

Activity and Time Budgets of Three Grasshopper Species (Orthoptera: Acrididae) from a Sandhills Grassland

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ABSTRACT: Time and activity budgets (locomotion, courtship, feeding, and quiescence) were constructed for three grasshopper species (*Amphitornus coloradus*, *Melanoplus confusus*, and *Mermiria bivittata*) from a sandhills, mixed-grass prairie in Nebraska. Distributions of time spent in these activities differed among the species although the majority of the time (ca. >80%) was spent in quiescent activity. Feeding was infrequent and the actual bouts typically short; feeding by these species occurred in different microhabitats. Daily shifts in activities and microhabitat use were observed. Face cleaning was frequently associated with movement.

Activity budgets describe the proportion of the available time that an animal spends in particular behaviors. They also allow a comparison of the frequency of particular behaviors during specific portions of the day. Although relative time spent in each activity does not necessarily indicate the relative importance of particular behaviors to an individual's fitness, quantification of the time budget may present a picture of the mix of activities employed by an organism to solve a variety of environmental problems. The resulting pattern should often represent a compromise among many alternative and often conflicting behaviors comprising the overall sequence of activities best suited to the environment (Baum and Rachlin, 1969; McCleery, 1978).

Grasshoppers (Orthoptera: Acrididae) exhibit a variety of activities including feeding, courtship and mating, movement (walking, jumping or flying), thermoregulation, hiding from predators, resting, etc. In some instances, behaviors conflict in that performing one activity means another cannot be performed. In other cases, more than one activity may be simultaneously accomplished (such as thermoregulating while maintaining crypsis). Of course, it may be that compromise is needed even in such cases as well in that microclimates optimal for adjusting body temperature may not be congruent with microhabitats which maximize the background matching ability of an individual. Such compromises undoubtedly change throughout the day as microclimates of particular microhabitats change or as crypsis may become less important at some times of day than others.

In this study, we describe the general activity budgets of three grasshopper species which are commonly found in a sandhills grassland. These species include both forb and grass feeding species which use different microhabitats (Joern, 1983). We fully recognize that some of the activities we describe may be fulfilling more than one function (e.g., quiescent activity) and that we will not be able to tease apart the functions responsible for particular activities being performed at particular times. However, our understanding of the functions and adaptive significance of each set of activities will be guided by knowing how much of the available time a grasshopper species actually allocates to a specific activity.

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Methods

STUDY SITE: This study was performed at Arapaho Prairie, a site located in the Nebraska Sandhills (Arthur Co.). This is a mixed-grass prairie located on sand dunes. Vegetation structure greatly varies depending on the local plant species composition and recent history of disturbance. Available microhabitats vary from open sand to closed vegetation canopy. A full description of the site is given elsewhere (Barnes and Harrison, 1982; Keeler et al., 1980).

GRASSHOPPER SPECIES: Three grasshopper species were observed: *Amphitornus coloradus* (Thomas), *Melanoplus confusus* Scudder, and *Mermiria bivittata* (Serville). Both *A. coloradus* and *M. bivittata* are grass feeders while *M. confusus* is a forb feeder (Joern, 1983). Phenologically, *M. confusus* have peak adult population densities a few weeks before the other two species although all species are present as adults by early July (Joern, 1982). In terms of general microhabitat use as observed in this study, *M. bivittata* tends to be found in more densely vegetated microhabitats (especially grass clumps) and the other species in more open microhabitats.

ACTIVITY BUDGETS: Time and activity budgets of these grasshopper species were constructed in naturally chosen microhabitats throughout the day (0600–1930) from 1 July to 10 August 1983 for *A. coloradus* and *M. bivittata* and from 1–22 July 1983 for *M. confusus*. Sampling was fairly uniform across all periods of the day (Table 2) for two of the species. Once an individual was located through arbitrary wandering by the observer, duration of activities was recorded for that individual until it was lost from sight. Individuals observed for less than 5 minutes were not included. General activity was categorized as: 1) *locomotion* (walking or jumping), 2) *courtship activity*, 3) *feeding* and 4) *quiescence* (little visible movement or other activities listed above). Height in the vegetation, substrate, feeding heights, and face-cleaning were also quantified according to the amount of time spent in each activity. A running tally was kept so that if, for example, an individual changed its height in the vegetation, this was reflected in the final activity summary.

Results and Discussion

Overall time and activity budgets for each species are outlined in Tables 1 and 2. Distributions of behaviors are significantly different among all species pairs based on total time for each activity (χ^2 contingency test, $P \ll 0.001$ for all comparisons). *Melanoplus confusus* spends proportionately more time moving, *M. bivittata* more time feeding, and *A. coloradus* more time in quiescent activities than the other species. Most of the time spent by all species was clearly in quiescent activity, however. Courtship activity was only observed in *A. coloradus* (7.5% of the individuals observed) even though it is clear that all species must participate in such activity. No observations of courtship behavior of any type in two species may represent real overall differences in time allocation to courtship or may represent only seasonal differences and hence sampling artifacts for the species since the life cycles are not exactly synchronized. However, observations were made throughout the period during which adults were present.

A striking similarity among species is observed for quiescence. At least 80% of the day is spent in quiescent activity although it may decrease during certain portions of the day for some species (Table 1).

Table 1. Time and activity budgets for three grasshopper species. Values in parentheses indicate 95% confidence intervals.

	<i>Amphitornus coloradus</i>	<i>Melanoplus confusus</i>	<i>Mermiria bivittata</i>
Number of individuals	53	71	51
Total observation time (minutes)	1187.2	1585.6	1887.3
Avg. time/individual (minutes)	22.4 (2.5)	22.3 (2.6)	31.1 (4.2)
Range (minutes/individual)	5–100	5–82.1	5–160.1
General activity (% time)			
Quiescence	92.5	88.5	88.4
Locomotion	2.6	7.6	1.3
Feeding	4.7	3.9	10.3
Courtship	0.2	—	—
Other activities			
Average feeding period (minutes)	1.7 (2.4)	1.3 (2.1)	1.6 (2.0)
Face cleaning (#/hour)	1.9 (1.8)	8.4 (6.5)	1.2 (1.0)
Time on litter (%)	63.1	75.6	33.1

Daily shifts in some activities are evident (Table 2) although often subtle. Pronounced changes included increased feeding activity in *M. bivittata* during the morning and late afternoon periods (this may also be true of *M. confusus*) and increased movement by *M. confusus* in the morning compared to afternoon. Since *M. confusus* feeds on a variety of forbs (Joern, 1983, 1985) which are uncommon (compared to grasses) at this site, increased movement to find suitable host plants is expected.

Position in the vegetation canopy differs among species (Fig. 1A). *Mermiria bivittata* is found at greater vegetation heights than the other species and *A. coloradus* is found at greater heights than *M. confusus* (χ^2 contingency test, $P <$

Table 2. Activity budgets throughout the day (% of time): early morning (0600–0900), morning (0900–1230), afternoon (1300–1530), and late afternoon/evening (1530–1930). Values in parentheses for each time period for each species indicate the percentage of the total observation time from this period of the day. Late afternoon values for *M. confusus* are not included since the sample was so small.

	Quiescence	Locomotion	Feeding	Courtship
<i>Amphitornus coloradus</i>				
Early morning (22.6)	97.0	2.3	0.7	—
Morning (26.6)	94.8	3.4	1.5	0.3
Afternoon (27.5)	95.6	1.4	3.0	0.5
Late afternoon (23.3)	94.8	3.3	1.9	—
<i>Mermiria bivittata</i>				
Early morning (21.9)	95.5	2.0	1.6	—
Morning (38.3)	88.0	1.9	10.1	—
Afternoon (20.0)	95.7	1.0	3.3	—
Late afternoon (19.8)	84.9	2.3	13.8	—
<i>Melanoplus confusus</i>				
Morning (77.3)	72.4	21.4	6.2	—
Afternoon (22.7)	94.8	5.2	0.1	—

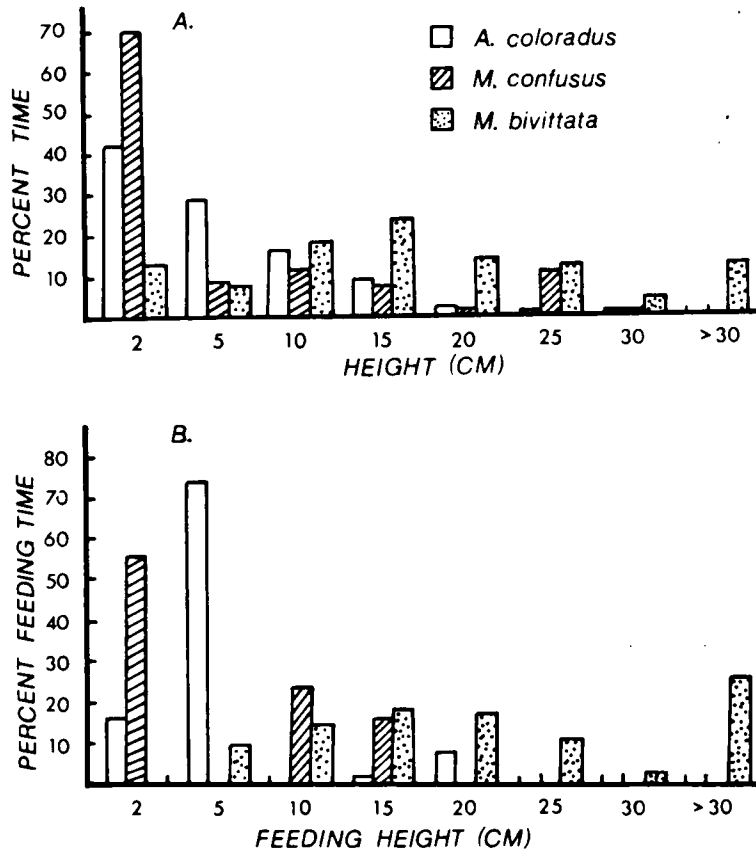


Fig. 1. A. Heights of microhabitat use by three grasshopper species. Sample sizes for A are given in Table 1. B. Feeding height of three grasshopper species. Only individuals which were actually observed feeding are included in B. Sample sizes for B are: *A. coloradus*—9, *M. confusus*—13, and *M. bivittata*—20. Each species is shown in the same sequence for each height interval for both A and B.

0.001 for all comparisons); analyses are based on total time. Feeding heights also differ among these species (Fig. 1B). Comparisons based on the total time at each height interval while feeding were significantly different among all species comparisons (χ^2 contingency tests, $P < 0.001$). *Melanoplus confusus* feeds primarily at ground level, *A. coloradus* at intermediate levels, and *M. bivittata* at the highest levels.

Length of feeding bouts (Table 1) did not differ among species (t -test among all species pairs, $P > 0.35$ in all cases). Lengths of feeding bouts were similar to those reported for *Hesperotettix viridis* feeding on *Gutierrezia microcephala* where 76% of the feeding bouts were less than 3 minutes (Parker, 1984). The overall percentage of time spent feeding in these species (Table 1) is much less than the 15% observed for *Locusta migratoria* nymphs in the laboratory (Ellis, 1951) or the 30–35% of the day spent feeding by *Nomadacris septemfasciatus* (Chapman, 1959). High and low temperatures inhibit feeding (reviewed in Uvarov, 1977) so little feeding is expected in early morning or mid-afternoon. This is observed at Arapaho Prairie (Table 2) for the grass-inhabiting *M. bivittata* but not in *A.*

coloradus; sufficient data are not available for *M. confusus*. Grasshoppers were observed feeding on dead or dry leaf material. Of the total time actually spent feeding, *M. confusus* spent 19.1%, *M. bivittata* spent 10.7%, and *A. coloradus* spent 48.1% of the time feeding on dead or severely dry foliage. Much time is actually spent on litter by each of these species (Table 1). The fact that *M. bivittata* spends more time in dense vegetation where litter is less common compared to the more open dwelling habits of the other species may explain the difference in litter habitation among species. This difference is not unexpected in that *M. bivittata* is cryptic against grass clumps and both *A. coloradus* and *M. confusus* are cryptic against their respective common backgrounds (Joern, pers. obs.).

Face cleaning, where the first or second pairs of legs were drawn over the head and antennae, were also scored (Table 1). In *A. coloradus* and *M. bivittata*, all face cleaning followed movement of some type while 53.6% of the face cleaning in *M. confusus* followed movement. However, not all movement was followed by face cleaning. About half of the movement was followed by face cleaning. Although we do not have sufficient information to evaluate the true significance of face cleaning, it suggests that grooming is important in association with movement. It may be that pathogens (e.g., fungal or protozoan parasite spores) are partly defended against in this manner.

All three species were primarily quiescent from ca. 1930 to 0600 hr and typically crawled up onto vegetation during this period. No displacement throughout the night was observed in several marked individuals.

Activity budgets of these species present an important overview concerning time allocation in grasshoppers. Factors responsible for the actual patterns of time allocation to various activities are clearly complex and most likely represent a series of compromises among activities which must be performed to survive and reproduce. Perhaps the most striking result is the large proportion of time which is spent in quiescent activity. Several reasons may explain this result. Predation has been shown to be very intense at this site from both robber flies (Joern and Rudd, 1982) and birds (Joern, in press). In each case, movement attracts attention to the individual and increases the probability of being eaten. Birds detect non-moving prey as well which also makes choice of background by a grasshopper important. Thermoregulation affects many important physiological processes and is greatly influenced by microclimate and posture (Anderson et al., 1979; Uvarov, 1977). Quiescent activity is clearly compatible with this requirement as actual movement is not repeatedly required for thermoregulation once the individual is positioned and postured. The relatively small proportion of time which grasshoppers spend feeding or in reproductive activities is obviously not commensurate with the effect these activities have on fitness. One would predict that males should spend more time in courtship activity (e.g., stridulation) than females. We did not have sufficient courtship activity to test this notion. Although additional studies are required to fully examine the role of time allocation on fitness or the associated functional reasons leading to the evolution of a particular time budget, the observed patterns of these three ecologically different grasshopper species from the same site provide a good initial overview of the pattern.

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