

Small-scale Displacements of Grasshoppers (Orthoptera: Acrididae) Within Arid Grasslands

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ABSTRACT: Small-scale linear displacement of 4 species of grasshoppers within an arid grassland was determined from marked individuals; movement was followed on a mapped grid of approximately one hectare. Species studied were: *Cordillacris crenulata* (Bruner), *Dactyloctenium variegatum* (Scudder), *Trachyrhachys kiowa* (Stål), and *Trimerotropis pallidipennis* (Burmeister). An estimated average range of displacement for individual species was between 60 and 80 meters. Average daily displacement of those individuals which did not leave the study site did not differ significantly among these species even though one species was flightless. Populations of 3 of the 4 species could be considered viscous. Although small-scale displacement was similar for individuals of these species, *T. pallidipennis* exhibited a greater propensity for dispersal than the other species.

Population structure of grasshopper species and the attendant movement of individuals is poorly known. A determination of the range of movements of individuals is important since many important questions concerning populations are involved, including the limits of a population, calculation of neighborhood size, determination of potential gene flow, and other spatially-dependent parameters of interest. In addition, knowledge of individual movement might explain much of the heterogeneity in population abundance and distribution typically seen in natural systems (Roughgarden, 1977).

Skellam (1951, 1973) argued that theoretical individuals will move outwardly from an initial starting point with increasing time because of random movement. Clark (1962) and Clark et al. (1969) have demonstrated that displacement of adults in the manner suggested by Skellam is the rule for the Australian *Phaulacridium vittatum* (Sjost.) and *Chortoicetes terminifera* (Walk.), although the displacement of the grasshoppers ceased after an initial period of dispersal. However, vegetation is more likely to affect the rate of movement than the outward distance moved from an initial point based on random processes (Clark, 1962; Uvarov, 1977, p. 63) since habitat structure often determines microhabitat choice (Anderson, 1964; Anderson and Wright, 1952; Dempster, 1955; Joern, 1982).

In this study, movements of individual adult grasshoppers of 4 species coexisting within a single habitat are described. Rather than releasing all individuals from a central point, individuals were located in their "chosen" microhabitats and subsequent movement monitored. This approach permits a more accurate portrayal of population movement because of the lack of extended disturbance as well as the lack of extreme population densities associated with release experiments

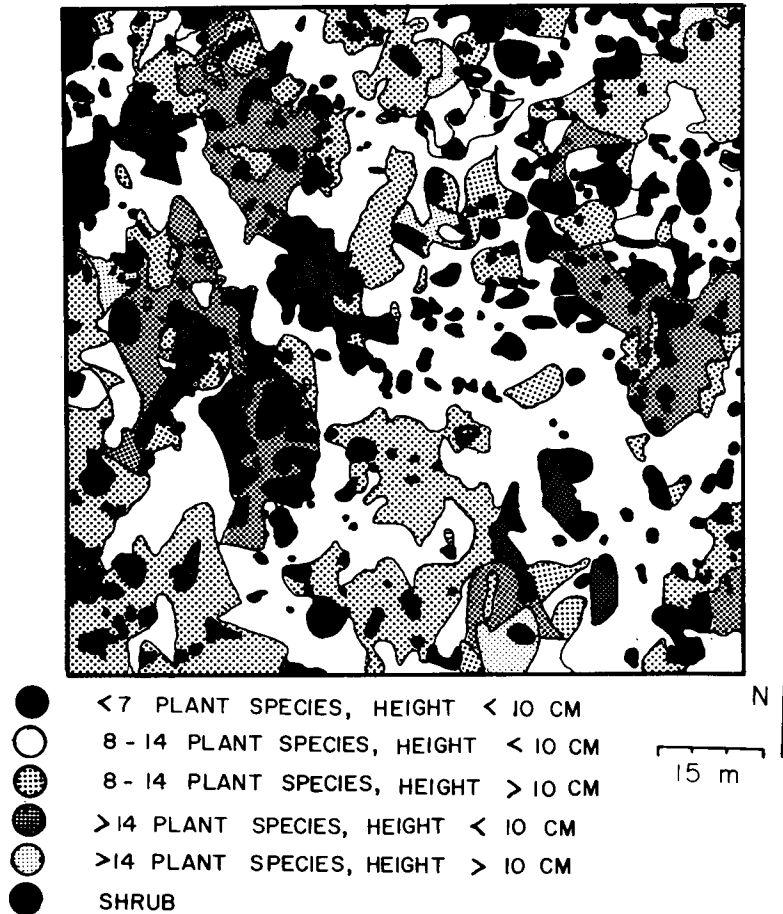


Fig. 1. Structure of vegetation at Altuda. Categories are based on the average height of vegetation within a patch and the total number of plant species.

which might enhance movement. Small-scale displacement includes movement done during the normal activities of a grasshopper excluding dispersal to a new area.

Description of Study Site

Individual movement was studied in 1975 at a permanently gridded site in an arid grassland plain of western Texas, 24 km east of Alpine (Brewster Co.). This region is dominated by the grasses *Bouteloua gracilis*, *B. eripoda*, and *Buchloe dactyloides*. The vegetation is quite heterogeneous and patchy resulting in a mosaic of both taxonomic and structural differences throughout the plot (Fig. 1). Large, open areas exist which consist primarily of bare soil and a sparse cover of grasses (*B. gracilis*, *B. dactyloides*, *Leptoloma cognata*, and *Scleropogon brevifolia*). The soil texture is finely particulate with a few larger rock particles. A more detailed description is found in Joern (1979).

The site is characterized by a low cloud cover and unpredictable summer rains.

Wind is generally present and varied in both magnitude and direction. There is usually an easterly component in the wind direction although it shifted considerably from day to day.

Grasshopper Species Studied and Microhabitat Use

Movements of the adults of four grasshopper species are documented in this paper: *Cordillacris crenulata* (Bruner), *Dactyloptum variegatum* (Scudder), *Trachyrhachys kiowa* (Stål) and *Trimerotropis pallidipennis* (Burmeister). *Cordillacris crenulata* is a relatively small species (about 14.5–17.6 mm long) and a strong flier over short distances. It is generally found in open microhabitats with sparse vegetation, and was often found on bare soil associated with short clumps of grass such as *B. gracilis*. Maximum adult population was estimated to be 589 individuals per hectare (SE = 462) (Joern, 1979). *Dactyloptum variegatum* is a flightless species with well developed walking and jumping capabilities. It is capable of traversing open areas of the habitat rapidly. It is larger (20.6–32.2 mm long) than *C. crenulata* and more robust. It is found in many microhabitats and appears to show little selectivity for microhabitats with any particular structure or plant species identity (Joern, 1982). This species was found in denser vegetation more often than the other three species. Estimated maximum adult population size was 198 individuals per hectare (SE = 177) (Joern, 1979). *Trachyrhachys kiowa* is a strong flier and is intermediate in size (16.5–20.6 mm in length). It also is found in sparsely vegetated microhabitats and tends to be on open soil near a low grass clump. Maximum population of adults was estimated to be 289 individuals per hectare (SE = 229) (Joern, 1979). *Trimerotropis pallidipennis* is an excellent flier and the largest of the three flying species studied (about 17.6–32.7 mm in length). It is found almost exclusively in open, bare microhabitats. The maximum density of adults was estimated to have been 128 individuals per hectare (SE = 173) (Joern, 1979, 1982).

Food plants were generally present in the vicinity of microhabitats chosen by the grasshoppers, and increased movement caused by lack of food was not probable. It appeared that structural qualities of the habitat were more important than availability of food plants in predicting where a particular species would be found (Joern, 1979).

The probability of finding suitable microhabitat within this one hectare study area was approximately equal for all of these species: *C. crenulata*—0.42; *D. variegatum*—0.39; *T. kiowa*—0.46; *T. pallidipennis*—0.42. This was determined by dividing the area of patches of microhabitat in which individuals of these species were actually found by the total area of the gridded plot.

Grasshoppers readily mated during this period and numerous pairs were encountered *in copula*.

Methods

Movement patterns were determined by following adults on a 95 m × 95 m permanently marked grid for a 6.5-week period beginning on 22 July 1975, and ending 6 September 1975. The plot was censused by slowly moving through the site, capturing with a net all grasshoppers seen, recording the location on the grid (and the specific microhabitat) and marking the individual (if not already marked) with a unique code. Each grasshopper was released at the point of capture. Cen-

suses were made frequently at irregular times. Records were typically taken at 2–3 day intervals; during late August, observations were suspended for 7 days. Released individuals generally remained within about a meter of where they were replaced; those moving great distances immediately after replacement were noted and not used to determine subsequent displacement.

Individual grasshoppers were marked with quick-drying Testor's enamel paint using unique sequences of marks. Only inconspicuous colors (grey, brown, black, and white) were used, and individuals usually had to be recaptured in order to be identified. Marks were placed on the pronotum, hind femora, and the tegmina and did not appear to affect behavior. Marks lasted the duration of the study.

Linear displacement between two capture points was used to estimate displacement. This distance was the radius of dispersal from the initial known point and did not include irregular movement about this straight line. Because of this, the measure is an underestimate of actual movement.

To estimate relative rates of movement among the species, the average distance moved per day, the maximum distance measured for a single day, and the root mean square of the distance moved after a given time were calculated. The root mean square (RMS) is calculated as:

$$\text{RMS} = \sqrt{\frac{\sum_i x_i^2}{n}}$$

where x_i is the distance moved by individual i after a given number of days and n is the number of individuals in the sample (Clark, 1962). The parameter can give the approximate range of small-scale displacement of individuals in a population. With increasing time, the root mean square of the distance will increase to a certain point and then either drop or level off. The value at which the RMS levels off represents the average range of small-scale displacement (Clark, 1962). Distance moved per day was calculated as the linear displacement between recaptures divided by the elapsed time (days) between recaptures. This will only be approximate, and more error is incorporated into the estimate when longer time periods are included. All recaptures are included in this analysis.

Results

Individual movements based on successive recaptures (Fig. 2) demonstrate the scale of movement within a habitat. The maximum measured distances include 64 m in one day for *C. crenulata* and 91 m in 3 days or 111 m in 16 days for *T. kiowa*. These distances, of course, represent minimal estimates of movement since some individuals could easily have moved longer distances off the plot. Total displacement for individuals of each species, irrespective of elapsed time between recaptures, is shown in Fig. 3. For individuals which were recaptured more than once, the distance from the most recent location was used to determine displacement. The flightless *D. variegatum* had about the same average displacement within a confined area as the strong-flying *T. pallidipennis*.

A general directional component of movement, toward the northwest, is seen in *C. crenulata* (Fig. 2). No obvious trend is seen in the other species. Statistics of local movement are presented in Table 1. *Cordillacris crenulata* exhibited the lowest average displacement per day and *T. pallidipennis* the greatest. Because of

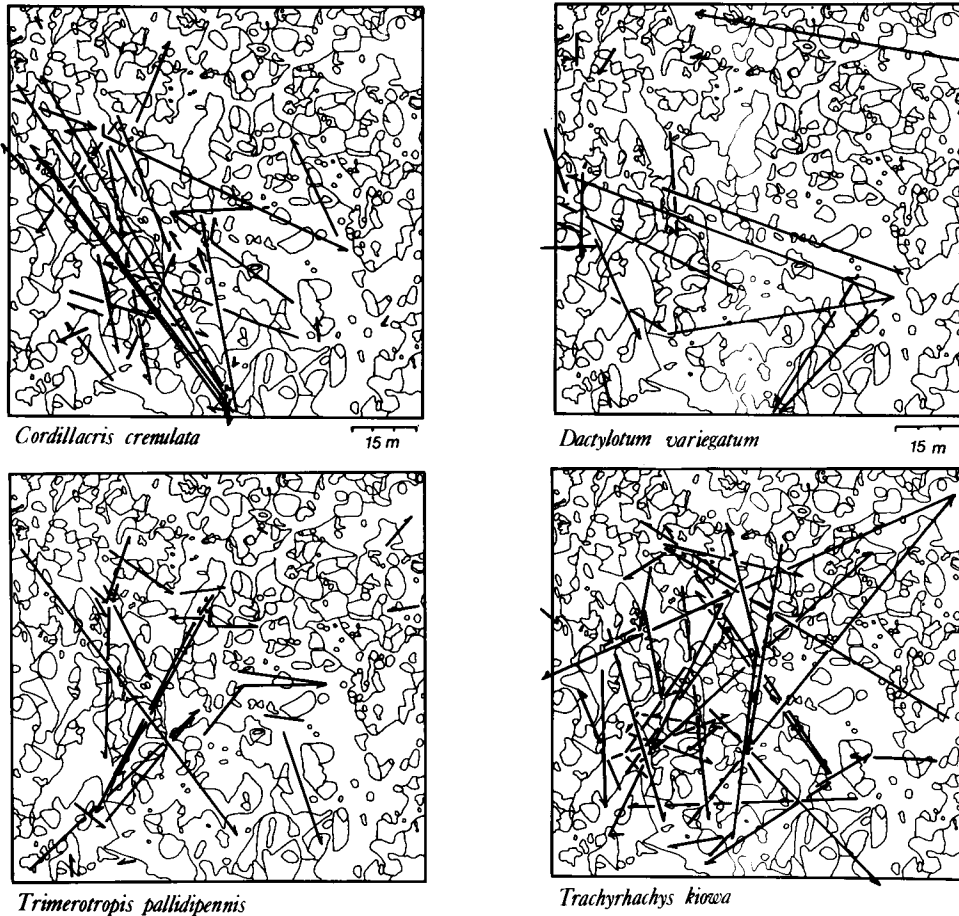


Fig. 2. Directed movement by individuals of four species of grasshoppers. Total linear displacement between recaptures of individuals are shown on the 95 m \times 95 m mapped study plot. No time element is incorporated; only total distance moved is shown. The vegetational mosaic is included in the background.

the great variability associated with these estimates, the values are not significantly different. The coefficient of variation allows the relative variability of movement to be compared; none of these estimates of the coefficient of variation is statistically significant at the 0.05 level.

Root mean square values for distance moved in increasing periods of elapsed time are presented in Table 2. *Cordillacris crenulata* showed a peak value of about 40–45 m after 4 days and another peak of about 60–70 m after 9–14 days. *Dactylotum variegatum* had a peak value of about 65 m after 5 days, while it was about 60 m after 4 days for *T. pallidipennis*. *Trachyrhachys kiowa* exhibited two peaks, at about 40–45 m after 4 days and at about 80 m after 14 days.

A positive correlation between distance moved and elapsed time was significant for *T. kiowa* and *T. pallidipennis* but not for *C. crenulata* or *D. variegatum*. Even though the correlation was significant for these first two species, a large fraction of the variance in distance moved is not explained. For *T. kiowa*, 34% of the

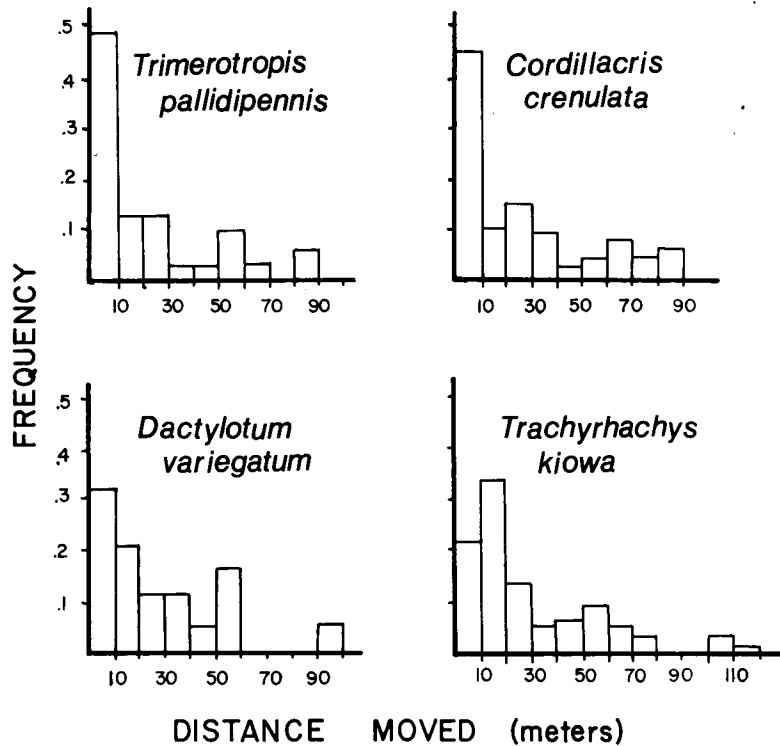


Fig. 3. Frequency of total displacement for all individual grasshoppers which were recaptured. No time element is incorporated; only total distance moved is indicated.

Table 1. Movement and recapture of 4 species of grasshoppers in an arid grassland study site. Distance was measured as a straight line between the release point and the point of recapture. The standard error of distance moved per day is in parentheses. The correlation coefficient (r) is between distance moved and elapsed time. Percent recaptured is the percent of all individuals marked which were recaptured at least once; multiple recaptures were not considered.

Species	Number individuals recaptured	Percent recaptured	Median no. days elapsed to recapture	Maximum no. days elapsed to recapture	Average distance per day (m)	Coefficient of variation (CV/100)	Maximum distance in one day (m)	r correlation (distance and time)
<i>Cordillacris crenulata</i>	55	53	6	34	4.9	1.92	64	0.17
<i>Dactylotum variegatum</i>	18	18	5	31	5.3	1.09	20	0.28
<i>Trachyrhachys kiowa</i>	76	36	4	27	6.9	1.52	30	0.58**
<i>Trimerotropis pallidipennis</i>	31	25	4	14	8.1	1.42	21	0.35*

* $P < 0.05$

** $P < 0.01$.

variance is explained and for *T. pallidipennis* 12% of the variance is explained by elapsed time alone.

Recapture information is also presented in Table 1. *Cordillacris crenulata* had the highest percentage of marked individuals recaptured, the largest number of individuals recaptured after relatively long periods of time, and the longest period of time from marking until last recapture. *Trimerotropis pallidipennis* had the lowest median number of days to recapture, the lowest maximum days of a recapture, and a low percentage of recaptures; only *D. variegatum* had a lower percentage of recaptures.

Discussion

Average movement per day for those individuals that remained within the study site was remarkably similar for the four species of grasshoppers which represented a range of sizes and flight capabilities. However, because of small sample sizes at many time intervals, conclusions must be considered somewhat tentative. Smaller species appeared to move at a slower rate although samples are too small for accurate determinations. The maximum distances moved in one day are similar to the movement of other grasshoppers such as early instar nymphs of *Camnula pellucida* (Scudder), which moved a maximum of about 35 m in one day, but are much lower than the maximum movement of adult *Melanoplus sanguinipes* (Fabr.), which moved a maximum distance of about 90 m per day (Riegert et al., 1954). These differences may not be biologically meaningful since the species in this study were followed under natural conditions, while the others were released *en masse* on a barren, tilled field. Average movements of grasshoppers from this study are similar to results of other reports. Solitary individuals of *Schistocerca gregaria* (Forsk.) moved an average of 23 yards over a 1–25 day period (Waloff, 1963), and Chapman (1959) reported that *Nomadacris septemfasciatus* (Serville) (6th instar nymphs) moved a maximum distance of about 100 yards in 4 days and an average of 30 yards over 3–5 day period. British grasshoppers tend to move only short distances (Richards and Waloff, 1954), often only a few feet.

Similarities in the range of movement are evident for the four species studied here as well. Each of the species tended to move within areas with a major axis of about 60 m from a few days to about two weeks. A general description of such individual movement is shown in Fig. 3. In all species the relationship of distance moved with time is either not statistically significant or explains very little of the variance. Although data are not available, it seems likely that after two weeks, *T. pallidipennis* traveled a much larger distance than the present estimate; such movement would not be detected on a grid of the size employed here. This view is supported by the smaller number of recaptures of this species beyond the first week after marking. High percentages of recapture for individuals of the other species suggests that they are more sedentary.

Obvious directional components of movement were evident only for *C. crenulata*. It seems likely that the long-distance flight ability of this species is not as great as in *T. kiowa* or *T. pallidipennis* and is more easily influenced by wind. Winds from the east are common (and often strong) at this site, which might partly explain the northwestern bias in flight. Riegert et al. (1954) found that wind influenced movement in various ways: early instar nymphs moved with the wind and adults flew into the wind.

Much variability in movement exists among individuals of the same species; *D. variegatum* was the least variable and *C. crenulata* the most variable, even though the average distances moved per day were almost identical for the two species. This may be explained by the fact that *D. variegatum* shows much less microhabitat specificity than does *C. crenulata* (Joern, 1982). *Cordillacris crenulata* may be less likely to move than *D. variegatum*, but may move farther when it does move in order to find a suitable microhabitat. Experiments have demonstrated the importance of habitat structure to small-scale movement (Dempster, 1955). Clearly, additional work is needed to identify the importance of microhabitat selectivity on small-scale movement.

Acknowledgments

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Literature Cited

- Anderson, N. S. 1964. Some relationships between grasshoppers and vegetation. *Ann. Entomol. Soc. Amer.* 57:763-742.
- Anderson, N. S., and J. L. Wright. 1952. Grasshopper investigations on Montana rangelands. *Mont. Agr. Exp. Sta. Tech. Bull.* 486. 46 pp.
- Chapman, R. F. 1959. Field observations on the behavior of hoppers of the red locust. *Anti-Locust Bull.* 33. Anti-Locust Research Centre, London. 51 pp.
- Clark, D. 1962. An analysis of dispersal and movement in *Phaulacridium vittatum* (Sjost.). *Austr. J. Zool.* 10:382-399.
- Clark, D., P. Ashnall, Z. Waloff, and L. Chinnick. 1969. Field studies on the Australian plague locust. *Anti-Locust Bull.* 44. Anti-Locust Research Centre, London. 101 pp.
- Dempster, J. P. 1955. Factors influencing small-scale movements of some British grasshoppers. *Proc. R. Entomol. Soc. Lond.* 30:145-150.
- Joern, A. 1979. Resource utilization and community structure in assemblages of arid grassland grasshoppers (Orthoptera:Acrididae). *Proc. Acad. Nat. Sci. Phila.* 105:253-300.
- . 1982. Vegetation structure and microhabitat selection in grasshoppers (Orthoptera:Acrididae). *Southwestern Naturalist* 27:197-209.
- Richards, O. W., and N. Waloff. 1954. Studies on the biology and population dynamics of British grasshoppers. *Anti-Locust Bull.* 17. Anti-Locust Research Centre, London. 182 pp.
- Riegert, P. W., R. A. Fuller, and L. G. Putnam. 1954. Studies on dispersal of grasshoppers (Acrididae) tagged with phosphorus-32. *Can. Entomol.* 86:223-232.
- Roughgarden, J. 1977. Patchiness in the spatial distribution of a population caused by stochastic fluctuations in resources. *Oikos* 29:52-59.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196-218.
- . 1973. The formation and interpretation of mathematical models of diffusionary processes in population biology. In M. S. Bartlett and R. W. Hiorns (eds.), *The Mathematical Theory of the Dynamics of Biological Populations*. Academic Press, New York. Pp. 63-85.
- Uvarov, B. 1977. *Grasshoppers and Locusts*. Vol. 2. Centre for Overseas Pest Research, London. 613 pp.
- Waloff, Z. 1963. Field studies on solitary and *transiens* desert locust in the Red Sea area. *Anti-Locust Bull.* 40. Anti-Locust Research Centre, London. 93 pp.