

Territorial Behavior of *Boottettix Argentatus* Bruner (Orthoptera: Acrididae)

ABSTRACT: At low male densities territorial behavior was observed in male creosote-bush grasshoppers (*Boottettix argentatus* Bruner). Males defend individual shrubs or shrub complexes and exclude conspecific males. Experimental introduction of males into occupied shrubs resulted in a maximum of one male per shrub. Aggressive interactions between males occurred more frequently in shrubs also harboring females. A hypothesis relating behavior and density to host plant condition is discussed.

INTRODUCTION

Wilson (1975) considered defense of occupied areas to be the diagnostic feature of territoriality. Although male orthopterans maintain spacing by means of acoustic displays (Alexander, 1961; Morris, 1971; Otte, 1972, 1977; Otte and Joern, 1975), relatively few orthopteran species have demonstrated territoriality by Wilson's definition. Alexander (1961) and Otte (1977) showed that ground-dwelling gryllids defend territories around burrows. Among acridids territorial defense has only been observed for *Ligurotettix coquillettii* McNeill, which defends creosote bushes in the Sonoran Desert (Otte and Joern, 1975).

Boottettix argentatus Bruner is a related desert gomphocerine grasshopper restricted in habitat to creosote bushes in the southwestern United States and Mexico (Otte and Joern, 1975, 1976). Otte and Joern (1975) did not observe physical conflict between males at high densities. This led these authors to consider *Boottettix* behavior as a stage in the evolution of territorial behavior described for *Ligurotettix*. In this paper we present evidence of territorial defense by *Boottettix* at low densities and suggest that behavior and density are related to host plant palatability.

METHODS

This study was conducted primarily on the mesa between New Mexico State University and Tortugas Mountain SE of Las Cruces, New Mexico, between September and December 1975, and during July and August 1976. The area was dominated by creosote bush (*Larrea tridentata* Cav.), but *Acacia greggii* Gray, *A. constricta* Benth., *Prosopis juliflora* (Sw.) and several species of cacti were also present. Small to medium creosote bushes rarely exceeded 1 m high or 1 m wide. The density of *Boottettix* in creosote bushes was directly counted in a 30 m × 30 m study plot on 5 October 1975. Observations from the Las Cruces area, including the study plot, were pooled with additional observations made in the Chihuahuan Desert 13 km N of El Sueco, Chihuahua, Mexico, during October 1975. The vegetation near El Sueco resembled that of the Las Cruces area.

RESULTS

The study plot included 55 creosote shrubs or shrub complexes harboring 15 males and 13 females. The population density was 0.031 m⁻² or 0.51 shrub⁻¹. Male density was 0.017 m⁻² (0.27 shrub⁻¹) compared to densities of 0.37 m⁻² (4.3 shrub⁻¹) estimated from data presented by Otte and Joern (1975).

Males rarely shared a shrub or shrub complex with another male. Only eight of 92 male-inhabited shrubs observed in the Las Cruces and El Sueco areas harbored more than one male. Six of these held two males. In each of these cases one male was singing, the call consisting of a short buzz of 0.5 sec duration with silent intervals of 20-180 sec; the other male was silent. Two silent males interacted with females in the shrubs. The remaining two shrubs were larger than average and harbored four and six males, as well as three females each.

Thirty-nine of these shrubs also harbored females. Males in six shrubs without females spontaneously vacated within 30 min after observation began. Males cohabiting with females, however, were not observed to leave voluntarily. Such shrubs provided the setting for 19 of the 20 encounters between males. Twelve of these ended when one of the males vacated the shrub.

Confrontations followed a distinct pattern, resembling that of *Ligurotettix* (Otte and Joern, 1975). Advertisement by a second male was followed by an exchange of the rival's call (*sensu* Morris, 1971), consisting of two sharp ticks produced in a period of 0.5 sec. During this exchange the rivals turned toward each other and converged by hopping from branch to branch. Physical conflict was generally avoided when one of the rivals retreated. In all but two of the encounters, the first male to produce the rival's call won the encounter. Pursuit of its adversary occurred five times. In one case the pursuing male caught the retreating male and bit its

pronotum and wing before the victim escaped from the shrub. Confrontation involving a silent male was observed only once.

Aggressive behavior was further investigated in eight trials, each involving a resident singing male and an introduced singing male collected from a neighboring shrub. Results included three retreats by introduced males, three retreats by resident males, one shrub vacated by both males and one shrub in which the intruder remained as a silent male. One of these trials indicated that shrub complexes may be defended. When an introduced male began to sing after displacing the resident male, a singing male at the other end of the 2-m-wide, three-shrub complex hopped across, displacing a silent male en route, and landed near the introduced male. This encounter ended with the retreat of the resident, but when it was captured and replaced in the shrub, a female approached and this male then chased the other out of the shrub.

Females were rarely found alone in creosote bush. Of 43 shrubs containing females, only four did not also harbor a male. Thirty-three harbored a single female, six harbored two, and four held three females.

The ratio of females to males in shrubs shared by both was 1.12, while for all male-inhabited shrubs, the figure was 0.53. These data are similar to low-density values for *Ligurotettix* (Otte and Joern, 1975).

DISCUSSION

In contrast to the findings of Otte and Joern (1975), our results showed that *Boottettix* males defend creosote bushes, particularly those harboring females, and more readily vacate shrubs without females. The difference in behavior between these two studies may be the result of density differences. Alexander (1961), Otte (1977) and Otte and Joern (1975) discussed abatement of territorial defense at high densities for other orthopterans. For these insects territorial behavior does not regulate density, but seems oriented instead toward maximizing mating success.

Among other factors food supply may regulate density. White (1974) suggested that shortage of suitable food is the deciding factor influencing survival most of the time in the life history of most insect species. Creosote bush produces a resin which reduces the palatability of its leaves for grasshoppers (Otte and Joern, 1976; Rhoades, 1977; Rhoades and Cates, 1976). Food may thus be limiting under normal conditions for creosote-bush grasshoppers. We suggest that creosote-bush suitability regulates grasshopper density directly and grasshopper behavior indirectly.

Females protect their greater investment in offspring by exhibiting preferences in mate and habitat selection (Thornhill, 1976; Trivers, 1972), thus forcing territorial males to compete for areas in which females are most likely found (Mayr, 1972; Parker, 1970). Habitat selection may be largely influenced by host plant suitability (Otte and Joern, 1975). Shrubs occupied by *Ligurotettix* had a significantly lower resin content in the preferred leaves than did the same set of leaves from unoccupied shrubs (Otte and Joern, 1976; Rhoades, 1977; Rhoades and Cates, 1976).

Under normal conditions we expect host plant suitability and herbivore density to be low (Otte and Joern, 1976; Rhoades, 1977; Rhoades and Cates, 1976; White, 1969, 1974). At low densities competition for territories would be least intense (Alexander, 1961; Otte and Joern, 1975) and large nearest-neighbor distance would minimize predation upon cryptically colored grasshoppers (Hamilton, 1964; Price, 1975). The cost of aggressive behavior would be low relative to the increased mating success achieved through territoriality (Parker, 1970).

Mattson and Addy (1975) and Rafees *et al.* (1964) suggested that stress may force plants to reduce production of antiherbivore compounds in order to meet current metabolic needs. White (1969, 1974) noted that stressed plants are richer in nitrogen, which is normally limiting for herbivores, and are therefore subject to increased herbivore populations. White (1974) suggested that water stress maintained for a few years results in outbreaks of defoliator populations.

Water-related stress might cause a decrease in the resin content or an increase in nutritional value of creosote-bush leaves. Grasshopper populations would rise with increasing host suitability. Territorial defense would become a liability at high densities as increased time spent in aggressive activity would reduce mating success and attract predators. We expect predation or improved creosote-bush condition to effect a reduction of herbivore density under such circumstances.

Acknowledgments.—We would like to thank Drs. M. S. Blum, D. A. Crossley, Jr., H. R.

Hermann, C. G. Jones, R. W. Matthews and J. W. Webb, University of Georgia, for critically reviewing the manuscript. This research was supported in part by the US/IBP Desert Biome Program, Jornada Validation Site under NSF Grant GB 15886.

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