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Dynamics of two Montana grasshopper populations: relationships among weather, food abundance and intraspecific competition

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Abstract The population dynamics of two grasshoppers (*Melanoplus femurrubrum* and *M. sanguinipes*) were studied using experimental microcosms over 8 years at a Palouse prairie site in Montana. Grasshopper density, survival and reproduction in the experimental populations responded in a density-dependent fashion to natural and experimental changes in food availability for all grasshopper developmental stages, both within and between all years. We observed that field populations of the grasshoppers at the site exhibited density, survival and reproductive responses similar to the experimental populations over the period of the study. Because we could not identify any differences between the field and microcosm environments or the grasshopper individuals in them, we contend that field populations were ultimately limited by food within and between years. Density-dependent food limitation occurred for all age categories over the entire summer, because food abundance declined relative to grasshopper food requirements over the summer. Food limitation occurred between years, because in years with the lowest food abundance, the populations produced more hatchlings for the next year than could be supported by the highest observed food abundance. Finally, the observed annual changes in food abundance were correlated with the annual variation in weather (rainfall and temperature), which indicated that the long established relationship between grasshopper densities and weather conditions does not imply population limitation by density-independent processes.

Key words Orthoptera · Acrididae · Grasshoppers
Population dynamics · Food limitation

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Introduction

Grasshopper densities are often correlated with the previous year's temperature and precipitation; pest managers use these relationships to predict outbreaks (Smith 1954; MacCarthy 1956; Edwards 1960; Bird and Romanow 1966; Bird et al. 1966; Riegert 1968; Gage and Mukerji 1977; Rodell 1977). Even though the processes underlying these correlations are not well understood (Lockwood and Lockwood 1989, 1990, 1991), the correlations have led ecologists to argue that grasshopper populations are largely limited by density-independent processes (Dempster 1963; Andrewartha and Birch 1984), i.e., retarded development, time for ovipositing, and fungal infection with moisture. Nonetheless, when the previous year's grasshopper density is included in correlations, a density-dependent effect emerges (Lockwood and Kemp 1988; Kemp and Dennis 1993).

A correlation between density and weather need not imply that density-independent factors principally limit a population. First, if the population is primarily limited by density-dependent processes which do not vary over time, a correlation with weather can emerge when the less important density-independent processes change with weather (Horn 1968). Second, if a population's carrying capacity varies with weather, a population's numbers can be correlated with weather, even if it is limited by density-dependent processes (veiled density-dependence, sensu Strong 1984, 1986a,b). Therefore, correlations between density and weather do not elucidate the mechanisms limiting a population. Rather, specific population mechanisms must be investigated to determine how each might vary with weather and population density (Varley et al. 1973).

We have reported on a 6-year experimental study of the effects of predation on grasshopper (Orthoptera, Acrididae) populations at a site in Montana, finding that predation did not reduce total grasshopper numbers, but actually increased numbers, possibly by reducing competition for food (Belovsky and Slade 1993). We also found that grasshopper numbers varied among years and

Table 1 Vegetation and weather parameters (precipitation and temperature for the plant growing season: April–Sept.) at the study site in Montana

Year	% Grass	Total plant biomass (g/m^2)	Mean plant quality (% soluble)	Edible (g soluble) m^2)	Precipitation (cm)	Temperature (°C)
1981	70.3	171.4	34.4	59.0	16.1	14.7
1982	88.3	98.3	27.4	26.9	16.4	15.7
1983	93.9	132.2	31.9	42.2	17.6	16.1
1984	93.1	24.5	38.5	9.4	10.9	15.9
1985	73.4	51.9	46.3	24.0	18.6	16.8
1986	94.8	38.2	39.8	15.2	17.8	17.4
1987	73.1	65.0	35.5	23.1	17.2	16.4
1989	74.0	40.8	37.6	15.3	16.9	16.5

that this variation was correlated with changes in food abundance. We report here the results from experiments conducted at the same site with the two most common grasshopper species (*Melanoplus femurrubrum* and *M. sanguinipes*) to determine whether competition for food limits their survival and/or reproduction. Observing food limitation would be counter to generally held views of how grasshopper and other terrestrial herbivore populations are thought to be limited (Hairston et al. 1960; Slobodkin et al. 1967; Lawton and Strong 1981; Strong et al. 1984; Hairston 1989).

We employed experimental populations in microcosms (cages) in the field; cages maintain field abiotic conditions (Belovsky and Slade 1993), so that density-independent processes are unchanged. To support the idea of food limitation for these grasshoppers, we must observe: (1) that grasshopper densities attained in control cages are not different from their densities in the field, and (2) cages receiving supplemental food have higher grasshopper survival and/or reproduction than controls. We examined which grasshopper developmental stages (if any) are affected most by food limitation, and related changes in the plant resource over the summer to changes in survival and reproduction. We also examined the ability of the grasshopper populations to "track" changes in the plant resources between years by producing sufficient offspring to assure food limitation in the next year.

Materials and methods

Study site

We conducted the study (1980–1989, except 1988) on 2 ha of the National Bison Range, Moiese (Lake and Sanders Counties), Montana, at an elevation of 800 m. The site is typical intermountain prairie of the Pacific Northwest (i.e., Palouse) dominated by C_3 grasses. Dominant grasses (Poaceae) at the site were *Poa pratensis* (L.) and *Elymus smithii* (Rydb.), while the composites (Asteraceae), *Achillea millefollium* (L.), *Aster falcatus* (Lindl.) and *Heterotheca villosa* (Pursh), were dominant forbs. These five plant species comprised over 90% of plant biomass (24.5–171.4 g/m^2 in September during the study: Table 1). During the study, the plant growing season's (May–August) mean daily air temperature was 16.2°C (14.7–17.4°C: Table 1) and precipitation was 16.4 cm (10.9–18.6 cm: Table 1), based on measurements made at the National Bison Range headquarters located less than 500 m from the study site. The most common grasshoppers were *Melanoplus femurrubrum* (DeGeer) and *M. sanguinipes* (Fabr.) which are univoltine, feed on both grasses and forbs, overwinter as eggs, and begin to hatch in mid-June. These grasshoppers accounted for 82% (57–91% in different years) of grasshopper individuals in June-September.

Field and microcosm populations

For microcosm populations to be relevant for deciphering field population dynamics through density and food manipulation, they must exhibit similar population dynamics to those observed in the field, and the individuals comprising both populations must be similar in their nutrition (diet composition and food intake) and body mass, which are traits related to survival and reproduction.

Field

We sampled field grasshopper densities in a 100 m^2 area using a catch-effort technique (Southwood 1978). To contain the grasshoppers, the area was surrounded with nylon netting (1.25 m wide). Two people caught grasshoppers within the area for three to four 15 min periods over 2 h in a day, and placed them in 70% ethyl alcohol for later examination (see below). The x-intercept of the regression line for the sum of prior catches (independent variable) versus the current catch (dependent variable) for each period is an estimate of density. In 1986–1987 and 1989, densities were sampled outside the cages in a different 100 m^2 area every 2 weeks from the 1st week of July through September. In 1981–1985, we sampled densities only in mid-September.

Because nymphs are very patchily distributed at hatching and do not move much in their first few weeks, they were sampled by placing a cardboard box (0.5 m×0.5 m×0.5 m) coated with pitch over a patch of vegetation so that all the individuals in the patch were caught. Twenty patches of vegetation were sampled each year (1983–1985) at the time of peak hatching (late June) to estimate the range of densities at hatching.

We used alcohol-preserved grasshoppers to measure relative abundance of the two species, their sex ratios, their adult body masses (wet), adult absolute food intake, adult diet composition and reproductive output. Food intake is the wet mass of plants in the foregut dissected from the grasshoppers. Relative diet composition was measured using microhistological techniques to identify foregut contents as the proportion of grass versus forb fragments (Ueckert 1968; Ueckert et al. 1972). Egg pods are difficult to find in the soil, so the number of developed ovarioles in dissected females was used as an index of reproductive potential, because this value is positively correlated with female egg production (Uvarov 1966). Developed ovarioles are larger than undeveloped ones and "yellowish" in color, because they have been provided with nutrients during and after vitellogenesis (Uvarov 1966). Most ovarioles were not actively producing eggs and, therefore, were not counted.

Microcosm

Grasshopper populations were established in field cages made of aluminum screen with a basal area of 0.10 m^2 and a height of 0.90 m. Each cage was buried in the ground and secured with stakes to minimize wind damage; the top of the cage was closed with clips which permitted easy access. Cages were placed in a grid separated by at least 2 m and were assigned treatments randomly. Each year, cages were placed in a different area to avoid pseudo-replication and the effects of past herbivory from experiments. We placed each cage over a similar patch of vegetation including some of the dominant grass and forb species, but could not ensure that cages contained equal plant biomass or similar relative abundances of plant species. However, replicates for the different treatments helped minimize any differences between cages. Grasshoppers were caught at an adjacent site with similar vegetation, kept in terraria for 2 days prior to stocking, and provided with ad libitum fresh food collected from the site twice a day. Holding grasshoppers for 2 days minimized using injured individuals.

Experimental treatments included: (1) grasshopper species stocked in the cage (two species), (2) grasshopper developmental stage stocked in the cage (three stages), and (3) grasshopper density stocked in the cage (three levels). We used all treatments in some, but not all, years (Table 2), due to time limitations. Each cage was stocked only with individuals of a single species and developmental stage (early instars: first to third; late instars: fourth to fifth; adults). Developmental stage was identified by wingpad characteristics. No effort was made to ensure an equal sex ratio with early instars, since their sex is not easily discerned, but equal sex ratios were used for late instars and adults. Cages were stocked with nymphs during the last week of June, and cages with adults in the 1st week of August. The different densities of grasshoppers (Table 2) placed in cages depended upon whether nymphs or adults were used and spanned the range of nymphal densities observed in patches of vegetation at peak nymphal emergence (late June). In each year, field densities varied from 1.4 to 24.3 nymphs/0.1 m^2 (cage-equivalent area) in patches of vegetation, while the mean was 7.0–10.1 individuals/0.1 m^2 of vegetation (see *Field*).

Every 2 days, two observers censused the grasshoppers in each cage. They recorded numbers of survivors and their developmental stages along with recent bodies (not dry). Body counts provided a check on the census. Survival was measured as the proportion of individuals surviving between developmental stages: (1) the percentage of early instars molting to late instars, (2) the percentage of late instars molting to adults, and (3) the percentage of late instars surviving to the constant adult density which was maintained until late September, when cold nights (<–7°C) began to kill grasshoppers. In 1983, the length and dry mass (60°C for 48 h) of each dead body in the cages initially stocked with adults was measured and compared with surviving individuals.

Caged grasshopper densities expressed on a square meter basis could not be directly compared to field densities (see *Field*), since cages were only placed over patches of vegetation. Therefore, the cage density was multiplied by the proportion of the field area that was covered by vegetation, and by the ratio of mean plant biomass in patches of vegetation in the field to patches in the cages at the end of the experiment (see *Food resources*). At the end of the experiment (mid- to late September), we preserved surviving grasshoppers in 70% ethyl alcohol to measure body mass, diet analysis, food intake and reproductive output (see *Field*). Reproductive output was measured as developed ovarioles (see *Field*), because egg pods were difficult to recover from the soil, especially when they were frequently deposited along the edges of the cage and broke apart when the cage was removed. In addition, we attempted to leave the cages in position over the winter to measure hatchling emergence next June, but the cages did not withstand winter winds and large mammal activity very well. To estimate the hatchability of eggs, ten *M. sanguinipes* egg pods were collected from cages in 1985 and placed in five 0.25 l jars (two pods/jar) containing vermiculite. The jars were kept outdoors from October 1985 to July 1986, and the hatchlings that emerged were counted; in late-July, we opened the egg pods and counted the unhatched eggs.

Food resources

To examine the role that food resources may play on population processes, the characteristics of natural vegetation in the field and cages can be correlated with density, survival and reproduction. In addition, food can be supplemented in cages and the population responses can be measured.

Field

All green-plant tissue does not constitute food for an herbivore. Identifying what portion might be edible for grasshoppers is problematic given the wide array of plant nutritional, toughness, phagostimulatory and secondary compound characteristics that influence diet selectivity by grasshoppers (Chapman 1990; Simpson 1990; Bernays and Bright 1993; Hinks et al. 1993). However, plant solubility in HCl and pepsin (Terry and Tilley 1964) may provide a simple and predictive index of nutritional value, because it is correlated with other chemical characteristics of plants, including protein content (Heidorn and Joern 1987). To determine whether solubility is an index of plant nutritional quality for these grasshoppers, we correlated solubility of different plant species with the in vivo digestibility of these plants for the grasshoppers.

M. sanguinipes' in vivo digestibility was measured in feeding trials during the summers of 1986 and 1987. Five individuals were placed in a 1 l jar for 3 days and provided with ad libitum amounts of a single plant species at 8:00 a.m. and 4:00 p.m. each day. Prior to the feeding trial, these grasshoppers were taken from the field and fed the plant species for 24 h. The fresh vegetation was weighed before providing it to the grasshoppers; weights were converted into dry mass using equivalent calibrated samples of the plants. At the time of the next feeding, the remaining vegetation was removed, dried and weighed to measure the dry mass consumed as the difference. The vegetation provided to the grasshoppers was kept fresh by placing it in a vial containing water. At the end of the experiment, we collected and weighed the frass. ADM (assimilated dry matter) was measured as:

ADM = (dry mass of food consumed - dry mass of frass)/dry mass of food consumed.

Mean ADM was calculated for each plant from five feeding trials [grasses: *Dactylis glomerata* (L.), *Poa pratensis* in 2 years, *Agropyron cristatum* (L.), and *Elymus smithii*; forbs: *Melilotus officinalis* (L.), *Taraxacum officinale* in 2 years, *Heterotheca villosa*, *Achillea millefolium*, and *Symphocarpus occidentalis* (Hook.)]. Mean ADM values were correlated with HCl and pepsin solubilities measured from plant samples.

In mid- to late September, the proportion of the site covered by vegetation was measured using 25 toe-points with each point recorded as striking bare ground or vegetation (Daubenmire 1947). At this time, ten 0.1 m^2 plots were placed in randomly selected patches of vegetation and the vegetation was clipped. In 1985–1987 and 1989, the vegetation was sampled every 2 weeks starting with the 1st week of July. We clipped only living (green) plants and divided them into grasses and forbs. The samples were dried for 48 h at 60°C and then weighed, ground in a Wiley Mill (40 mesh screen), and digested (0.5 g) in HCl and pepsin (Terry and Tilley 1964).

Microcosm

Food abundance was supplemented for grasshoppers in cages during some years by providing additional water to the vegetation (Table 2), because water limits plant growth in semi-arid regions such as our site. Water was sprayed on the soil in the cage; this minimized the grasshoppers' ability to drink water, while providing water for plants. Water was added every 2 days, and the amount (150 ml/cage) increased availability over each year's natural precipitation by 88–150%. Ten cages without grasshoppers were used to show how additional water changed the vegetation; five received no

Table 2 The microcosm experiment in each year of the study. Developmental stages of *Melanoplus femurrubrum* and *M. sanguinipes*, density levels and supplemented food (*no* natural; *yes* natural and supplemented) are defined in the text

Year	Species	Density levels – supplemented food			Cages (replicates – total)
		Developmental stage Early instars	Late instars	Adults	
1981	*M. femurrubrum*			10/cage-no	3–3
	M. sanguinipes			10/cage-no	3–3
1982	*M. femurrubrum*			10/cage-no	6–6
	M. sanguinipes			10/cage-no	6–6
1983–84	*M. femurrubrum*			10/cage-no	5–5
	M. sanguinipes			10/cage-no	5–5
1985	*M. femurrubrum*	10, 15 or 20/cage-no	10, 15 or 20/cage-no	10/cage-yes	5–40
	M. sanguinipes	10, 15 or 20/cage-no	10, 15 or 20/cage-no	10/cage-yes	5–40
1986	*M. femurrubrum*	6, 10 or 16/cage-no	6, 10 or 16/cage-no	10/cage-yes	5–40
	M. sanguinipes	6, 10 or 16/cage-no	6, 10 or 16/cage-no	10/cage-yes	5–40
1987	*M. femurrubrum*	6, 10 or 16/cage-yes	6, 10 or 16/cage-yes		5–60
	M. sanguinipes	6, 10 or 16/cage-yes	6, 10 or 16/cage-yes		5–60
1989	*M. femurrubrum*	6, 10 or 16/cage-yes	6, 10 or 16/cage-yes	10/cage-yes	5–70
	M. sanguinipes	6, 10 or 16/cage-no	6, 10 or 16/cage-no	10/cage-no	5–35

added water (controls) and five received water. Finally, the vegetation in cages was clipped and analyzed in the same way as the field vegetation at the end of the experiment (mid- to late September).

Statistical analysis

All statistics were computed using SYSTAT (Wilkinson 1990). Survival measures (p) were LOGIT transformed [log p - log $(1-p)$] to normalize values and to eliminate autocorrelation in assessing density dependence (Hails and Crawley 1992). Because survival can equal 0 or 1, and the LOGIT transformation of these values is undefined, the LOGIT transform was computed using the correction: log $(p + 1/6)$ - log $(1-p + 1/6)$ (Mosteller and Tukey 1977). Regression and unbalanced ANOVA and ANCOVA were employed. Unbalanced designs were needed because all treatments were not represented by the original number of replicates due to cages lost to wind and animal damage (i.e., deer), and because some treatments could be pooled.

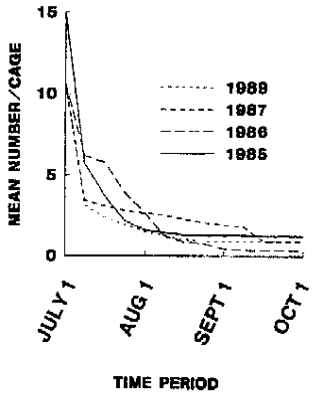

Fig. 1 The decline in mean numbers of the univoltine grasshoppers in cages with natural vegetation during four summers. Values are averaged for all cages regardless of species or initial density stocked in the cage

Results

Comparison of field and microcosm populations

Estimates of field population densities had coefficients of variation ranging from 8 to 15%. In cages, counts of dead bodies accounted for only 30–50% of missing early instar nymphs because their small size made them hard to see and easily removed by ants which entered cages. However, 80–98% of missing late instar nymphs and adults were found as bodies. Therefore, we were confident in the accuracy of our density and survival estimates.

Grasshopper numbers in the cages declined over the summer to a constant number that was maintained until the experiment's end (Fig. 1). In cages stocked with nymphs, the decline to constant density required 30–40 days, and the constant density was maintained for 50–60 days. In cages stocked with adults, the decline was more rapid (6–10 days) and the constant density was maintained for up to 45 days.

Density

The constant adult densities in cages did not differ between the two grasshopper species (Table 3: $F = 0.004$, $df = 1, 10$, $P \leq 0.93$), so their densities were averaged. Consequently, we compared the average for the constant adult densities observed each year for the two species in cages to that year's combined field densities for the two species in mid-September (Table 3). The correlation was very good (Fig. 2a: $r^2 = 0.96$, $n = 6$, $P \leq 0.001$); the slope of the regression was not different from 1.0 (0.87, SE = 0.21), and the intercept was not different from zero (0.05, SE = 0.05). For cages started with nymphs, we

Table 3 Characteristics of grasshopper (*Melanoplus femurrubrum* and *M. sanguinipes*) populations in the field and cages initially stocked with adults. Standard deviations (±) and sample sizes (in parentheses) are presented

Year	Density (no/m²)	Cage density (no/cage)		Sex ratio (males/females)		Developed ovarioles (no/female)		Females body mass (mg wet mass)	
		M. femur.	*M. sang.*	*M. femur.*	*M. sang.*	*M. femur.*	*M. sang.*	*M. femur.*	*M. sang.*
Field									
1981	12.32			2.09	0.76	27.00±6.88 (13 females)	27.38±9.2 (23 females)	392±62 (13 females)	492±68 (23 females)
1982									
1983	10.26			0.75	0.67	22.75±2.25 (10 females)	23.80±3.1 (13 females)	359±27 (10 females)	460±50 (13 females)
1984	2.67			0.35	0.53	17.40±4.40 (20 females)	20.04±4.00 (25 females)	356±48 (20 females)	375±59 (25 females)
1985	4.22				0.93		24.24±5.70 (21 females)		418±61 (21 females)
1986	6.99			0.94	0.80	21.11±3.26 (12 females)	21.88±4.80 (18 females)	300±38 (12 females)	359±90 (18 females)
1989	10.61			1.00	0.81				
Cages									
1981	13.8	4.33±1.15 (3 cages)	6.33±1.15 (3 cages)	0.25	0.00	17.00 (2 females)	16.40±5.30 (8 females)	234 (2 females)	398±48 (8 females)
1982		3.50±2.24 (6 cages)	3.80±2.87 (6 cages)	0.14	0.00	16.50±2.64 (7 females)	17.30±5.60 (7 females)	308±36 (7 females)	392±35 (7 females)
1983	10.35	4.40±2.50 (5 cages)	5.20±1.79 (5 cages)	1.37	1.20	16.00±2.32 (10 females)	10.00±4.83 (11 females)	296±26 (10 females)	481±76 (11 females)
1984	2.31	2.00±1.00 (3 cages)	2.33±0.58 (3 cages)	0.00	0.00	14.00 (2 females)	16.50 (2 females)	312 (2 females)	356 (2 females)
1985	3.85	4.80±2.68 (5 cages)	4.40±0.55 (5 cages)						
1986	5.76	3.40±1.34 (5 cages)	4.00±0.71 (5 cages)	0.57	0.22	12.00±6.27 (9 females)	10.00±1.10 (7 females)	219±52 (9 females)	359±90 (7 females)
1989	10.83	2.44±1.67 (5 cages)	3.25±1.67 (5 cages)	0.50	1.09				

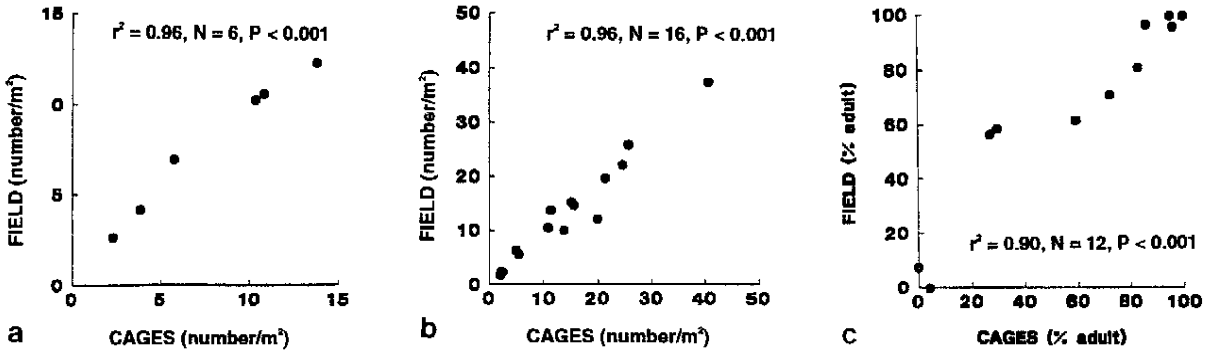

Fig. 2a–c The average numbers for both grasshopper species combined are compared between the caged populations with natural vegetation and field populations. Densities are presented on a square meter basis. **a** Comparison of the constant adult density in the cages and the mid-September density of adults in the field for each year; **b** comparison between the bi-weekly cage and field population numbers (see text); **c** comparison between the bi-weekly age structure for caged and field populations for 1986, 1987 and 1989

compared densities (Fig. 2b) in mid-September in 1985, and bi-weekly in 1986 (August - September), 1987 and 1989 (July - September). The correlation was good ($r^2 = 0.96$, $n = 16$, $P \leq 0.001$); the slope of the regression did not differ from 1.0 (0.90, SE = 0.05), and the intercept was not different from zero (0.55, SE = 0.89). Therefore, densities in cages were not different from the field.

Age structure

Combining data for the two grasshopper species, we found that the bi-weekly relative abundance of develop-

Table 4 Characteristics of individual grasshoppers inside and outside the cages in 1983 are presented. Standard deviation (±) and sample size (*n*) are provided. We examined only ten of the individuals (five males and five females) for diet composition (*ns* not significant, *n* number of individuals)

Species	Trait	Inside	Outside	Significance
Melanoplus femurrubrum	Adult mass (mg live mass)	271±36 *n*=19	300±67 *n*=20	*t*=1.67 *ns*
	Food in crop (mg fresh)	14±7 *n*=19	10±6 *n*=20	*t*=0.50 *ns*
	Diet (% forb fragments)	54±29 *n*=10	68±27 *n*=10	*t*=1.10 *ns*
M. sanguinipes	Adult mass (mg live mass)	423±83 *n*=22	420±62 *n*=23	*t*=0.14 *ns*
	Food in crop (mg fresh)	24±12 *n*=22	15±9 *n*=23	*t*=2.85 *P*<0.01
	Diet (% forb fragments)	47±19 *n*=10	47±35 *n*=10	*t*=0 *ns*

mental stages in cages initially stocked with early instars was not different from field distributions (Fig. 2c: arcsine square root transformation, $r^2 = 0.90$, $n = 12$, $P \leq 0.001$), because the slope was not different from 1.0 (0.93, SE = 0.10) and its intercept was not different from zero (0.16, SE = 0.11). Therefore, the developmental rate of grasshoppers in cages was not different from the field.

Sex ratio

The mean ratio of males to females for adults of both grasshopper species in cages was lower than in the field in 7/10 cases (Table 3), and the slope of the regression (0.12, SE = 0.10) was significantly less than 1. Therefore, male survival was lower relative to female survival in the cages than the field.

Body mass, food intake and diet

No differences in body mass and diet composition were observed between grasshoppers in the field and cages, but a significant difference for food intake (Table 4) was found, and this was the opposite of the expectation that food intake in cages may be reduced due to restricted movement preventing individuals from finding suitable food plants. Therefore, we could not identify any individual differences between grasshoppers in the cages and field that might modify population processes due to anticipated cage-effects.

Reproductive output

No significant differences between the mean number of developed ovarioles per female of either species in the cages and field were observed for each year, but the mean number was not significantly correlated between the cages and field (Table 3: $r^2 = 0.08$, $n = 8$, $P \leq 0.50$), with a trend for lower reproduction in cages. *M. sanguinipes* egg pods kept in the field from October 1985 through July 1986 had 31.8% hatchability.

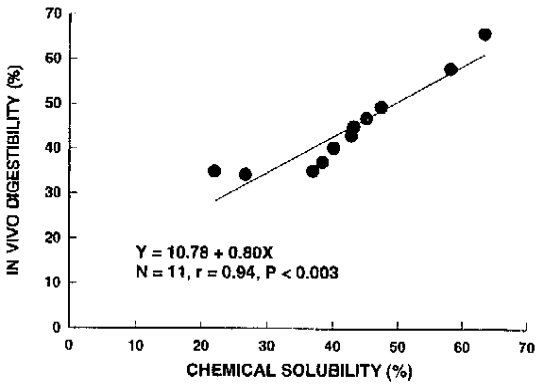

Fig. 3 The in vivo dry matter digestibilities of different plant species, and the same plant species in different years, compared with the plants' solubilities in HCl and pepsin

Food resources

Plant quality

We found a very strong correlation between the solubility of plants in HCl and pepsin and *M. sanguinipes*' in vivo digestibility (ADM) of the plants (Fig. 3).

Field and cages

At the end of the microcosm experiments (mid- to late September), mean total living-plant biomass did not differ between the field and cages ($F = 1.74$, $df = 1, 202$, $P < 0.19$). The relative abundance of grass was lower in the field than cages ($t = 2.36$, $df = 12$, $P < 0.05$): this was expected, because we placed cages over a combination of grasses and forbs, and forbs were more patchily dis-

Table 5 Comparison of vegetation in supplemental watered and natural vegetation cages without grasshoppers at the end of the experiment. Standard errors (±) and sample sizes (*n*: cages) are provided. In the ANOVA (unbalanced) tables, the sign (in parentheses) represents the correlation effect of the treatment

Year/ treatment	Biomass			Chemical solubility	
	Grass (g/m^2)	Forb	Total	Grass (% soluble)	Forb
1985					
Natural (n=10)	5.05±0.79	1.99±0.56	7.04±0.78	38.73±1.43	54.83±1.72
Water (n=10)	5.92±0.71	2.63±0.87	8.54±0.63	36.96±0.94	49.50±0.74
1986					
Natural (n=8)	3.64±0.65	0.40±0.20	4.41±0.56	45.14±2.06	58.48±1.63
Water (n=4)	3.83±0.75	0.76±0.22	4.23±0.77	39.53±2.58	48.80±2.89
1987					
Natural (n=3)	7.16±2.22	1.37±1.23	8.53±2.55	40.77±3.35	61.60±2.15
Water (n=3)	5.67±2.07	4.50±2.94	10.2 ±1.05	43.43±3.56	45.50±1.59
1989					
Natural (n=5)	3.64±0.77	0.70±0.26	4.34±0.96	37.80±1.63	58.68±1.03
Water (n=5)	5.82±1.99	2.28±1.30	8.10±1.64	32.90±1.77	43.78±1.25

Categorical variable	ANOVA tables for					
	Total biomass			Chemical solubility		
With or without supplemental water	F=5.09	df=1, 40	P<0.03 (+)	F=26.17	df=1,77	P<0.001 (–)
Year	F=7.86	df=3, 40	P<0.001	F=4.02	df=3,77	P<0.01
Grass vs. Forb	not applicable			F=169.66	df=1,77	P<0.001
Year×water	F=1.24	df=3, 40	P<0.31	F=2.02	df=3,77	P<0.12

tributed than grasses in the field. The mean solubilities in HCl and pepsin for grasses and forbs in the field were not different from cage values.

Supplemented food

Supplemental watering of cages without grasshoppers significantly increased plant biomass and decreased plant solubility in HCl and pepsin (Table 5). The increased plant biomass, even though plant quality declined, may have increased food for the grasshoppers.

Density with supplemental food

For cages started with *M. sanguinipes* nymphs (Fig. 4a–c), supplemental water increased densities of all developmental stages, but the effectiveness of water in increasing density varied among years. Effectiveness decreased in years with greater precipitation, because added water should increase plant production more in dry years. For cages started with adults of either grasshopper species, supplemental water increased constant adult densities (Fig. 4d). Adding water per se did not have an effect, because when water was provided for grasshoppers in the form of wet paper towelling, their density and survival was not increased (Belovsky and Slade, unpublished data). Therefore, the added water appeared to increase food availability.

Reproduction with supplemental food

Sufficient reproductive data was only obtained in 1986 (for supplemented food: *M. femurrubrum* – Seven females in four cages; *M. sanguinipes* – nine females in five cages), because too few females survived to the experiment's end in most years. Supplemented food increased the mean number of developed ovarioles per female ($F = 4.62$; $df = 1,15$, $P < 0.05$).

Population dynamics in cages

Density

We compared the density of the next developmental stage to three variables: density of individuals at the previous stage, whether the cage was initially stocked with the previous stage or an earlier stage, and year. For cages started with nymphs, adult density did not depend upon whether cages were stocked with early or late instars, but only the initial number of late instar individuals and the year (Table 6). For cages started with nymphs, constant adult density did not depend upon the initial number of late instars or whether we stocked the cage with early or late instars, but only the year (Table 6). Furthermore, for 1985, 1986 and 1989, constant adult densities in cages started with nymphs in June were highly correlated with constant adult densities in cages started in August with adults for both species ($r^2 = 0.98$, $n = 6$, $P \leq 0.01$). The slope of the regression was not different from 1.0 (0.89, SE = 0.31) and the intercept was not different from zero

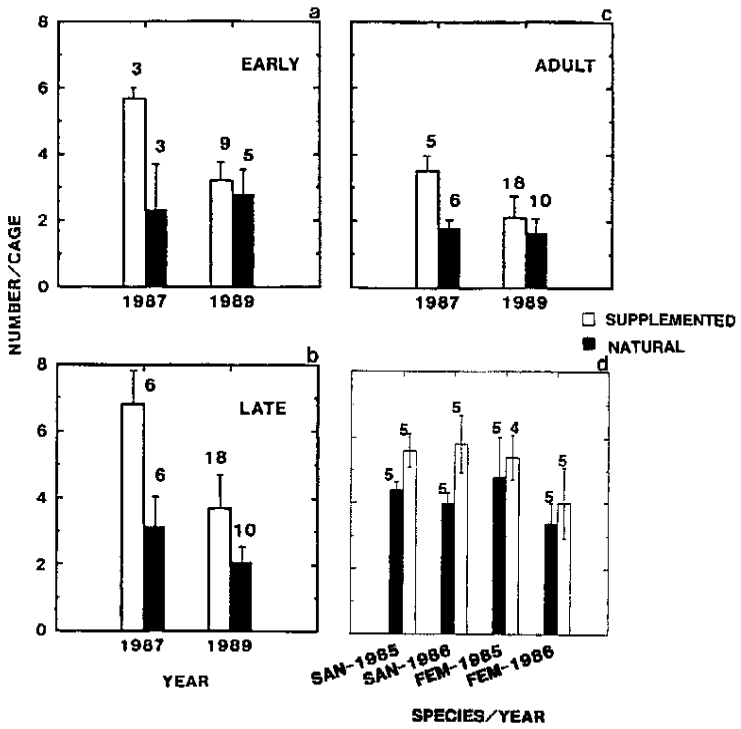

Fig. 4a–d Individuals surviving between developmental stages (see text) in cages receiving supplemented and natural food (see Table 1). For *Melanoplus sanguinipes* nymphs: **a** survival from early to late instars increases with added food ($F = 4.30$, $df = 1,16$, $P < 0.05$); **b** survival from late instars to adults increases ($F = 12.29$, $df = 1,36$, $P < 0.001$); **c** survival from late instars to the constant adult density increases ($F = 4.54$, $df = 1,35$, $P < 0.04$). **d** For cages started with *M. femurrubrum* (*FEM*) and *M. sanguinipes* (*SAN*) adults, survival to the constant adult density increases ($F = 4.02$, $df = 1,31$, $P < 0.05$). SDs and samples (n = number of cages) are indicated

Table 6 Density results (for *Melanoplus femurrubrum* and *M. sanguinipes*) from the microcosm experiments with natural food levels. We conducted all analyses using unbalanced ANCOVA

	Grasshopper species					
	M. femurrubrum			*M. sanguinipes*		
Number of adults produced						
Continuous variable						
Initial density of late instar individuals	F=24.87	df=1, 65	P<0.001	F=56.65	df=1, 63	P<0.001
Categorical variables						
Year	F=5.91	df=3, 65	P<0.001	F=2.91	df=3, 63	P<0.041
Cage started with early or late instars	F=1.69	df=1, 65	P<0.20	F=0.04	df=1, 63	P<0.84
Number of adults maintained until the end of experiment						
Continuous variable						
Initial density of late instar individuals	F=0.03	df=1, 59	P<0.86	F=0.24	df=1, 63	P<0.63
Categorical variable						
Year	F=4.29	df=3, 59	P<0.008	F=3.83	df=3, 63	P<0.014
Cage started with early or late instars	F=0.94	df=1, 59	P<0.34	F=0.07	df=1, 63	P<0.79

(0.98, SE = 0.98), indicating that adult densities were independent of nymphal stocking densities. Therefore, microcosm results were pooled and repeated-measure statistics were not needed, because past effects did not carry over between developmental stages. Finally, there was a negative effect of density on survival for both grasshoppers at all developmental stages and survival varied among years (Fig. 5; Table 7). Therefore, survival in the cages was density-dependent, but the intensity of density-dependence varied among years.

Sex ratio

We found that the ratio of males to females (0.45, SD = 0.51 males/female, n = 12) was significantly less than an equality (i.e., biased against males: arcsine square root transformed, $t = -3.56$, $df = 10$, $P \leq 0.01$) (Table 3). Therefore, males had much lower survival in the cages than females.

Body mass

Adults dying in cages during 1983 had a lower body mass (dry) for a given body length (mm) than individuals that survived (ANCOVA – continuous variable of body length: $F = 586.45$, $df = 1, 179$, $P \leq 0.001$; categorical variable of surviving versus dying: $F = 12.51$, $df = 1, 179$, $P \leq 0.001$). We know from a small subsample of the individuals that were weighed prior to stocking that individuals dying tended to decrease in body mass, and those

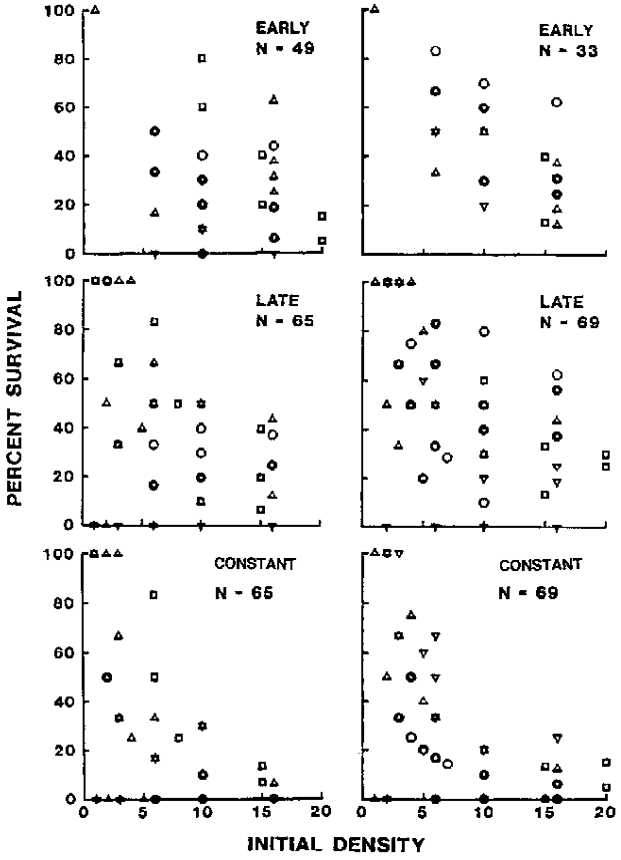

Fig. 5 Percentage survival between different developmental stages of *Melanoplus femurrubrum* and *M. sanguinipes* [*squares* 1985, *circles* 1986, upward triangles 1987, *down-turned triangles* 1989, *early* survival from an early instar nymph to late instar nymph, *late* survival from a late instar nymph to adult, *constant* survival by late instars to the constant adult density (see text), *N* total number of caged populations over 4 years – based upon experimental design, cages destroyed over the course of each year's experiment, and "pooling" of data (see text), the numbers of cages for each developmental stage and summer varied between 3 and 26]

surviving tended to maintain body mass or increase in mass.

Reproduction

The cages provided limited data on female reproductive output, because few females survived until the experiment's end. When we compared the mean number of developed ovarioles per female with constant adult density maintained in the cages during a given year (Table 3), the categorical variables of year ($F = 41.07$, $df = 4,2$, $P < 0.02$) and grasshopper species ($F = 3.53$, $df = 1,2$, $P < 0.04$) were significant, and the continuous variable of body mass provided a significant negative correlation ($F = 45.25$, $df = 1,2$, $P < 0.02$), while density provided an almost significant positive correlation ($F = 9.64$, $df = 1,2$, $P < 0.09$). For the field, we also observed a positive correlation with density ($F = 10.62$, $df = 1,7$, $P < 0.014$), but no species or body mass effects emerged.

Vegetation

Mean plant characteristics (total biomass, percentage grass, and solubility estimates) for cages comprising a treatment differed by less than 15% within a year, indicating relatively uniform vegetation. We examined plant biomass in cages at the end of the experiments in terms of the cage's population treatment (initial density, stage of development and grasshopper species stocked) and year. Density and developmental stage had no effect, but year ($F = 26.89$, $df = 7, 142$, $P < 0.001$) and species ($F = 12.19$, $df = 1, 142$, $P < 0.001$) did. Cages containing the larger-bodied *M. sanguinipes* had less plant biomass, but the difference was less than 10%.

Table 7 Survival results from unbalanced ANCOVAs (arcsine square root transformed) for the microcosm experiments (on *Melanoplus femurrubrum* and *M. sanguinipes*) with natural food levels

	Grasshopper species					
	M. femurrubrum			*M. sanguinipes*		
Proportion surviving from early instar to late instar						
Continuous variable						
Density of early instars	F=17.55	df=1, 44	P<0.001	F=44.35	df=1, 28	P<0.001
Categorical variable						
Year	F=2.69	df=3, 44	P<0.05	F=1.65	df=3, 28	P<0.20
Proportions surviving from late instar to adult						
Continuous variable						
Density of late instars	F=15.52	df=1, 60	P<0.001	F=19.82	df=1, 64	P<0.001
Categorical variable						
Year	F=9.16	df=3, 60	P<0.001	F=2.32	df=3, 64	P<0.08
Proportion surviving from late instar to the constant adult density maintained in cages						
Continuous variable						
Density of late instars	F=27.96	df=1, 60	P<0.001	F=33.79	df=1, 64	P<0.001
Categorical variable						
Year	F=3.93	df=3, 60	P<0.01	F=2.63	df=3, 64	P<0.05

Weather and populations

Density

Each year's constant adult densities for the two grasshopper species in the cages were correlated with precipitation and temperature during that year's plant growing season (May - September: Table 1), and a significant multiple correlation was found ($r^2 = 0.63$, $n = 14$, $P \leq 0.004$).

Vegetation

Stepwise regression was used to compare weather and plant parameters. Plant biomass increased with precipitation (partial correlation, $P \leq 0.02$) and decreased with temperature (partial correlation, $P \leq 0.003$) (Table 1: $r^2 = 0.87$, $n = 8$, $P \leq 0.006$). Plant quality decreased with precipitation (partial correlation, $P \leq 0.04$) and increased with precipitation squared (partial correlation, $P \leq 0.04$) (Table 1: $r^2 = 0.62$, $n = 8$, $P \leq 0.09$).

Discussion

Comparison of field and microcosm populations

Similar densities, survival, reproduction and individual traits (body mass and diet) were observed in the caged and field populations. The similarities may be surprising, since cages are often thought to produce aberrations. First, no cage effects were found in pilot data, when the same constant adult density was obtained in cages of different areas (0.1–9 m^2: Belovsky and Slade, unpublished data). Second, mortality in small populations can be dominated by chance events that obscure dominant processes operating in large populations. This is not a concern in our study because the same densities were obtained in cages and the field. In addition, when all grasshoppers died within 4 days of stocking (13 of 433 cages) we restocked them, and all individuals again died within less than a week. This suggested that results were repeatable, not due to chance. Finally, abiotic conditions (Belovsky and Slade 1993), initial densities and vegetation for the cages were comparable to the field. Therefore, it appears that the processes operating on caged populations to limit them are also operating in the field.

The only difference between cage and field populations was a larger field ratio of males to females. Because field and cage densities were comparable, this means that male survival was lower in cages than in the field, and female survival was greater. This was not expected given that males are more frequently caught by predators (Belovsky et al. 1990). Caged females tended to reproduce less: this might account for their greater survival if they invested more resources in survival than reproduction, but this would not account for lower male survival. We believe that both the tendency for lower reproduction by females and reduced male survival in cages emerge from paternal investment effects. Paternal investment in eggs can be twice as much as maternal investment for these grasshoppers; paternal investment is obtained when females receive numerous spermatophores in an extended copulation with a male and this is repeated with several males (G. E. Belovsky, J. Chase and J. B. Slade, unpublished data). Furthermore, we know that males spend considerable time displaying to females and interacting with other males for access to matings, and attempting to disrupt copulations by other males, which reduces time spent feeding. We suggest that males in cages encounter other males and females more frequently than in the field due to their restricted mobility. This can reduce male food intake and increase their energy expenditures, which reduces their survival. Also, fewer males would lower paternal investment, reducing female reproduction.

Food resources

Similarities between field and cage populations suggest that similar processes are limiting both, and the observation that supplemental food increased cage densities, survival, and reproduction suggests that food was limiting. Furthermore, a density-dependent decline in survival is expected and this was observed.

Other observations support food limitation of these populations. First, the individuals that died in the cages decreased in body mass, as expected if mortality was due to food deprivation. Second, adults in the laboratory provided with water, but no food, die in 6–10 days, the same time period that cages stocked with adults required to achieve constant density (Belovsky and Slade, unpublished data). Third, from other experiments, we know that the survivors in cages are individuals that are better able at finding food (Belovsky and Slade, unpublished data).

Other alternative limiting mechanisms can be discounted. First, abiotic conditions were comparable between the cages and field (Belovsky and Slade 1993); thus, direct limitation by abiotic conditions was not supported, especially as they often operate in a density-independent fashion. Second, cages eliminated natural enemies, which could not then be limiting. In addition, experimental studies on predation with these populations found that predators did not reduce grasshopper numbers (Belovsky et al. 1990; Belovsky and Slade 1993), and parasitoids attacked less than 10% of the grasshoppers (M. Lietti de Guibert, personal communication). Third, infectious diseases increase mortality as density increases. We discount diseases as a limiting factor because field-caught grasshoppers maintained in the laboratory with ad libitum food at greater than 50 times the field densities did not exhibit increased mortality, but reduced mortality (<1%) (Belovsky and Slade, unpublished data).

Food abundance and competition for food appeared to limit these populations. The proximate cause for declining

field populations over a summer could be starvation (as in the cages), but also could occur through dispersal or killing by natural enemies of surplus individuals in relation to the available food. Nonetheless, the *ultimate* mechanism limiting field populations appeared to be food.

Changing food resources – the impact on populations

Food availability at a given time (Table 1) was estimated as the sum of the product of grass biomass and its solubility and the product of forb biomass and its solubility, since these grasshoppers consume grasses and forbs.

Density

Food availability (mid- to late September) was correlated with the constant adult density maintained in cages for that year (Fig. 6: $r^2 = 0.88$, $n = 14$, $P \leq 0.001$). The correlation between density and food was 15% better than that between density and plant biomass, indicating the impact of plant nutritional quality. Therefore, as expected if food is limiting, adult densities in cages varied among years with changing food resources.

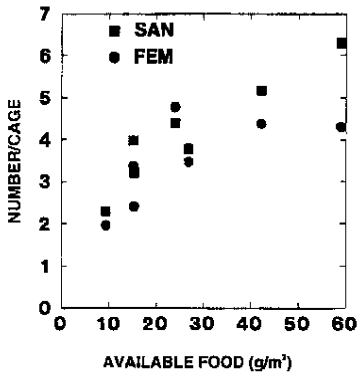

Fig. 6 The mean constant adult density (*Melanoplus femurrubrum FEM, M. sanguinipes SAN*) in cages stocked with adults are compared with the mid- to late September available food (see text)

Survival should be positively correlated with the year's measure of food availability and negatively correlated with grasshopper density in the cages, because less food is available per capita as density increases. For cages started with nymphs, the survival of both grasshopper species from one developmental stage to the next was correlated with available food (mid- to late September, the only measure available for all years) and the number of individuals in the cage at the previous developmental stage (Table 8). Grasshopper susceptibility to food availability might vary between developmental stages, and the regression slopes relating these variables for the different stages (Table 8) would reflect this; but t-tests showed no differences in slopes. The importance of intraspecific competition might vary between developmental stages, and differences in the regression slopes relating these variables would reflect this, but *t*-tests showed competition intensifying with greater development. This is expected with food competition, because larger body mass requires greater food consumption.

Reproduction

The mean number of developed ovarioles per female increased with the constant adult density in both the cages and the field (Table 3). This seems counterintuitive, because reproduction should decline with density if food competition occurs. We correlated constant adult density, total food available, per capita food available, and the mean ratio of males to females with the ovariole counts using stepwise regression ($r^2 = 0.83$, $n = 19$, $P < 0.005$). Food available per capita (partial correlation, $P \leq 0.001$) and the number of males per female (partial correlation, $P \leq 0.11$) were positively correlated with ovariole counts. The positive effect of constant adult density arose because density increased with available food. Second, the sex ratio effect supports our earlier contention that reduced paternal investment may explain the tendency to observe lower reproduction in cages.

Food availability and competition for food, even in terms of paternal investment, consistently emerge for

Table 8 Multiple regressions relating grasshopper (*Melanoplus femurrubrum* and *M. sanguinipes*) survival between developmental stages to population density and available food in cages with natural vegetation in different years

Species	Developmental	Independent variable						Overall regression		
		Inverse of density of starting development stage			Available food			*n*	*r*	*P*
		Slope	S.E.	*P* for partial correlation	Slope	S.E.	*P* for partial correlation			
M. femurrubrum	Early to late	−0.09	0.04	0.01	0.08	0.02	0.001	41	0.62	0.001
	Late to adult	−0.19	0.03	0.001	0.06	0.01	0.001	50	0.70	0.001
	Late to constant adult density	−0.24	0.04	0.001	0.04	0.01	0.04	30	0.79	0.001
M. sanguinipes	Early to late	−0.09	0.02	0.001	0.04	0.01	0.005	33	0.60	0.001
	Late to adult	−0.12	0.02	0.001	0.06	0.01	0.001	49	0.61	0.001
	Late to constant adult density	−0.20	0.03	0.001	0.04	0.01	0.001	49	0.77	0.001

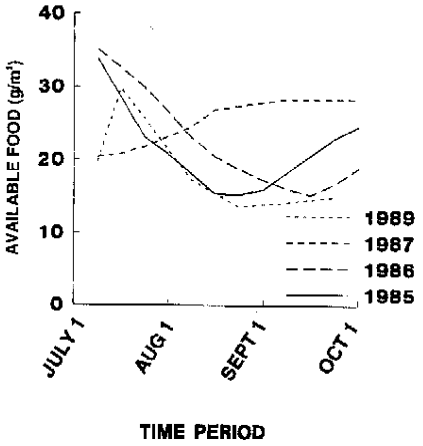

Fig. 7 Bi-weekly available food (see text) over four summers (early July - late September) is presented as the LOWESS smoothing function (Wilkinson 1990) to illustrate changes within a grasshopper generation

field and cage populations. Furthermore, the mechanism for this density-dependent response would appear to be exploitation, rather than interference, because we have not observed any behavioral interactions that would reduce food consumption (e.g., individual distance, territoriality, and aggression), even though interference is observed among males in mate acquisition (Belovsky and Slade, unpublished data). In fact, we observe a tendency for individuals that are not feeding to move towards individuals that are feeding, and for them to feed together. This is not surprising since both species will aggregate and travel in swarms on occasion (Pfadt 1988). However, laboratory studies on other grasshopper species (Smith 1970; Wall and Begon 1986) have observed interference, and some species exhibit spacing behavior through aggressive interactions in the field (Lockwood 1988).

Changing food resources within and between years – the role of weather

The paper opened with the observation that grasshopper densities have been correlated with temperature and precipitation, and this led ecologists to argue for their density-independent limitation. Up to this point, we have concentrated on food and density-dependent competition for it. Therefore, what is the role of weather?

Within a summer, food availability was relatively constant (1987) or declined (1985, 1986, 1989) with increasing aridity until late September when rains occur (Fig. 7). Because the annual cohort of these grasshoppers is large and individuals require more food as they grow over the summer, this explains why survival for all developmental stages was food limited. Therefore, the within-year weather creates the pattern of food availability that leads to consistent food limitation. Different within-year weather patterns could create a different survival pattern: e.g., early summer aridity and late summer rains may create food limitation early but not late in the summer. The within-year weather pattern at our site is typical of many temperate grasslands.

Between years, plant biomass increased with precipitation and decreased with temperature, while plant quality decreased and then increased with precipitation. Increases in plant biomass with greater precipitation dominated the food availability relationship in our study. We also observed these patterns with supplemental watering in cages (Table 5). Therefore, annual variations in food availability were driven by weather.

Our correlation between grasshopper density and weather (r^2 = 0.63) was 40% less than observed for available food (r^2 = 0.88). We found that precipitation was positively correlated and temperature was negatively correlated with density, which is counter to studies in other northern North American grasslands (Smith 1954; MacCarthy 1956; Edwards 1960; Bird et al. 1966; Bird and Romanow 1966; Riegert 1968; Gage and Mukerji 1977; Rodell 1977). Furthermore, correlations between weather and density reported in studies from other regions and populations at different densities are not consistent (Capinera 1987; Capinera and Horton 1989; Lockwood and Lockwood 1990, 1991). These inconsistencies could reflect food limitation where food availability is drought-limited in some areas and cold-limited in others. Alternatively, these differences could reflect populations limited by food versus weather-induced increases in mortality. Therefore, simple correlations between weather and grasshopper densities may have little utility for understanding the processes limiting grasshopper populations.

Our study indicates that correlations between weather and grasshopper density may not imply population limitation by density independent processes (Dempster 1963; Andrewartha and Birch 1984), but can reflect changing carrying capacities and density-dependent competition for food (i.e., density-veiled dynamics sensu Strong 1984, 1986a,b). White (1976, 1978) claimed in a frequently cited paper that grasshopper densities are limited by food quality which is greater during a drought. On the surface, White's explanation would appear similar to our findings; however, he claims that this limitation of grasshopper populations is density-independent.

Our results differ with White's (1976, 1978) interpretation on several points. First, White claimed that early instar survival did not depend upon their abundance or food abundance, rather it depended solely upon weather conditions that increased plant protein content which improved survival. In contrast, we found that competition for food, a density-dependent process, limited survival. Second, White claimed that adult grasshopper density was limited by the survival of early instars. In contrast, we found that all grasshopper developmental stages were food limited. Third, White claimed that there existed no shortage of food per se for grasshoppers, since densities of older grasshoppers, which ate more and could be limited by food abundance, seldom attained the necessary high densities due to low early instar survival. In con-

trast, we found that adult densities were not limited by the number of early instar individuals and their survival, and even under the most severe food limitation during our study (1984) sufficient offspring were produced so that adults in the next year were food limited.

How robust is food limitation between years?

Based on experience, Scharff (1954) claimed that *M. sanguinipes* populations were consistently food limited in Montana; our experiments demonstrate that his intuition was correct for our site over 8 years. However, for populations to consistently "track" changing food resources between years (Roughgarden 1975; Chesson 1986), so they are *ultimately* food limited can be problematic. "Tracking" can occur in two ways. First, the population can produce so many eggs each year that more hatchlings are available to start the next year's population than the available food can support. Second, the dispersal of surplus individuals from adjacent populations could impose food limitation. The former case represents a source population, while the latter is a sink (sensu Pulliam 1988).

We believe our site contains a source population. First, we assume that each female surviving to the constant adult density during a year produces only one egg pod which contains the number of eggs equal to the number of developed ovarioles per females in cages for that year. This is conservative, since (1) females tend to produce more than one pod, (2) some females failing to survive to the constant adult density still produce a pod(s), and (3) females in cages tended to have fewer developed ovarioles than field females. Second, the product of the mean number of females in cages at the constant density for a given year, the above estimate of female reproduction for that year, and the proportion of eggs hatching (a conservative estimate, since literature values were higher; Pfadt and Smith 1972) provided an estimate of hatchlings expected per cage for the next year. Third, if the above value is greater than six hatchlings, the smallest stocking density that still exhibits food limitation in the year with greatest food, then the population will "track" food resources. We estimated that 7.5–33 hatchlings/cage were produced over the years of our study. Given that food availability varied by more than sixfold during the study, we contend that the ability to "track" food resources between years is robust for these grasshoppers.

Conclusion

Our experiments indicate that grasshopper populations over 8 years on a native Montana prairie with abundant natural enemies and highly variable weather were food limited, a strong density-dependent process. The study highlights the need to experimentally examine population dynamics for species like grasshoppers, which are noted for their variability, in order to assess the importance of food limitation and other density-dependent processes. This may explain why analyses of census time series have been hard pressed to resolve issues about population limitation (Hassell and Sabelis 1987; Strong 1987; Stiling 1988; Hassell et al. 1989; Turchin 1990; Woiwood and Hanski 1992; Holyoak 1993; Royama 1993), especially when carrying capacity varies temporally.

Our results question two generalizations about the population dynamics of grasshoppers and herbivores. First, *terrestrial* herbivores are seldom food limited, but often predator limited (Hairston 1989). Second, herbivorous insect populations seldom exhibit strong density dependence (Strong 1983, 1984, 1986a, b; Strong et al. 1984). Neither claim was supported by our study. This does not imply that the ideas are false for grasshoppers or generally for herbivores, but questions current empirical support for them, which is seldom based on experimentation. However, because the grasshoppers reported on here are frequently cited as evidence for the absence of food limitation and the action of predator or density-independent limitation, the generalizations must be questioned.

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