

# Radiotelemetry reveals differences in individual movement patterns between outbreak and non-outbreak Mormon cricket populations

PATRICK D. LORCH<sup>1</sup>, GREGORY A. SWORD<sup>2</sup>, DARRYL T. GWYNNE<sup>3</sup> and GERALD L. ANDERSON<sup>2</sup> <sup>1</sup>Department of Biology, University of North Carolina at Chapel Hill, U.S.A., <sup>2</sup>Northern Plains Agricultural Research Laboratory, United States Department of Agriculture, Agricultural Research Service, Sidney, Montana, U.S.A. and <sup>3</sup>Biology Department, University of Toronto at Mississauga, Canada

**Abstract.** 1. Outbreaks of insect pest populations are common and can have devastating effects on natural communities and on agriculture. Little is known about the causes of these outbreaks or the causes of *en masse* migrations during outbreaks.

2. Flightless Mormon crickets (*Anabrus simplex*) were the focus of this study. They are a katydid species that forms large, dense, mobile groups (migratory bands) during outbreak periods, eating vegetation in their path.

3. Radiotelemetric methods were used to measure differences in movement rate and directionality in outbreak and non-outbreak populations, testing the hypothesis that these populations differ in their travel rate and consistency of direction.

4. Daily individual movement in outbreak populations differs substantially from non-outbreak populations that are at much lower density. In addition to large differences in distances travelled (1.6 km as compared with 1 m) and rates of travel, there is evidence for collective movement among individual Mormon crickets travelling in migratory bands.

5. These data suggest that the direction of group movement may be influenced by local environmental conditions such as wind direction and movement of nearby band members. This work forms the basis for ongoing work testing hypotheses about mass migrations in outbreak populations.

**Key words.** Collective movement, insect migration, marching, radio tracking.

## Introduction

Insect outbreaks are common (see references in Hunter, 1995). When they occur in pest species, outbreaks of species such as gypsy moths (Lepidoptera: Lymantriidae: *Lymantria dispar*), pine borers (Coleoptera: Cerambycidae), and locusts (Orthoptera: Caelifera: Acrididae: *Locusta migratoria*) can have devastating consequences for humans and for ecological

communities. Controlling rising population densities in such insects is a major focus of applied ecology. However, relatively little is known about the causes of outbreaks, and particularly why within species they occur in some populations and not in others (Speight *et al.*, 1999). Even less is known about what causes groups of insects in outbreak populations to migrate *en masse* (Dingle, 1996). These migratory groups are often observed as flying swarms or marching bands in insects such as the African armyworm *Spodoptera exempta* (Lepidoptera: Noctuidae) and a number different locust species (Uvarov, 1977; Rose, 1979). Coordinated, long-distance group movements by these organisms are in large part responsible for their devastating pest status throughout the world (Dingle, 1996).

Correspondence: Patrick D. Lorch, Department of Biological Sciences, Kent State University, Rm. 256, Cunningham Hall, Kent, OH 44242-0001, U.S.A. E-mail: plorch@kent.edu

Outbreaks resulting in bands of marching insects occur but are poorly understood among katydids in the orthopteran suborder Ensifera (Gwynne, 2001). The movements of the flightless Mormon cricket [*Anabrus simplex* (Haldeman) (Orthoptera: Ensifera: Tettigoniidae)], widespread in western North America, were examined in detail. This species forms large mobile groups during outbreak periods. Radiotelemetric methods were used to describe differences in movement rate and directionality between Mormon crickets in outbreak and non-outbreak populations. The long-term goal is to find ways of predicting the direction and rate of movement, both to improve understanding of the causes of outbreaks and to reduce their impact on natural and agricultural resources.

Radiotelemetry is a valuable tool for understanding animal movement patterns. The ability to reliably track individual movements at the landscape scale has facilitated a greater understanding of animal migration patterns, home range sizes, habitat selection, and population demographics (White & Garrot, 1990; Dingle, 1996; Millspaugh & Marzluff, 2001). Data from these studies also form the basis for the development of animal movement models (Turchin, 1998; Millspaugh & Marzluff, 2001). This knowledge in turn has been used in various biological disciplines such as ecology, behaviour, conservation, and management (Millspaugh & Marzluff, 2001). Large transmitter size had limited radiotelemetric studies primarily to vertebrates (Cooke *et al.*, 2004). However, the reduced weight of newer transmitters has recently allowed studies of the movement of smaller organisms, including insects such as the Mormon cricket (Lorch & Gwynne, 2000; Cooke *et al.*, 2004; Sword *et al.*, 2005). In fact, since the study of Lorch and Gwynne (2000), the weight of transmitters used to track Mormon crickets has nearly halved to 0.45 g, much reducing the potential effects of transmitter load on these 2–3 g insects.

Mormon crickets are shield-backed katydids (subfamily Tettigoniinae). Under outbreak conditions, these insects form large cohesive groups called migratory bands, containing millions of insects that have been observed to travel *en masse* up to 2 km per day (Cowan, 1929, 1990). The behavioural mechanisms underlying their cohesion and directionality are very poorly understood (MacVean, 1987). In low-density non-outbreak populations, Mormon crickets do not march in migratory bands and appear to be much more sedentary (Lorch & Gwynne, 2000). Insects from these populations also differ from band-forming counterparts in coloration, mating system, size (Gwynne, 1984, 2001) and even life history (there is some evidence that non-band-forming crickets mature to adulthood several weeks later: D. T. Gwynne & N. Bailey, unpublished data). With the exception of variation in mating systems, the mechanisms underlying the observed phenotypic differences between Mormon crickets have not been fully explained. The possibility of genetic differences between band-forming and non-band-forming populations is currently under investigation (N. Bailey, M. G. Ritchie & D. T. Gwynne, unpublished data). Recent laboratory

behavioural assays suggest that movement in band-forming populations is environmentally determined and induced simply by short-term inter-individual interactions among conspecifics under high population density conditions (Sword, 2005). Recent field experiments also suggest that dense band-formation and movement evolved in response to the protection from predation afforded by band membership ('selfish herd effects'; Sword *et al.*, 2005).

The data presented below demonstrates that the daily movement patterns of individual Mormon crickets in band-forming populations differ substantially from that of individuals in much more sparse non-band-forming populations that are orders of magnitude lower in density. In addition to marked differences in distances travelled, there is evidence for collective movement among individual Mormon crickets travelling in migratory bands. The data suggest that the direction of group movement may be influenced by local environmental conditions such as wind direction. This work forms the basis of a broader effort to develop models of Mormon cricket movement and enhance understanding of collective movement in migratory insects.

## Methods

### *Effect of radio transmitters on movement behaviour*

The behavioural effects of transmitter load on an individual's movement were assessed by observing insects with and without radio transmitters in a laboratory arena. Fifty-three recently moulted adult insects were collected from a large mobile Mormon cricket band at the Wilkins site (40°23'24"N, 109°04'12"W, 2381 m elevation) on 7 July 2003, maintained in a 30-cm<sup>3</sup> screen sleeve cage overnight for  $\approx$  18 h, and observed the following day. Rearing conditions, observation, and analysis protocols were as described in Sword (2005) except that the arena was circular (26.6 cm diameter, 36.8 cm high). Transmitters were attached, as in the field, to 23 insects (16 female, 7 male) with a drop of hot glue on the dorsal surface of the pronotum with the radio transmitter antenna oriented toward the rear of the insect. After the glue hardened, the insects were placed in small cages that were blackened to block out most light, and allowed to settle for 5 min prior to observation in the arena as per Sword (2005). Thirty (15 female, 15 male) insects without transmitters were similarly observed for comparison. All insects were observed alone in the arena for 5 min.

Six behaviours, three turning-related and three walking-related, were quantified from digital video recordings using the EthoVision 4.0 ColorPro Video Behavioral Analysis System (Noldus Information Technology, 2002). These behaviours were as follows: (1) Walk Time (%), percentage of the assay spent walking; (2) Speed (cm s<sup>-1</sup>), average distance moved per unit time; (3) Distance (cm), total distance moved during the assay; (4) Turn Angle (°), average absolute change in direction between two consecutive samples; (5) Turning Rate (° s<sup>-1</sup>), average absolute change in

direction of movement per unit time; and (6) Meander ( $^{\circ}\text{cm}^{-1}$ ), average absolute change in direction relative to distance moved (see Noldus Information Technology, 2002 for detailed information about the calculation of these variables). Non-parametric Kruskal-Wallis  $H$  one-way ANOVA tests (using StatView 5.0.1; SAS Institute 1998) were used to test the hypothesis of no difference between groups of each sex  $\times$  radio transmitter combination for each behavioural variable.

#### Study sites for radio-tracking

Band-forming Mormon crickets were tracked at three different sites on a high desert plateau south of Dinosaur National Monument in the Blue Mountain region of north-east Utah and north-west Colorado, U.S.A. Mormon cricket bands had formed annually for a number of years prior to this study and the area has a history of band formation dating back at least 60 years (Wakeland, 1959). Vegetation at all tracking sites was dominated by sagebrush, *Artemesia tridentata*. Other common forbs and grasses included *Achillea millefolium*, *Agropyron smithii*, *Amelanchier alnifolia*, *Artemesia nova*, *Astragalus* spp., *Balsamorhiza sagittata*, *Bouteloua gracilis*, *Cercocarpus montanus*, *Gutierrezia sarothrae*, *Juniperus scopulorum*, *Juniperus osteosperma*, *Lupinus* spp., *Opuntia polyacantha*, *Stipa comata* and *Symphoricarpos occidentalis*. Topography in the region was variable, containing relatively flat areas, rolling hills interspersed with local drainages, and extremely rugged areas characterised by steep rocky slopes and cliff faces. The three tracking sites were Stuntz Ridge (Stuntz; 40°26'4"N, 109°04'37"W; 2363 m) where individuals within a band were tracked from 22 to 27 June 2003, Plug Hat (40°18'03"N, 108°55'52"W; 2320 m) tracked from 29 June to 4 July 2003, and Wilkins Cabin (Wilkins; see coordinates above) tracked from 5 to 10 July 2003. Local Mormon cricket densities within the tracked bands were visually estimated to vary from between 1 and 100 insects  $\text{m}^{-2}$ .

Non-band-forming Mormon crickets were tracked at three sites in the Poudre River Canyon in the Rocky Mountains of north-central Colorado, U.S.A. Populations in this area have no recorded history of outbreaks or band-formation (Wakeland, 1959; Gwynne, 1984; Lorch & Gwynne, 2000). Densities at these sites have always been observed to be low (Gwynne, 1984; Lorch & Gwynne, 2000), with visual estimates of much less than 1 insect per 10  $\text{m}^2$ . Study sites were flat grassy meadows adjacent to the Poudre River, embedded within Ponderosa Pine forest (see Gwynne, 1984 for additional site information). The three tracking sites were Kelly Flats (Kelly; 40°40'41"N, 105°28'57"W, 2038 m), upper Indian Meadows (Indian; 40°41'47"N, 105°31'51"W, 2115 m), and lower Indian Meadows (Indian2; 40°41'45"N, 105°31'15"W, 2097 m). Due to ease of tracking insects at these sites relative to band-forming sites, all insects were tracked concurrently from 11 to 17 July 2003.

Immediately prior to tracking, portable weather stations (Vantage Pro Weather Station, Davis Instruments, Hayward, CA, U.S.A.) were set up at each site to record local weather conditions. Weather parameters were saved to a data logger at 15 min intervals over the duration of tracking and downloaded to a laptop PC computer. Due to a technical error, weather data were not recovered at the Stuntz site. Temperature variation among sites that might influence insect movement rates was tested using an ANOVA on mean daily temperature at each site over the tracking duration. Variation was partitioned in the analysis into main effects of population type (band-forming vs. non-band-forming) and tracking site nested within population type.

#### Radio-tracking protocol

Twelve insects (six male and six female) at each band-forming site and six (three male and three female) at each non-band-forming site were affixed with radio transmitters, released, then relocated once daily over the course of 5 days. Tracking for longer is difficult given average travel distances and a transmitter detection range of  $\sim 500$  m on flat ground. Insects within a band were initially collected into 50 ml centrifuge tubes at 20 m intervals along a transect running perpendicular to the perceived direction of band movement. Insects were collected on foot at non-band-forming sites, and were released where they were found. Collection positions were marked with flags, and insects were taken in centrifuge tubes to a nearby vehicle to be weighed and affixed with a radio transmitter, applied as described above (Fig. 1).

Radio transmitters were 0.45 g Micro-Pip tags (Biotrack Limited, Dorset, U.K.) with specific individual frequencies between 173 and 174 MHz. With an inter-pulse interval of 2 s these tags last over 3 weeks under field conditions. Tagged insects were released at their original capture site and relocated once daily using a LA12-Q receiver and a hand-held Yagi directional antenna (AVM Instrument Company, Ltd., Colfax, CA, U.S.A.). One-day recapture intervals were used because longer intervals would result in loss of fast-moving migratory individuals and shorter intervals would reduce the number of individuals that could be tracked. Shorter intervals seemed unnecessary for the non-band-forming populations – although they were tracked at different times of day, they were always found close to where they had been released previously. Position and time of initial release as well as all subsequent relocations were recorded using a sub-metre accurate Trimble TSC1 Asset Surveyor<sup>TM</sup> DGPS System. Differentially corrected GPS data were exported from Pathfinder Office 2.51 (Trimble Navigation Ltd., Sunnyvale, CA, U.S.A.) into ArcMap 8.3 (ESRI Inc., Redlands, CA, U.S.A.). For each insect, 'as the crow-flies' distance and heading from magnetic north were calculated between successive daily recapture intervals.



**Fig. 1.** Mormon crickets (*Anabrus simplex*) with radio transmitters attached. Non-band-forming female (top) is shown carrying a spermatophylax and is slightly smaller than the band-forming female (bottom; Reproduced from Sword *et al.*, 2005).

#### Radio-tracking data analysis

Daily distances were converted to daily rates of movement to standardise for variation in sampling intervals among individuals. Directionality of movement was quantified using the consistency of the circular mean direction ( $r$ ; Zar, 1999). Consistency varies from 0 to 1 as the directedness of a group increases from random (dispersed) to completely consistent (concentrated). The probability of  $r$  being different from zero is assessed using the Rayleigh test of uniformity (Zar, 1999).

To determine if movement rates and directional consistencies were different between the sexes, average daily rate ( $\text{m h}^{-1}$ ) and circular mean direction of travel (unitless) were calculated for each individual over the tracking duration. The hypothesis of no effect of sex on rate or consistency was tested using a nested ANOVA to separately partition variation attributable to sex, population type (band-forming vs. non-band-forming), and tracking site nested within population type. Rates and directional consistencies were calculated for individuals over 5 days.

To compare the rate of travel between population types, a nested repeated-measures ANOVA was used. Site and day effects were controlled for by nesting site within population

type and using day as the repeat effect. Differences in the directional consistency between population types were examined by comparing the consistency of each group of insects at each site over each sampling interval in a nested ANOVA. The effects of population type were tested, controlling for site nested within population type.

## Results

### *No effect of radio transmitters on movement behaviour*

Carrying a radio transmitter had no apparent effect on the short-term movement behaviour of either male or female Mormon crickets assayed in the lab. Kruskal-Wallis tests revealed no significant differences in movement parameters between groups of males or females either with or without transmitters (Walk Time,  $H_3 = 3.229$ ,  $P = 0.358$ ; Speed,  $H_3 = 2.046$ ,  $P = 0.563$ ; Distance,  $H_3 = 1.474$ ,  $P = 0.688$ ; Turn Angle,  $H_3 = 2.687$ ,  $P = 0.442$ ; Turning Rate,  $H_3 = 2.186$ ,  $P = 0.688$ ; Meander,  $H_3 = 3.775$ ,  $P = 0.287$ ).

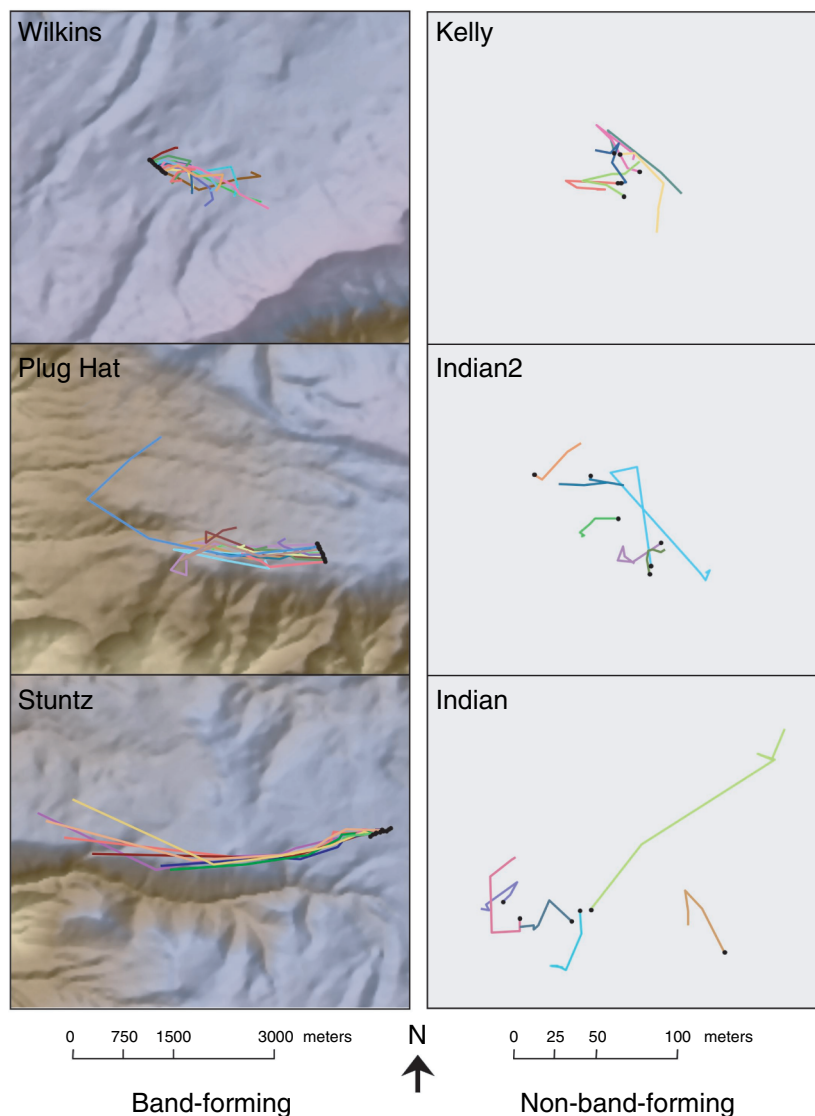
### *No sex or temperature effects on movement*

No effect of sex in either rate of movement or consistency of direction was found in the nested ANOVA model that controlled for variation due to population type and site (rate:  $F_{1,50} = 1.326$ ,  $P = 0.255$ ; consistency:  $F_{1,50} = 0.0015$ ,  $P = 0.969$ ). Thus, sex was ignored in all subsequent analyses. A similar model detected no significant variation in daily mean temperatures, either between population types ( $F_{1,21} = 0.02$ ,  $P = 0.88$ ) or among tracking sites nested within population type ( $F_{1,21} = 0.55$ ,  $P = 0.58$ ). This indicates that differences in temperature among sites are insufficient to explain observed differences in movement.

### *Band-forming vs. non-band-forming movement*

There were striking differences in both rate of movement and consistency of direction between band-forming and non-band-forming populations (Fig. 2). Daily movement rates were significantly greater among band-forming than among non-band-forming populations (Fig. 3; Table 1). There was no significant variation in movement rates among sites nested within population type (Table 1). On average, individuals in band-forming populations travelled at a rate of  $331 \text{ m day}^{-1}$  (range =  $1.4\text{--}1959.1 \text{ m}$ ), with six individuals observed to travel over 1 km ('as-the-crow-flies') in a single day. In contrast, individuals in non-band-forming populations travelled at a much lower average rate of only  $0.66 \text{ m day}^{-1}$  (range =  $0.5\text{--}87.7 \text{ m}$ ).

On a given day, individuals within bands all tended to move in the same direction, while the movements of individuals in non-band-forming populations were not



**Fig. 2.** Movement patterns of band-forming and non-band-forming Mormon crickets. Line colours represent different individuals and each line segment depicts 1 day of movement. Black dots indicate the initial release points. Topographic change from low to high elevation is represented by the transition from yellow to brown to blue in the migratory population maps. Background colour of the sedentary population maps is arbitrary because topographic features were unresolved at such a small spatial scale. Note that band-forming individuals spatially separated from each other often turned in the same direction at the same time.

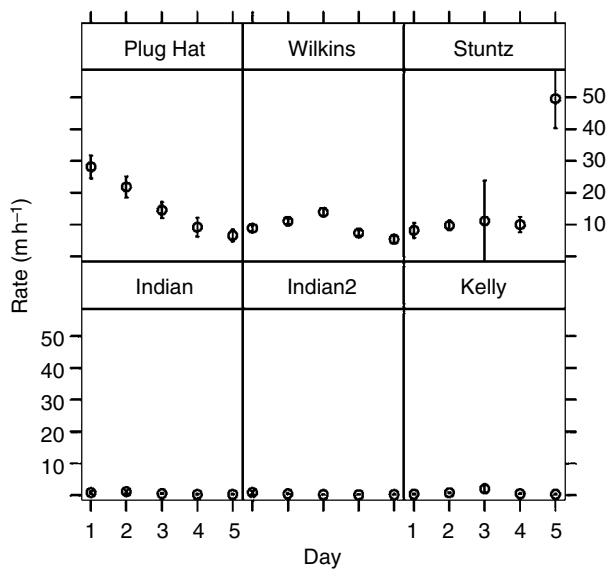
directional. This difference was demonstrated by the significant effect of population type on consistency (Table 2). Not only were daily consistency measures higher in band-forming relative to non-band-forming populations, but their consistency indices within days were also more often significantly different from zero [13/15 days in band-forming vs. 0/15 days in non-band-forming populations based on Rayleigh test of uniformity (Fig. 4)]. There was no evidence for significant variation among sites nested within the different population types (Table 2).

## Discussion

These results provide a robust demonstration of differences in directedness and rate of movement between band-forming and non-band-forming populations of Mormon crickets. Insects in band-forming populations travel significantly

faster and are significantly more directional as a group than insects in non-band-forming populations.

A preliminary and less quantitative study of Mormon cricket movement using radiotelemetry described similar differences in directedness and rate (Lorch & Gwynne, 2000). However, the study used only two insects per population (all females) that were tracked for 2 days and lacked sufficient replication for rigorous statistical analysis. The present study vastly increased the number of sampled populations, the number of individuals of both sexes sampled within each population, and the number of consecutive sampling days. Larger sample sizes used in this study enabled the use of circular statistics to compare variance in directionality that was not possible in Lorch and Gwynne (2000). In addition, tracking for five consecutive days allowed for a more thorough investigation of individual and group-level movement patterns over time.



**Fig. 3.** Mean  $\pm$  SE rate of travel calculated among individuals for a given site and day.

The possibility that all Mormon crickets make extensive movements but that these movements simply go unnoticed when the insects are at very low population densities can be ruled out. Mormon crickets in band-forming populations walked much greater distances per day than conspecifics in non-band-forming populations (Figs 2 and 3; Table 1). Individuals in migratory bands travelled an average of  $0.33 \text{ km day}^{-1}$ . One individual was observed to have moved almost 2 km in 24 h. This appears to be the longest recorded daily movement for any flightless insect. This maximum is in line with historical estimates of maximum band travel distance (Cowan, 1929), but the actual maximum distance these insects are capable of travelling is likely even greater. Observed rates of movement should be underestimates of the actual rate of travel because they are based on insects carrying extra weight and do not take topography or tortuosity of movement (i.e. deviation from straight-line travel) into account. Extrapolation using the maximum rate predicts that bands have the potential to move over 60 km per month.

**Table 1.** Nested, repeated-measures ANOVA of travel rate comparing band forming and non-band-forming populations (Population Type). The factor Site nested within Population Type controlled for differences between sites. Repeated measures of rate were taken using the same individuals over 5 days. Day was entered as a repeated measure to control for differences between days (non-significant Day effect:  $F_{4,30} = 2.44$ ,  $P = 0.07$ ). The whole model was significant ( $F_{5,33} = 10.44$ ,  $P < 0.0001$ ).

Source	d.f.	<i>F</i>	<i>P</i>
Site[Population Type]	4, 33	0.36	0.83
Population Type	1, 33	26.70	<0.0001

**Table 2.** Nested ANOVA of circular concentration comparing band-forming and non-band-forming populations (Population Type). The factor Site nested within Population Type controlled for differences between sites. The whole model was significant ( $F_{5,24} = 5.75$ ,  $P = 0.0013$ ) and it explained 45% of the variance.

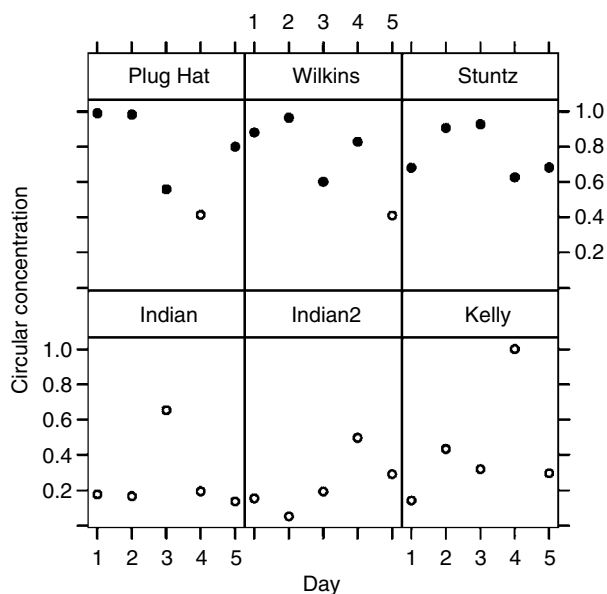
Source	d.f.	SS	<i>F</i>	<i>P</i>
Site[Population Type]	4, 24	0.12	0.56	0.69
Population Type	1, 24	1.42	26.54	<0.0001

By tracking over consecutive days it was possible to observe a number of synchronised turns among the migratory insects in which a majority of the band members changed directions in a similar manner at the same time (Fig. 2). This synchrony among members is further supported by the fact that the consistency indices of the migratory insects were significant in all but 2 days over the entire duration of tracking (Fig. 4). Importantly, insects appeared to turn in the same direction regardless of their position in the band (Fig. 2). This suggests that individuals may have changed direction in a similar manner in response to some landscape-scale environmental cue. Individual taxis in response to the same environmental cue could provide an underlying mechanism for the consistency of direction that was repeatedly observed. On the other hand, given that Mormon cricket movement appears to be induced by short-term inter-individual interactions (Sword, 2005), another possibility is that turning is a collective event propagated through the band via interactions among individuals analogous to turns observed in bird flocks or schools of fish (Radakov, 1973; Couzin & Krause, 2003).

Although this study was not specifically designed to elucidate the mechanisms underlying migratory band movement, the data do offer some insights and suggest future hypotheses for testing. At first inspection it may appear as though topographic features such as ridges influenced band direction, especially at the Stuntz and Plug Hat sites (Fig. 2). This seems unlikely though, because bands have been observed to traverse similar terrain on other occasions. Furthermore, closer inspection of the movements at Plug Hat (Fig. 2) reveals similar direction changes by insects experiencing quite different topography.

Sword (2005) suggested that migratory band movement might be best understood as a self-organising system in which inter-individual interactions result in group-level collective movement patterns (see Couzin & Krause, 2003). An array of movement models in which individuals modify their rate and direction in response to conspecifics have shown that group direction can arise from local inter-individual interactions as a result of self-organisation (Krause & Ruxton, 2002; Couzin & Krause, 2003). If both the initiation of Mormon cricket movement as well as group directionality are collectively determined and not influenced by extraneous environmental cues, it might be expected that the direction of band movement from day to day would be random. This was clearly not the case. Bands repeatedly moved in the same direction over successive days (Fig. 2).





**Fig. 4.** Circular concentration calculated among individuals for a given site and day. Closed circles show daily concentration estimates that were significantly different from zero ( $P < 0.05$ , based on the Rayleigh test). All of these were in band-forming sites (Plug Hat, Wilkins, and Stuntz). One non-banding site had high concentration (0.99), but it was based on two individuals and was not significantly concentrated.

Although the activation of Mormon cricket movement appears to be collectively determined (Sword, 2005), perhaps the direction of group travel is either directly or synergistically influenced by one or more local environmental cues.

Wind direction is an obvious cue that might account for the daily movement directions that were observed. Wind is thought to influence the direction of band movement in marching locust nymphs, but its effects can be species specific and vary with wind speed (Uvarov, 1977). Preliminary data suggest Mormon crickets may use morning wind direction to set their travel direction when they leave their evening roosts and begin to march each morning (MacVean, 1987; Gwynne, 2001). Positive correlations were found between prevailing wind direction and average daily band direction during 1 h intervals from 06.00 to 09.00 hours (although the only significant correlation was during the 09.00 hours interval; data not shown). Another possibility is that while a majority of Mormon crickets stop moving and seek shelter at night, on multiple occasions individuals have been observed moving across open ground during the evening, albeit much more slowly due to lower night-time temperatures. Perhaps these individuals seed band directionality the next day and can help to explain the directional consistency of band movement across days.

An important consideration in radio-tracking studies is to ensure that the tags do not adversely affect the behaviour of the study organism (White & Garrott, 1990). Radio transmitters were found to have had no significant effect

on short-term movement behaviours including speed, distance, and turning. The possibility that the radio transmitters slow down individuals over the long term cannot be ruled out, but any effect appears to be minor given that the maximum individual rate of travel observed was consistent with other published estimates. Additional observations support the notion that radio transmitters did not impair the natural behaviour of Mormon crickets. First, seven tagged females of both population types were observed 'carrying the hominy' (Cowan, 1990), the large bilobed spermatophylax, a nuptial meal transferred with the spermatophore during copulation (Gwynne, 2001) and carried by the female for hours after mating (see Fig. 1). Second, three radio-tagged males were observed calling, showing that attachment of the radio transmitter to the pronotum did not prevent them from raising their tegmina to stridulate. Also, no discernible sex differences were found in directedness or rate of travel, despite the fact that males are smaller than females and therefore more likely to be affected by additional weight. The lack of a sex difference also indicates that the apparently greater movement of females than males in a band as they actively search for mates (Gwynne & Dodson, 1983) is minor compared to the very long distances travelled after the morning mating period that precedes marching (Gwynne, 2001).

Future studies will examine the role of wind direction as well as other environmental and social variables on Mormon cricket migratory band movement. Results of these analyses along with the estimates of directional consistency and rate obtained here will be integrated into models that can further understanding of the dynamics and mechanisms underlying landscape-scale group movement patterns. These models have the potential to enhance Mormon cricket management during outbreaks by identifying where bands are likely to go, thereby enabling control operations to be more discriminate and precise. The benefits of such an approach can include reductions in the manpower and cost necessary to treat Mormon cricket bands along with minimising the potentially harmful effects of chemical control on the environment.

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