

SUSCEPTIBILITY TO PREDATION FOR DIFFERENT GRASSHOPPERS: AN EXPERIMENTAL STUDY¹

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Abstract. A study was conducted in western Montana to determine the impact of different predators on grasshopper populations. By placing grasshoppers of different species, sexes, ages, and body masses on monofilament tethers in the field, rates of predation could be estimated. These rates are consistent with other estimates obtained from population studies in the same environment, but provide a far more detailed assessment of which grasshoppers are most vulnerable to predators and which predators are most important. Immature individuals are more vulnerable at small body sizes and adults are more vulnerable at large body sizes; this is because the principal predators on immature individuals are arthropods, and on adults, vertebrates. Male grasshoppers were 2–3 times as vulnerable as females. The subfamily Oedopodinae was more vulnerable than the Gomphocerinae or Melanoplinae. Predation rates indicate that predators are only able to impact seriously (reduce life expectancy below the suitable abiotic period for existence) the largest Oedopodinae, making predation of little consequence for most grasshopper populations in this environment.

Key words: birds; body size; field experiment; grasshoppers; predation; predation rates.

INTRODUCTION

The importance of predation in limiting populations is an often-debated issue in ecology, but it is difficult to assess due to the problems in conducting experiments (Sih et al. 1985). Even when experimental studies can be conducted to address the importance of predation, they often provide only a gross portrayal of predatory dynamics, since the difficulties of experimentation limit sample size and the range of conditions that can be examined. In this paper, an experimental study on grasshoppers in a native Palouse prairie was used to assess predation rates on different species, sexes, body sizes, and ages, providing a more complete representation of predatory dynamics than has been generally available.

Grasshoppers are known to have many predators, and many grasshoppers are eaten by predators (Dempster 1963, Greathead 1963, Lavigne and Pfadt 1966). They also are known to possess behavioral and color adaptations to avoid predators (Isley 1938, Rowell 1971, Uvarov 1977, Schultz 1981, Gillis 1982). A number of studies have argued that predators are important in reducing grasshopper densities (Stower and Greathead 1969, Joern and Rudd 1982), and some have demonstrated this experimentally by comparing

densities in areas with and without predators (Kajak et al. 1968, Joern 1986, G. E. Belovsky and J. B. Slade, *unpublished manuscript*). These studies either examine a single grasshopper species population or take a community approach by combining all grasshopper populations together; unfortunately both of these approaches ignore or mask what determines vulnerability to predators and consequently prevents a determination of the conditions under which predators might limit grasshopper populations.

To determine what influences a grasshopper's susceptibility to predation, a field experiment was conducted using individuals of 12 species for which age, sex, and body size were known. Since sex, age, body size, and taxonomic relationships are important determinants of vulnerability, a detailed determination could be made of which grasshopper populations are potentially limited by predators and at what stages in their life cycles limitation might occur.

In addition, the experiments permitted us to determine which predators are most important, what times of day predators are most successful in capturing grasshoppers, and whether grasshoppers reduce their activity at these times in response to the threat of predation. These aspects of predation cannot be addressed by simply comparing grasshopper densities in areas with and without predators. We thus obtained a more complete examination of the conditions under which predators might limit grasshoppers.

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STUDY SITE

The study was conducted at the National Bison Range, Montana. A 4-ha area of native Palouse prairie at an elevation of 760 m was chosen as the study site, the same area used for the experiments reported in G. E. Belovsky and J. B. Slade (*unpublished manuscript*). Approximately 70% of the vegetation is composed of grass by dry mass, total plant biomass averages 189 g/m², and 40% of the area is bare ground. Dominant grasses include *Agropyron spicatum*, *A. smithii*, *Festuca scabrella*, *F. idahoensis*, *Poa pratensis* and *Koeleria cristata*. Dominant forbs include *Achillea millefolium*, *Taraxacum* sp., *Aster fulcatus*, *Tragopogon dubius* and *Chrysopsis villosa*.

Twelve grasshopper species were used in the study; they compose >99% of the individuals and >70% of the Acrididae species at this site. Four species were in the subfamily Gomphocerinae: *Chorthippus curtipes*, *Amphitornus coloradus*, *Ageneotettix deorum*, and *Pseudopomala brachyptera*. Four species were in the subfamily Oedopodinae: *Trachyrhachys kiowa*, *Camnula pellucida*, *Arphia pseudonietana* and *Dissosteira carolina*. The remaining four species were in the subfamily Melanoplinae: *Melanophus dawsoni*, *M. femur-rubrum*, *M. sanguinipes* and *M. bivittatus*.

The predators on grasshoppers included birds, rodents, spiders, and ants. The most common avian predators were the Western Meadowlark (*Sturnella neglecta*), the Grasshopper Sparrow (*Ammodrammus savannarum*) and the Eastern and Western Kingbirds (*Tyrannus tyrannus* and *T. verticalis*). The most common rodent predators were *Peromyscus maniculatus* and *Microtus pennsylvanicus*. The most common spider predators belonged to the families Clubionidae and Licosidae.

METHODS

Ideally, predation rates are best studied by observing over time the fates of large numbers of prey individuals in order to determine the characteristics of the individuals killed and the types of predators. Given the small size, high mobility, and cryptic coloration of grasshoppers, and an observer's unavoidable disturbance of predators and prey, close observation of individuals is difficult. These difficulties can be overcome by tethering grasshoppers in the environment and periodically examining them to see whether predation has occurred. Any restriction of a prey's movement will modify the predatory interaction; therefore, these potential problems must be considered and shown to minimize behavioral changes that affect vulnerability.

Tethering.—Tethering was accomplished by attaching individuals to a 50-cm piece of monofilament. Adult grasshoppers and larger nymphs (>10 mm overall length) were attached to the monofilament using a noose. The noose was allowed to slide under the metazonal disk of the pronotum before tightening, which pre-

vented the grasshopper from sliding the noose over its head and escaping. Smaller grasshoppers (≤ 10 mm overall length) were attached using cyanoacrylic glue on the pronotum. Monofilament diameters between 0.05 and 0.2 mm were used for tethers, lighter monofilament for smaller individuals so movement was less impeded, and heavier monofilament for larger individuals to reduce their chewing through the monofilament and escaping.

Tethering impact studies.—Studies to investigate the impact of tethering were conducted in the laboratory and field. The frequency of movement was compared for tethered and untethered individuals in 0.20-m² terraria. Movement was defined as walking, hopping, or flight by the individual, i.e., displacements of >1 cm. Distance moved was not used since tethering restricts the linear distance travelled to a 50-cm radius, and movement per se rather than distance may attract predators. Individuals when initially tethered "struggled" against the restraint, but this appeared to subside after 30 min unless tethered individuals became entangled with each other in the terraria. Therefore, individuals were not used in studies within 30 min of tethering; if individuals became entangled their movement was not counted and they were untangled.

Individuals of both sexes in all 12 species were compared. Two terraria with three tethered or three untethered individuals were observed simultaneously. Three individuals per terrarium provided densities higher than observed in late August (Fig. 3), but within the ranges observed in July and early August (8–35/m²). The individuals were examined every 5 min for movement. Frequency of movement is the number of instances of movement divided by the total number of 5-min periods.

Since movement was considered the most important behavior attracting predators, no systematic comparison of other behaviors was made. However, the occurrence of other behaviors was noted for tethered individuals in the field.

Field studies.—Field studies of predation were conducted in July and August, 1985–1987. During these months grasshopper nymphs, adults, and their predators are most abundant. Each individual used in the field studies was identified to species, sex, and degree of development (nymph or adult), and its length was measured (fastigium to end of abdomen). The body mass for each individual was not measured since hundreds of individuals were used and handling was minimized to reduce damage to individuals. Therefore, body mass had to be computed. For nymphs, a regression between length and mass was developed using nymphs not included in the experiment. Adult body masses were determined using a separate sample of individuals of each sex and species.

The experiment was conducted by placing tethered individuals in the study site with the free end of the monofilament fastened to a nail inserted in the ground.

The nail was also inserted through a 4-cm² piece of orange plastic flagging to help in relocating the grasshoppers. The flagging might have attracted predators to tethered individuals. However, this did not appear to occur since there was no evidence of adjacent tethered individuals being captured, as might be expected if predators "trap-lined" from flag to flag. Also, the tethered individuals were up to 50 cm away from the flag.

A 50-cm radius provided the grasshopper with enough latitude for movement to find the variety of microhabitats required for survival and substrates against which it might be cryptic. The individuals were placed along transect lines to help in relocation. They were spaced far enough apart (10–20 m apart) so the regular location would not attract predators, and there was no artificial increase in the absolute or relative prey abundance which might attract predators.

Tethered individuals were examined in the field at the end of set time periods (0600–0800, 0800–1000, 1000–1200, 1200–1400, 1400–1600, 1600–1800, 1800–2000, 2000–0600), and any tethers found tangled in vegetation were untangled. An individual entangled with vegetation increased its rate of movement only when it was left with a very short tether (<5 cm). Our observations indicated that this occurred <5% of the time. Approximately equal numbers of individuals ($\pm 12\%$) were presented for each time period. At the end of each time period, the observer recorded whether the grasshopper was present; if it was missing, the individual was replaced. Grasshoppers might be missing if they escaped, or were eaten by a predator, or died and were subsequently scavenged.

Non-predatory deaths probably were due to injury in tethering, to hypothermia, or to hyperthermia or desiccation when tethered individuals became tangled. This source of mortality is not natural and is small, 4.2% (243/5794). These individuals were observed to be moribund in one time period and over half were being scavenged by ants when observed next.

Escapes were identified by a loosened, empty noose or a chewed-through noose or tether which was covered with dried "spittle." This represented a small loss, 1.6% (90/5794), and was comparable to that observed in the laboratory when tethered individuals had less time to chew on the tether, 0.7% (8/1190). Individuals from the subfamily Gomphocerinae were the most adept at chewing through their tethers or nooses, because their mouths are better positioned to chew on a loosened noose.

The remaining missing individuals were killed by predators, and in most cases the type of predator was determined. Spiders were often still feeding on the grasshopper, or the grasshopper was found in a web. Ants were observed to kill nymphs, but were only observed as scavengers on dead adults. Ants usually required >2 h to consume an individual, so they were

generally observed still feeding. Birds often broke the tether when flying off with the grasshopper. If they did not remove the individual, the wings and possibly the legs were left after consumption. Rodents usually did not break the tether, because they consumed the individual on the spot; however, they left the grasshopper's wings and legs behind as well as their own feces. Occasionally, the observer actually saw the bird or rodent consuming the grasshopper.

Predation rates.—Predation rates were measured in several ways. A crude predation rate was computed as the number of individuals eaten by predators divided by the number of individuals presented per time period, and was multiplied by 100 to measure predation as a percentage. This value could be determined for species, degree of development, sex, and body size categories, and was used for comparative purposes. The crude predation rate (percent eaten in 131 min) is only a relative estimate of predation intensity since it contains a number of biases:

- 1) The study's time period may not reflect average climatic, in particular thermal, conditions which affect grasshopper activity. By measuring the study's thermal conditions (air temperature, °C) and comparing them with the known average, and using a relationship for activity vs. thermal conditions (Belovsky and Slade 1986), a correction can be computed.

- 2) The experiment may present grasshoppers to predators at times of the day when the grasshopper might normally be inactive and hidden in dense vegetation, making them less vulnerable. When the grasshopper was first placed in the environment at times that it would normally be inactive, it might search for a place to become inactive, or simply remain in the open, making it more conspicuous and vulnerable to predators. By using the known daily activity cycle of grasshoppers (Belovsky and Slade 1986) to weight the crude predation rate at each time period, a correction can be made.

- 3) Grasshoppers will hop or fly great distances in trying to escape from predators, and then hide in dense vegetation; the experiment eliminated this ability. By scaling the crude predation rates by the observed capture success rate of birds in the field, a correction can be made. Capture success rate was measured by watching foraging birds from an elevated point (hill or truck) at distances <50 m. In this way, we determined whether ground- and aerial-foraging birds successfully captured a grasshopper after chasing it. The grasshoppers and birds observed were free-roaming; the observations were restricted to birds since they were the most important predator (see Results) and easiest to observe.

The first two biases could either overestimate or underestimate predation rates depending upon experimental conditions, while the third bias will always overestimate predation rates. All other possible biases (e.g., flagging, increasing grasshopper densities, in-

creased movement with entanglement) will overestimate predation rates.

RESULTS

Control studies

Control studies to determine the effects of tethering were examined using a MANOVA. There were no statistically significant differences in movement frequency between tethered and untethered individuals in the terraria (Table 1; MANOVA: $F = 0.02$; $df = 1,46$; NS); movement did not differ between the sexes (MANOVA: $F = 0.80$; $df = 1,46$; NS); movement did differ among the species (MANOVA: $F = 3.35$; $df = 11,46$; $P < .004$). Therefore, movement frequency did not change with tethering. If movement per se attracts predators, tethering might not affect the predator's ability to locate grasshoppers.

Tethered individuals fed, copulated, and oviposited normally. Copulations were frequently observed between tethered and untethered individuals in the field. Finally, all nymphs were observed to initiate molt activity normally while tethered, but those attached with a noose could not complete the molt, while those attached with cyanoacrylic glue could. Therefore, other than linear distance travelled, including escape ability (see Methods: Predation Rates: (3), above), tethering did not seem to modify grasshopper behavior.

Field studies

Field studies provided the crude predation rates (proportion eaten) for nymphs of different body sizes (Table 2) and for adults of each species and sex of different body sizes (Table 3). All statistics for predation rates are based on arcsine transforms. Comparisons of crude predation rates with different grasshopper characteristics indicate:

1) Nymph predation rates were negatively correlated with body size (Fig. 1A), where mass is a better correlate ($r = 0.65$, $N = 17$, $P < .004$) than length. Length is not significant when included with mass in a stepwise multiple regression. The major predators for nymphs were ants and birds (Table 4). Due to the abundance of nymphs of *Melanoplus femur-rubrum* and *M. sanguinipes*, these composed the majority of nymphs used in the study. Nymphs were identified to species (Brusven 1972, Scoggan and Brusven 1973), but instars were not determined, to reduce excessive handling which damages individuals.

2) Adult crude predation rates (Table 3) are significantly different between some species pairs using a chi-square test (19/66 species pairs are significantly different at $P < .05$). More important, the crude predation rates are positively correlated with the average species body size (Fig. 1B), where mass is a better correlate ($r = 0.86$, $N = 12$, $P < .0003$) than length. Length

is not significant when included with mass in a stepwise multiple regression. The major predators for adults are birds and rodents (Table 4).

The adult crude predation rates can be examined by sex and subfamily (Table 3). A significant difference exists between males and females, independent of body mass (MANCOVA: $F = 22.56$; $df = 1,18$; $P < .0001$). Males were more than twice as susceptible to predation as females (Fig. 1B). Also, significant heterogeneity was found among different subfamilies of Acrididae, independent of body mass (MANCOVA: $F = 3.37$; $df = 2,18$; $P < .02$). Predation rates increased from the Gomphocerinae to the Melanoplinae to the Oedopodinae, when body mass and sex were held constant. Overall, body mass and sex each account for 27% of the variance in predation rates, with subfamily accounting for 13%, for a total explained variance of 67%. While species differences were not significant when subfamily, sex, and mass were included in a MANCOVA, they would account for an additional 9% of variance explained.

3) Intensity of predation at different time periods could be compared using the crude predation rates for all tethered individuals present in each time period (Table 5); significant differences were observed ($\chi^2 = 129.23$, $df = 6$, $P < .0001$). Predation in the period 0600–0800 was nearly 2.5 times as great as the next highest value. Values were combined for all species to maintain an adequate sample size.

4) Capture success rates of birds feeding on grasshoppers were based upon 90 observed attacks by birds of which 20 were successful, giving a success rate of 22.2%. Twenty-six of these attacks were observed by us and 64 were provided by Mark Ritchie (*personal communication*) from his studies in the same area. Ground-foraging birds accounted for 68% of the observations, and had a success rate of 21.3%, which was not significantly different from the 24.1% success rate for aerial-hunting birds ($\chi^2 = 0.11$, $df = 1$, NS).

DISCUSSION

Predation rate differences between nymphs and adults

Predation rate differences emerged, with nymphs being more susceptible to predation when small, while adults are more susceptible when large. Invertebrate predators are more important for nymphs, while vertebrate predators are more important for adults (Table 4: $\chi^2 = 36.83$, $df = 4$, $P < .0001$). Since invertebrate predators are smaller than vertebrate predators, they might prefer smaller prey, which can be subdued and handled more easily. Larger vertebrate predators might prefer larger adult grasshoppers since they will not have any difficulty handling even the largest individual, and small individuals may be too difficult for them to find in the vegetation and may provide too little food per

TABLE 1. The results of movement frequencies for tethered and untethered individuals in the laboratory, the species listed in ascending order of body size.

Species	Subfamily	Tethered			Untethered		
		Pre-sented	Moved	Ratio	Pre-sented	Moved	Ratio
<i>Melanoplus dawsoni</i> Average	Melanoplinae	72	27	0.38	72	20	0.28
<i>Chorthippus curtipennis</i> Female Male Average	Gomphocerinae	48 42 90	7 11 18	0.15 0.26 0.20	48 42 90	11 11 22	0.23 0.26 0.24
<i>Amphitornus coloradus</i> Female Male Average	Gomphocerinae	48 42 90	15 5 20	0.31 0.12 0.22	48 42 90	15 11 26	0.31 0.26 0.29
<i>Ageneotettix deorum</i> Female Male Average	Gomphocerinae	72 42 118	18 15 33	0.25 0.36 0.28	72 42 118	24 11 35	0.33 0.26 0.30
<i>Pseudopomala brachyptera</i> Female Male Average	Gomphocerinae	42 43 85	10 11 21	0.24 0.26 0.25	42 43 85	14 5 19	0.33 0.12 0.22
<i>Trachyrhachys kiowa</i> Female Male Average	Oedopodinae	24 63 87	7 10 17	0.29 0.16 0.20	24 63 87	4 5 9	0.17 0.08 0.10
<i>Melanoplus femur-rubrum</i> Female Male Average	Melanoplinae	30 30 60	9 14 23	0.30 0.47 0.38	30 30 60	12 13 25	0.40 0.43 0.42
<i>Camnula pellucida</i> Female Male Average	Oedopodinae	48 72 120	17 31 48	0.35 0.43 0.40	48 72 120	21 35 56	0.44 0.49 0.47
<i>Melanoplus sanguinipes</i> Female Male Average	Melanoplinae	29 58 87	12 14 26	0.41 0.24 0.30	29 58 87	6 8 14	0.21 0.14 0.16
<i>Arphia pseudonietana</i> Female Male Average	Oedopodinae	72 72 144	9 10 19	0.12 0.14 0.13	72 72 144	15 13 28	0.21 0.18 0.19
<i>Melanoplus bivittatus</i> Female Male Average	Melanoplinae	42 48 90	9 21 30	0.21 0.44 0.33	42 48 90	12 29 41	0.29 0.60 0.46
<i>Dissosteira carolina</i> Female Male Average	Oedopodinae	75 72 147	11 26 37	0.15 0.36 0.25	75 72 147	10 24 34	0.13 0.33 0.23

unit of feeding time. These considerations, which emerge from foraging theory (Schoener 1969, 1971, Stephens and Krebs 1986), may explain the way in which predation rates on nymphs and adults vary with body size.

Why do sexual and subfamily differences emerge in predation rates?

Male grasshoppers are smaller than females (Table 3), but they are far more susceptible to predators. Our

laboratory studies of movement (Table 1) did not indicate any differences in the frequency of tethered movement between the sexes that might influence vulnerability (MANOVA: $F = 0.25$; $df = 1, 22$; NS). However, males may be more vulnerable if they expose themselves more than females do by the manner they choose to move (e.g., flight) and the microhabitats (e.g., bare ground) they seek. Males fly or hop more frequently, while females walk more often, making them less visible. Males expose themselves on bare ground

TABLE 2. The results of the tethering experiments for nymphs. The "real" rate (percent eaten per day) refers to the corrections described in Discussion: What Are the Real Predation Rates?

Length (mm)	Body mass (mg)*	Pre-sentations	No. eaten	Crude rate†	"Real" rate	Half-life (d)
5	6.2	8	0	0.0	0.000	1000‡
6	9.9	17	2	11.8	0.033	21
7	14.9	16	2	12.5	0.035	20
8	21.1	62	2	3.2	0.009	77
9	28.8	50	5	10.0	0.028	24
10	37.9	64	2	3.1	0.009	79
12	61.2	32	1	3.1	0.009	79
13	75.4	65	2	3.1	0.009	79
14	91.6	48	1	2.1	0.006	117
15	109.7	69	2	2.9	0.008	85
16	130.0	55	0	0.0	0.000	1000‡
17	152.3	29	2	6.9	0.020	36
18	177.0	10	0	0.0	0.000	1000‡
19	203.9	29	0	0.0	0.000	1000‡
20	233.2	27	0	0.0	0.000	1000‡
21	265.0	14	0	0.0	0.000	1000‡
24	376.0	14	0	0.0	0.000	1000‡

* Body mass was computed using the regression: mass = 0.000091 · length^{2.62}; $r = 0.96$; $N = 28$; $P < .001$.

† Crude rate = (no. of individuals eaten by predators) ÷ (no. of individuals presented per time period) × 100.

‡ The calculated value is infinity.

or high in the vegetation, while females tend to burrow into the vegetation. In accord with this, males of most species were more easily caught with insect nets than were females.

Males may be more vulnerable because they expose themselves more in their search for females. Uvarov (1977) claims that males move more, faster, and greater distances in their search for mates. Finally, males of some subfamilies (Gomphocerinae and Oedopodinae) produce sounds (crepitation and/or stridulation) to attract females which may also attract predators.

Differences in predation rates by subfamily, when body mass is statistically held constant, might be due to differences in movement. While there is no relationship between the frequency of tethered movement (Table 1) and subfamily (MANOVA: $F = 1.45$; $df = 2, 22$; ns), some qualitative parallels can be drawn.

The three subfamilies rank in the same order for their predation rates and their use of flight: the greater the use of flight the more vulnerable they are as adults. Perhaps flight attracts predators. In particular, the Oedopodinae are represented only by flying forms, unlike the Gomphocerinae, of which two species are brachypterous (flightless; *Pseudopomala brachyptera* and *Chorthippus curtippennis*), and the Melanoplinae, of which one species is brachypterous (*Melanoplus dawsoni*). In addition, many of the Oedopodinae, unlike those in the other subfamilies, have brightly colored wings.

This raises the question whether flight is really an anti-predator adaptation, since it may increase vul-

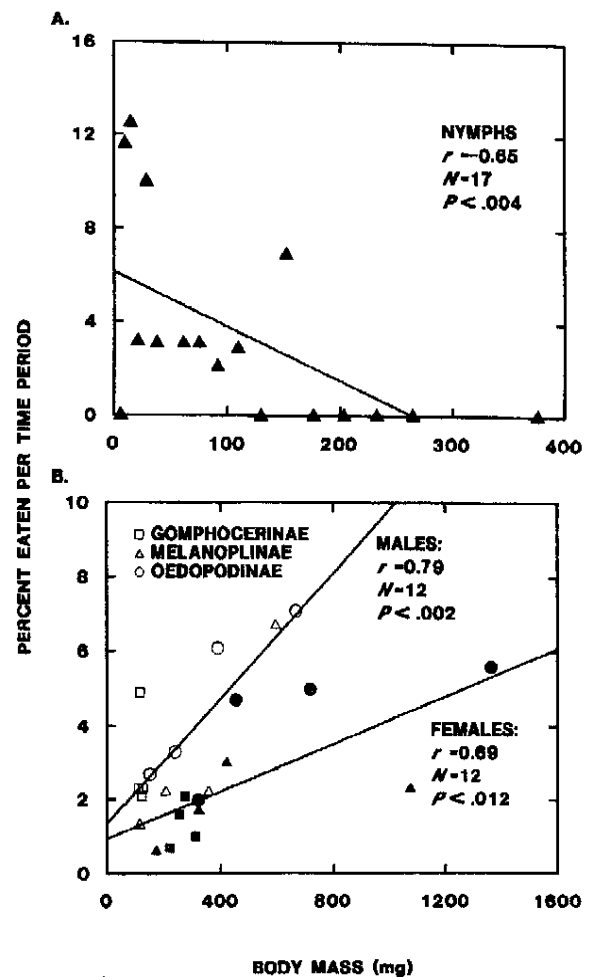


FIG. 1. The measured crude predation rates (percent eaten per 131 min) are plotted vs. body mass for nymphs (A) and adults (B). For adults, observations are plotted separately for males (open symbols) and females (solid symbols); separate symbols are used for each subfamily of Acrididae.

nerability. Perhaps flight is an adaptation to exploit scarce food resources. First, some Acrididae have non-migratory brachypterous or near-flightless forms and migratory winged forms. The migratory forms appear when weather or density conditions lead to diminished food resources (Uvarov 1966, 1977). Second, predation rates were dramatically reduced for tethered Oedopodinae if their wings were glued closed using cyanoacrylic glue (Mark Ritchie, *personal communication*).

Predation rate differences might arise from different microhabitat and feeding site choices. Three of the four Oedopodinae species (*Trachyrhachys kiowa*, *Arphia pseudonietana*, and *Dissosteira carolina*) tend to occur on bare ground, and, rather than climbing on plants to feed, they tend to cut a plant part at the base and consume it on the ground. All four Melanopline species tend to be found in or on vegetation. Two of the Gomphocerine species (*Ageneotettix deorum* and *Amphi-*

TABLE 3: Results of the tethering experiments with adults. N = sample size. The "real" rate (percent eaten per day) refers to the corrections described in Discussion: What Are the Real Predation Rates?

Species	Subfamily	Body mass (mg)		Length (mm)	
		$\bar{X} \pm SD$	(N)	$\bar{X} \pm SD$	(N)
<i>Melanoplus dawsoni</i>	Melanoplinae	Female			
Male		174 ± 40	(17)	19.3 ± 1.0	(13)
Average		115 ± 18	(24)	16.2 ± 0.8	(20)
		145		17.8	
<i>Chorthippus curtippennis</i>	Gomphocerinae	Female			
Male		220 ± 61	(14)	22.1 ± 2.2	(15)
Average		124 ± 12	(20)	17.1 ± 1.0	(20)
		172		19.6	
<i>Amphitornus coloradus</i>	Gomphocerinae	Female			
Male		254 ± 35	(27)	22.7 ± 1.4	(16)
Average		128 ± 12	(15)	17.9 ± 0.8	(18)
		191		20.3	
<i>Ageneotettix deorum</i>	Gomphocerinae	Female			
Male		275 ± 44	(27)	19.3 ± 1.5	(29)
Average		113 ± 28	(25)	14.6 ± 1.4	(33)
		194		17.0	
<i>Pseudopomala brachyptera</i>	Gomphocerinae	Female			
Male		313 ± 63	(20)	31.9 ± 1.9	(15)
Average		116 ± 27	(16)	25.0 ± 1.1	(32)
		215		28.5	
<i>Trachyrhachys kiowa</i>	Oedopodinae	Female			
Male		323 ± 43	(24)	21.3 ± 1.5	(12)
Average		152 ± 29	(26)	16.3 ± 1.5	(14)
		238		18.8	
<i>Melanoplus femur-rubrum</i>	Melanoplinae	Female			
Male		324 ± 61	(29)	20.0 ± 1.8	(38)
Average		207 ± 25	(25)	18.3 ± 0.9	(39)
		266		19.2	
<i>Camnula pellucida</i>	Oedopodinae	Female			
Male		456 ± 100	(28)	25.7 ± 2.9	(33)
Average		239 ± 51	(25)	18.9 ± 1.4	(33)
		348		22.3	
<i>Melanoplus sanguinipes</i>	Melanoplinae	Female			
Male		423 ± 84	(61)	21.9 ± 2.7	(22)
Average		358 ± 44	(53)	22.8 ± 1.8	(27)
		391		22.4	
<i>Arphia pseudonietana</i>	Oedopodinae	Female			
Male		719 ± 202	(25)	26.0 ± 2.0	(25)
Average		391 ± 71	(29)	22.0 ± 1.4	(35)
		555		24.0	
<i>Melanoplus bivittatus</i>	Melanoplinae	Female			
Male		1076 ± 263	(25)	31.9 ± 5.4	(26)
Average		597 ± 91	(37)	26.9 ± 2.4	(25)
		837		29.4	
<i>Dissosteira carolina</i>	Oedopodinae	Female			
Male		1364 ± 488	(25)	33.9 ± 2.9	(28)
Average		668 ± 140	(35)	28.7 ± 2.2	(34)
		1016		31.3	

* See footnote †, Table 2.

tornus coloradus) are similar to the majority of Oedopodinae, preferring bare ground, and cutting plant parts before feeding on them, while the other two Gomphocerinae (*P. brachyptera* and *C. curtippennis*) and one of the Oedopodinae (*Camnula pellucida*) are more similar to the Melanoplinae. While these differences might account in part for the predation rates and need to be further investigated, they do not provide a clear-cut pattern to explain the subfamily differences.

Do grasshoppers modify activity to avoid times with highest predation rates?

Using data on a grasshopper's daily activity cycle at the study site (Belovsky and Slade 1986), each of the seven daylight time periods were ranked by predation rate (Table 5) and by intensity of grasshopper activity. A Spearman rank correlation was not significant ($r_s = 0.21$, $df = 7$), indicating that grasshopper activity was

TABLE 3. Continued.

Presentations (animals/h)	No. eaten	Crude rate*	"Real" rate	Half-life (d)
154	1	0.6	0.0017	408
155	2	1.3	0.0037	187
309	3	1.0	0.0028	248
153	1	0.7	0.0020	347
192	4	2.1	0.0059	117
345	5	1.4	0.0040	173
244	4	1.6	0.0045	154
132	3	2.3	0.0065	107
376	7	1.9	0.0054	128
238	5	2.1	0.0059	117
220	5	2.3	0.0065	107
458	10	2.2	0.0062	112
310	3	1.0	0.0028	248
264	13	4.9	0.0138	50
674	16	2.4	0.0068	102
151	3	2.0	0.0057	122
182	5	2.7	0.0076	91
333	8	2.4	0.0068	102
234	4	1.7	0.0048	144
227	5	2.2	0.0062	112
461	9	2.0	0.0057	122
232	11	4.7	0.0133	52
180	6	3.3	0.0093	75
412	17	4.1	0.0116	60
298	9	3.0	0.0085	82
278	6	2.2	0.0062	112
576	15	2.6	0.0073	95
221	11	5.0	0.0141	49
180	11	6.1	0.0172	40
401	22	5.5	0.0155	45
257	6	2.3	0.0065	107
178	12	6.7	0.0189	37
435	18	4.1	0.0116	60
195	11	5.6	0.0158	44
210	15	7.1	0.0201	34
405	26	6.4	0.0181	38

* See footnote †, Table 2.

not related to predation risk. As might be expected with an ectotherm, activity is probably a function of thermal conditions (Belovsky and Slade 1986).

Are the measured capture success rates for birds realistic?

Our measure of capture success rate (22.2%) is much lower than the rate (85.3%) reported by Joern (1988) from aviary experiments in natural vegetation. He used

TABLE 4. The incidence of predation attributed to different predators in the field experiment.

Predator	No. killed	
	Nymph	Adult
Ant	7	6
Spider	3	4
Rodent	0	34
Bird	5	82
Unknown	6	30

many of the same grasshopper species as this study, plus a ground-foraging bird, the Grasshopper Sparrow, which also is common at our study site. Aviary experiments in natural vegetation at our study site, using the grasshopper species reported on here and a ground-foraging bird, the Brown-headed Cowbird (*Molothrus ater*), provided a capture success rate of $28.8 \pm 6.4\%$ ($\bar{X} \pm SD$, $N = 11$) (Belovsky 1990). These results are not different from the rates observed in the field (arc-sine transform: $t = 0.98$, $df = 9$, ns). Why did Joern (1988) observe different capture success rates?

The predator we used in our aviary studies, although a different bird than the one used by Joern (1988), should not provide the explanation for different capture success rates, since cowbirds are considered only second to the Western Meadowlark as a grasshopper predator (Bent 1965). We believe that differences in the vegetation between our site and Joern's (1988) may account for the different capture success rates. The sandhill grassland site in Nebraska studied by A. Joern (*personal communication*) may have more bare ground than our site. This may account for the greater capture success rate, since a study at our site (Check 1989) found that predation rates decreased by 20% when vegetation cover was increased by 60%. Differences such as these indicate the need for comparative studies at different sites.

What are the real predation rates?

As pointed out in the Methods (Predation Rates section), crude predation rates (percent eaten per 131 min)

TABLE 5. The time period distribution of predation on tethered adult individuals.

Time period	No. presented	No. eaten	Crude rate*	Activity rank†
0600-0800	711	72	10.1	7
0800-1000	564	7	1.2	6
1000-1200	616	25	4.1	1
1200-1400	620	15	2.4	2
1400-1600	602	18	3.0	3
1600-1800	704	9	1.3	5
1800-2000	718	10	1.4	4
2000-0600	650	0	0.0	‡

* See footnote †, Table 2.

† Belovsky and Slade (1986); a larger number indicates lesser activity.

‡ Grasshoppers are not active at this time due to thermal conditions (Belovsky and Slade 1986).

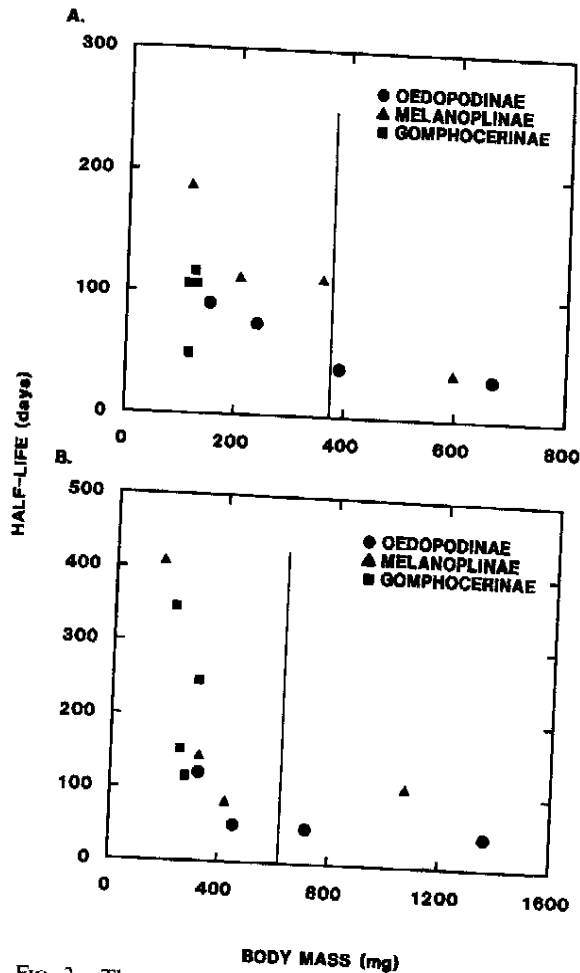


FIG. 2. The computed population half-life, or expected individual survival, is presented for adult males (A) and females (B). A vertical line separates the plots into two zones: species whose average body mass is < 500 mg and those larger (see Discussion: What Are the Real Predation Rates? for rationale).

are biased by (1) non-average thermal conditions modifying grasshopper activity, (2) presentation of tethered individuals at times when grasshoppers would normally be inactive, and (3) the inability of tethered individuals to escape when located by a predator.

Belovsky and Slade (1986) reported that grasshoppers at this site are feeding (exposed to predators) for ≈ 239 min/day. We found that our experiments were conducted on days with below-average air temperatures (17.9°C vs. 18.6°), which would increase grasshopper feeding by 7% (Belovsky and Slade 1986), requiring a reduction by 7% in calculated predation rates. Furthermore, when the presentation of tethered individuals is weighted by the proportion of grasshoppers observed active in each time period (Belovsky and Slade 1986), the measured predation rates should be reduced by 25%. Finally, the capture success of avian predators was observed to be 22.2%.

Using the above values, "real" predation rates (percent eaten per day) can be estimated as:

$$\text{"real" rate} = \text{crude rate} (0.93)(0.75)(0.22) \\ (239 \text{ min/day}) / (131 \text{ min/period}),$$

giving a daily rate rather than a rate per period of observation (Tables 2 and 3: crude rate). Predation rates are not meaningful in themselves, but they can be converted into a half-life for a population, or the expected time an individual will live until a predator kills it (life expectancy). This half-life (HL), using an exponential decline of the population, is:

$$\text{HL} = \ln 0.5 / -\text{"real" rate}.$$

The "real" rate and the half-life values are presented in Tables 2 and 3, and half-life values are plotted against body mass in Fig. 2.

Adult grasshoppers have at most 90 and more commonly 60 d to live at the study site between maturing (eclosure) and the onset of fatal freezing temperatures. It is evident from the half-life values (Fig. 2) that predators might not be exerting much of a controlling influence on smaller adults since their predation half-lives are much greater than the suitable period for existence. However, for larger adults (average species body mass > 500 mg), the half-lives are smaller than the suitable period. This is enhanced from a population perspective, since females, the productive population members, are less affected by predation than males. Even with the largest species, predators may reduce adult numbers through male mortality, but have little effect on the egg production, since females are less vulnerable.

Given the combination of variables with potentially large measurement errors used to compute the "real" predation rates and half-life values, the reliability of these computed values must be questioned. The sensitivity (reliability) of our estimates to errors in parameter estimation can be addressed using parameters from our aviary experiments (see Discussion: Are the Measured Capture Success Rates for Birds Realistic?, above). These experiments gave comparable parameter values to those reported here and standard deviations for the values which were not obtainable in the present study (capture success: $28.8 \pm 6.4\%$, $N = 11$; overlap of bird and grasshopper daily activity: $76 \pm 4\%$, $N = 4$). Employing the upper 95% confidence interval values for these parameters, the "real" predation rates and half-life values were re-computed to estimate the maximum values that might be expected.

The half-life value is more sensitive to change since it is an exponential function of the "real" predation rate, but it only decreased by 35% with these maximum parameter values. This change would lead to three more adult sex/species categories being added to the list of those potentially impacted by predators, rather than the original estimate of 7/24. If sex differences are ignored and only species are examined, there are no changes in the original list of species impacted by predation. Finally,

the body masses (> 500 mg) impacted by predation are unchanged. Therefore, the results presented above on predation rates are very robust, and these additional parameter estimates indicate a coefficient of variation of 14% for the predation rate and half-life values presented in Table 3.

The above results are borne out from manipulations of predator populations at our study site (G. E. Belovsky and J. B. Slade, *unpublished manuscript*). The only grasshoppers to increase in density when birds are excluded are those > 500 mg. Furthermore, the reduced density of large grasshoppers when birds are present is comparable to that expected from the predation rates: 72 vs. 61%.

While our predation rates are comparable to those reported by others: 0.3–2.5%/day (Stower and Greathead 1969, Joern and Rudd 1982, Joern 1986), the importance of predation cannot be assessed from rates alone, since food is in short supply for the grasshoppers at this site and intra- and interspecific competition for food occurs (G. E. Belovsky and J. B. Slade, *unpublished manuscript*). Therefore, predation may be compensatory (Errington 1946a, b, 1956) if the grasshoppers killed by predators are those that would die from competition or lack of food.

The interpretation of predation rates for nymphs is even more difficult since they change with ontogeny. Given the growth rates of *Melanoplus femur-rubrum* and *M. sanguinipes* nymphs (Brusven 1972), the time that an individual is expected to remain in each body mass category can be determined, and an average predation rate can be computed for the nymphal period. For these nymphs, the loss to predators is $\approx 41\%$ over their 48-d nymphal period. Given the large initial density of nymphs at this study site (≥ 50 individuals/m²), and their large mortality ($\geq 90\%$) in the absence of predators due to shortages of and competition for food (G. E. Belovsky and J. B. Slade, *personal observation*), the importance of predators again cannot be addressed from predation rates alone.

Do predation rates change between years?

For *M. femur-rubrum* and *M. sanguinipes* sufficient presentations of tethered individuals were made in each of the study's 3 yr to compare predation rates between years and with the density of grasshoppers in the environment (G. E. Belovsky and J. B. Slade, *unpublished manuscript*). To ensure an adequate sample size, the observations for the two species were combined and plotted against density in Fig. 3. A positive correlation is found between density and "real" predation rates (Spearman rank correlation: $R = 1.00$, $N = 3$, $P < .05$), and the rates are statistically different between years ($\chi^2 = 7.15$, $df = 2$, $P < .03$). Whether this relationship reflects changing numerical and/or functional responses by the predators, or there are more "weakened" grasshoppers that are vulnerable to predators at

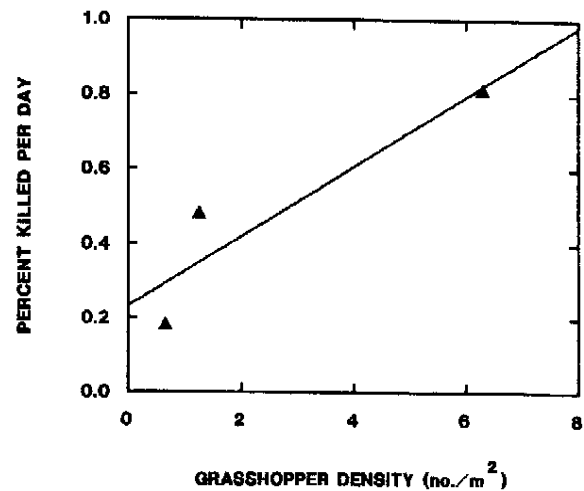


FIG. 3. The real predation rates (percent eaten per day) for *Melanoplus femur-rubrum* and *M. sanguinipes* in three different years (\blacktriangle) are compared against the yearly densities of grasshoppers at the study site. "Real" predation rates are calculated from crude rates, as described in Discussion: What Are the Real Predation Rates?

high densities due to intra- or interspecific competition cannot be ascertained.

CONCLUSION

The results illustrate the types of mechanistic relationships that can be obtained by experimental presentations of prey to predators in the field. The method is not without drawbacks, as evidenced by the biases and corrections discussed. Nonetheless, interesting body-size, taxonomic, and sexual differences in predation rates clearly emerge, and these help explain population and community observations and experiments conducted in this system (G. E. Belovsky and J. B. Slade, *unpublished manuscript*). However, the measurement of predation rates alone does not necessarily translate into a better understanding of the importance of predation for population and community dynamics (Sih et al. 1985), since predation may be compensatory.

How the results obtained at our Palouse prairie site relate to other grasshopper communities with different vegetation cover, daily activity periods for predators and grasshoppers, predator abundance, food for grasshoppers, grasshopper species, etc., cannot be assessed here. However, given the differences between our results and those reported in the literature for predation on grasshoppers (e.g., Joern and Rudd 1982, Joern 1986, 1988), the causes of these differences pose interesting problems.

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