Oecologia (2001) 128:416–421
DOI 10.1007/s004420100666

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Tasty on the outside, but toxic in the middle: grasshopper regurgitation and host plant-mediated toxicity to a vertebrate predator

Received: 1 June 2000 / Accepted: 31 January 2001 / Published online: 24 March 2001

Abstract Regurgitation by arthropods is often considered to be a rudimentary form of defense against predators. In phytophagous insects, regurgitate composition will vary with diet, and plant secondary compounds from host plants can contribute to the effectiveness of regurgitate deterrence. Regurgitation in response to predator attack is particularly common in grasshoppers. However, there is little empirical evidence in favor of grasshopper regurgitation as an effective antipredator mechanism in natural predator-prey systems. In particular, studies of the effect of grasshopper diet on regurgitate deterrence to vertebrate predators are lacking. This study investigated the relationship between diet and predator defense in the grasshopper, *Schistocerca emarginata* (=*lineata*) (Orthoptera: Acrididae). Using the insectivorous lizard, *Anolis carolinensis* (Iguanidae), as a predator, I demonstrate that consumption of *Ptelea trifoliata* (Rutaceae) by *S. emarginata* can confer distastefulness as well as toxicity. Regurgitate deterrence is mediated strictly by host plant material in the gut and does not require an enteric contribution from the grasshopper. Regurgitation by *Ptelea*-fed *S. emarginata* can result in rejection prior to ingestion by *A. carolinensis* and can enable grasshoppers to survive predator attacks.

Keywords *Schistocerca emarginata* (=*lineata*) · *Anolis carolinensis* · Grasshopper · Predator · Host plant

Introduction

Many arthropods regurgitate their gut contents when disturbed (Whitman et al. 1990). This behavior is most common among the grasshoppers (Eisner 1970) and is often referred to as “spitting tobacco juice” because of its resemblance to the human habit of chewing tobacco leaves and spitting an unpleasant brown sticky fluid. Despite the widely observed correlation between grasshopper regurgitation and molestation, there is very little empirical evidence in support of regurgitation as an adaptive predator defense mechanism.

Grasshopper regurgitate is a complex mixture of digestive enzymes, salivary secretions, and partially digested food plants (Freeman 1967, 1968; Knecht et al. 1974; Lymbery and Bailey 1980). Topical administration of *Locusta migratoria* regurgitate to the eyes of birds induced obvious stress (Freeman 1968), and oral administration induced vomiting and diaphragm contractions in guinea pigs, sheep, and goats (Curasson 1934). Evidence of its deterrence to invertebrate predators was provided by Eisner (1970), who found that regurgitation by tethered *Romalea microptera* (=*guttata*) and *Brachystola magna* caused dispersion of attacking *Pogonomyrmex* ants. Grasshopper body parts treated with regurgitate were also rejected, whereas those left untreated were accepted by foraging *Pogonomyrmex* workers. Digger wasps were observed to be reluctant to sting grasshoppers which had spread regurgitate over their bodies, and vigorously groomed following contact with the regurgitate (Steiner 1981). In the only study addressing grasshopper regurgitation as a deterrent to vertebrate predators, regurgitating *Goniaea* sp. were rejected by skinks, spiders, and ants, as were mealworms treated with *Goniaea* regurgitate (Lymbery and Bailey 1980).

In phytophagous insects, regurgitate composition will vary with host plant diet. Regurgitate deterrence mediated by ingested plant secondary compounds has been suggested as a widespread and common form of predator defense (Eisner 1970; Blum 1981; Peterson et al. 1987;

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Whitman et al. 1990). Only two studies, both conducted with invertebrate predators, have demonstrated an effect of diet on regurgitate deterrence in grasshoppers. Eisner (1970) showed that when fed two of its natural host plants, *Eupatorium capillifolium* (Asteraceae) and *Salix nigra* (Salicaceae), the regurgitate of *R. microptera* was deterrent to ants (not directly identified in the text, but inferred to be *Pogonomyrmex*). However, diets of lettuce or *Myrica cerifera* (Myricaceae) resulted in non-deterrent regurgitates. Ortego et al. (1997) showed that *Schistocerca americana* regurgitate was more strongly deterrent to *Crematogaster opuntia* ants when the grasshoppers were fed wheat seedlings than when fed lettuce. Ortego et al. (1997) also demonstrated that both the organic and aqueous phases of the regurgitate were deterrent to ants following extraction with ethyl acetate. Deterrence of the organic phase was attributed to the presence of plant secondary compounds, while deterrence of the aqueous phase was attributed to enteric components such as digestive enzymes. *Crematogaster* ants typically forage for honeydew and nectar (Sudd and Franks 1987) while *Pogonomyrmex* ants are seed-harvesters and rarely take live prey (Taber 1998). Thus, neither *Crematogaster* nor *Pogonomyrmex* are likely to be major predators of large mobile grasshoppers, with possible exceptions being encounters during hatching, molting, or injury. Importantly, no studies to date have shown an effect of grasshopper diet on regurgitate deterrence to vertebrate predators.

Some populations of the grasshopper, *Schistocerca emarginata* (=*lineata)*, in Texas, USA, feed primarily on either *Ptelea trifoliata* (Rutaceae) or *Rubus trivialis* (Rosaceae) as juveniles (Sword and Dopman 1999). Sword (1999) demonstrated that *S. emarginata* nymphs from *Ptelea*-feeding populations exhibit density-dependent aposematism with deterrence to predators conferred through host plant use. Nymphs from *Ptelea*-feeding populations can be unpalatable to insectivorous *Anolis carolinensis* (Iguanidae) lizards when reared on *Ptelea*, but not when reared on *Rubus*. In the Sword (1999) experiments, rejected *Ptelea*-reared grasshoppers were either vomited by the lizards or released prior to ingestion. Of six *Ptelea*-reared grasshoppers that were released prior to ingestion, two survived and appeared to be uninjured (Sword, unpublished data). Observations of these predator attacks suggested that regurgitation of grasshopper gut contents elicited rejection of the grasshoppers prior to ingestion by the lizards.

Here I investigate the relationship between host plant use and predator deterrence in *S. emarginata*. I demonstrate that (1) grasshopper diet directly affects the deterrence of *S. emarginata* regurgitate to *A. carolinensis* lizards, (2) deterrence is strictly the result of plant material in the gut and requires no enteric contribution whatsoever from the grasshoppers, and (3) regurgitation by *Ptelea*-fed *S. emarginata* can facilitate individual survivorship by eliciting rejection by *A. carolinensis* lizards prior to ingestion.

Materials and methods

Lizard feeding trials

Deterrence to predators was assessed using *A. carolinensis* lizards as a bioassay. *A. carolinensis* shares a niche with small avian predators in North America and forages exclusively for insects in trees and shrubs as well as on the ground (Roughgarden 1995). This lizard was common in the *S. emarginata* habitats studied by Sword and Dopman (1999) and I have observed it basking and moving about in *Ptelea* shrubs on numerous occasions. Field-captured adult lizards were obtained from a commercial supplier in Louisiana, outside the range of *S. emarginata* (Hubbell 1960). Lizards were maintained in the laboratory in 1-m^3 screen sleeve cages with 150-W incandescent lamps provided as a heat sources for basking on a 14 h light:10 h dark regime. Lizards were daily offered an ad lib diet of water and live crickets, *Acheta domestica* (Orthoptera: Gryllidae), obtained from a commercial supplier. This diet was occasionally supplemented with non-aposematic grasshoppers (no *Schistocerca*) collected at the University of Texas, Brackenridge Field Laboratory (BFL).

Prior to testing, lizards were individually marked and isolated in 3.5-l clear plastic tubs with plastic mesh-covered lids. Each cage contained a stick for roosting and a water dish. Cages were maintained in a walk-in environment chamber at 30°C, 14 h light:10 h dark. Lizards were then offered a standardization meal of one adult *A. domestica* cricket to control for motivational state. Feeding trials were conducted 1 day following consumption of the standardization meal by removing the lizards from the individual plastic tubs and placing them in a 1-m^3 screen cage housed in the same environment chamber with a 150-W incandescent lamp provided overhead for basking. Lizards were allowed to settle and then offered an insect from one of the treatment groups described below. Lizard feeding trials were conducted for a maximum of 3 h and observed continuously. Attack and consumption of an insect without regurgitation for 24 h was scored as acceptance. Rejection was scored as attacking and either releasing voluntarily (as opposed to grasshopper escape due to hind leg autotomy) or as consumption followed by regurgitation within 24 h of ingestion. Uneaten insects were removed from the cage at the end of the testing period. Lizards that did not attack were tested in subsequent trials on successive days until an attack occurred. Each lizard was used only once.

Treatments

Regurgitates

To determine if regurgitate from *S. emarginata* grasshoppers reared on either *Ptelea* or Romaine lettuce, *Lactuca sativa* var. *longifolia* (Asteraceae), could elicit predator rejection, lizards were offered live adult *A. domestica* crickets with 20 μl of *S. emarginata* regurgitate evenly applied across their dorsal surface. Treated crickets were released into the lizard observation cage and appeared to move about the cage in a normal fashion. Regurgitate was obtained from final-instar *S. emarginata* reared exclusively on diets of either *Ptelea* or Romaine lettuce. Grasshoppers were collected as first instars from a *Ptelea*-feeding population at BFL (Sword and Dopman 1999) and reared in groups at 30°C,14 h light:10 h dark in 8-l clear plastic tubs with wire mesh lids. Fresh *Ptelea* cuttings were obtained daily from different trees at BFL and offered in a 300-ml beaker of water to prevent desiccation. Romaine lettuce was commercially obtained and fresh leaves were offered daily. Individual insects were grasped between the thumb and forefinger and gently squeezed about the pronotum until they regurgitated. Regurgitate was collected into a glass pipette and deposited into a small screw top glass vial. Regurgitate was collected daily for 2 weeks from approximately 30 grasshoppers per plant, frozen between collection bouts, and thawed to 30°C before use in lizard feeding trials.

Plant pastes

To determine if regurgitate deterrence was strictly due to the presence of plant material, or due to a synergistic effect of host plant and enteric factors, lizards were offered adult crickets with 20 µl of a plant paste evenly applied across their dorsal surface. Treated crickets were released into the lizard observation cage and appeared to move about normally. Romaine lettuce paste was prepared by grinding 2.4 g of liquid nitrogen-frozen leaf (petiole removed) in a mortar and pestle. Following grinding, 0.5 ml of dH_2O was added. *Ptelea* paste was similarly prepared by grinding 1.8 g of leaf (petiole removed) frozen under liquid nitrogen. Due to the lower water content of *Ptelea* leaves, 2 ml of dH_2O was added so that both pastes had similar consistencies. Plant pastes were stored separately in screw-top glass vials and frozen until being thawed to 30°C for use in the feeding trials. Freezing was assumed to have no effect on the composition of either the plant pastes or the regurgitate samples.

Loss of deterrence

To determine the effect of dietary change on deterrence, lizards were offered fourth- and fifth-instar *Ptelea*-reared *S. emarginata* grasshoppers from BFL that had been switched to Romaine lettuce for either 24 h or for a single meal. Insects in the 24-h treatment were removed from a *Ptelea*-reared stock cage and allowed to feed on Romaine lettuce for 24 h at 30°C, 14 h light:10 h dark prior to being offered to a lizard. Insects in the single-meal treatment were removed 15 at a time from a *Ptelea*-reared stock cage and individually observed feeding at 30°C on Romaine lettuce in 101.25-cm^3 clear plastic conical cages with wire mesh tops. Insects were offered to the lizards following an initial meal of at least 4 min of continuous feeding on lettuce. Average meal length was 6.0 min.

Statistics

Differences in the number of insects accepted and rejected were assessed between different treatment groups with Fisher's exact test.

Results

Regurgitates

Crickets treated with regurgitate from *Ptelea*-reared *S. emarginata* were highly deterrent to *A. carolinensis* and rejected more often than those treated with regurgitate from lettuce-reared *S. emarginata* ($P<0.0001$) (Fig. 1). All rejections occurred prior to ingestion. Lizards would commonly rub the sides of their mouths against the cage floor immediately after rejection and would continually open and close their mouths for up to a minute following attack. The rejection behaviors observed during this experiment were similar to those exhibited by other insectivorous lizards following experience with unpalatable prey (Boyden 1976).

Plant pastes

Crickets treated with a paste of *Ptelea* were highly deterrent and rejected more often than crickets treated with a similar preparation of Romaine lettuce ($P<0.0001$) (Fig. 2). The response of predators to crickets treated with either *Ptelea* or Romaine lettuce paste was nearly identical to those treated with regurgitate from either *Ptelea* or Romaine lettuce-reared *S. emarginata* (Figs. 1, 2). Rejection behaviors of the lizards were also similar, and all rejections occurred prior to ingestion.

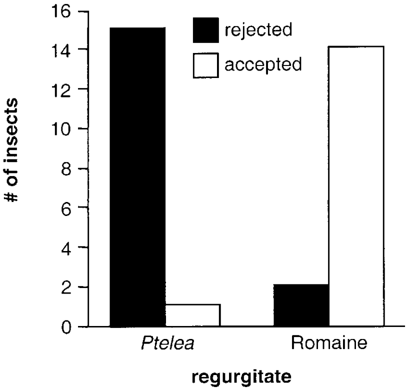

Fig. 1 *Anolis carolinensis* response to crickets treated with regurgitate from *Schistocerca emarginata* grasshoppers reared on either *Ptelea* or Romaine lettuce

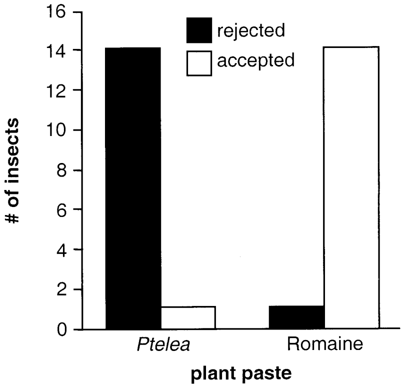

Fig. 2 *A. carolinensis* response to crickets treated with host plant pastes of either *Ptelea trifoliata* or Romaine lettuce

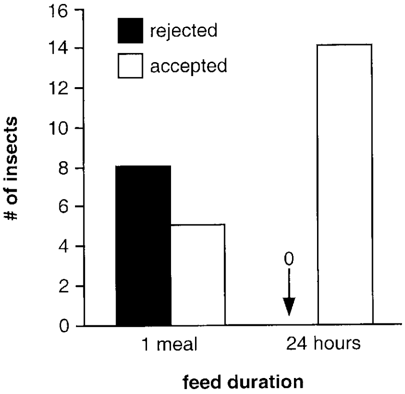

Fig. 3 *A. carolinensis* response to *Ptelea*-reared *S. emarginata* fed on Romaine lettuce for either one meal or for 24 h

Loss of deterrence

S. emarginata reared on *Ptelea* and then allowed to feed for 24 h on Romaine lettuce were accepted without exception. In contrast, *S. emarginata* that had fed on lettuce for a single meal were rejected in 61.5% of the encounters (*P*=0.0006) (Fig. 3). Of the eight grasshoppers rejected by the lizards, three were regurgitated and five were released prior to ingestion. Two released individuals survived attack, one injured and the other apparently unharmed. The behavior of lizards rejecting prior to consumption was similar to the previously described rejection behaviors.

Discussion

The regurgitation response of grasshoppers and other arthropods can facilitate predator contact with prey gut contents prior to consumption of the prey itself. Host plant use has previously been shown to affect the deterrence of grasshopper regurgitate (Eisner 1970; Ortego et al. 1997). This study concurs with these findings, but is distinguished by three features: (1) regurgitate deterrence to a vertebrate predator can be affected by grasshopper diet; (2) deterrence can be mediated entirely by plant material in the gut, and (3) regurgitation can facilitate individual survivorship of predator attacks.

Diet directly affects regurgitate deterrence

S. emarginata produces a regurgitate that is highly deterrent to *A. carolinensis* when reared on *Ptelea*, but not when reared on Romaine lettuce (Fig. 1). Importantly, deterrence of the regurgitate can be entirely attributed to the presence of plant material and does not require an enteric contribution from the grasshopper (Fig. 2). Complete loss of deterrence to predators occurs within 24 h of feeding on non-toxic host plants, but requires more than a single meal (Fig. 3). Thus, simply ingesting a noxious host plant can provide insects with an effective chemical defense, while regurgitation can function as a simple delivery mechanism. This scenario should be broadly applicable to foliage-feeding herbivorous insects.

Attacked *S. emarginata* invariably regurgitated. Contact with grasshopper regurgitate mediated predator rejections prior to consumption. During these experiments and those described in Sword (1999), lizards only released *Ptelea*-fed *S. emarginata* when the ventral portion of a grasshopper’s head enterered their mouth. On one occasion, a grasshopper was initially captured by the hind leg and the leg was immediately lost by the grasshopper, presumably due to autotomy. The lizard masticated the leg, swallowed it, and promptly reattacked the grasshopper. It subsequently released the grasshopper, but only after maneuvering the insect's head into its mouth. Consumption of body parts and release only after contact with the ventral head region would not be expected if the deterrent employed by the grasshopper were cuticular or systemic. This, coupled with the demonstrated deterrence of *Ptelea* regurgitate (Fig. 1), clearly indicates that contact with regurgitated gut contents mediated prey rejections prior to ingestion.

Regurgitation enhances survivorship

Of particular importance is that some grasshoppers survived their encounter with the predator. *S. emarginata* feeding on *Ptelea* not only repelled, but survived lizard attack. During experiments described in Sword (1999), two of six *S. emarginata* reared on *Ptelea* were rejected prior to ingestion and survived apparently unscathed. In this study, two of eight individuals reared on *Ptelea* and then fed a single lettuce meal also survived attack, although one was injured. These examples clearly demonstrate that regurgitation in response to attack can enhance individual survivorship when an individual has recently been feeding on a noxious host plant.

Gut content-mediated toxicity

Although *Ptelea*-fed *S. emarginata* can be rejected prior to ingestion by lizards, regurgitation by grasshoppers did not account for all of the observed lizard rejections. Feeding on *Ptelea* confers distastefulness, as evidenced by pre-ingestion rejections, but *Ptelea*-fed *S. emarginata* were also attacked, consumed, and then regurgitated by lizards following ingestion. Lizard regurgitation of *Ptelea*-fed grasshoppers suggests that *Ptelea*-feeding confers toxicity as well as distastefulness to predators.

In contrast to these findings, the effects of insect diet on their palatability to predators can be much more subtle. Lizard predators developed aversions to juveniles of the closely related desert locust, *Schistocerca gregaria*, that were fed *Hyoscyamus muticus* (Solanaceae) (Sword et al. 2000). In this case, the effects of toxic plant material in the locusts’ guts were not immediately apparent because the lizards neither rejected locusts prior to consumption nor did they ever regurgitate the locusts. Nevertheless, lizards that had previously consumed a locust fed *Hyoscyamus* were much less likely to consume another *Hyoscyamus*-fed locust relative to lizards that had previously eaten locusts fed different host plants.

Most grasshopper predators do not feed on foliage and are not adapted to metabolize plant compounds (Whitman 1990). Indeed, this must be true of many generalist predators that feed on phytophagous insects. An insect feeding on leaves and consumed by a predator can be viewed as a foliage-filled capsule. The offending predator may be subjected to the defenses of the prey’s host plant by inadvertently ingesting a noxious dose of plant secondary compounds. Thus, foliage-feeding insects, by way of their gut contents, can employ plant secondary compounds for their own defense and serve as an opportunistic extension of their host plant's chemical defenses (Eisner 1970).

There are a number of examples in which insects employ enterically unaltered plant compounds for defense against predators, but these typically involve some form of active sequestration by the insects (Bowers 1990). For example, two classic studies by Eisner et al. (1974) and Morrow et al. (1976) showed that sawfly larvae from different genera sequester pine terpenes and eucalyptus oils in foregut pouches known as diverticula. These repellent compounds are regurgitated along with the gut contents in response to predator attack. The influence of diet on the compounds available for predator defense has been clearly demonstrated in *Romalea guttata* (=*microptera*) (Acrididae). This generalist grasshopper can sequester a variety of noxious secondary compounds from an assortment of unrelated host plants. Following storage in metathoracic glands, these compounds are emitted as part of a potent defensive secretion from the metathoracic spiracles (see Whitman 1990 for review). Although the sequestration of plant compounds for defense is fairly common in insects, this study supports the idea that the passive utilization of ingested substances can also be a substantial mode of predator defense (Eisner 1970; Blum 1981; Peterson et al. 1987; Whitman et al. 1990).

Ptelea and other species in the Rutaceae are known to produce an abundance of furanocoumarins (Dreyer 1969; Gray and Waterman 1978) that are toxic to a broad range of organisms. Furanocoumarins are UV phototoxic and can react with duplexed DNA to form irreversible crosslinks, with amino acids to result in protein denaturation, with unsaturated fatty acids to form cycloadducts, and with ground state oxygen to result in toxic oxyradicals that can oxidatively damage a number of biomolecules. (Berenbaum 1991). *S. emarginata* in *Ptelea*-feeding populations must have acquired adaptations to deal with furanocoumarins. The grasshoppers may either detoxify them, as do some lepidopterans feeding on furanocoumarin-rich plants (Berenbaum 1995), or withstand the compounds in unaltered form. Unaltered furanocoumarins may be responsible for the toxicity of *S. emarginata* feeding on *Ptelea*, but additional study is necessary to identify the actual source of toxicity. *Ptelea* and other rutaceous plants also produce a number of alkaloids (Dreyer 1969; Waterman 1975) including toxic furanoquinoline, β-carboline, and benzylisoquinoline alkaloids (Leslie and Berenbaum 1990). Again, further investigation is required to determine the roles of these compounds in conferring toxicity to *S. emarginata*.

To fully appreciate the function of a specific prey defense, we must understand the interaction between the defense and the diversity of potential predators with varying foraging strategies (Malcom 1992). Despite hours of observation, I have not witnessed predation in the field on *S. emarginata* by *Anolis* lizards or any other vertebrates. The difficulty inherent in observing natural predation was likely exasperated in this case by predator learning and subsequent avoidance of *S. emarginata* warning coloration (Sword 1999). I have, however, observed the rejection of *Ptelea*-fed *S. emarginata* by other vertebrate predators in the laboratory. *Ptelea*-fed grasshoppers were attacked and rejected prior to ingestion by Gould's monitor lizards, *Varanus gouldii* (Varanidae), consumed then regurgitated by a rough green snake, *Opheodrys aestivus* (Colubridae), and accepted then subsequently refused by a Woodhouse's toad, *Bufo woodhousei* (Bufonidae). Observations of avian predation are lacking, but are clearly required to better understand the breadth of protection against vertebrate predators afforded to *S. emarginata* by *Ptelea* consumption. Not surprisingly, *S. emarginata* nymphs from *Ptelea*-feeding populations are vulnerable to predation and are frequently attacked by invertebrate predators. I have seen nymphs taken in the field on many occasions by *Polistes* sp. wasps (Vespidae), assassin bugs (Reduviidae), and a number of different spiders. In the lab, *Ptelea*-fed *S. emarginata* nymphs were also readily consumed by a Carolina mantid, *Stagmomantis carolina* (Mantidae), and an unidentified wolf spider (Lycosidae). When the suite of potential *S. emarginata* predators is considered, these anecdotal observations suggest that *Ptelea*-mediated deterrence primarily acts as a defense against vertebrate as opposed to invertebrate predators. The possibility of *Ptelea*-feeding as a defense against parasitoids or pathogens remains unexplored.

Implications

So why might grasshoppers tend to regurgitate when disturbed? In contrast to most phytophagous insect groups, grasshoppers are considered to be polyphagous feeders (Chapman 1990; Chapman and Sword 1997). Grasshoppers often feed selectively on plants from multiple unrelated plant families and can be polyphagous as species, populations, and individuals. Hypotheses accounting for the prevalence of individual polyphagy in grasshoppers are reviewed in Bernays and Bright (1993), but the proximate result of individual polyphagy can often be a mixture of plants in the gut. Individuals whose gut contents are a mixture of toxic and non-toxic plants can still be deterrent to predators (Fig. 3) and survive attacks, which suggests that regurgitate can be deterrent despite dilution by non-toxic plant material. Grasshoppers will feed on a broad array of host plants including plants that are unsuitable for survival and development (Chapman and Sword 1994). Unsuitability may be due to nutritional deficiency or the presence of toxic plant secondary compounds. In the field, even grasshoppers with relatively specialized feeding habits will sample and take occasional meals on different host plants (Braker 1991; Chambers et al. 1996). Conversely, other species appear to need variety in their diet and frequently switch among plants (Bernays et al. 1992). In each of these instances, presence in the gut of plant material deterrent to predators could provide the grasshoppers with a simple, passive chemical defense. This is not to imply that diet mixing in grasshoppers is an anti-predator adaptation or that their gut contents will always be deterrent, but simply that deterrence can feasibly arise as a coincidental effect of dietary mixing. The timely regurgitation of potentially deterrent gut contents could serve as an opportunistic defense against either vertebrate or invertebrate predators and may spare a grasshopper's life.

Among phytophagous insects in general, passive gut content-mediated deterrence may be an important precursor to the evolution of sequestration of noxious plant secondary compounds as a predator defense. Host plant specificity in conjunction with gut content-mediated deterrence may facilitate the evolution of sequestration (Eisner 1970; Bowers 1990), although it should not be considered as a prerequisite (Jones et al. 1988, 1989).

Acknowledgements Special thanks to Sean McMahon, John Botti, and Steve Phelps for assisting with the lizard maintenance and observations. Larry Gilbert, Mike Singer, and Rich Patrock provided logistical support and critical comments. This project was funded by grants from the Orthopterists' Society Research Fund, Sigma Xi, and the Lorraine I. Stengl Endowment to the UT Department of Zoology.

References

Berenbaum MR (1991) Coumarins. In: Rosenthal GA, Berenbaum MR (eds) Herbivores, their interaction with plant secondary metabolites. Academic Press, San Diego, pp 221–250

Berenbaum MR (1995) Photoxicity of plant secondary metabolites: insect and mammalian perspectives. Arch Insect Biochem Physiol 29:119–134

Bernays EA, Bright KL (1993) Dietary mixing in grasshoppers: a review. Comp Biochem Physiol 104A:125–131

Bernays EA, Bright K, Howard JJ, Raubenheimer D, Champagne D (1992) Variety is the spice of life: frequent switching between foods in the polyphagous grasshopper *Taeniopoda eques* Burmeister (Orthoptera: Acrididae). Anim Behav 44:721–731

Blum MS (1981) Chemical defenses of arthropods. Academic Press, New York

Bowers MD (1990) Recycling plant natural products for insect defense. In: Evans DL, Schmidt JO (eds) Insect defense: adaptive mechanisms and strategies of prey and predators. State University of New York Press, New York, pp 353–386

Boyden TC (1976) Butterfly palatability and mimicry: experiments with *Ameiva* lizards. Evolution 30:73–81

Braker HE (1991) Natural history of a Neotropical gap-inhabiting grasshopper. Biotropica 23:41–50

Chambers P, Sword G, Angel JE, Behmer S, Bernays EA (1996) Foraging by generalist grasshoppers: two different strategies. Anim Behav 52:155–165

Chapman RF (1990) Food selection. In: Chapman RF, Joern A (eds) Biology of grasshoppers. Wiley, New York, pp 39–72

Chapman RF, Sword GA (1994) The relationship between plant acceptability and suitability for survival and development of the polyphagous grasshopper, *Schistocerca americana* (Orthoptera: Acrididae). J Insect Behav 7:411–431

Chapman RF, Sword GA (1997) Polyphagy in the Acridomorpha. In: Gangwere SK, Muralirangan MC, Muralirangan M (eds) Bionomics of grasshoppers, katydids and their kin. CAB, Wallingford, pp 183–195

Curasson G (1934) Sur le toxicité de la sécrétion buccale des Sauterelles. Bull Acad Vet Fr 17:337–382

Dreyer DL (1969) Coumarins and alkaloids of the genus *Ptelea*. Phytochemistry 8:1013–1020

Eisner T (1970) Chemical defense against predators in arthropods. In: Sondheimer E, Simeone JB (eds.) Chemical ecology. Academic Press, New York, pp 157–217

Eisner T, Johnessee JS, Carrel J, Hendry LB, Meinwald J (1974) Defensive use by an insect of a plant resin. Science 184: 996–999

Freeman MA (1967) Proteolytic enzymes of the crop fluid from *Locusta migratoria* L. Comp Biochem Physiol 20:1013–1015

Freeman MA (1968) Pharmacological properties of the regurgitated crop fluid of the African migratory locust, *Locusta migratoria* L. Comp Biochem Physiol 26:1041–1049

Gray AI, Waterman PG (1978) Coumarins in the Rutaceae. Phytochemistry 17:845–864

Hubbell TH (1960) The sibling species of the Alutacea group of the bird-locust genus *Schistocerca* (Orthoptera, Acrididae, Cyrtacanthacridinae). Misc Publ Mus Zool Univ Mich 116

Jones CG, Whitman DW, Silk PJ, Blum MS (1988) Diet breadth and insect chemical defenses: a generalist grasshopper and general hypotheses. In: Spencer KC (ed) Chemical mediation of coevolution. Academic Press, San Diego, pp 477–512

Jones CG, Whitman DW, Compton SJ, Silk PJ, Blum MS (1989) Reduction in diet breadth results in sequestration of plant chemicals and increases efficacy of chemical defense in a generalist grasshopper. J Chem Ecol 15:1811–1822

Knecht M, Hagenmaier HE, Zebe E (1974) The proteases in the gut of the locust, *Locusta migratoria*. J Insect Physiol 41: 461–470

Leslie AJ, Berenbaum MR (1990) Role of the osmeterial gland in swallowtail larvae (Papilionidae) in defense against an avian predator. J Lepid Soc 44:245–251

Lymbery A, Bailey W (1980) Regurgitation as a possible antipredator defensive mechanism in the grasshopper *Goniaea* sp. (Acrididae, Orthoptera). J Aust Entomol Soc 19:129–130

Malcom SB (1992) Prey defence and predator foraging. In: Crawley MJ (ed) Natural enemies. Blackwell, Oxford, pp 458–475

Morrow PA, Bellas TE, Eisner T. (1976) Eucalyptus oils in the defensive oral discharge of Australian sawfly larvae (Hymenoptera: Pergidae) Oecologia 24:193–206

Ortego F, Evans PH, Bowers WS (1997) Enteric and plant derived deterrents in regurgitate of the American bird grasshopper, *Schistocerca americana*. J Chem Ecol 23:1941–1950

Peterson SC, Johnson ND, LeGuyader JL (1987) Defensive regurgitation of allelochemicals derived from host cyanogenesis by eastern tent caterpillars. Ecology 68:1268–1272

Roughgarden J (1995) *Anolis* lizards of the Caribbean. Oxford University Press, Oxford

Steiner AL (1981) Anti-predator strategies. II. Grasshoppers (Orthoptera, Acrididae) attacked by *Prionyx parkeri* and some *Tachysphex* wasps (Hymenoptera, Sphecinae and Larrinae): a descriptive study. Psyche 88:1–24

Sudd JH, Franks, NR (1987) The behavioural ecology of ants. Chapman & Hall, New York

Sword GA (1999) Density-dependent warning coloration. Nature 397:217

Sword GA, Dopman EB (1999) Developmental specialization and geographic structure of host plant use in a polyphagous grasshopper, *Schistocerca emarginata* (=*lineata*) (Orthoptera: Acrididae). Oecologia 120:437–445

Sword GA, Simpson SJ, El Hadi OTM, Wilps H (2000) Density-dependent aposematism in the desert locust. Proc R Soc Lond B 267:63–68

Taber SW (1998) The world of the harvester ants. Texas A&M University Press, College Station

Waterman PG (1975) Alkaliods of the Rutaceae: their distribution and systematic significance. Biochem Syst Ecol 3:149–180

Whitman DW (1990) Grasshopper chemical communication. In: Chapman RF, Joern A (eds) The biology of grasshoppers. Wiley, New York, pp 357–391

Whitman DW, Blum MS, Alsop DW (1990) Allomones: chemicals for defense. In: Evans DL, Schmidt JO (eds) Insect defense: adaptive mechanisms and strategies of prey and predators. State University of New York Press, New York, pp 289–351