The Feeding Behavior of *Atlanticus testaceus* (Orthoptera: Tettigoniidae)[1,2]

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ABSTRACT

The feeding behavior of *Atlanticus testaceus* (Scudder), a decticine katydid, was investigated in 1958–61 in Livingston County, southeastern Michigan. The ecology, local and seasonal distribution, and behavior of the insect were observed in the field; and, in the laboratory, the animal's mandibular morphology, crop contents, food selection, and food restriction were studied. Although *Atlanticus* prefers animal food, its diet consists more of plant than of animal materials because suitable prey are insufficiently available. Its choice of food plants is wide, including the leaves and especially the flowers of forbs, the fruits of certain woody plants and occasionally their leaves, and even the flowers of grasses. Its animal food is obtained partly by scavenging and partly by predation; the prey consists largely of small insects that are abundant in its environment, but it sometimes catches and eats larger, more powerful insects, especially when they are disabled. It is also cannibalistic. These observations, together with the strongly carnivorous adaptation of the mandibles, suggest that *Atlanticus* is a carnivore by preference but an omnivore by necessity.

The shield-backed katydids of the genus *Atlanticus* are members of the subfamily Decticinae. Several reports have dealt, in part, with their systematics (Blatchley 1920, Caudell 1907, Hebard 1934, Rehn and Hebard 1916, Scudder 1894), while others have been concerned largely with their distribution and habits (Cantrall 1943; Davis 1893; Gangwere 1960, 1961). Of the 2 papers by the present author, the first (1960) was an annual report in which the feeding of *A. testaceus* was tentatively discussed, and the second (1961) was a monograph which contained a brief reference to *Atlanticus* in a study of feeding in Orthoptera as a group.

A. testaceus (Scudder) is the commonest shield-backed katydid in the North-Central United States, and is found throughout Michigan. Its body is comparatively large, and its habits are somewhat curious. The little that is known about its feeding suggests that the insect is a combination plant-feeder, scavenger, and predator. Food habits of such complexity have yet to be studied intensively with respect to Orthoptera. These facts prompted an investigation into this insect's food selection, the results of which follow.

The project was carried out during the 1958–61 field seasons at the Edwin S. George Reserve. This biological preserve, operated by the University of Michigan, is situated near the village of Pinckney, Livingston County, Mich., approximately 70 miles west-northwest of Detroit. The general area was described in detail by Cantrall (1943) in his excellent report on the ecology of the Reserve's Orthoptera, and in less detail in the author's monograph (Gangwere 1961). One of the specific sites of the present study, Southwest Field, has been described by the author (Gangwere 1965), and a discussion of the other, Southwest Woods, follows.

TECHNIQUES

1. *Field Observations.*—Individuals of *Atlanticus*, free in the field, were observed on numerous occasions for several hours at a time, both by day and by

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night. This activity yielded feeding records and information on distribution and behavior.

2. *Baiting.*—One hundred areas of ground, each 12 inches in diameter, were denuded and permanently marked with identification stakes. These feeding stations were situated in each of the several major habitats of the field and woods, and were arranged in sequence along a winding trail 4650 feet long. They served as markers for all field studies and were especially useful in baiting. On several occasions dry flakes of bran and oats were distributed on each; the trail was followed at fixed intervals for an entire 24-hour period; and the number and location of *Atlanticus* at bait were recorded. These activities gave indications of the species' periodicity (which is incompletely nocturnal), its habitat selection, and its numbers within the environment.

3. *Community Analysis.*—Feeding is not only a function of food preferences, but is also related to the distribution and abundance both of food and of feeders. This fact suggests a need for certain community studies. The distribution and abundance of the feeder, *Atlanticus,* were investigated by transects, by methods just listed (nos. 1 and 2), and by marking-recapture experiments that involved paint applied to the pronotal disk of adult animals. The distribution, abundance, and comparative availability for feeding of various vascular plants, the major kind of food, were determined by making (a) a list of the plant species of the field and woods, (b) visual estimates of plant abundance at different times during the growing season, and (c) belt transects of selected habitats.

4. *Differential Feeding Tests.*—Two types of differential feeding tests were employed in the laboratory; one kind involved vegetation as food and the other kind animal prey. In the vegetation experiments, test groups of 10–20 individuals of *Atlanticus* were confined, each group within a screen cage (18 in. high, 9 in. diam). Each was given various combinations of grasses, forbs (broad-leaved herbs), and woody plants common in Southwest Woods, Southwest Field, and adjacent areas of the Reserve. The animals' food preferences were determined according to the comparative damage they inflicted by feeding and on the basis of the debris they left on the cage floor after 1 day's exposure to the potential food plants. In the animal food experiments, test groups of *Atlanticus* caged as just described or individual *Atlanticus,* each in a private, smaller, screen cage (9 in. high, 4 in. diam), were given assortments of living and dead insects and other foods of animal origin. The percentage of individuals of each prey species eaten after several days was taken as the index of food selection.

5. *Mouthpart and Crop Content Analysis.*—Specimens of *Atlanticus* were collected from Southwest Field and Southwest Woods on a biweekly basis. After preservation in 80% alcohol, the mouthparts were examined in the laboratory in situ. The labrum was lifted and the mandibles separated by a dissecting needle, making visible the dentes and other mouthpart structures. The crop was then exposed, slit, and the contents made into permanent preparations (with Turtox CMC–10 mounting medium) and analyzed using standard procedures.

6. *Food Restriction Experiments.*—Two series of food-restriction experiments were conducted. In the first series, groups of 20 individuals of *Atlanticus* were confined together in the larger-type cages described here. One such cage was provided with vegetation only; a second with a scavenging diet of household, nonanimal foods; and a third with household meats and dead insects. In the second series of tests, the insects were confined individually in cages of the smaller type; some were given access to vegetation and some to various species of living and dead insects and horsemeat. Mortality was recorded in each series.

HABITAT RELATIONS

Southwest Field.—Southwest Field is a dry, abandoned pasture in the extreme southwestern corner of the E. S. George Reserve. It is bounded by scattered trees, a marsh, an apple orchard, and, toward the northeast, by Southwest Woods. Much of the field is dry upland dominated by *Aristida purpurascens, Poa compressa, Rubus* spp., and *Rumex acetosella.* To the north and south, the field slopes downward into swales, or depressions, where the vegetation is noticeably more luxuriant. The vegetation here is dominated by *Poa pratensis,* but includes much *Asclepias syriaca, Berteroa incana,* and *Setaria* sp. The vascular plants of the field total 154 species of 47 families. The relative abundance of these species (hence, their availability as food) was estimated by analysis of density and frequency data from the belt transects (Gangwere 1965). This information need not be repeated here.

Southwest Woods.—Southwest Woods, an example of Cantrall's shady oak-hickory habitat, borders and shares an ecotone with Southwest Field. The part investigated most intensively approximates a triangle bounded on 2 sides by the field and on the third by an unimproved road. The northerly directed base of this triangle is 342 feet long and each side, approximately 684 feet. The surface slopes gently eastward and provides drainage into a neighboring swamp. The soil is predominantly Bellefontaine sandy loam. The elevation is 950–975 feet.

A list of the vascular plants of Southwest Woods compiled during the project totals 136 species of 49 families. The tall tree stratum is dominated by the hickories *Carya glabra* and *C. ovata* and the oaks *Quercus alba* and *Q. velutina;* the low tree stratum by *Corylus americana, Hamamelis virginiana, Prunus serotina,* and *Sassafras albidum;* and the shrub stratum by *Gaylussacia baccata.* These woody plants are only occasionally used for perching and seldom as food by *Atlanticus* and, therefore, were not systematically sampled.

The ground stratum of the woods has a more direct influence on *Atlanticus.* The abundance of its plants

was estimated by analysis of density and frequency data from the belt transects. A synopsis of the results follows. *Carex pensylvanica* is the most abundant and ubiquitous plant of the ground cover. *Amphicarpa bracteata* is slightly less abundant. Saplings of *Carya* spp., *Quercus* spp., and the forb *Desmodium nudiflorum* are common. Somewhat less common are the forbs *Aster* spp., *Desmodium glutinosum, Galium* spp., the grass *Poa pratensis,* and the woody plant *Sassafras albidum.* Still less frequently encountered are the forb *Helianthus divaricatus,* the woody plant *Prunus serotina,* and the grasses *Hystrix patula* and *Poa compressa.* Many other species contribute to the ground cover, but in no case are they sufficiently dense or ubiquitous to require discussion. This highly varied assemblage of forbs, grasses, sedges, ferns, and saplings takes root from a forest floor strewn with leaf litter and broken branches and twigs.

Distribution of Atlanticus testaceus.—In southern Michigan, *A. testaceus* overwinters in the egg stage and hatches toward the end of March and beginning of April. In the spring it passes through the several nymphal stages and reaches maturity in early June. Within a week or two after the onset of maturation in the population, peak numbers of adults are attained, and the males first begin to stridulate. Toward late summer and fall, the insect gradually declines in numbers until, at the time of the killing frosts, it disappears entirely.

Young nymphs in Southwest Woods and Southwest Field are localized in the field-wood ecotone and in an extension of it, the entry of a road into Southwest Woods. They frequent those sunny places of the ecotone where there is sparse vegetation, bare ground, and dry leaf litter. Older nymphs and adults may be found in the ecotone but are also encountered throughout the field, within the woods, the orchard, and even in a neighboring marsh. Toward late summer the adults are commonest in the field (especially its swales), though some can be heard calling from within the woods, the ecotone, and the orchard.

FOOD SELECTION

Feeding Records.—Forty feeding records were amassed for *A. testaceus* free in its natural environment. Slightly less than three-fourths of the records were taken after dusk, while the remainder were obtained during late morning or late afternoon. The 2 sexes were about equally represented among the feeding individuals.

Approximately two-thirds of the field feeding records involved plants. The parts taken were mostly flowers but included some leaves and stems. One of the plant records involved a nonflowering species, two of them were on woody plants, and the remainder on forbs. The food plants and number of records in excess of one are as follows: a mushroom; the woody plants *Quercus* sp. and *Rubus flagellaris;* and the forbs *Achillea millefolium, Anemonella thalictroides, Asclepias syriaca* (11 records), *Asparagus officinalis* (5 records), *Galium pilosum, Monarda fistulosa, Rumex acetosella,* and *Verbascum thapsus* (4 records).

Twelve of the field feeding records involved either predation or scavenging on animals. The prey and number of records in excess of one are as follows: a pentatomid bug; the orthopterans *A. testaceus* (4 records), *Gryllus pennsylvanicus* Beutenmuller, and *Melanoplus confusus* Scudder; the coleopteran *Phyllophaga* sp.; a lepidopterous caterpillar (2 records); and 2 flies, *Chrysops* sp., and an unknown species of Diptera Cyclorrhapha. The 4 records of *Atlanticus* as food are examples of cannibalism on weakened or injured individuals.

Differential Feeding Tests: Vegetation Series.—Forty-seven of these experiments were conducted, which gave caged *A. testaceus* access to 113 species of plants and, for comparison, a few species of living aphids and horse meat. In all cases the vegetation was of lower preference value than the animal materials, which were accepted 100% of the time. Of all the plants offered, 47 species (or slightly less than half) were eaten on one or more occasions. Usually they were attacked at the flowers, but occasionally at the leaves, stems, or fruits. In no instances were roots eaten. Certain plant groups, such as the mosses (1 sp.), the mushrooms (1 sp.), the horsetails (4 spp. of *Equisetum*), and the ferns (*Onoclea sensibilis*), were rejected whenever given. However, 1 group, the flowering plants, included some acceptable species.

There was a wide range of acceptability among the flowering plants. The grasses, sedges, and rushes (accepted only 8% of the time) proved of distinctly lower preference value than the forbs (accepted 30% of the time) and had no consistently acceptable species. Among the forbs found acceptable are *Chenopodium album, Convallaria majalis, Lychnis alba, Plantago lanceolata, P. major, Rumex acetosella, R. obtusifolius, Trifolium repens, Viola pensylvanica,* and *V. sororia.* Also acceptable are several composites, particularly *Arctium lappa, Erigeron philadelphicus, E. pulchellus, E. strigosus, Lactuca sativa,* and *Taraxacum officinale.* The Compositae was accepted as a group 31% of the time.

Woody plants were less often taken than were forbs. As a group, their foliage was accepted only 12% of the time, though *Prunus serotina* and *Rhus typhina* seemed somewhat more attractive. The undistinguished performance of woody plants as foods was, however, dramatically improved when they were in the form of fleshy fruits rather than foliage alone; with the availability of fruits, these plants were accepted 90% of the time. Examples of woody plants whose fruits were found attractive are blueberry (*Vaccinium* sp.), mulberry (*Morus* sp.), blackberry (*Rubus allegheniensis* and *R. flagellaris*), and strawberry (*Fragaria virginiana*).

The results of the differential feeding experiments on plants tested more frequently (5–26 times each) merit more detailed presentation (Table 1). This table lists frequently tested plants according to category of preference value. The categories, each sepa-

Table 1.—Results of differential feeding experiments with *Atlanticus testaceus* on plants tested frequently. The sequence from bottom to top is that of increasing average preference value. (V) = foliage and other vegetative parts eaten; (F) = flowers and other floral parts eaten; (VF) = both vegetative and floral parts eaten.

Preference value	Plant species
High	*Rumex obtusifolius* (V), *Taraxacum officinale* (VF)
Moderate	*Verbascum thapsus* (F)
	Berteroa incana (V), *Daucus carota* (V), *Erigeron strigosus* (F)
Low	*Rudbeckia serotina* (VF)
	Achillea millefolium (F), *Desmodium paniculatum* (VF), *D. sessilifolium* (V), *Panicum oligosanthes* (F), *Phleum pratense* (VF)
	Monarda fistulosa (V)
	Solidago juncea (V)
	Carya sp. (V), *Circaea quadrisulcata* (V), *Panicum latifolium* (F), *Panicum* sp. (VF)
	Amphicarpa bracteata (V), *Rosa carolina* (V)
	Desmodium glutinosum (V), *Helianthus divaricatus* (V)
	Festuca obtusa (V)
	Hystrix patula (V)
	Carex pensylvanica (V)
	Dactylis glomerata (VF), *Poa pratensis* (F)
	Poa compressa (F)
Rejected	*Asclepias syriaca*, *Quercus velutina*

rated by the symbol ↑, are listed in order of increasing preference value from bottom to top of the page. Plants listed above the symbol are, on the average, more acceptable than those below it, and those listed together in the same category have essentially the same preference value. Additional symbols (V, VF, and F) are appended to the name of each plant to denote the parts eaten; V refers to foliage and other vegetative parts, F to flowers and other floral parts, and VF to a combination of the two.

Differential Feeding Tests: Prey Series.—Twenty-two differential feeding experiments were conducted, which gave caged *A. testaceus* access both to horse meat and to 40 species of insects, either alive (for possible predation) or dead (for scavenging). The results obtained on prey species tested 3 or more times (up to the maximum of 33 presentations) are sufficiently reliable for tabulation and discussion (Table 2).

The results of the tests were subject to modification by altering either prey or conditions of confinement. With respect to prey, disabled or weakened animals were more often eaten by *Atlanticus* than those that were intact and vigorous; living prey were more readily taken than were dead animals; and the newly

dead, in turn, were more readily accepted than were dry or decomposed, long-dead animals. With respect to conditions of confinement, several *Atlanticus* were often able to dispatch a powerful prey organism that 1 individual could not overpower. Time is also a factor, for certain powerful prey escaped predation for several days until, weakened by attack, they succumbed.

Mouthparts.—The mouthparts of 58 nymphal and adult male and female specimens of *A. testaceus* were studied in the laboratory. The mandibles were characterized by the carnivorous-type adaptation, in which the dentes are fanglike protuberances for tearing flesh. The only variation observed, a shortening and increased obtusity of the dental apices, was a result of abrasive wear. Such wear was most pronounced in senescent individuals.

Crop Contents.—The crops of a total of 58 specimens of *A. testaceus,* both nymphs and adults, were examined for content. Eight (14% of all crops) were empty. The full or partly full crops largely contained dicotyledonous plant remains, as indicated by the characteristic plant "hairs" and epidermal cells; much of this content (74%) was composed of both leaves and flowers of forbs and woody plants. The remainder of the content was of grass (1%), dicot pollen (8%), and insect remains (17%), the latter including fragments of body and head sclerites and appendages occasionally referable to the Holometabola.

Food Restriction Experiments.—These experiments, consisting of 2 separate series of tests, indicated certain trends (Table 3). The first series, carried out during the 1960 field season, exposed a cage of 20 nymphal *Atlanticus* to a vegetation diet, another to such a nonanimal scavenging diet as would be suitable for a domestic cockroach or domestic cricket, and a third to an animal scavenging diet. The 3 diets were as follows, with the foods of each arranged in order of decreasing preference value. The vegetation diet included garden lettuce (*Lactuca*) (usually riddled), a species of grass, 1 of plantain (*Plantago*), and dried leaves of oak (*Quercus*) (generally nibbled or refused outright); the nonanimal scavenging diet included oat flakes (a favorite), bran flakes, and cheese (generally untouched); and the animal diet included dry bodies of *Atlanticus* and dead mosquitoes (both preferred) and ham and horse meat (both largely untouched). Survival over a period of 1 month was inferior on the animal diet but better on the nonanimal scavenging and the vegetation diets. There were, however, obvious differences in the size and vitality of individuals exposed to the 2 low-mortality diets; those given the nonanimal scavenging diet were stunted, while those on the vegetation diet were large, active, and apparently healthy.

The apparent superiority of the vegetation diet, as indicated by the 1960 tests, seemed inconsistent with results from other field and laboratory studies. A second series of tests, more representative of field conditions, was undertaken in 1961. It featured more realistic alternative diets. The cannibalism that must have distorted the 1960 results was avoided this time by placing the katydids in individual cages. Some *Atlanticus* were given access to a vegetation diet consisting of 2 favored food plants, *Taraxacum officinale*

Table 2.—Results of differential feeding experiments with *Atlanticus testaceus* on certain frequently tested potential prey.

Percent eaten	Insect species offered	Order and Family
100	*Chrysopa* sp.	Neuroptera, Chrysopidae
	Chrysops sp.	Diptera, Tabanidae
	Tipula sp.	Diptera, Tipulidae
	Philaenus spumarius (L.)	Homoptera, Cercopidae
80–83	*Ischnura verticollis* (Say)	Odonata, Coenagriidae
	Archasia pallida (Fairmaire)	Homoptera, Membracidae
	Unidentified species	Coleoptera, Curculionidae
50–60	*Halisidota tesselaris* (J. E. Smith)	Lepidoptera, Arctiidae
	Unidentified caterpillar	Lepidoptera
	Tabanus sp.	Diptera, Tabanidae
	Oecanthus quadripunctatus[a] Beutenmuller	Orthoptera, Gryllidae
	Unidentified species	Trichoptera
25–40	*Anomoea laticlavia* (Forster)	Coleoptera, Chrysomelidae
	Macrodactylus subspinosus (F.)	Coleoptera, Melolonthidae
	Tetraopes femoratus LeConte	Coleoptera, Cerambycidae
	Leptoterna dolabrata (L.)	Hemiptera, Miridae
	Nabis sp.	Hemiptera, Nabidae
	Unidentified species	Hemiptera, Pentatomidae
14–22	*Alydus eurinus* Say	Hemiptera, Alydidae
	Atlanticus testaceus[b] Scudder	Orthoptera, Tettigoniidae
	Gryllus pennsylvanicus Burmeister	Orthoptera, Gryllidae
	Melanoplus confusus Scudder	Orthoptera, Acrididae
	Unidentified species	Hymenoptera, Formicidae
0	*Acheta domesticus* (L.)	Orthoptera, Gryllidae
	Unidentified species	Coleoptera, Coccinellidae

[a] Juveniles. [b] Dead.

Table 3.—Results of maintenance of *Atlanticus testaceus* on certain restricted diets.

Year[a]	Diet	Survival[b]	Condition of survivors
1960	Animal scavenging	Less than 25%	—
	Nonanimal scavenging	Approx. 75%	Stunted
	Vegetation	Approx. 75%	Healthy
1961	Vegetation	0%	—
	Prey-scavenging	Approx. 75%	Healthy

[a] *Atlanticus* caged together in 1960, individually in 1961.
[b] At end of 2 months for 1961 prey-scavenging class; at end of 1 month for all others.

and *Rumex obtusifolius,* and others were provided a prey-scavenging diet composed of a wide variety of living and dead insects and horse meat. The experiment continued for 2 months. All animals on the vegetation diet, unable to resort to occasional cannibalism, were dead by the end of the first month. In contrast, nearly three-fourths of those on the prey-scavenging diet were alive and healthy at the end of the experiment, and death of most of those that died was a result of unsuccessful molting. Prey, incidentally, was preferred over dead animals in these cages.

DISCUSSION

Atlanticus *as a Carnivore.*—The fact that *A. testaceus* is a carnivore by preference is indicated by its mouthparts (that are strongly carnivorous type in adaptation) and by field and laboratory observations. All differential feeding tests that compared animal with plant substances disclosed that animal materials are of higher preference value. However, this partiality for animal tissue is even more deep rooted than that fact would indicate. Based on the food restriction tests, live animal foods are also of higher survival value.

Animal foods, living or dead, exhibit obvious differences in texture, condition, and accessibility, and in its behavior *Atlanticus* proved responsive to gross differences of this type. The insect prefers living animals to those that are newly dead, and, in turn, newly dead animals to those that are long dead, dry, or decomposed. Furthermore, it survives better on prey than it does on animal substances taken by scavenging. Aside from these gross differences, *Atlanticus* exhibits comparatively little specificity in its carnivory; 1 species of prey of a given size and strength is much like another in attractiveness. Thus, *Atlanticus* resembles many other predaceous Orthoptera in that it takes prey largely on the basis of size and availability. It specializes in eating the small, weak, often soft-bodied insects that abound in the situations it frequents. Deerflies, small caterpillars, lacewings, damselflies, bugs, aphids, and leafhoppers (insects that are frequently eaten in the laboratory and abundant in Southwest Field and Southwest Woods) are probably common victims. Ants proved unattractive, probably protected by their bodily secretions. Certain large beetles that are protected by their tough exoskeleton were found resistant to attack, as were large grasshoppers and crickets that are protected by their size, strength, and agility. Nevertheless, even the most powerful insects are eaten if injured, bleeding, weakened by disease or old age, or incapacitated by molting. Sometimes several *Atlanticus* combine in their efforts to overcome the prey.

Cannibalism was observed several times in the field and rather more often in the laboratory. It does not occur to any great extent in healthy, intact *Atlanticus* capable of violently leaping away from their would-be predator comrades. When the prospective prey is molting, ill, or otherwise disabled, the result is often quite different.

The act of predation differs according to the size, strength, and agility of the prey. Small, sluggish prey are attacked without hesitation. An individual of *Atlanticus* eating aphids, for example, simply lunges about from cluster to cluster of the helpless prey, grabbing at individual animals with the mandibles and chewing momentarily on the body of each until large numbers (up to 20 or so specimens) have been consumed. The manner of taking larger prey is different. The *Atlanticus* awaits or stalks the prey and then leaps on it, using the body and legs to pin its prospective meal against the substrate. The predator's spiny legs are not raptorial but together form a barbed enclosure in which the prey is effectively trapped. Even flies on the wing may be caught in this fashion. The trapped prey is held by the predator's forelegs (sometimes aided by the midlegs) while the katydid perches on the remaining legs. Then the mandibles are brought into play on any convenient part of the wriggling prey. Once the victim ceases kicking, the pace of feeding is more leisurely until the predator has had its fill. Often only parts of the wings, legs, and occasional body and head sclerites remain uneaten.

Atlanticus *as a Vegetarian.*—There was a preponderance of plant materials in the analyzed *Atlanticus* crops, and approximately two-thirds of the feeding records taken in nature involved plant species. Moreover, the food restriction tests showed that individuals of *Atlanticus* can live for several weeks on vegetation alone, and, when this diet is augmented with occasional animal prey, they may survive on it for months. On the other hand, all differential feeding tests that compared plant with animal materials demonstrated the insect's preference for the latter. This seeming contradiction is resolved by the fact that, in nature, plants are more available as food than are prey and dead animal matter. Thus, plants are important—though not necessarily preferred—items of diet.

The data of the differential feeding tests (Table 1) examined in light of information from the density and frequency studies of plants important in Southwest Field and Southwest Woods indicate that *Atlanticus* has no fixed, customary food plants in this area. Fourteen frequently tested plants are abundant in one or another of the *Atlanticus* habitats of Southwest Field and Southwest Woods, but these plants are all of low preference value and not likely to be eaten

often. The 2 frequently tested plants that are of high preference value, *Rumex obtusifolius* and *Taraxacum officinale,* are uncommon in Southwest Field and Southwest Woods. Two other frequently tested plants, *Berteroa incana* and *Erigeron strigosus,* are abundant in the swales and ecotone, respectively, and combine this comparative availability with a moderate preference value when in the floral state. Both are in flower when *Atlanticus* is adult and prone to ascend the vegetation nightly. In view of the relatively slight stem that is characteristic of each, neither plant offers a suitable perch; their flowers can be eaten only infrequently.

If one turns to the feeding records taken in nature, several apparent inconsistencies are noted. Six of the 10 species on which field feeding records were taken were also tested frequently in differential feeding experiments, but 5 of the 6 proved of low preference value. Only one, *Verbascum thapsus,* was even moderately attractive. Another plant, a species of mushroom, both rejected in the feeding tests and of low availability in Southwest Field and Southwest Woods, was the host plant of a feeding record in nature.

Patterns of Food Selection.—The aforementioned facts, together with the wide latitude in feeding that is characteristic of *A. testaceus,* suggest that the insect's food selection is based less on preferences than on fortuity, distribution, and perching habits. The young nymphs are restricted to the field-wood ecotone, where their food selection is necessarily dependent on the assemblage of plants, animals, and dead materials found there. The last-stage nymphs and adults occur throughout Southwest Field and Southwest Woods, but the availability of perches (along with a need for sunlight during the daytime) tends to concentrate them in the swales. The marking-recapture studies indicate that adults of *Atlanticus,* upon finding a shrub or concentration of stout herbs suitable for perching, tend to stay there, perhaps remaining associated with a single plant for many days at a time. In consequence, the selection of food plants and prey available to them are as limited as those to which the immatures have access.

Numerous feeding patterns are suggested. The flowers of many plants and the leaves and fleshy fruits of a few are favored and may be eaten when found by a hungry *Atlanticus;* the attractive fruits of *Rubus,* for example, are likely to be eaten whenever encountered. In contrast is the pattern associated with plants that are unattractive as foods but attractive as perches; *Asclepias syriaca,* the foliage of which was consistently rejected in the feeding experiments, was the host plant of 11 separate floral feeding records taken in nature. Its availability in a habitat frequented by *Atlanticus* in middle and late summer, its flowering condition at that time, and its ideal form for perching account for its astonishing field acceptance. Somewhere between the 2 aforementioned patterns lies the utility of plants such as *Verbascum thapsus.* This species, of moderate preference value in the differential feeding tests, is available only in the swales, where at best it is scarce. The several feeding records based on it are explicable only on the basis of perch selection.

This interpretation of food selection in last-stage nymphs and adults of *A. testaceus* is complicated by the species' periodicity. The insect is incompletely nocturnal (Gangwere 1958). It hides during the day under leaf litter or vegetation at ground level and only occasionally moves, stridulates, or feeds diurnally, especially on cloudy days. It becomes more active toward dusk, when the adults begin their nocturnal ascent of the vegetation. Immediately after dusk, most *Atlanticus* are on the vegetation and do not descend until the early hours of the next morning. Inasmuch as the katydids move about and feed lightly during the day, their food selection at that time is determined by the conditions at ground level. At night, feeding is maximal from immediately after dusk to midnight and proceeds on the perch according to the patterns mentioned earlier.

Feeding According to the Literature.—Earlier authors have made brief comments on the food selection and feeding behavior of this interesting insect. McNeill (1891) noted that *A. testaceus* shows a decided taste for animal foods and is at least partly carnivorous in the wild state. Davis (1893) found that it is fond of many kinds of fruits ranging from raspberries to watermelon. Caudell (1907) stated that *Atlanticus* spp. eat animal as well as vegetable foods and probably do not confine themselves to a vegetable diet in nature. Blatchley (1920) reported that *Atlanticus* spp. in captivity feed as readily on animal as on vegetable foods and probably feed on such bodies of dead animals as they can find in nature. Finally, Cantrall (1943), observing captive *A. testaceus* eating disabled individuals of the grasshopper *Melanoplus sanguinipes,* described the katydid as an omnivore but stressed its predatory habits.

The present study is generally consistent with these earlier reports, serving to extend them and to bring them into perspective. Its especial contribution is toward a better understanding of the role that environmental influences play in modifying the insect's food selection, both in carnivory and herbivory.

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REFERENCES CITED

Blatchley, W. S. 1920. Orthoptera of Northeastern America with Especial Reference to the Faunas of Indiana and Florida. Nature Publ. Co., Indianapolis. 784 p. (p. 586–600).

Cantrall, I. J. 1943. The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Univ. Michigan Mus. Zool. Misc. Pub. 54. 182 p. (p. 144–6).

Caudell, A. N. 1907. The Decticinae of North America. Proc. U. S. Nat. Mus. 32: 285–410.

Davis, W. T. 1893. The song of *Thyreonotus*. Can. Entomol. 25: 108–9.

Gangwere, S. K. 1958. Notes on the feeding periodicity of various Orthoptera. Pap. Michigan Acad. Sci., Arts, Letters 43: 119–32.

1960. Feeding habits of the insect species *Arphia sulphurea* (Fabricius) and *Atlanticus testaceus* (Scudder). Rep. Grant. no. 242, Johnson Fund (1959). Yearbook Amer. Phil. Soc.: 294–8.

1961. A monograph on food selection in Orthoptera. Trans. Amer. Entomol. Soc. 87: 67–230. (p. 107–8).

1965. Food selection in the oedipodine grasshopper *Arphia sulphurea* (Fabricius). Amer. Midland Nat. 74: 67–75.

Hebard, M. 1934. The Dermaptera and Orthoptera of Illinois. Bull. Illinois Nat. Hist. Surv. 20: 125–279. (p. 218–9).

McNeill, J. 1891. A list of the Orthoptera of Illinois. Psyche 6: 24.

Rehn, J. A. G., and M. Hebard. 1916. A revision of the species of the genus *Atlanticus*. Trans. Amer. Entomol. Soc. 42: 33–100.

Scudder, S. H. 1894. A preliminary review of the North American Decticidae. Can. Entomol. 26: 177–84.

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