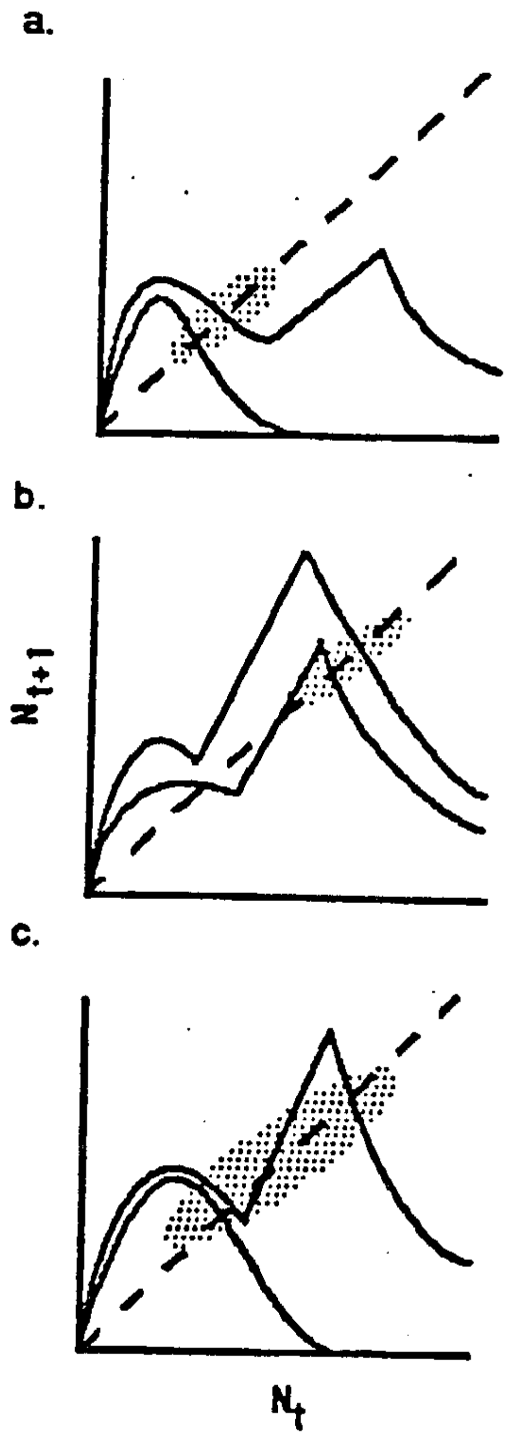


FIG. 3.

In each plot, two Ricker Curves are presented to depict the extreme annual conditions in an environment (low food - high abiotic-induced mortality vs. high food - low abiotic-induced mortality). This annual variability prevents populations from reaching equilibria, but the equilibria act as "attractors" to create a domain (shaded region) in which the population will vary. In a) natural enemy/abiotic factors dominate to limit the population; in b) food/competition dominate; and in c) natural enemies/abiotic factors and food/competition can dominate in different years.



4) If a Ricker Curve predicts a population limited by predation/abiotic factors or food/competition (Case A - Condition 3), then hatchling density ($N_t$) was used to determine which alternative should occur (observed $N_t$ vs. the value at Point D: Table 1, Fig. 2c).

## RESULTS:

Initial data used to develop the Ricker Curves were obtained at the Hill Site from 1981-1987 and 1989. Over these 8 years, *M. sanguinipes* populations were predicted to exhibit Case B/Condition 3 in 5 years, and Case B/Condition 2 in 3 years (Fig. 4). Furthermore, $N_t$ values were large enough when Case B/Condition 3 was predicted, that food/competition-limitation should be observed, rather than predator/abiotic factor-limitation. Therefore, populations were never predicted to be predator/abiotic factor-limited, and in 4 years (1985-1987, 1989), predator-limitation was not observed (avian exclosures), but food/competition-limitation was indicated (similar field and cage densities). This, however, was not an independent test of the model, since data used to test the model had been used to construct it.

Testing the model required data from years/sites where the Ricker Curve model had not been developed. Studies at the Hill, Tower 2, and Trisky Creek in 1990 and 1991 provided the needed data. Two parameters (food-based carrying capacity and adult lifespan modifying reproductive output) were measured; other parameters were from previous Hill studies.

Hill populations continued to demonstrate Case B/Condition 3 (Fig. 5) and food/competition-limitation, as observed in previous years. Therefore, over 10 years at the Hill site, Case B/Condition 2 and Case B/Condition 3 were equally observed.

At Tower 2 and Trisky Creek, Case B/Condition 3 was observed in 1990 (Fig. 5), and $N_t$ values were large enough so that food/competition appeared to be limiting, rather than predator/abiotic factors. In 1991, Tower 2 approached Case B/Condition 1, but $N_t$ was large enough to prevent predator/abiotic factor-limitation. However, Trisky Creek was defined by Case B/Condition 1 (Fig. 5), and predator-limitation was observed. At Tower 2 and Trisky Creek in 1991, predator-limitation was possible, because green vegetation disappeared in late summer due to desiccation, given each sites' slope/aspect and poor soil moisture retention.

The ratios of $N_{t+1}$ to $N_t$ at Point E (Table 1) were correlated with the ratios of population densities in the controls to exclosures (see MATERIALS AND METHODS). As expected, the ratios were highly correlated (Fig. 6: $r^2 = 0.98$, $N = 6$, $P \leq 0.001$); the greater the ratio at Point E, the less likely that predator-limitation was observed.

## DISCUSSION:

Results indicate that Domains B and C are observed in populations of *M. sanguinipes*. At the Hill site, predator-limitation was not observed over 10 years; however, at Trisky Creek and possibly Tower 2, predator-limitation occasionally occurred. Domain A was never observed, but these populations probably exist (*e.g.*, Joern 1986, in press; Fowler *et al.* 1990),

FIG. 4.

Basic Ricker Curve parameters (Table 1) measured at the Hill site during 1981-1987, 1989 are presented, along with the conceptualized shapes of the resulting extreme annual Ricker Curves.

| PARAMETER | VALUE |
|---|---|
| a | 0.093 deaths *per capita* |
| i | 0.35 - 0.70 deaths *per capita* |
| R | 25.0 - 33.8 hatchlings *per capita* |
| R' | 5.5 hatchlings *per capita*/g food ingested *per capita* |
| c | 0.021deaths *per capita* |
| b | 0.864 deaths |
| f | 9.2 - 59.0 g food/m² |
| C | 0.2 g food required *per capita* for maintenance |

CRITICAL VALUES ON RICKER CURVE

| | LOW FOOD - HIGH DENSITY INDEPENDENT MORTALITY | | HIGH FOOD - LOW DENSITY INDEPENDENT MORTALITY | |
|---|---|---|---|---|
| | $N_t$ | $N_{t+1}$ | $N_t$ | $N_{t+1}$ |
| A: | 1.61 | 6.04 - 8.18 | 3.49 | 28.40 - 38.39 |
| B: | 2.79 - 2.91 | 2.79 - 2.91 | 6.55 - 6.67 | 6.55 - 6.67 |
| C: | 3.16 | 0.48 - 0.65 | 3.61 | 28.13 - 38.04 |
| D: | 3.46 - 3.61 | 3.46 - 3.61 | 1.42 - 1.47 | 1.42 - 1.47 |
| E: | 5.20 - 5.60 | 17.46 - 19.83 | 11.54 - 16.53 | 212.94 - 238.33 |
| F: | 7.56 | 7.56 | 67.92 | 67.92 |

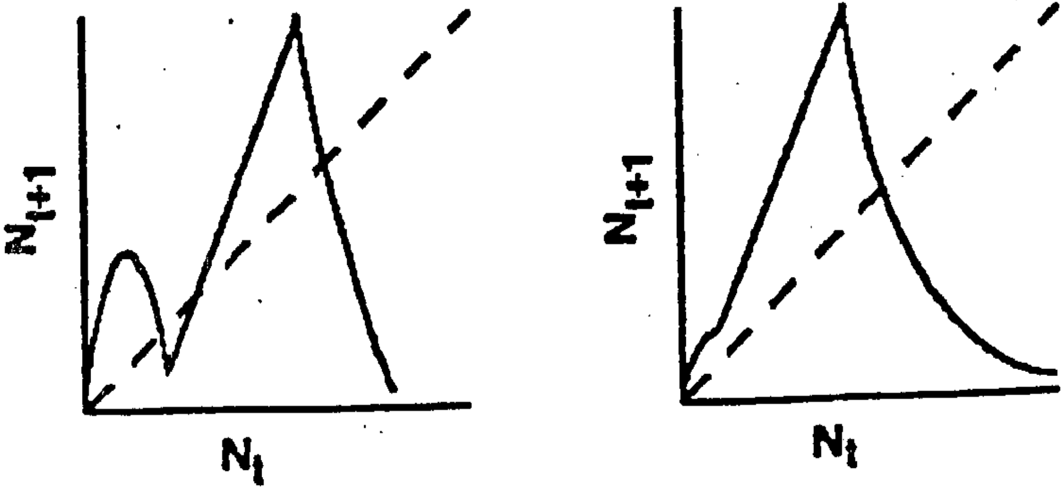


FIG. 5.

The Ricker Curve parameters that changed between three sites and over two years are presented, along with a plot of the Ricker Curve's conceptualized shape. The shape is depicted by varying the position of the reference line (striaght line: $N_{t+1} = N_t$).

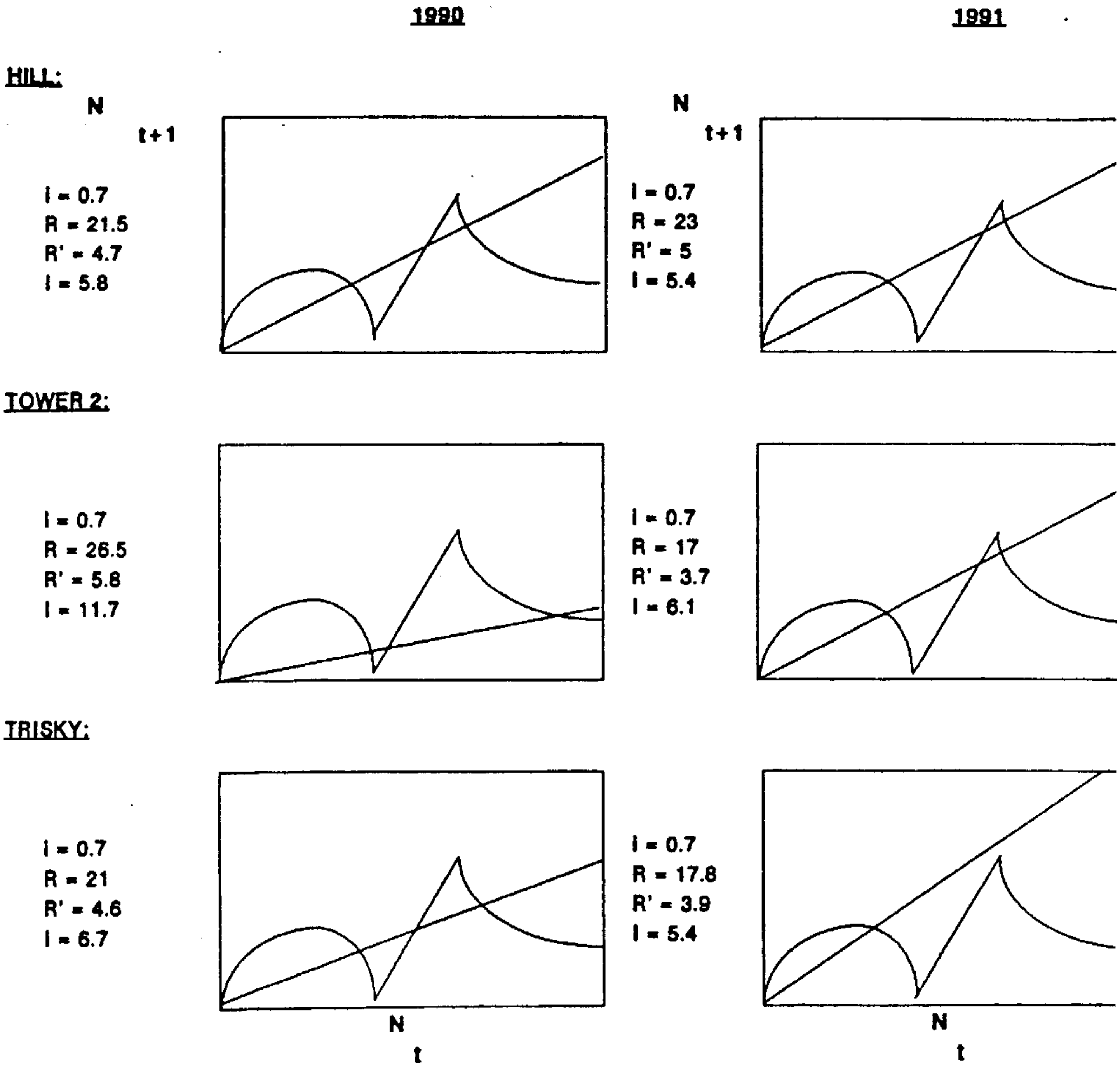
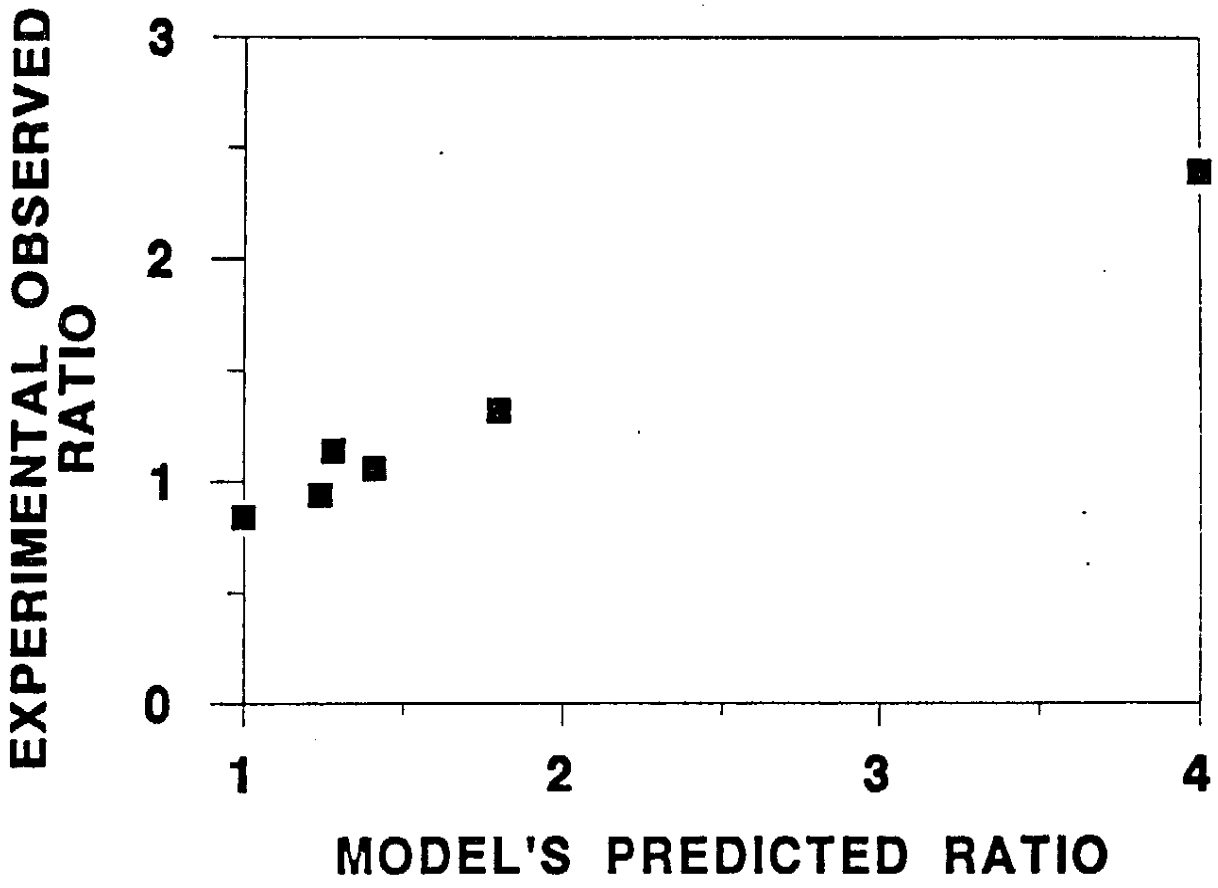


FIG. 6.

The $N_{t+1}/N_t$ at Point E (Fig. 3a) for the Ricker Curve for each site/year is plotted with the ratio of grasshopper numbers measured in the controls and avian exclosures at the site/year. This constitutes a test of the Ricker Curve model (see MATERIALS AND METHODS).



and I plan to study such a population. Domain A populations are probably characterized by soil and slope conditions that lead to desiccated vegetation early in the summer, which prevents grasshopper populations from attaining a level at which food-limitation can operate.

Annual shifts by populations from limitation by predation/abiotic factors and food/competition (Domain C) are consistent with methods of fitting grasshopper populations to Catastrophe Theory (Lockwood 1990, 1991). However, populations in Domain A or B would not be amenable to such modelling, and may be the reason that Catastrophe Theory models work for some populations, and not others. Therefore, Ricker Curve models, based upon explicit ecological mechanisms, potentially explain Catastrophe Theory predictions.

While my study results are still tentative, the technological value of identifying the three potential Domains is that they may indicate the need for different pest control strategies.

1) **Domain A** may not require control, since populations are maintained at low densities by predation/abiotic factors. This was not observed in my study.

2) **Domain B** produces <u>chronic</u> high density populations that can cause economic damage. These populations require less monitoring by pest managers, because they regularly approach pest levels. This was observed for two populations in my study.

3) **Domain C** occasionally produces outbreaks that cause economic damage; this will also require costly monitoring to know when populations approach economic levels and require control. This was observed for one population in my study.

Domains B and C are the main concern of pest managers, and the most efficient long-term control of these populations may be to force them into Domain A. Augmentation of natural enemies cannot accomplish this, since the populations are not susceptible to natural enemies, and pesticides cannot do this without continual application. Perhaps, this can be accomplished through habitat manipulations that change population parameters, and developing these methods will require greater understanding of grasshopper population ecology.

## <u>CONCLUSIONS</u>:

My preliminary results for grasshopper population ecology indicate:

1) Populations may be limited within Domains that are controlled by predators/abiotic factors, food/competition, or both in different years.

2) The Domains can be explicitly defined by a few biological parameters that can be measured and used in a Ricker Curve model.

3) Comparing predicted population behavior with that observed, the Domains have been identified in field populations.

4) These population differences are important for the monitoring of pest populations, and the development of novel long-term control strategies.

## LITERATURE CITED:

Belovsky, G. E. 1989. Grasshopper competition. USDA-APHIS-PPQ, Grasshopper Integrated Pest Management Project Annual Report (FY-90), Boiese, Idaho. pp. 45-50.

Belovsky, G. E . 1990a. Grasshopper competition and predation: biological control options. USDA-APHIS-PPQ, Grasshopper Integrated Pest Management Project Annual Report (FY-91), Boiese, Idaho. pp. 37-44.

Belovsky, G. E. 1990b. How important are nutrient constraints in optimal foraging models or are spatial/temporal factors more important? pp. 255-278. *In* Hughes, R. N. (ed.), Behavioural Mechanisms of Food Selection. NATO ASI Series, Vol. G 20, Springer-Verlag, Berlin.

Belovsky, G. E. 1992. Modelling avian foraging: implications for assessing the ecological effects of pesticides. *In* Kendall, R. J. and T. E. Lacher, Jr. (ed.s), The Population Ecology and Wildlife Toxicology of Agricultural Pesticide Use: a modelling initiative for avian species. Lewis press.

Belovsky, G. E. and J. B. Slade. in press a. Grasshopper survival: relationships among weather, food abundance and intraspecific competition. Ecology.

Belovsky, G. E. and J. B. Slade. in press b. Grasshopper reproduction: response to food and density. Ecology.

Belovsky, G. E., J. B. Slade, and B. A. Stockhoff. 1990. Susceptibility to predation for different grasshoppers: an experimental study. Ecology 71: 624-634.

Fowler, A. C., R. L. Knight, T. L. George and L. C. McEwan. 1991. Effects of avian predation on grasshoppers in North Dakota grasslands. Ecology 72: 1775-1781.

Joern, A. 1986. Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in sandhills grassland. Oikos 46: 243-249.

Joern, A. in press. Variable impact of avian predation on grasshopper assemblies in sandhills grassland. Oikos.

Lockwood, J. A., and D. R. Lockwood. 1990. Catastrophe theory. USDA-APHIS-PPQ, Grasshopper Integrated Pest Management Project Annual Report (FY-90), Boiese, Idaho. pp. 39-44.

Lockwood, J. A., and D. R. Lockwood. 1991. Predictive modelling of grasshopper population dynamics using catastrophe theory. USDA-APHIS-PPQ, Grasshopper Integrated Pest Management Project Annual Report (FY-91), Boiese, Idaho. pp. 32-36.

Varley, C. G., G. R. Gradwell, and M. P. Hassell. 1973. *Insect Population Ecology: An Analytical Approach.* University of California Press, Berkeley.