INSECT TERRITORIALITY AND ITS EVOLUTION: POPULATION STUDIES OF DESERT GRASSHOPPERS ON CREOSOTE BUSHES

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INTRODUCTION

Territorial behaviour has been viewed as any 'site-dependent display behaviour that results in conspicuousness and in avoidance by other similarly behaving individuals' and which is not restricted to site-dependent defensive or aggressive behaviour (Fretwell 1972). By this broad definition a number of grasshopper species may be territorial. However, territorial defence, a component of site-dependent behaviour is extremely rare in grasshoppers (Acridoidea). The only species now known to defend territories (among more than 150 species studied—Jacobs 1953; Otte 1970) is *Ligurotettix coquillettii* McNeill, a gomphocerine grasshopper living on creosote bushes (*Larrea divaricata* Cav.) in the Sonoran Desert. Elucidation of factors selecting for territoriality is difficult because other species living on creosote bushes in both North and South America fail to display any territorial defence. Both *Ligurotettix* and another gomphocerine species, *Bootettix argentatus* Br., advertise their whereabouts acoustically by stridulating, and both feed on creosote leaves. *Bootettix* resembles creosote leaves in colour and remains on the foliage day and night, while *Ligurotettix* resembles the grey stems, resides on stems during the daytime and feeds on the foliage at night. Several *Bootettix* males commonly inhabit the same bush or even the same branch, whereas *Ligurotettix* males tend vigorously to defend bushes against other males and may even avoid occupation of adjacent bushes. Such behavioural differences are evidently responsible for the considerable differences in population density between the two species.

*Goniatria planum* Bruner, a close relative of *Ligurotettix*, lives on southern blackbrush (*Florenzia cernua* DC) in the Chihuahuan Desert (Tinkham 1948). This species also does not defend territories but appears to have characteristics which could easily lead to territorial defence, given a change in bush size. In Argentina several species of the prosco-piid genus *Astroma* are host-specific on several *Larrea* species. They also display no territorial defence system and may reach densities in excess of 15 males per bush.

Territorial defence in insects appears to be more common in groups which are capable of recognizing and returning to unique points in their landscape, e.g., Odonata (Jacobs 1955) and certain Hymenoptera (Lin 1963; Wilson 1971). But insects which remain in small, clearly bounded, and defensible places may also be territorial even though they are incapable of distinguishing among similar sites.

Our objectives here are to present results of observations and experiments on populations of *Larrea*-inhabiting grasshoppers occurring in North and South American deserts and to discuss general features of territoriality in relation to distribution and density in insects. Marking experiments and manipulations of population densities were carried out mainly in *Ligurotettix coquillettii*, but observations on other species allow us to illustrate
several other strategies of desert species. Other species that we considered are Bootettix argentatus and Cibolacris parviceps (F. Walker) in the Sonoran Desert, Goniatron planum in the Chihuahuan Desert, and several Astroma species from the Monte Desert of Argentina.

METHODS

The study was carried out 56 km west of Tucson, Arizona, on the Silver Bell Bajada, along the eastern slope of the Silver Bell Mountains. The study site is dominated by creosote bush (Larrea divaricata Cav.) and is intersected by washes containing Cercidium floridum Bentham, Acacia constricta (Woot.), and Prosopis julifora (Sw.). Most data were gathered at three localities henceforth designated site I, about 16 km east of sites II and III, about 1 km apart. Field data were collected between 10 July and 23 August 1972, and between 14 July and 11 August 1973. Site I comprised a stretch of level ground between two washes and consisted almost exclusively of four plant species: 3 perennial bushes, Larrea divaricata, Franseria damosa Gray, and F. deltoidea Gray, and an annual grass, Bouteloua aristidoides Humboldt, Bonpland & Kunth. As many as six grasshopper species inhabited the site: Ligurotettix coquilletti, confined to Larrea bushes; Cibolacris parviceps, which feeds on Larrea at night and rests on the ground in the day time; and Trimerotropis pallidipennis (Burmeister), Trachyrachis mexicana Saussure, and Psolissa texana Scudder which live on open ground and feed on the grass Bouteloua aristidoides. Bootettix was not found on the site but was fairly abundant nearby.

At Site I a map was made of all bushes. It consisted of a 45 m x 90 m grid of 3 m x 3 m squares marked with small painted stones. Larrea bushes growing close together and with considerable foliage overlap were mapped as a single bush complex. These complexes were later shown to constitute single Ligurotettix territories. Areas covered by individual creosote bushes were estimated for the most part, but in some cases diameters were measured. Bush height and number of stems were not estimated, but these features tend to be correlated closely with the diameter of the plant. The fullness of the bush (amount of foliage per stem) was variable and not noticeably dependent on bush size.

All males of Ligurotettix on the grid were individually marked (below). Since they sing all day and into the night, all males within an area can be quickly located. They are easily captured with the fingers, marked, and returned to the bushes without seeming to be disturbed. Initially, individuals were marked with paint spots on the pronotum, wings and legs. Later males were marked with small numbered labels glued to the pronotum with rubber cement. Both methods resulted in a population of uniquely identified males, which could later be identified without being recaptured. Males were first marked on 14 July 1972, and returned to their bushes. Censuses were taken roughly twice a week on 17, 21, 25, 28, 31 July and 9, 11, 16 and 22 August. In 1973 censuses were taken on 26, 28, and 30 July and on 13 August. The male population was increased on three occasions by addition of new marked individuals. These were captured elsewhere, marked in the laboratory and introduced into the study site the following day.

In 1973 we marked females at all three intensive sites to estimate population size and rates of movement. Muted colour, browns, greens, and blues of Testors paints were used to reduce conspicuousness and hence predation. All females marked on a given day were given the same code.

Crop contents provided information on diet.

1. Host plants and diet

More than 90% of Ligurotettix males were found on creosote bushes. In areas where other plants were abundant (and possibly when the density of males was relatively the number of suitable bushes available) males occasionally occupied other plant species. At the edge of washes and at higher elevations, occasional individuals were found on Lycium berlandieri Dunal and Cercidium microphyllum (Torrey). The species also inhabited and fed on both Larrea and Atriplex polycarpa (Torrey) where these bushes occur together in the Avra Valley. At Saguaro National Monument (south) three males were found singing on Simmondsia sp. at night. Of these one had eaten only Simmondsia leaves, one had eaten both Larrea and Simmondsia leaves and one had eaten only Larrea. A female taken from the ground near Marana had eaten grass. In high density areas a small but regular proportion of males were found on burr sage (Franssaria deltoidea) during the day. No males were found on this plant at night, at which time animals feed. In four daytime censuses the proportion of the total male population at Site II and Site III found on Franssaria varied from 5-1% to 8-8%.

2. Daily activity cycles

Males tend to sing all day, commencing about 8 a.m. and stopping around 11 p.m. in July and August. Singing activity is somewhat dependent on temperature. On one cool evening males sang until dusk and then stopped. Later in the evening a sudden warm breeze caused large numbers of males to sing again. Songs consist of single, double, or triple clicks which can be heard over a distance of 50 m or more (Otte 1970).

The intensity of activity varies regularly during the day and seems to reach a peak between 10 a.m. and 1 p.m. Activity then slowly declines, reaching a minimum shortly after sundown. In the late afternoon, males are very sensitive to our movements and were difficult to capture. After dark, activity increases once again and remains intense for several hours. By midnight most singing has stopped.

Creosote bushes consist of long naked grey stems radiating from the ground and giving rise to foliage distally. Males and females resemble the stems in colour and are difficult to locate without practice. At night individuals move on to the foliage and feed.

3. Bush preference

Bushes varied in a number of parameters, such as number of stems, height, and foliage density. All but the last parameter increased with bush circumference. Males are more likely to occupy and to remain for longer periods on larger bushes. This preference is illustrated in Figs 1 and 2. Since smaller bushes greatly outnumber larger ones, more males were found occupying smaller bushes, but the average length of occupancy is significantly greater for larger bushes. Thus, more males land on smaller bushes, but they spend less time there. The mean length of occupancy was determined by summing the days that grasshoppers occupied bushes of each size class and dividing this by the total number of bushes in that class. Also, a larger proportion of small bushes was never occupied, and the known frequency of repeated occupancy of one bush was higher for larger than for smaller bushes. Thus 35% of larger bushes (more than 5-4 m²) were found to be occupied at least twice, while only 5% of smaller bushes (5-4 m² or less) were found to be occupied at least twice. The proportion of males found inhabiting the same
bush for at least 3 days was 47% for larger bushes (more than 5-4 m²) and 30% for smaller bushes (5-4 m² or less) (χ² test, P < 0.01). Very small bushes, although more abundant, were occupied by very few males. This may be due in part to the fact that they constitute smaller targets, hence are encountered less frequently by moving males. The very largest bushes may also be occupied for shorter periods than somewhat smaller bushes. Location of females, as a function of relative-bush volume (approximated by elliptic cones), is shown in Fig. 2. The frequency distribution of males and females on the various size classes is shown to be very similar.

4. Residence

Four males remained in the same bush for at least 30 days. The longest stay recorded in our 44-day study was 39 days. The rate at which a given group of males (i.e., all males counted at any one time) depart from their bushes over successive time intervals is reasonably constant (Fig. 3). Roughly one-third of the males censused on any one day move to another bush during the initial 3-day period, but only about one-sixth of those remaining depart during later intervals. Thus the probability that a male will remain in a bush after he first settles there is initially low but increases the longer he stays there. Proportionately fewer males became established on bushes for lengthy periods later in the season. If most females may be inseminated at this time, males may spend more time moving and searching.

More than half the female population marked on any one day departs from its bushes within the initial one-day interval, but in 1972 some females at Site I remained stationary in one bush for several weeks.
5. Dispersion patterns

Coefficients of dispersion (C.D.) (Sokal & Rolf 1969) of bushes and Ligurotettix males are compared in Table 1. The relatively low C.D. values for bushes indicate repulsion or negative interaction among bushes, or at least bush complexes. Slight repulsion of males is evident in early censuses, during which time the number of males remained relatively light and constant. Later, under lower densities, distribution of males was random. Since quadrats differ in bush frequency, they have different probabilities of containing males. For this reason we examined the distribution of males among blocks each containing ten bushes. Slight repulsion among males distributed within such blocks is again evident. Nearest neighbour analysis (Clark & Evans 1954) on both bushes and grasshoppers shows a nearly random distribution of males. Clearly, territoriality occurs within bushes and among bushes with overlapping foliage but there is no strong evidence that it occurs between non-overlapping bushes.

Table 2. Number of males per bush in regions differing in male density and bush size. The Larrea flat has a large number of small and intermediate sized bushes and shows essentially no multiple occupancy. Remaining sites had a higher proportion of large bushes and a significantly higher proportion of multiple occupancy. Percentage is given in parentheses.

<table>
<thead>
<tr>
<th>Number of males/bush</th>
<th>Site I*</th>
<th>No. of bushes</th>
<th>Site II†</th>
<th>Site III†</th>
<th>Site III†</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>309-6 (91-1)</td>
<td>37 (40-2)</td>
<td>10 (32)</td>
<td>13 (46)</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>30 (0-8)</td>
<td>44 (47-8)</td>
<td>15 (48)</td>
<td>13 (46)</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0 (0-0)</td>
<td>10 (10-9)</td>
<td>2 (6)</td>
<td>1 (4)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>0</td>
<td>1 (3)</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>1 (1-1)</td>
<td>2 (6)</td>
<td>1 (4)</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>0</td>
<td>1 (3)</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Total bushes</td>
<td>340</td>
<td>92</td>
<td>31</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Mean/10 bushes</td>
<td>0-9</td>
<td>7-4</td>
<td>12-9</td>
<td>6-8</td>
<td></td>
</tr>
</tbody>
</table>

* Mean for five census periods.
† Some males also found on Franseria deltoidea shrubs.
‡ A plot sampled 50 m east of Site III.

Table 2 illustrates bush utilization patterns in two fields differing in size distribution. Site II contained a larger proportion of large bushes and the frequency of double occupancy was clearly more prevalent. We present a model below which explains why some bushes are doubly occupied while others remain unoccupied, even though males compete for bushes.

6. Population density

The 90 x 45 m grid (Site I) contained 346 Larrea bushes and bush complexes (Figs 4–8). The actual number of individual plants exceeded this number, since many bush complexes consisted of several plants growing in close proximity. The densities of Ligurotettix males varied little from one census period to another and peak densities were very similar in two successive years even though rainfall regimes were quite different in the two years (Fig. 9). To determine whether density was influenced by territorial spacing of males, we doubled the population of males on 25 July 1972. On this day 34 males were resident on the grid. To this number we added 29 new males—15 males on to already occupied bushes.
Fig. 4. 90×45 m grid at site I (a Larrea-Fransaria association), position of males on 14 July 1972: ○, Larrea divaricata; ◦, Fransaria dumosa; ▲, F. deltoidea; ●, location of males of Ligurotetix.

Fig. 5. Position of resident males (●) and introduced males (▲) at the time of introduction on 25 July 1972.
Fig. 6. Position of all males three days after the 25 July introduction, indicating a return to pre-introduction levels and distribution patterns.

Fig. 7. Position of resident males (○) and introduced males (▲) at the time of introduction on 11 August 1972. The number and distribution of males returned to pre-introduction levels within three days.
and 14 males on to unoccupied bushes equivalent in size to occupied bushes. Occupied and unoccupied bushes were randomly selected. After three days no bushes contained more than one male, and the population in the grid had returned to 32 males. The results of this introduction are summarized in Table 3. Interactions between males forced to occupy the same bush had the following outcomes: in nine cases both males vacated the bush and in six cases the resident retained the bush. The mean daily departure rate of resident males (excluding the 25–28 July interval) was 3-7 males/day. But the 25–28 July departure rate of residents was 6-6 males/day. It seems likely that even males remaining alone on a bush experienced encounters with the introduced males. Introduced males were less successful at remaining on bushes than resident males ($X^2$ test, $P<0.05)$ and were least successful when placed on to already occupied bushes.

On 11 August, two groups of unmarked males were introduced on to empty bushes in two subplots, one male to a bush (Fig. 7). By 16 August, the population had again returned to the pre-introduction level of 22 males. A few introduced males remained on subplot B, but none remained on subplot A.

We do not understand why the population dropped to 22 males after the 11 August

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**Table 3. Behaviour of resident and introduced males following the 25 July introduction of 30 new males. N, number of males remaining or leaving during the 25–28 July interval.**

<table>
<thead>
<tr>
<th></th>
<th>Resident alone</th>
<th>Introduced alone</th>
<th>Resident and introduced together</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Remaining</td>
<td>Leaving</td>
<td>Remaining</td>
</tr>
<tr>
<td>N</td>
<td>9</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>%</td>
<td>47</td>
<td>53</td>
<td>29</td>
</tr>
</tbody>
</table>
1972 introduction, rather than to the 32 male level which we thought represented some saturation level. Since a good number of introduced males remain in the field, we cannot attribute the drop to the fact that all introduced males automatically leave the field. Saturation levels could perhaps decrease during the season because of changing behaviour patterns in males. Males may search more late in the adult season when most females would be expected to be inseminated and thus increase the number of male aggressive encounters. In a previous season (Residence) we showed that males are indeed less sedentary later in the season.

In 1973 the grid again contained between 30 and 34 males at the end of July. On 28 July we added 20 males to randomly selected unoccupied bushes. Within 2 days the population returned to its original level. These data may suggest that factors other than aggression are operating to keep male densities low. It is possible that the bushes we selected were unsuitable for habitation. But since there is a constant reshuffling of males between censuses, aggressive interactions could, of course, still be prevalent. The evidence that territoriality places constraints on male population levels remains somewhat circumstantial. It consists of two observations: (a) aggression between males (see section 8) makes multiple occupation of a bush less probable, and (b) population levels are resistant to change. We can by no means rule out predation or the existence of unpalatable bushes as important factors influencing density.

Populations in 1972 and 1973 declined at almost precisely the same rate even though rainfall regimes for the two years were quite different. In 1972 there was essentially no spring or early summer rain, but an abundance of rain and annual plant growth in the latter half of July and in August. In 1973 spring rainfall was abundant, but study areas were very dry during July and August; creosote bushes had a drier appearance, and many summer annuals were absent.

7. Behaviour of females and ratio of females to males

Information on females can be summarized as follows: (1) females seem to have the same daily activity cycles as males; (2) they do not signal acoustically; (3) they are attracted to the songs of males when they are sexually receptive; (4) more than one female was often found on the same bush as the male, even in low density sites, and all but one of 103 females we located were found in bushes containing males; (5) females were found closer to males in the high density sites ($\bar{x} = 30.17$ cm; s.d. = 22.09) than in low density sites ($\bar{x} = 48.38$ cm; s.d. = 33.96) ($P<0.05$; F test); and (6) three estimates of female population size (Table 4) indicated roughly the same number of females in high density sites but more females than males in the low density site. Because of the small population sizes, these estimates must be considered rough estimates only, and they probably underestimate the actual size of the population.

The number of females per male on a bush varies with density. At site I, where the ratio of territories to males was high, males did not share females. At the two high density sites, sharing of females by males was more common. This difference is made more meaningful when one computes the mean number of females per male in low and high density sites (Table 5). Clearly, the number of females per male is potentially high under low density conditions.

8. Territorial defence and aggression

The simultaneous occupation of one bush by two males is relatively rare. At sites II and III where bushes were larger and male densities higher, the incidence of two males occupy-
directly in front of or behind him. Once in close proximity, both males performed a leg raising movement which involved raising the hind femora and making up and down movements of the hind tibiae. Following such an exchange (lasting five seconds or so) one or the other male (in our observations, usually the introduced male) lunged at the opponent, grappling and biting. All legs became involved in the struggle, with the result that the males usually fell to the ground. Here they continued to fight, by biting and by kicking with the hind tibiae. Sometimes kicking separated the two males and attacks were sometimes repeated. The outcome of fights staged in this way cannot be predicted; either resident or introduced male emerged as winner and remained on the bush. In several cases, both males vacated the bush. Introductions of males in experiments described above indicated that resident males have a higher probability of retaining the bush. Staged fights were artificial in the sense that both males probably "viewed" the other as an intruder. There was some variation in the length of fights and details of the fight sequences. The longest fight lasted more than five minutes and the shortest less than one minute. We could not see what damage had been done in the fights, if any. Mandibles could easily sever an opponent's limbs and this could seriously handicap a male in further interactions.

Indirect evidence of aggressive interactions exists in high density sites (II and III) where a relatively constant percentage (mean = 7.4%) of males moved to Fransaria deltoidea during the day. At night, when it would be more difficult for a territory holder to detect an intruder, and when individuals feed, no males were found on Fransaria.

Aggressive tendencies seem to vary with population density. On the grid males reacted very quickly and aggressively to males sharing their bushes. But at sites II and III where Larrea plots contained a high density of males, more than one male often occupied a single bush. In bushes with more than one male, aggressive interactions were rare, even when males were close to one another (less than 6 in). Often no recognition by one male of the other was observed under these circumstances. Nevertheless, most bushes in high density sites still contained only one male.

B. Bootettix argentatus Bruner

This species has a wider geographic range than Ligurotettix. Its distribution follows creosote bush more closely. It remains on Larrea foliage continuously and feeds exclusively on Larrea. A much larger size range in bushes is inhabited in dense populations. But of special interest here are differences in relations between males and their possible effect on population density. Interactions are typical of those of grasshoppers in general. They possess signals which cause males in close proximity to separate from one another, but physical conflict does not occur. Males also attract females with good signals (Otte 1970). These songs can be heard day and night, but intervals between songs are long (0-5-3-0 minutes vs. every few seconds in Ligurotettix) and the sound is less intense.

In the Silver Bell area, population densities were low. Higher densities were found north of Needles, California, in Organ Pipe National Monument, Arizona, and between Marathon and Big Bend National Park, Texas. At the latter locality, extremely high densities were encountered in October 1972. Bushes were small to intermediate in size and rarely more than waist high. But all bushes appeared to contain at least several males, and some contained ten or more, sometimes with several males to a branch. Even very small plants a few inches in height sometimes contained two or three males. Similar densities in our study grid would have resulted in a population in the vicinity of 1500 males.

We noticed a great deal of flying among bushes by both sexes in the high density Texas population. Whether there is a real difference in the tendency of individuals to fly as population density increases was not determined, but such a change may well occur.

C. Cibolacris parviceps (F. Walker)

This third gomphocerine species also feeds primarily on Larrea, although less than does the previous species. It resembles the desert floor in colour and remains on the ground during the day. Late in the afternoon individuals fly into Larrea bushes and begin to feed. Several males and females may typically occur in the same bush at night. Mating takes place on the ground in the daytime. This species also possesses signals which attract females and cause males to separate, but contact aggression does not occur.

D. Goniatoron planum Bruner

This species is a close relative of Ligurotettix but does not defend bushes, or appears not to do so under the conditions in which we observed them. Goniatoron is restricted to the Chihuahuan Desert where it lives almost exclusively on southern blackbrush (Flourensia cernua). For reasons unknown to us it does not inhabit Larrea even when these are abundant in their habitat. Intermale relations in Goniatoron planum may be summarized as follows.

1) Males have two noisy calls, differing in function. A buzzing phrase is produced mainly by solitary males and consequently probably functions primarily to attract females. Clicks are also produced by solitary males but more commonly by males that must have been displaced or by two males that are very near one another. Clicks therefore probably have a sex identification and/or male-spacing function.

2) Singing males may be attended by one or more silent males and are themselves well-spaced in the field, one singing male to a bush. Were it not for the presence of silent males, the population would have superficially resembled a population of Ligurotettix. One bush contained three silent males and one singing male. In this instance, we chased the four males out of the bush, and all alighted on the ground (a behaviour never seen in Ligurotettix) and produced a series of clicking sounds. We then chased the singing male (male A) into another bush already occupied by a singing male (male B). Male A remained silent as the resident (B) continued singing. Then we chased A into a third unoccupied bush, and within a minute he resumed singing as before.

3) We believe that silent males in a sense use the singing male to attract females into the bush without themselves having to expend energy and that singing males are not aware of the presence of potential competitors. Silent males are very likely sensitive to the movements of individuals entering the bush (as in Ligurotettix) and therefore stand a good chance of intercepting females attracted to the singing male. Similar usurpation of females by silent males occurs in the genus Syrbus (Otte 1972).

4) We saw no fighting among males, even though the opportunities existed. The population we observed evidently contained more males than bushes, a situation not usually seen in Ligurotettix. Possibly males are aggressive under lower densities.

5) Males and females are prone to leaving their bushes, evidently on account of the bushes' small size. Therefore bushes may not be habitable for prolonged periods and hence may not be worth defending. The main differences in the habitats of Goniatoron and Ligurotettix are bush size and number of hiding places. Table 6 summarizes some differences in bush structure and the behavioural differences which appear to be a direct consequence of them.
Table 6. **Summary of differences between Larrea and Flourenzia bushes and the behaviour of their respective herbivores, Ligurotettix and Goniatrion (two closely related species). Structural differences may provide the different selective pressures which account for behavioural differences**

<table>
<thead>
<tr>
<th></th>
<th>Flourenzia</th>
<th>Larrea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bush size</td>
<td>small</td>
<td>larger</td>
</tr>
<tr>
<td>No. stems</td>
<td>few</td>
<td>many</td>
</tr>
<tr>
<td>(= hiding places)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grasshopper</td>
<td>Goniatrion</td>
<td>Ligurotettix</td>
</tr>
<tr>
<td>Residentiality</td>
<td>low</td>
<td>high</td>
</tr>
<tr>
<td>Defence of bush</td>
<td>apparently low</td>
<td>high</td>
</tr>
<tr>
<td>Bush inhabited by several males</td>
<td>frequent</td>
<td>rare</td>
</tr>
</tbody>
</table>

E. Astroma spp.

The Monte desert of Argentina has four Larrea species. Several Astroma species in the acridoid family Prosopilidae are host-specific on Larrea divaricata and L. cuneifolia Cav. Densities in these species are highly variable but become very high on occasion. At Andalgala (Provincia Catamarca) we found as many as 10 adult males (and as many females) on a single intermediate sized bush, and J. Schultz (personal communication) has found as many as 40 individuals on a single bush. Thus, population densities in these species may be higher than those of any other Larrea-specializing grasshopper species. Astroma species also are much larger than North American Larrea specialists and do considerably more damage to bushes (J. Schultz, personal communication). Males display no aggressive behaviour. Sexual size dimorphism is pronounced, and the smaller males frequently ride around on the backs of the females even when not copulating. Other males attempting to mount such females are probably removed by kicking.

DISCUSSION

A. Territoriality and density dynamics

Our results point indirectly to the conclusion that territorial defence is an important component in keeping populations of Ligurotettix males at relatively low levels. We suggest, however, that this control is quite incidental to the attempts of individual males to increase their quota of females by exclusive use of bushes likely to harbour females.

The present comparison of desert grasshoppers suggests that we are dealing with an array of species in which upper density limits are controlled in quite different ways. Numbers of Ligurotettix males appear to be controlled by the classical density-governing factor of Nicholson (1957), in this case intraspecific competition for females. We have not as yet attempted to demonstrate a return from a downward displacement. Below this carrying capacity fluctuations may be largely due to density-independent factors. Field studies on other species considered here have not been carried out in sufficient quantitative detail to permit anything more than speculation. At site 1 Ligurotettix maintained constant adult populations over two-seasons at the same time that marked changes in the density of a ground-dwelling annual plant-feeding grasshopper, Trimerotropis pallidipennis were taking place. In 1972 there was essentially no spring rainfall and little annual plant growth, while in 1973 spring rains were abundant and resulted in a large crop of spring and early summer annuals. The small T. pallidipennis population in 1972 and the very large population in 1973 were probably a direct consequence of these rainfall differences. Because it lives on resilient perennials, Ligurotettix appears to be well buffered against rainfall fluctuations, in addition to responding to intraspacific aggressive constraints.

But what of the overall patterns of density change and movement of individuals over extensive areas? We have focused on small subsets of a large, essentially continuous distribution of individuals which varies in density from place to place in relation to vegetation and rainfall patterns and perhaps to soil (oviposition) conditions. We propose that some of the following processes occur within larger areas.

1. Male populations in suitable areas (areas containing females) build up to a carrying capacity which is determined largely by the ratio of males to bushes, and excess males (non-territory holders) disperse into surrounding areas of lower density. Since females are not competing for males or bushes they should not be expected to depart as readily as males. Hence one should expect to find the sex ratio skewed in favour of females in suitable areas and in favour of males at the margins of suitable areas. Data bearing on this point are not available.

2. Rainfall in the Sonoran Desert tends to be patchy, with thunder-showers drenching certain areas and missing others nearby, thus producing stretches of good habitat alternating in an irregular fashion with poor habitat. Consequently, there may usually be areas of low density which absorb excess males from regions of high density.

3. Areas which have very low average rainfall may be suitable most years but have highly suitable occasionally. An individual that emigrates from a high density site could then by chance arrive at sites which are temporarily highly suitable, both on account of climate and low male density. However, one would expect selection to favour males that seek new sites only if there were good chance of encountering females there. We found females flying to lights (along with species that were obviously making long-distance flights) indicating that some kind of long-distance displacement by females does occur.

4. For females we predict the following movements. As the habitat deteriorates, females will tend to leave before the males, since they would not be dependent on the presence of males (once fertilized) and would be expected to be more sensitive to declining conditions locally, because they are the ones that must convert plant food into offspring (see further discussion below). Thus, an area that has recently become suitable adjacent to a deteriorating one might be expected to contain an excess of females over males. Males would be less inclined to move and would tend to do so only when the females (their critical resource) had already departed.

B. Site-dependent behaviour

Fretwell (1972) discusses three kinds of site-dependent behaviour resulting in regular spacing of animals. These are summarized in Fig. 10. Territoriality in Ligurotettix is of the density-limiting type, and territorial defence appears to be the principal reason for the large differences in population size occurring between this and other creosote-inhabiting species. Observations on Bootettix and Astroma indicate that creosote bushes can support much larger numbers of individuals without suffering significant damage and suggest that for Ligurotettix food would only be limiting at very much higher densities. Since several females are commonly found on the same branch, they evidently do not compete for bushes. It appears probable that territorial defence stems from competition among males for bushes that are attractive to females—perhaps those with food and oviposition sites of the right kind and affording adequate protection. Parental investment by a male is minimal, and his contribution to survival of offspring may be limited to the sex cells he
furnishes, or, if predators are differentially attracted to singing males, he could in addition improve the survival probability of his mates. Since members of the sex which invests less will compete among themselves for the sex which invests more (Trivers 1972), it is probable that females ultimately determine the bush category most suitable for males. But

what is suitable for females may not be best suited to males. Female preference may, for example, increase with bush size, but males may not prefer very large bushes because they are difficult to defend and must more frequently be shared with other males. Since females must mate, and they do so by first being attracted to males, males to some extent deter-

mine the particular bush (with the general size class suitable to females) that a female settles in.

C. Habitat occupation patterns

It seems odd that in a field where males are competing intensely for bushes, some bushes should remain unoccupied while others are doubly occupied (Table 2). There are several factors which could influence this distribution. (1) Some bushes appearing to be

suitable may in fact be unsuitable; plant chemistry might render certain bushes unpalatable, or the number and structure of stems may not afford adequate refuge against predators. In the present study we encountered a number of large bushes which were never occupied. (2) Territories occasionally include several bushes so that even an empty bush might elicit attacks from territory holders. (3) Males search for suitable bushes in a random fashion and happen to miss some suitable plants.

If a randomly searching male's threshold to settle decreases steadily as he encounters only small bushes or bushes already occupied, a point may be reached where a choice

FIG. 10. Visual representation of Fretwell's (1972) classification of site-dependent behaviour by animals, which results in even spacing of individuals. Two habitat types are depicted, with habitat A being more suitable than B when both are empty. Left column: Rows 1 and 2: animals begin to occupy habitat A first. They use signals to indicate that a site is occupied and, hence, less suitable. Rows 3 and 4: use of habitat A decreases in suitability to that of B, then entering animals enter A and B in such a fashion that suitability in the two habitats remain roughly equal. The result is an ideal-free distribution of animals. Central column: Row 1: animals occupy habitat A. Row 2: they defend their occupied sites, forcing newcomers into habitat B before suitability of habitat A is reduced to that of B. Rows 3 and 4: habitat B fills up and subsequent newcomers become outcasts; they are aggressively prevented from settling in either habitat. The result is an ideal-dominant distribution of males. Right column: The signals of individuals do not indicate anything about the suitability of the habitat. They facilitate spacing within A, but animals use other cues to determine suitability. Thus, they remain crowded but spaced until some essential resource is in short supply, at which time they move to habitat B.

FIG. 11. Left: Hypothetical changes in habitat suitability with increasing density. L₀, unoccupied large bushes; L₁, large bushes occupied by one male; S₀, unoccupied small bushes; S₁, small bush already occupied by one male. A species which has no difficulty in locating bushes of highest suitability might be expected to utilize the habitat in a stepwise fashion, switching to the next most suitable category only when the most suitable category was exhausted. To a species which has difficulty in locating the most suitable areas, the suitability of the habitat will decline according to the curved line (see text for derivation of the curve). Top right: suitability versus density under Allee's principle (Allee et al. 1949). Suitability of large (L) and small (S) bushes may be low at very low densities, due to difficulties in locating males.
must be made—to continue searching, to share a bush with another male, or to occupy a small bush. The suitability of a field into which a male enters can therefore be viewed as being determined by the territory to male ratio, the proportion of relatively suitable to unsuitable bushes, and the capacity of animals to locate suitable bushes. To illustrate how these factors might interact, imagine a portion of a field which contains 20 bushes (10 large and 10 small) in which large empty bushes have a suitability of 10, small bushes have a suitability of 6, large bushes with a resident male a suitability of 4 and a small bush with a resident male a suitability of 2. An ideal species which has no difficulty in locating bushes of highest suitability might be expected to occupy all large bushes first, then begin to occupy all small bushes and, when all bushes contain one male, to double up, beginning with large bushes (Fig. 11). In reality males are probably incapable of quickly finding bushes of highest suitability. Given this limitation, the suitability appears to be lower for a male that, upon entering the field, immediately encounters either smaller bushes or already occupied large bushes. The suitability curve cannot be determined with accuracy. But it is possible to construct a hypothetical curve by simulating a colonizing sequence. The assumptions used in the simulation then become interesting if the distribution of settlers corresponds to the natural situation. To do this we consider the portion of a field with 20 uniformly distributed bushes of suitability as described above. We now introduce 25 males into the field, and repeat the procedure ten times. Introductions are random (each bush having an equal probability of being the starting point). Only large and unoccupied bushes are settled the first time they are encountered. A male’s threshold to remain in a bush decreases with each unsuitable bush he encounters, as follows. After encountering two unsuitable bushes he is willing to accept a small unoccupied bush (suitability 6), but none with lower suitability; after three unsuccessful encounters he is willing to settle in a large bush with one male (suitability 4), but none with lower suitability; after four unsuccessful encounters he is willing to settle in a small bush containing one male, and so on. Thirdly, the direction of departure from an unsuitable bush is to one of the four nearest surrounding bushes, but the direction taken is random. If a male leaves the portion of the field under consideration he does not return. Of 25 males, 16–20 (mean 17.7; n = 10) males settled in the field; the rest departed. Of the large bushes, 7% remained unoccupied and 27% were occupied by two males. The apparent suitability of the habitat to entering males decreases as the density of males already present increases. The overall suitability at each density level was calculated using the formula:

\[ S = \frac{p(10) + q(6) + r(4) + s(2)}{10} \]

where \( p \) is the proportion (in 10 runs) of 1st, 2nd, 3rd, ... and nth males entering the field and settling on large, unoccupied bushes of suitability 10; and \( q, r, \) and \( s \) are the proportions settling on bushes of suitability 6, 4, and 2 respectively. A line through points plotted in this fashion gives one a hypothetical curve of apparent suitability. The curve shape will, of course, change with the threshold values and with other parameters, but it always shows that even a field with density 0 appears to be less suitable than it actually is and that at certain densities the suitability for the field is higher than would be expected if animals were much more capable in finding suitable bushes. In reality a continuous gradation from highly unsuitable to highly suitable bushes exists, and bush suitability cannot be subdivided into discrete categories. Nevertheless, the principle of habitat occupation just outlined should still apply.

Clearly, very low densities are also undesirable from the standpoint of locating mates.

For this reason, habitat suitability, in relation to density, will increase initially to some maximum and then decline (Fig. 11). The density which maximizes suitability could very well be different for the two sexes, that for females possibly lying to the right of that for males. As yet we have no way of evaluating what the optimal density for females would be.

D. Defence strategy in relation to density

We present now a model which predicts that the number of females inseminated (female quota) by the most successful males will initially increase as density increases, i.e., that relatively fewer males will father the next generation. But at some point defence becomes prohibitively costly in terms of time and/or energy. At this point we can suppose that aggressive behaviour will decrease as density increases. Fig. 12 illustrates graphically the changes in aggressive behaviour and the female quota in relation to changing territory: male ratio. At very low densities there are many more suitable territories than males, and the female quota is close to one (assuming a sex ratio of 1:1). As the number of available territories becomes scarce, females continue to be attracted to bushes of high suitability, but other males cannot enter these bushes because they are defended by the resident, who gains by not sharing. We make the assumption here that females are attracted to bushes of high suitability and especially those containing singing males and they continue to be attracted regardless of density. This seems reasonable given the fact that bushes can tolerate very high grasshopper densities. The result is that the female quota of territory holders increases steadily at first. But with further increases in male density (or reduction of the territory: male ratio) a male spends an increasing proportion of his time and energy defending the territory against challengers, both because they are more
numerous and because they can be expected to challenge more vigorously as the number of females per suitable bush increases. We should expect that the resident will stop defending at some density level below which defence takes up all or most of his time or energy (at which point his quota drops to 0). The resident may choose instead to settle for a non-aggressive existence, but one in which he stands to inseminate at least some females. At high densities, therefore, the maximum number of females inseminated drops to near 1 again.

An alternate strategy for males of a territorial species is to migrate out of an area when densities reach certain levels. It can be seen that the strategy of a non-territory holder (or the holder of an inferior territory) would depend on density levels. At intermediate levels where all females are adequately defended by territorial males a male may be better off leaving the area altogether on the chance of finding more favourable conditions, but at higher densities when aggressive tendencies of resident males have abated he can share females and would be better off staying.

E. The road to territoriality

The literature on territoriality is vast (see Brown & Orians 1970; McLaren 1972). Consequently, we shall merely focus our attention on what we believe to be important in the animals treated here. Several factors are believed to select for (or predispose an animal for evolving) territorial defence (Brown 1964; 1969; Baker 1972). Some of them are: (1) that some limiting resource be relatively localized and permanent; (2) that the resource is defensible; (3) that the resource be obtained in greater quantity if animals remain in a suitable region rather than moving among suitable regions; (4) that animals obtain more of the resource by defending the area against competing individuals; and (5) that individuals claiming an area advertise this fact, even while absent, to potential rivals. In this connection, females constitute a male resource that is essentially always in short supply. The more matings that a male can get the better, except in essentially monogamous species where male parental investment is high and where infidelity entails certain risks (Trivers 1972). It would seem on these grounds alone that territoriality would be more likely to involve competition for females than competition for other resources and that, whenever females are relatively localized, the males who appropriate areas containing females would be rewarded with exclusive sexual rights to those females.

In Ligurotettix we believe that, since bushes are likely to harbour females, males, by defending such bushes, reduce the probability that females who enter the bush will be intercepted by another male. There seems to be a tendency among acoustically signalling orthopteran males to become parasitic on other males and to use the attracting power of a neighbour and then intercept the attacked females (Otte 1972). Such parasitic interactions evidently occur in Goniatron (above). Ligurotettix has evidently circumvented this by taking the next step, which is to be highly vigilant and to exclude any male that enters his territory and attempts to intercept or share his females.

In non-colonial insects territoriality appears generally to evolve in association with increasing the female quota; such seems to be the case in cicada killers (Lin 1963), butterflies (Baker 1972) and crickets (Alexander 1961). But territoriality is clearly related to foraging in social Hymenoptera, particularly in ants (Wilson 1971).

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