

July 1966

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Recommended Citation

Gangwere, S. K. 1966. "Relationships between the Mandibles, Feeding Behavior, and Damage Inflicted on Plants by the Feeding of Certain Acridids (Orthoptera)," *The Great Lakes Entomologist*, vol 1 (1)

DOI: <https://doi.org/10.22543/0090-0222.1006>

Available at: <https://scholar.valpo.edu/tgle/vol1/iss1/3>

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RELATIONSHIPS BETWEEN THE MANDIBLES, FEEDING
BEHAVIOR, AND DAMAGE INFLICTED ON PLANTS BY
THE FEEDING OF CERTAIN ACRIDIDS (ORTHOPTERA)¹

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In 1960 the author described three fundamental patterns of feeding in Orthoptera and their allies and emphasized the close correlation that exists between the insects' mouthpart structure, food, and feeding pattern. An article by Anderson (1964) made reference to these described patterns and discussed possible modifications of them. To the author's knowledge these are the only reports available that make other than casual mention of the characteristic damage by Orthoptera to food plants. Numerous other papers include figures that depict orthopteran damage, and still others verbally describe the damage inflicted by various economically important species. In all these reports at least one basic consideration has been all but ignored: the possible relationships between mandibular form, pattern of use, and the resulting damage to food plants. Findings with respect to this topic are given below.

METHODS

Living grasshoppers were caged individually, together with their food, in small glass chambers placed on the stage of a binocular dissecting microscope through which feeding could be observed in minute detail. Other grasshoppers were photographed as they fed. The 16 mm camera used was a Ciné-Kodak Special II, with a 63 mm f2.7 lens and an 8-inch extension tube, and set at 64 frames per second. Illumination was provided by three microscope lamps fitted with heat filters to protect the insects. To assure immediate feeding all experimental animals were denied access to food for twelve hours prior to a test.

OBSERVATIONS

The 21 acridids studied are listed in Gangwere (1960). In every case the feeding pattern the grasshoppers exhibit fits the type called margin-feeding; that is, feeding at the margins of leaves or flowers or sometimes along a midrib, fold, or other prominence. In so doing, a rather invariable sequence of activities is followed.

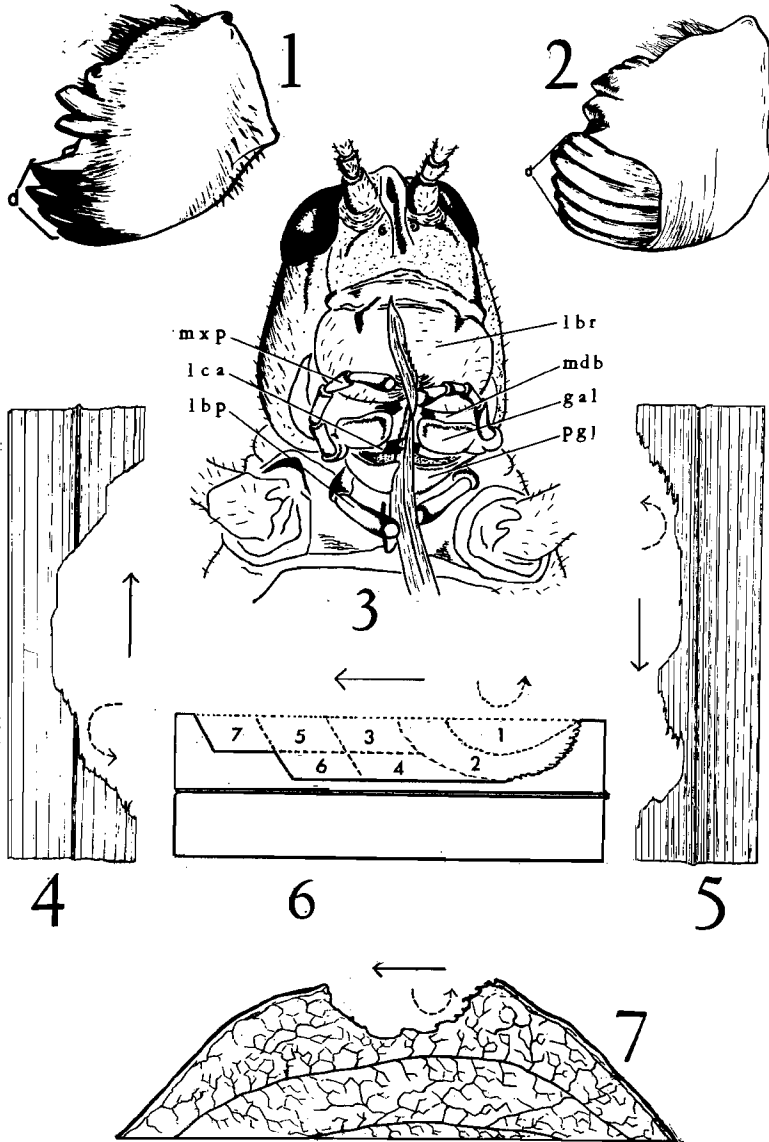
A grasshopper, given access to coarse grasses, usually begins by straddling the leaf edge. The animal swings its head forward and upward, bringing its hypognathous mouthparts into their most forward

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position. The head then moves in a backward and downward path while the mouthparts cut food from the leaf edge (Fig. 3). This downward and backward movement of the head during incision never varies, for the apically located incisor dentes of the mandibles must come into contact with the food first. (If the animal tried to eat using a forward and upward movement, the molar dentes would meet the food first and be unable to incise it properly.) By these actions a small, concave excavation is made in the leaf margin (Fig. 6, cut no. 1). It is deepened and elongated during successive swaths (Fig. 6, cut no. 2). When the excavation has been enlarged to a point where it cannot be deepened easily, the first phase of the insect's feeding has been completed. The second and more extensive phase begins as the animal moves a short distance forward to an intact portion of the leaf, where it begins feeding anew. Here it undertakes another backward- and downward-directed swath until a fair-sized piece has been partially loosened. This morsel is then completely removed by a combination of incision by the mandibles and splitting of the grass between the parallel veins (Fig. 6, cut no. 3). A later series of "bites," parallel to, but deeper than the last, together with splitting, brings the excavation down to or even well below the midrib (Fig. 6, cut no. 4). All subsequent feeding proceeds in the same step-like fashion, and the resulting excavation is angulate (Fig. 6, cuts nos. 5, 6, 7).

EXPLANATION OF FIGURES

- Fig. 1. Dorsal aspect of the left mandible of the cantantopine *Melanoplus a. angustipennis*, showing the forbivorous-type adaptation. d = incisor lobe.
- Fig. 2. Dorsal aspect of the left mandible of the truxaline *Syrbula admirabilis*, showing the graminivorous-type adaptation. (Abbreviation as in Fig. 1.)
- Fig. 3. Frontal view of a grasshopper head showing the relationships between its mouthparts and a grass leaf on which it is feeding. This is an example of margin-feeding. gal = galea; lbp = labial palpus; lbr = labrum; lca = lacinia; mdb = mandible; mxp = maxillary palpus; pgl = paraglossa.
- Fig. 4. Section of a grass leaf showing the angulate, comparatively even-margined cut caused by the graminivorous-type mandibles of the truxaline *Syrbula admirabilis*.
- Fig. 5. Section of a grass leaf showing the somewhat irregular cut caused by the herbivorous-type mandibles of the oedipodine *Spharagemon collare*.
- Fig. 6. Section of a grass leaf eaten by a graminivorous grasshopper. The numbers on this diagrammatic figure indicate the general sequence of feeding: areas labelled nos. 1 and 2 are removed by the early concave cuts and those labelled nos. 3 to 7 by the later angulate cuts.
- Fig. 7. Section of a forb leaf showing the escalloped, irregular cut caused by the oedipodine *Spharagemon b. bolli*. This damage is
(continued on next page)



EXPLANATION OF FIGURES (continued from preceding page)

typical of that produced on forbs by either herbivorous-type or forbivorous-type mandibles.

Figs. 4-7. The solid arrows indicate the feeders' forward progression and the dotted ones the direction taken by the mouthpart swaths.

The pattern of damage discussed above is characteristic of graminivorous grasshoppers. Acridids with different food-habits deviate from this pattern in the damage they inflict on their food plants, though the feeding sequence remains much the same; examples are found among woody plant foliage-feeders and forb-feeders. They eat ovoid, net-veined leaves rather than leaves that are linear and parallel-veined. Because of the venation, they are unable to remove morsels by a combination of incision and splitting between veins. The cut made—by incision only—is necessarily scalloped and irregular.

The inability of forbivorous acridids to leaf-split accounts only in part for the character of the damage they inflict. Damage is also a result of the shape of the mandibles. Mandibles exhibiting the forbivorous-type adaptation, as in many cantantopines, have an armature of irregular, sharp dentes (Fig. 1); those characterized by the graminivorous-type adaptation, as in the truxalines and acridines, have dentes in the form of parallel ridges often fused or worn into a semicontinuous cutting edge (Fig. 2); and those having the herbivorous-type adaptation, as in many oedipodines and some cantantopines, are intermediate between the preceding two, both in form and function. These three kinds of mandibles cause plant damage ranging from the scalloped and irregular cut (Fig. 7) caused by forbivorous-type mandibles to the intermediate one (Fig. 5) produced by herbivorous-type mandibles to the angulate and comparatively even-margined one (Fig. 4) made by graminivorous-type mandibles. The damage, thus inflicted, is sometimes of sufficient specificity to enable one to diagnose the taxonomic group to which the feeder belongs.

Finally, it is possible to determine the gross direction that a grasshopper moved during feeding as well as the direction taken by the individual mouthpart cuts. One need only locate the frayed portion of the animal's excavation. Fraying, produced by the early cuts when splitting is impossible and the mouthparts are in a relatively unfavorable position for efficient incision, indicates the early, more posterior part of the excavation, while the smooth portions and angulations are later and more anterior. Once the direction of individual cuts is established, one can easily deduce the feeder's forward progression; almost always it is opposite in direction to the cuts.

ACKNOWLEDGEMENTS .

Professors I.J. Cantrall, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, and W.L. Thompson, Department of Biology, Wayne State University, kindly read the manuscript of the foregoing report. Mrs. Patricia DeBlois, also of Wayne, typed the final copy of the manuscript. To these persons the author is indebted.

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