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SHORT COMMUNICATION

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Radio-telemetric evidence of migration in the gregarious but not the solitary morph of the Mormon cricket (*Anabrus simplex*: Orthoptera: Tettigoniidae)

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Abstract The Mormon cricket, *Anabrus simplex*, is one of just a few species of katydids (or bushcrickets, Orthoptera: Tettigoniidae) that, like migratory locusts, appear to have solitary and migratory morphs. Using radio telemetry we studied movements of individuals of two morphs of this flightless species. Individuals within each migratory band had similar rates of movements along similar directional headings whereas solitary individuals moved little and showed little evidence of directionality in movement. Our results also add to other recent radio-telemetry studies showing that flightless insects of 1–2 g in mass can be tracked successfully using these methods.

Introduction

Although not as well known as swarming by migratory locusts (Acrididae, Uvarov 1977) there are a few diurnal flightless tettigoniids (in several subfamilies on different continents) that form large, dense aggregations and march in large bands (reviewed by Gwynne, in press). This behavior is best known in coulee crickets (*Peranabrus scabricollis)* and Mormon crickets (*Anabrus simplex),* two North American shield-backed katydids (Tettigoniinae) that can be economically important when they invade crop fields (MacVean 1987).

There appear to be gregarious and solitary phases in the Mormon cricket (Cowan 1990; Gwynne, in press), a single morphological species (Gurney 1939). Solitary Mormon crickets do not form moving bands, have a cryptic green or brown coloration (typical of many tettigoniids: Gwynne, in press), and are found from sagebrush flats to alpine meadows. In contrast, gregarious individuals are conspicuous, dark-coloured insects from sagebrush habitats. Gregarious bands can be several kilometers wide and over 10 km long, with densities of up to several dozen adults per square metre (Cowan 1929; Wakeland 1959).

Little is known about the biology of migration in these insects. Bands appear to move because local food is quickly depleted (C.P. Gillette, cited in Cowan and McCampbell 1929) and coordinated group behaviour probably decreases predation (Gwynne, in press). Observations of bands in the same locality taking different directional headings appear to refute a number of suggestions for orientation cues such as using wind direction or the sun's position (Cowan 1929). As all observations of directionality have been anecdotal, a main purpose of our study was to determine if individuals within a band maintain similar headings as well as similar rates of movement. Such information may be useful in predicting whether Mormon crickets in native habitats are likely to encounter crop fields. A key aim of our study was to compare the movements of gregarious and solitary Mormon crickets in nature, our expectation being that solitary individual forms would not show directionality or long-distance movement. We used radio telemetry, so our final purpose was to demonstrate that small (approx. 0.85 g) radio-transmitters can be used effectively to monitor the movements of these 2- to 3-g insects.

Methods

Our preliminary estimates of the rate and direction of travel were obtained from four radio-tagged females in two solitary and two gregarious populations. The latter inhabited open areas of sagebrush: below a mesa in Echo Park, Dinosaur National Monument, Colorado, studied from 18 to 21 July 1999 (40°28.231′N, 109°2.126′W; 2300–2400 m altitude); and just below low hills near Vernon Utah, from 22 to 24 July (40°3.444′N, 112°25.279′W; 1700 m). At both sites Mormon crickets have long been known to form gregarious bands (Cowan 1929, 1990; Gwynne 1984) although solitary populations can also be found in nearby alpine valleys (D.T. Gwynne and P.D. Lorch, unpublished work). Our two solitary populations were in meadows on the east slope of the

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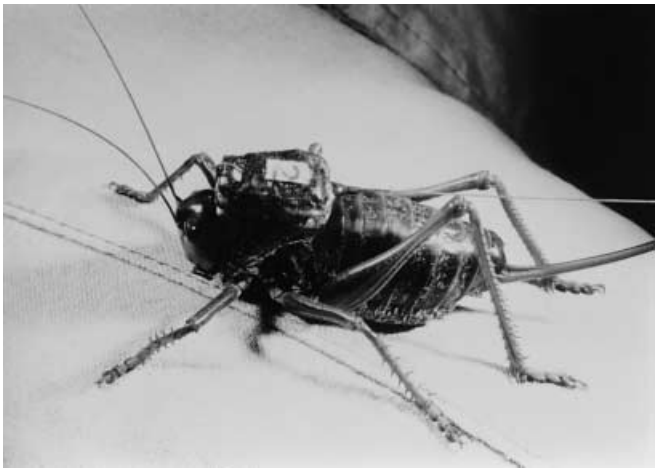

Fig. 1 A female Mormon cricket of the gregarious morph from the Dinosaur site showing the *radio-tag* glued to the *pronotum* and the *antenna* directed back over her *ovipositor*

Colorado Rocky Mountains: Kelly Flats in the Cache La Poudre Canyon, studied from 28 to 30 July (40°40.695′N, 105°28.963′W; 2100–2200 m), and a field near the Stove Prairie road from 29 to 30 July (40°38.775′N, 105°22.347′W; 2100–2200 m). Gregarious behavior has not been reported in this region of the Rocky Mountains (Wakeland 1959; Gwynne 1984).

To the pronotum of each female we glued (cyanoacrylate) radio-transmitters (0.85 g SM1 from AVM Instrument Co., http://www.avminstrument.com), with the antenna directed backwards (Fig. 1), which could be detected in brush or grass from approximately 500 m. We recaptured the tagged females at intervals over 24–48 h. After recapture, we estimated the distance and direction of travel (in degrees from north). Since time intervals for recapture varied between sites, rates of travel were estimated (m day^{-1}) and compared. In each of the four sites, between 23 and 41 h after tagging, we recaptured two females (initially tagged when approximately 100 m apart; for gregarious individuals one was in a dense part of the band whereas the second was closer to the band's edge).

Females at Dinosaur and Vernon were recaptured twice. For Dinosaur, data are indicated for the two females with subscripts a and b (Fig. 2). At Vernon the females did not move between first and second recaptures so only initial to first recapture data are shown in Fig. 2. To assess whether the morphs differed in rate and direction of travel we first compared the median speed by females using a conservative Mann-Whitney *U*-test. The two estimates of speed at Vernon and Dinosaur were averaged before testing for differences between morphs. To determine whether females travelled in a consistent direction within a site, we used one-way ANOVA to assess whether the variation about a mean direction varied more between sites than within sites. There are no comparable non-parametric tests for partitioning variance (repeated-measures ANOVAs were precluded by a lack of repeated data at some sites).

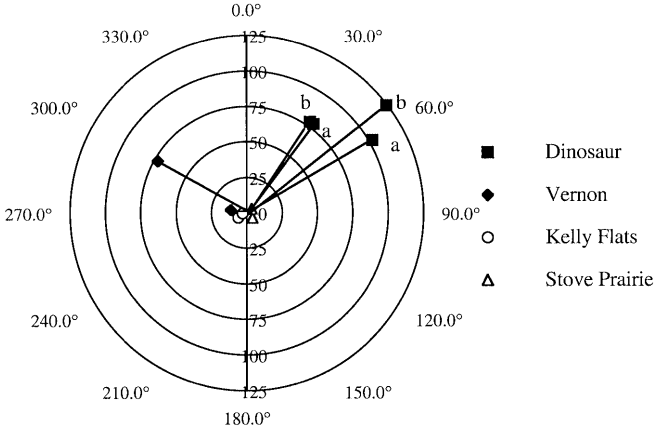

Fig. 2 Speed and direction of travel ofMormon cricket females (*open symbols* solitary morph females, *closed symbols* gregarious morph females). For Dinosaur, *a* indicates first recapture and *b* indicates second recapture

Results and discussion

As expected, gregarious individuals moved over greater distances than solitary females ($U=1$, $U'=15$, $z=-2.021$, one-tailed $P=0.02$) especially when measurements for non-moving individuals were excluded ($U=0$, $U'=16$, $z=-2.309$, one-tailed $P=0.01$). There was also significantly more variation in the direction of movement between sites than within sites ($F_{(3,4)}=29.27$, $P=0.0035$), indicating that individuals within a band tend to move in the same direction. Differences in migration behaviour did not appear to be due to topography, e.g. solitary individuals being prevented from long-distance movement by steep hillsides. Although the two gregarious sites were more open than one of the solitary sites, Mormon crickets are relatively unconstrained as they can move over obstacles such as buildings (Feilner 1864; Cowan 1929).

Gregarious crickets at Dinosaur were the only ones showing clear directional migration at each recapture of the two females, although the two gregarious individuals at Vernon had similar headings during their only recorded movements. During observations at Dinosaur, the band was clearly visible moving together in the same general direction as the two radio-tagged individuals. By contrast at Vernon both our tagged individuals, and the band itself, appeared to move much less. The band showed less obvious directional movement even though each morning many crickets spilled from overnight roosts in shrubs to move over open ground. The different behavior at Vernon may have been due to older individuals that migrate less. This hot Utah site was 600 m lower, and 24′ of latitude south of Dinosaur (the two solitary-cricket sites were similar in altitude to Dinosaur). Moreover, in Utah, eggs reportedly hatch in late February compared to hatching dates up to mid-April recorded for higher-altitude and higher-latitude sites in Utah, Colorado and Wyoming (Cowan 1990).

One other telemetry study of ensiferan Orthoptera used giant weta, *Deinacrida rugosa* (Stenopelmatidae), a very large species of 20 g or more (McIntyre, unpublished, cited in Szabo 1993) and a radio-tag (approx. 1 g) that was relatively light. Our results add to studies of other orders (Hayashi and Nakane 1989; Riecken and Raths 1996) showing that smaller flightless insects of about 2 g in body mass can also be successfully tracked with radio transmitters of about 1 g.

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