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THE BEHAVIOR OF ATLANTICUS TESTACEUS (ORTHOPTERA: TETTIGONIIDAE) ON THE E. S. GEORGE RESERVE, MICHIGAN[1,2]

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Several reports deal in part with the systematics, distribution, or habits of one or another of the shield-backed katydids of the orthopteran genus *Atlanticus*. Included are Blatchley (1920), Cantrall (1943), Caudell (1907), Davis (1893), Hebard (1934), McNeill (1891), Rehn and Hebard (1916), and Scudder (1894). One species of the genus, *A. testaceus* (Scudder), is found commonly throughout Michigan and has interesting habits. As the species' feeding behavior was poorly understood, the author undertook an investigation dealing with that subject. The results are in press. During the course of that study much information was obtained on certain non-feeding aspects of the species' behavior. Findings with respect to the latter are given below.

The project was carried out during the 1958-1961 field seasons at the University of Michigan's Edwin S. George Reserve, a biological preserve near the village of Pinckney, Livingston County, Michigan. The general area is described in detail in Cantrall's excellent report on the Reserve's Orthoptera (1943) and in less detail in the author's monograph on food selection in Orthoptera (1961). The specific sites of study, Southwest Field and Southwest Woods, are described in Gangwere (1965) and Gangwere (in press), respectively. The latter two reports may also be consulted for information on the techniques used during the study.

DAILY ACTIVITIES

Nymphs. The behavior of *Atlanticus testaceus* varies with age, time of day, and other factors. The juveniles are geophilous and always in close association with dry leaf litter. Their daily regime is as follows. They spend much time in the shade of fallen leaves, motionless, their antennae sometimes twirling. Occasionally they walk briskly a short distance (twirling their antennae and using their palpi as they move), or they hop rather than walk. Then they pause for a time but eventually resume their infrequent movements until they find themselves in a clump of vegetation, where they are likely to rest for a more protracted

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period. Always they remain alert. If they encounter suitable food and are hungry, they eat for a period of time usually less than 15 minutes. The above pattern of alternate activity and inactivity is characteristic of their daytime period. Toward dusk, the nymphs gradually accelerate their activities until movement is maximal and almost constant during early evening, but always the young animals remain near the ground. Finally, in early morning (2:00 A. M. or later), they become completely inactive, not to resume movement until late the following morning.

Adults and Last-Stage Nymphs. The behavior of adults is similar to that of young juveniles, except that they are slower in their movements. undergo a nocturnal ascent of the vegetation, and have certain activities peculiar to the sexually mature. Adults, like juveniles, have a periodicity best described as incompletely nocturnal (Gangwere, 1958); they are most active at night but also move significantly during the day, especially under cloudy conditions. They spend the daylight hours hiding beneath leaves and debris, often at the base of shrubs or stout herbs and only occasionally move over the surfaces of the leaves. (Caged animals perch on the sides of their container unless crumpled paper or dried leaves are placed on the cage floor, in which case they, too, hide during the day.) By late morning (approximately 10:00-11:00 A. M.) the adults exhibit a slight, temporary increase in movement and perhaps engage in light feeding and stridulation, always followed by resumption of inactivity. Toward late afternoon (3:00-5:00 P. M.), the males (still clustered on the ground near the bases of plants) begin a period of more accelerated stridulation. Then at dusk the last-stage nymphs and adults of both sexes become phytophilous; they climb the vegetation and perch horizontally atop leaves or branches or vertically on stems, from which position the males begin intensive and practically uninterrupted stridulation for the rest of the evening. They stop stridulating occasionally, move a short distance to the next higher position from which they resume calling, until eventually they reach the top of the plant (sometimes a height up to 10 or 15 feet from the ground). The males call from various positions on a limited number of plants, while the females move about from plant to plant, occasionally stopping to rest or eat. Females that climb plants holding perching males may mate. After midnight both sexes become increasingly inactive (though they remain alert and their antennae continue to twirl), and calling becomes depressed. Descent from the vegetation is initiated by 2:00 or 3:00 A. M., is most marked about 4:00 A. M., and is completed before dawn, when the animals come to rest on the ground and under leaf litter. The cycle begins anew the next day.

The stridulation of *Atlanticus testaceus* has been described in the literature (Cantrall, 1943, Davis, 1893, *et al.*), so its general character is well known. Other aspects of the stridulation and associated behavior are not as well known. The pitch of the call is altered under cool conditions and becomes a short, sputtery creak rather than its usual *zzzzp-zzzzp-zzzzp-zzzzp* expressed again and again. It appears

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that more than one kind of call characterizes the species. There may possibly be a distinct mating sound, for a mature female approaching a calling male may elicit a change in his even trill to a slower, interrupted clatter. There is sometimes an alarm call. *Atlanticus* males, when picked up or otherwise distrubed, sometimes emit a single loud *zik,* often in association with escape behavior. These *Atlanticus* perched on vegetation either dodge behind a leaf or stem or else leap to the ground where they hide. Those animals on the ground leap violently several times until they locate a hiding place, where they crouch motionlessly. If prodded, they crouch more deeply on their flexed hind legs and make ready to leap. They bite viciously if given the opportunity, but are not able to break the human skin.

PERIODISM

In southern Michigan *Atlanticus testaceus* is nymphal in early spring and matures during late spring and early summer. Within a week or two after the onset of maturation in the population, peak numbers of adults are encountered, and the males begin to stridulate. Toward late summer and fall the insects gradually decline in numbers until the killing frosts, when they disappear entirely. On the Reserve the author has taken nymphs as early as April 8; the first adults as early as June 4; and the last adults in fall as late as October 26.

HABITAT OCCUPANCY

There is unanimity in the literature that *Atlanticus testaceus* is a woodland species or at least is closely associated with woodland. Blatchley's statement (1920) that it "frequents for the most part dry open woodland, thinly wooded rocky slopes, and borders of thickets" is representative of accounts given in the older literature. Cantrall (1943) refined these observations with respect to the *Atlanticus* of the George Reserve but concurred in his emphasis on the insect's dependence on woodland conditions. He noted that early juveniles are nearly always located in sunny spots in rather open forest, older nymphs in woodland and in field margins seldom more than twenty yards from woodland, and adults in woodland including even shady forest situations. He concluded that, with maturity, those katydids that stray from their woodland habitations promptly die or make return migrations to the more favorable woodland environment.

Results of the present study suggest the need for a different interpretation of the species' habitat occupancy (at least with respect to the George Reserve). Young nymphs in Southwest Field and Southwest Woods are closely localized in the field-wood ecotone and in an extension of this ecotone, the mouth of a road leading into Southwest Woods. (A similar distribution is noted in other areas of the Reserve.) The young katydids frequent sunny places where there is sparse vegetation, bare ground, and dry leaf litter. At this stage they are not found in

Southwest Woods, in its "oak openings" (open places where the sunlight shines through onto the leaf litter), in the uplands of Southwest Field, or in the field depressions. Older nymphs and adults, in contrast, wander. They may be found in the ecotone but also are encountered throughout the field and, to a lesser extent, within the woods, the orchard, and even in neighboring Southwest Marsh (where they cannot live for long). Toward late summer the adults are most common in the field, particularly in its depressions, though some can be heard calling from within the woods and orchard.

This fluctuating habitat occupancy is a consequence of the species' changing needs at different times during the life cycle. Based on data of this investigation (*viz.*, occurrence of the youngest nymphs and a single oviposition record in nature), the *Atlanticus* of Southwest Field and Southwest Woods oviposit in the ecotone. (If they do so elsewhere, it is doubtful that the eggs hatch.) Once hatched, the young nymphs find the ecotone a suitable habitation where the requisite sunlight, sparse vegetation, and dry leaf litter are provided. They are limited to the ecotone at this stage, for they cannot long survive the rigors of either open field conditions (where there is no leaf litter or other protective debris) or shady woodland conditions (where there is leaf litter but no sunlight). They are possibly able to exist in "oak openings" of the woods, but this distribution involves departure from the more optimal conditions of the ecotone and travel through the shady woods. As the nymphs approach maturity, they become less dependent on protection afforded by leaf litter and can migrate to space themselves (territoriality?) or to seek mates on perching sites. They need not return to the ecotone proper except to oviposit.

What explains the disparity between these results and those of Cantrall, obtained in the same general area twenty years earlier? The explanation can be found in the effects of succession. It appears that *Atlanticus testaceus* is really an ecotonal--not a woods-dwelling--species. In the late 1930s, when Cantrall studied the insect, the character of the field was still largely determined by the cultivation and grazing practices to which it had so recently been subjected; it had progressed little beyond the stage of open pasture. The woods, too, were comparatively open and subject to thorough grazing by a large deer population that kept the undergrowth minimally developed. The field-wood ecotone was completely lacking. The extensive "oak openings" presumably offered the only sites for oviposition by adult females and occupation by newly hatched juveniles. Though the older nymphs and adults often migrated, they were obliged to return to the woods for oviposition and, above all, for perching. Both Southwest Woods and Southwest Field were, therefore, in a state of stress, from which they have now recovered. Today a distinct ecotone is developed for nymphal occupation and adult perching and oviposition. Furthermore, many parts of the field, now so overgrown that they themselves are almost ecotonal in nature, also afford suitable perching sites and habitations for older nymphs and adults.

Such an hypothesis requires demonstration that the sluggish, flightless *Atlanticus* last-stage nymphs and adults are capable both of migrations of the magnitude discussed above and of residence in one place over an extended period of time. Marking and recapture experiments were carried out. A total of 231 adult *Atlanticus* were marked by daubing the pronotum with paint. Of these, 40 individuals were recaptured one or more times. Maximal, average, and minimal distances that marked insects moved over a period of several weeks were, respectively, 550, 120, and 0.0 feet. All movements of individuals seemed random; no concerted migrations of major segments of the population from one habitat to another were detected. The results confirm the fact that individual animals can readily move throughout the two communities when the occasion demands or, on the other hand, may remain associated with a single plant for many days at a time.

The habitat selection outlined above for *Atlanticus testaceus* in Southwest Field and Southwest Woods is not necessarily characteristic of the species at other places in its range, though it could well be typical. According to Cantrall (personal communication), large populations of nymphs have been observed in other states in such places as along a fence row separating pastures of blue grass and in open pastures containing bramble. In such cases some factor other than leaf litter must provide the protection needed by the young *Atlanticus*. The fence and the taller vegetation growing in its shade could be the factor in the first example; numerous piles of cow dung, eminently suitable for protection, could be the factor in the second.

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