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APOSEMATIC COLORATION IN *DACTYLOTUM VARIEGATUM* (ORTHOPTERA: ACRIDIDAE): SUPPORT FROM VERTEBRATE FEEDING TRIALS

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ABSTRACT—The palatability of the brightly colored and flightless *Dactylotum variegatum* (commonly called the rainbow grasshopper), relative to apparently cryptically colored and generally winged sympatric grasshopper species, was tested using local predators. Sparrows killed no *D. variegatum* when both this and other grasshopper species were offered in feeding trials. Mice, however, killed grasshoppers randomly. When similar numbers of *D. variegatum* were offered alone, mice killed a greater proportion of grasshoppers than the birds killed. When offered only *D. variegatum*, mice consumed significantly more of the *D. variegatum* that they killed than did birds. Mice consumed proportionately more of the *D. variegatum* killed when offered only this species than when offered a mixture of grasshopper species. We also observed nests of Cassin's sparrows to determine whether *D. variegatum* were delivered to nestlings by adults. No *D. variegatum* were delivered despite forming 18% of the grasshopper population in the area surrounding the nests. Although this species is highly visible, and represents a large portion of the grasshopper fauna, it does not appear to be proportionately consumed by the local predators we studied. This avoidance by predators may be an important factor influencing the abundance of the rainbow grasshopper in the local habitat. We conclude that the coloration of *D. variegatum* is aposematic, and is directed primarily at the visually hunting avian predators, being less of a deterrent to nocturnal mice.

The coloration, flight capability, and behavior of the rainbow grasshopper (*Dactylotum variegatum* (Scudder) (Melanoplinae)) are unusual among the orthopterans commonly found in southeastern Arizona. *D. variegatum* exhibits a bold color pattern (with bright orange and yellow-green markings on a dark blue background) in both nymphs and adults. This coloration causes the grasshopper to stand out from the background vegetation, at least to the human observer and presumably to its visually hunting predators. Adults are brachypterous (i.e., have short wings) and, in contrast to most other grasshoppers of this area, are therefore flightless. This species also delays initiation of escape responses when approached or physically disturbed, in contrast to sympatric acridids (pers. obser.).

Despite characteristics which would appear to make this species susceptible to predation, *D. variegatum* is abundant among grasshoppers in our study area. Because these characteristics of apparent vulnerability are typical of aposematic animals that are distasteful, dangerous, or otherwise strongly defended (Wickler, 1968; Edmunds, 1974), we hypothesized that the bright coloration advertises a protective unpalatability or distastefulness to potential predators. Here we report the results of feeding trials in which *D. variegatum* and other local orthopteran species were offered to sympatric birds and rodents known to consume grasshoppers. We also list grasshopper species that were delivered to nests of one of the bird species used in the feeding trials.

MATERIALS AND METHODS—The study was conducted at the Research Ranch of the National Audubon Society in Santa Cruz County, Arizona (elevation 1,500 m). All test grasshoppers and predators tested were locally sympatric and were taken from semidesert grassland dominated by native perennial grasses, especially *Bouteloua gracilis, Lycurus phleoides,* and *Eragrostis intermedia.* The most common perennial shrubs in this area are *Happlopappus tenuisectus* and *Baccharis pteronoides* (Bock and Bock, 1986; Brady et al., 1989). The predators we tested were lark sparrows (*Chondestes grammacus*), Botteri's sparrow (*Aimophila botterii*), Cassin's sparrow (*A. cassinii*), and deermice (*Peromyscus maniculatus*). These predators are common at this site and a large portion of their diets in other areas has been reported to be grasshoppers (Cottam and Knappen, 1939; Martin et al., 1951; Baepler, 1968; Williams and LeSassier, 1968).

Two types of feeding trials were conducted. Predators were offered either a mixture of grasshoppers including *D. variegatum* or were offered only *D. variegatum.* Because nymph and adult *D. variegatum* coloration and behavior are similar, we used them indiscriminately in the feeding trials. In the mixed-species feeding trials the predators were offered, along with *D. variegatum,* a mixture of Acrididae in various subfamilies in approximate proportion to the diversity of these grasshoppers in the field at the time of the test. The subfamilies included Gomphocerinae (*Ageneotettix deorum* Scudder, *Aulocara femoratum* Scudder, *Eritettix simplex* Scudder, *Heliaula rufa* (Scudder), *Paropomala wyomingensis* (Thomas), *Psoloessa texana* Scudder, *Syrbula montezuma* (Saussure)), Melanoplinae (*Hesperotettix viridis* (Thomas), Oedipodinae (*Arphia pseudonietiana* Bruner), and occasionally other unidentified species from these subfamilies. None of these species bore any resemblance to *D. variegatum,* most appearing to be cryptic in pattern and coloration.

Feeding trials were conducted by releasing one predator into a 1.0-m × 1.6-m × 0.7-m cage. The cages were constructed either of clear plastic with wire mesh (6 mesh/cm) vents or entirely of fine wire mesh. During testing, each cage contained water and grain, as well as rock, soil, and clumps of grasses taken from the study area. Four to 17 grasshoppers were offered, depending on our ability to obtain grasshoppers in the field at the time of each test. A total of 151 *D. variegatum* individuals and 105 individuals of the other species were offered to 26 individual predators in 30 feeding trials. In nine of these trials, predators were offered only *D. variegatum.* The numbers of grasshoppers alive and intact, killed but not eaten, and killed and consumed were tallied at the end of each trial. New grasshoppers were captured for each trial.

We tested six individuals of lark sparrow (*Chondestes grammacus*), three of Botteri's sparrow (*Aimophila botterii*), and four of Cassin's sparrow (*A. cassinii*). Each bird was caught in a mist net and immediately released into its own cage; grasshoppers were added about 0.5 h later. The trial was stopped after 1.5 to 3 h, by which time the bird had generally killed one quarter to one half of the prey. Thirteen deermice (*Peromyscus maniculatus*) were tested. Each mouse was captured at night and held alone over the next day in the feeding trial cage supplied with water and grain. The trials began at dusk the next day when the grasshoppers were released into the cages. The numbers of grasshoppers alive, killed but not eaten, and killed and eaten were tallied early the next morning.

Feeding trials were conducted from mid-August to mid-September 1984, and from early July to early August 1985, when both grasshoppers and predators were most abundant. The data were tested for independence using the G-Statistic. Williams' correction for a 2 × 2 contingency table of small sample size was applied (Sokal and Rohlf, 1981). For all reported values, *d.f.* = 1.

Feeding observations at nests were conducted in August 1983, during peak nesting season at this site. The identity of grasshoppers delivered by adult Cassin's sparrows to young at two nests was noted. Nests on an upland mesa of the Research Ranch were observed through binoculars from a blind set up approximately 25 m from each nest. Each nest was watched on two consecutive days (4 and 5 August and 11 and 12 August 1983), for a total of 8.5 h (3.0 and 5.5 h respectively). Observations were made at peak feeding times during morning and afternoon. Grasshoppers were categorized as *D. variegatum* or "other" for the purposes of this study. Grasshoppers were counted in the vicinity of the nests during a concurrent study by counting and identifying individuals as they were flushed from wire hoops (Jepson, 1985; Jepson-Innes and Bock; 1989). The census was conducted during July and August 1983, and included the area in which the nests were located.

RESULTS—The results of the feeding trials, pooled for each species of predator, are shown in

Tables 1 and 2. All three species of birds were offered a mixture of *D. variegatum* and other grasshoppers, but only non-*D. variegatum* species were killed. This result differs significantly from the hypothesis that the birds would kill grasshoppers randomly with respect to their frequency in the mixture offered (feeding trials pooled by species; lark sparrows, $G = 24.307$, $P < 0.001$; Botteri's sparrows, $G = 13.333$, $P < 0.001$; Cassin's sparrows, $G = 28.486$, $P < 0.001$). However, when deermice were offered a mixture of species, *D. variegatum* was killed in proportion to its frequency in the pooled mixture ($G = 0.547$, $P > 0.5$).

In feeding trials including only *D. variegatum*, both birds and deermice killed grasshoppers. Deermice killed significantly more *D. variegatum* than did the birds (pooled) under these conditions ($G = 25.314$, $P < 0.001$).

Not all of the *D. variegatum* individuals killed were eaten. Birds killed and consumed *D. variegatum* only when no other grasshopper species were offered. Deermice consumed significantly more of the *D. variegatum* they killed when offered *D. variegatum* alone than when offered this species in a mixture with other species ($G = 5.606$, $P < 0.05$). Considering only trials offering *D. variegatum* alone, deermice consumed significantly more of the *D. variegatum* they killed than did the birds ($G = 4.245$, $P < 0.05$).

Grasshoppers made up over 90% of the total number of food items delivered to these nests; other items were praying mantids and lepidopteran larvae. The numbers of *D. variegatum* and non-*D. variegatum* grasshoppers brought to the two nests were pooled. The adult sparrows delivered a total of 69 grasshoppers; 69 were non-*D. variegatum* species and none were *D. variegatum*. This is significantly fewer *D. variegatum* than expected ($G = 15.15$, $P < 0.001$), given that they represented 18% of the total grasshopper population during July and August (Jepson, 1985).

DISCUSSION—Aposematic colors and patterns should be most effective with visually hunting predators. The birds we tested are all diurnal hunters. During the daylight hours (when the birds were tested), *D. variegatum* was easier for us to see in the cages than were the other grasshoppers. We assume, therefore, that the distinctive coloration of *D. variegatum* was not overlooked by birds in the feeding trials with the

TABLE 1—Fates of *D. variegatum* and other grasshoppers offered together to birds and to mice in feeding trials. Numbers of grasshoppers pooled for all feeding trials with each predator. Numbers in parentheses are the proportion of the total number of grasshoppers in each category following the feeding trials.

Predator	*D. variegatum*				Other grasshoppers				Number of trials
	Total offered	Alive	Killed, not consumed	Killed and consumed	Total offered	Alive	Killed, not consumed	Killed and consumed	
Deermice	30	2 (0.07)	9 (0.30)	19 (0.63)	38	1 (0.03)	0 (0.00)	37 (0.97)	11
Birds									
Lark Sparrow	16	16 (1.00)	0 (0.00)	0 (0.63)	47	18 (0.38)	0 (0.00)	29 (0.62)	4
Botteri's Sparrow	9	9 (1.00)	0 (0.00)	0 (0.00)	9	2 (0.22)	0 (0.00)	7 (0.78)	3
Cassin's Sparrow	11	11 (1.00)	0 (0.00)	0 (0.00)	11	0 (0.00)	0 (0.00)	11 (1.00)	3
All birds	36	36 (1.00)	0 (0.00)	0 (0.00)	67	20 (0.00)	0 (0.00)	47 (0.70)	10

TABLE 2—Fates of *D. variegatum* offered alone to birds and to mice in feeding trials. Numbers are to be interpreted as indicated for Table 1.

Predator	Total offered	Alive	Killed, not consumed	Killed and consumed	Number of trials
Deermice	33	12 (0.36)	4 (0.12)	17 (0.52)	3
Birds					
Lark Sparrow	47	43 (0.91)	4 (0.09)	0 (0.00)	5
Cassin's Sparrow	5	3 (0.60)	0 (0.00)	2 (0.40)	1
All birds	52	46 (0.88)	4 (0.08)	2 (0.04)	6

grasshopper mixture. Presumably, once this grasshopper is noticed, its slower escape behavior would cause it to be more readily captured if the birds chose to do so. We conclude that *D. variegatum* was perceived and actively avoided by these visually hunting predators. That the birds did kill *D. variegatum* when no other grasshopper species were present further corroborates this conclusion.

Deermice, however, are primarily nocturnal and forage using a well developed sense of smell. They would be less likely to detect the colors and pattern of their prey. Deermice were able to find and kill grasshoppers, but apparently did not discriminate between the *D. variegatum* and non-*D. variegatum* on the basis of color and pattern, as indicated by grasshoppers being killed at random with respect to their frequency in the mixed species tests.

Not all species with apparently aposematic coloration possess distasteful or dangerous characteristics. Since most of the *D. variegatum* killed by the birds were subsequently rejected as food and since we found no other species in the area that might serve as models for mimicry, we conclude that *D. variegatum* is not likely to be protected by a mimetic resemblance to another protected species. Our results suggest that *D. variegatum* itself possesses qualities that render it undesirable as food to these birds and that the bright coloration of *D. variegatum* serves an aposematic function. The brightly colored and closely related species *D. pictum* is reported to be inedible by "bantams, turkey, sparrows, mockingbirds, and others" (Isely, 1938).

Although deermice killed grasshoppers indiscriminately, *D. variegatum* is apparently less desirable as food. Having killed a grasshopper, a deermouse is less likely to consume *D. variegatum* than other species in the mixed species feeding trials. We assume that the characteristics that make *D. variegatum* undesirable as a food item for birds also affect the deermice. Because deermice consumed a greater proportion of the *D. variegatum* offered to them than did the birds in the *D. variegatum* only feeding trials, we conclude that the effect of the deterrent was apparently not as strong for the mice under our test conditions. Mice were held for a longer period before testing and may have had a higher hunger level. This may have caused them to consume more of the *D. variegatum* that they killed than did the birds.

In addition to the hunger level of the predator, the unpalatability of a food item could be influenced by the strength of the deterrent characteristic as perceived by a particular predator. We noticed that while the birds generally consumed portions of the thoracic and abdominal exoskeleton of *D. variegatum* along with the internal organs, the deermice often consumed only the interior contents leaving the exoskeleton. Because toxic products are frequently sequestered in cuticular reservoirs by insects (Blum, 1978) feeding in this fashion may allow deermice to avoid the postulated deterrent.

One candidate for the feeding deterent is gymnospermin (Miyakado et al., 1974) or a derivative of this diterpenic alcohol which has been isolated from *D. variegatum* (cited in Whitman, 1990). Gymnospermin is produced by *Baccharis glutinosa,* a genus heavily fed on by *Dactylotum* spp. (Ball, 1936; Whitman, 1990). This composite is common at our study site (pers. obser., Bonham, 1972).

Avian predators have been shown to significantly affect the density and species composition of grasshopper populations in grassland systems (Joern, 1986; Bock et al., 1992). The protected status of *D. variegatum* may in part explain the relatively high proportional representation of this species in our study site (Joern and Gaines, 1990; Bock et al., 1992).

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