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THE FEASIBILITY OF USE OF CAECAL AND DIVERTICULAR COLORATION IN FIELD DETERMINATION OF GRASSHOPPER DIET[1,2]

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INTRODUCTION

Many studies have been undertaken in the past on the food selection, food preferences, and economic damage of various grasshoppers and their allies. Among the more salient of these researches are those of Anderson (1961, 1964); Ball (1936); Bindra (1958); Boldyrev (1928); Blackith and Blackith (1966); Brues (1946); Chapman (1957); Dibble (1940); Gangwere (1959, 1960, 1961, 1965, 1965a, 1966, 1966a, 1967); Husain *et al.* (1946); Isely (1938, 1946); Isely and Alexander (1949); Joyce (1952); Mulkern and Anderson (1959); Mulkern, Anderson, and Brusven (1962); Mulkern *et al.* (1969); Pfadt (1949); Riley (1878); Roonwal (1953); Savin (1927); Weiss (1924); and Williams (1954). Techniques useful in the investigation of food selection are to be found in certain of the above reports. Especially noteworthy in this respect are those by Blackith and Blackith, Chapman, Gangwere (1961), Isely and Alexander, Joyce, Mulkern and Anderson, Pfadt, Roonwal, and Savin.

The relatively new technique of Blackith and Blackith (1966) involves the comparison of colorations in the ileal diverticula of morabine grasshoppers (Orthoptera: Eumastacidae). The digestive caeca of eumastacids were previously discussed by Slifer (1944), and those of other groups by Gangwere (1966) in a comprehensive paper dealing with the mechanical handling of food in the orthopteroid alimentary canal. There is also an extensive literature on the gut physiology of these insects, some of which is appropriate to a consideration of the caeca and diverticula.

The possibility that the method of Blackith and Blackith is applicable to other groups of Orthopteroidea prompted the present research, which is, in part, an attempt to test the feasibility of using gastric caecal and diverticular coloration in studying the food-habits of certain members of the Michigan fauna. Moreover, assuming that the method is applicable, and is utilized in an area of known floral composition, it should be indicative of the effect that availability of food plants has on the diets of the various species studied; that possibility is also investigated.

MATERIALS AND METHODS

During the field season of 1968, various species of Orthopteroidea (largely Acrididae) were collected at Proud Lake and Pontiac Lake Recreation Areas, Oakland County, and at Stoney Creek Metropolitan Park, Macomb County, Michigan. Laboratory populations of the captured insects were maintained for later study using the grasshopper rearing cages described by Gangwere (1960), slightly modified by the use of pie tins both as cage top and as bottom, and were given appropriate maintenance food plants in Erlenmeyer flasks.

During actual experimentation, individual grasshoppers were isolated in cages such as were described by Gangwere (1960) for rearing mantids. The insects were starved for 24 to 48 hours (emptying the gut), but during this period were given access to drinking water supplied in cotton-stoppered vials. Following starvation, a known species of food plant was introduced into each cage, and the animals were allowed to feed for 2 to 24 hours. The range of allowed feeding time was determined by the hours necessary to produce particular colorations and to study the mode of color change. The grasshoppers were then killed with ethyl acetate. Under a binocular dissecting microscope, the terminal portion of the abdomen was cut off, the animals were decapitated, and the freed gut was pulled through the foramen magnum to be placed on a clean, dry microscope slide. As the dissection was immediate, it

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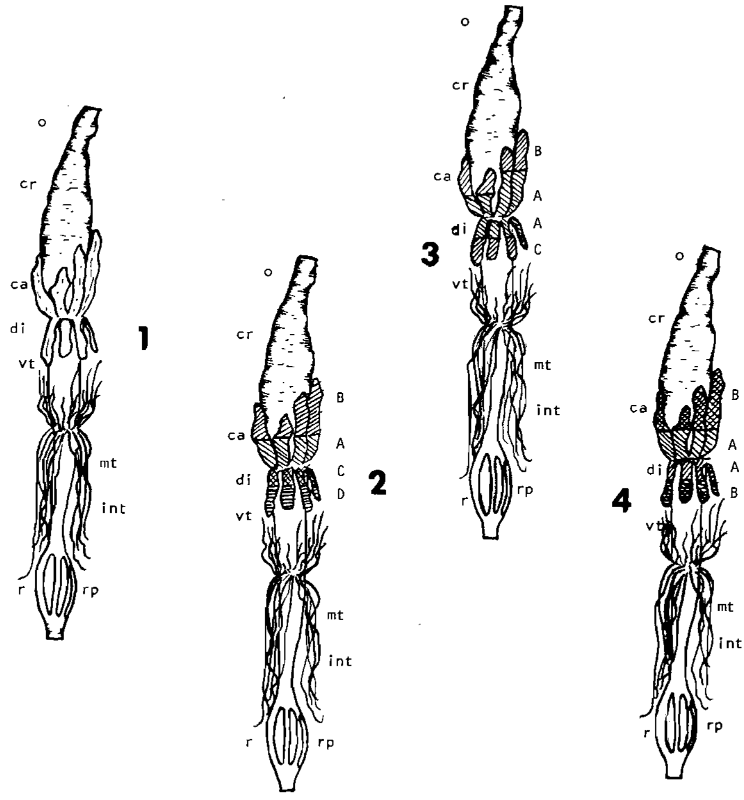

Fig. 1. Alimentary canal of the grasshopper, *Syrbula admirabilis* (Uhler), showing four of the six caeca and their caudal diverticula. ca, caecum; cr, crop; di, diverticulum; int, anterior intestine; mt, malpighian tubule; o, oesophagus; r, rectum; rp, rectal "pad"; vt, ventriculus ("stomach").

Fig. 2. Alimentary canal of *Syrbula admirabilis* showing the first sequence of color change in the caeca and diverticula. Sequence denoted respectively by a, b, c, and d.

Fig. 3. Alimentary canal of *Syrbula admirabilis* showing the second sequence of color change in the caeca and diverticula. Sequence denoted respectively by a, b, and c.

Fig. 4. Alimentary canal of *Syrbula admirabilis* showing the third sequence of color change in the caeca and diverticula. Sequence denoted respectively by a and b.

was not necessary to use an isotonic solution to maintain the gut tissues. This avoidance of the use of saline solution was actually desirable so as not to mix the gut contents. Coloration of the caeca and diverticula was recorded immediately, for the observed colors proved highly ephemeral.

The following species are investigated:

Acrididae: Gomphocerine (Slant-Facted Grasshoppers)
Chorthippus c. curtipennis (Harris)

Acridadae: Oedipodinae (Band-Winged Grasshoppers)
Arphia p. pseudonietana (Thomas)
Dissosteira carolina (Linnaeus)
Encoptolophus s. sordidus (Burmeister)
Pardalophora apiculata (Harris)
Spharagemon b. bolli (Scudder)

Acrididae: Catantopinae (Spine-Breasted Grasshoppers)
Melanoplus confusus (Scudder)
Melanoplus f.-r. femur-rubrum (De Geer)
Melanoplus s. sanguinipes (Fabricius)

Tettigoniidae: Phaneropterinae (Bush and Round-Headed Katydids)
Scudderia c. curvicauda (De Geer)

RESULTS

The results of the study are presented in Table 1 (Caecal and Diverticular Coloration of Selected Orthoptera).

DISCUSSION

The orthopteroid insects possess a number of blind pouches at the proximal end of the ventriculus (Fig. 1). They include the caeca (those pouches that project cephalad) and the diverticula (those that project caudad). Distinct colors and color patterns were observable in the caeca and diverticula of the species fed and studied in the present investigation (Table 1). These patterns proved to be superficially visible when the gut was first removed from the body, and were even brighter and more intense on its interior walls (as was indicated by observations on the slit gut). Moreover, within the exposed lumen there was, at times, a small volume of fluid with a slight hue generally indicative of the wall coloration. These several colors and color patterns were highly ephemeral, which necessitated immediate observation before they faded and were replaced by the dark hues of the death condition.

The guts of starved animals were always dark brown to black in color. This "starved" coloration changed promptly with feeding. Sequentially timed dissections after feeding demonstrated disappearance of the "starved" coloration in a rather prescribed manner: the "starved" coloration first disappeared from the proximal end of the caeca. This new coloration (in part attributable to the food source) then spread from the proximal to the distal end of the caeca, while simultaneously it replaced the "starved" condition in the proximal portion of the diverticula. The distal portion of the diverticula was generally the last area in which the coloration underwent food-induced change (Fig. 2).

Two relatively common variations to the above general pattern of color change were observed. In the first, coloration began simultaneously both in the proximal caeca and in the proximal diverticula, and then spread through the remaining area of the caeca and then of the diverticula (Fig. 3). In the second variation, there was a simultaneous, relatively synchronized spreading of color throughout the length both of the caeca and of the diverticula (Fig. 4), but at times lines or stripes of the "starved" condition coloration persisted, usually slightly lighter than their initial shade.

Large variations in coloration were seen, both within given species and between them. However, in all cases, the intensity and distinctiveness of the observed coloration appeared related to the amount of food present in the midgut. Thus, when the gut contents were concentrated in the hindgut, the caecal and diverticular coloration was less well defined.

The hoped for (but not expected) specificity of color based on food source was not encountered. There proved to be a wide range of color variation, but it was not sufficiently consistent to submit to classification. Individuals of a given grasshopper species were sometimes observed to develop different coloration when eating different parts—and sometimes even identical parts—of the same plant species. It is apparent that gut color variation is due, in part, to food source, but is also greatly modified by the animal's internal physiological state, which rules out use of the technique for field determination of Michigan grasshopper food-habits.

The possibility that caecal coloration is a function of genetic factors inherent within a single grasshopper population is also dismissed, based on the complete absence of any noticeable difference in the animals collected from different stations. It seems more likely that the observed patterns of coloration are the result of the extraction of plant pigments from the food, as modified and influenced by digestive enzymes and other substances present in the feeder's alimentary tract.

CONCLUSIONS

In light of the results of the present study, it appears that the gut coloration in non-morabine grasshoppers—at least in the species here investigated—is not sufficiently specific to submit to classification, and *cannot* be used as an index of food-habit. The observed colors and color patterns prove ephemeral, for they change with the onset of feeding, and are continuously altered as the food progresses along the length of the alimentary tract. These colors doubtlessly derive from substances within the food source, as modified by the internal state of the feeder.

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Table 1. Caecal and diverticular coloration of selected Orthoptera

Foods	Plant parts ingested[3]	Feeders	Caecal coloration	Diverticular coloration
Gramineae				
Agrostis sp.	L & S	*Pardalophora apiculata*	Golden; brown striped	Golden
” ”	F	” ”	Golden; brown striped	Golden
” ”	L & S & F	” ”	Golden; brown striped	Golden
Eleusine indica	F	*Melanoplus s. sanguinipes*	Yellow-green	Yellow-green
” ”	L & F	” ” ”	Brown	Brown
” ”	F	” ” ”	Olive	Olive
” ”	L	” ” ”	Yellow-green	Yellow-green
” ”	L	” ” ”	Yellow-brown	Black
” ”	L & S & F	” ” ”	Golden; brown striped	Golden-brown striped
” ”	L	” ” ”	Yellow-white	Dark green
” ”	L	” ” ”	Yellow-white with reddish brown tips	Black
” ”	L	” ” ”	Yellow-brown striped	Yellow-brown striped
” ”	L & F	” ” ”	Yellow	Yellow
” ”	L	” ” ”	Yellow-brown striped	Yellow-brown striped
” ”	L	” ” ”	Amber	Amber
” ”	L & F	” ” ”	Dark blue (distally); creamy brown (proximally)	Creamy brown
Grass sp.	L	*Dissosteira carolina*	White	White
” ”	L & F	*Melanoplus f.-r. femur-rubrum*	Dull pink	Dull pink
” ”	L	*Encoptolophus s. sordidus*	Pale golden	Golden brown & brown striped

Table 1 (Continued)

Grass sp.	L	” ” ”	Golden; brown striped	Pale golden
” ”	L	” ” ”	Golden; brown striped	Pale golden
” ”	L	” ” ”	Greenish yellow	Greenish yellow
” ”	L	” ” ”	Golden; brown striped	Golden
” ”	L	” ” ”	Golden; brown striped	Clear
Poa compressa	L	*Melanoplus confusus*	Black	Black-brown
” ”	L	” ”	Dark green-black	Dark green-yellow-striped
” ”	L	” ”	Black	Black
” ”	F	” ”	Brownish green	Brownish green
” ”	L & S	*Pardalophora apiculata*	Pale yellow	Milky white
” ”	L & S	” ”	Milky white	Milky white
” ”	S & F	” ”	Yellow	Pale yellow
Poa pratensis	S & F	*Dissosteira carolina*	Golden; brown striped	Golden; brown striped
” ”	F	*Melanoplus confusus*	Black (starved)	Black (starved)
” ”	L	” ”	Opaque yellow	Opaque yellow
” ”	L	” ”	Opaque yellow	Opaque yellow
Setaria viridis	L	*Melanoplus s. sanguinipes*	Pale greenish yellow	Pale greenish yellow
” ”	L	” ” ”	Yellow-green striped	Yellow
” ”	L	” ” ”	Pale green	Pale green
” ”	L	” ” ”	Yellow-green	Yellow-green
” ”	F	” ” ”	Pale yellow	Pale yellow
” ”	F	” ” ”	Yellow-green	Yellow-green
” ”	L	” ” ”	Green	Green
” ”	L	” ” ”	White-red tipped	White
” ”	F	” ” ”	Yellow-brown	Yellow-brown
” ”	L	*Melanoplus f.-r. femur-rubrum*	Greenish yellow	Green

Table 1 (Continued)

Cruciferae				
Lepidium virginicum	F	*Melanoplus confusus*	Golden; brown striped	Golden; brown striped
” ”	L & S	*Melanoplus s. sanguinipes*	Golden; brown striped	Golden
Fabaceae				
Lespedeza sp.	L & S & F	*Melanoplus s. sanguinipes*	Milky white	Milky white
” ”	L & S & F	” ” ”	White	White
Lythraceae				
Lythrum salicaria	S & F	*Scudderia c. curvicauda*	Purple	Purple
Umbelliferae				
Daucus carota	F	*Spharagemon b. bolli*	Yellow	Yellow
” ”	L	*Melanoplus confusus*	Pale green	Pale green
” ”	F	” ”	Golden	Transparent
Asclepiadaceae				
Asclepias tuberosa	L	*Melanoplus s. sanguinipes*	Dark brown (starved animal)	Dark brown (starved animal)
” ”	F	*Melanoplus confusus*	Black (starved animal)	Black (starved animal)
” ”	L	” ”	Black (starved animal)	Black (starved animal)
Labiatae				
Monarda fistulosa	L & S & F	*Melanoplus s. sanguinipes*	Yellow-white	Yellow-white
” ”	L & S & F	” ” ”	Golden green	Yellow to gold
” ”	L & S & F	” ” ”	White	White
Compositae				
Galinosoga parviflora	L	*Melanoplus s. sanguinipes*	Yellow-brown striped	Yellow
Lactuca sp.	L	*Pardalophora apiculata*	Pale to bright yellow (distally to proximally)	Cream
” ”	L & S	*Melanoplus s. sanguinipes*	Whitish yellow	Whitish yellow
” ”	F	*Melanoplus confusus*	Green	Pale black
” ”	L	” ”	Golden	Golden

Table 1 (Continued)

Rudbeckia hirta	F	*Melanoplus s. sanguinipes*	Black-gold striped	Black-gold striped
” ”	F	*Melanoplus confusus*	Black	Black
Solidago sp.	L & S & F	*Melanoplus s. sanguinipes*	Pale yellow	Light yellow
Taraxacum officinale	L	*Pardalophora apiculata*	Yellow	Light yellow
” ”	L	” ”	Transparent	Transparent
” ”	L	*Melanoplus s. sanguinipes*	Golden with single dark brown spot	Golden
” ”	L	” ” ”	Golden; brown striped	Golden; brown striped
” ”	L	” ” ”	Golden	Golden
” ”	L	” ” ”	Light brown	Light brown
” ”	L	” ” ”	Yellow-brown striped	Yellow
” ”	F	” ” ”	Yellow-brown striped	Black-green
Melanoplus s. sanguinipes (dead)		*Scudderia c. curvicauda*	Yellow-brown	Yellow-brown
Pardalophora apiculata (dead)		*Pardalophora apiculata*	Dark golden-brown lines	Semi-opaque; golden
Pardalophora apiculata (dead)		” ”	Gold with dark brown lines	Semi-opaque; golden

3L=leaves, S=stems, f=flowers and inflorescenses