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Diet breadth and anti-predator strategies in desert locusts and other Orthopterans

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Abstract

A density-dependent change from a cryptic to an aposematic antipredator strategy has recently been suggested as a possible functional explanation for phase change in the desert locust (*Schistocerca gregaria* Forskål). Predators learn to avoid locusts that have fed on toxic plants faster when they are in the brightly colored gregarious phase than when they are green and solitary. We review recent work comparing acquisition of a defensive compound via food selection between solitary, transiens (solitary locusts in transition to the gregarious phase) and gregarious locusts. Lab experiments showed that solitary locusts were deterred at first contact with hyoscyamine, a plant compound that protects against predators, but later habituated to the compound and incorporated it into the diet (*albeit* at a low rate). By contrast, gregarious and transiens locusts fed readily on the compound. A computer simulation showed how low-density, solitary locusts would not benefit much from consuming the compound, because they escape predation by avoiding detection. However, for high-density transiens and gregarious locusts, for whom crypsis is no longer an option, acquiring toxicity dramatically decreases predation risk. A survey of the literature showed that solitary locusts exhibit a narrower diet breadth than gregarious locusts, suggesting that solitary locusts avoid defensive plant compounds, whereas gregarious locusts use a mix of compounds in the gut as a defence against predators. Gut-mediated antipredator defences might be more widespread among Orthopterans, especially brightly colored species, than has previously been realized. In particular, it remains to be investigated whether density-dependent aposematism and changes in food selection toward chemical defense, play a role in phase change in other locust species.

Introduction

Density-dependent phase change has evolved several times within the Acrididae and appears to be a successful adaptation for grasshoppers living in arid environments where resources are patchy and unpredictable in both space and time (Despland 2004). The selective advantages of phase polyphenism, and specifically of phase-related color change, have long interested researchers, and numerous hypotheses have been proposed, including intraspecific signalling to keep migrating hopper bands together, thermoregulatory benefits, or side-effects of a heightened immune response (Wilson 2000).

Recent work has suggested that locust phase change represents a shift from a cryptic to an aposematic antipredator strategy. Sword *et al.* (2000) have shown that lizard predators develop aversions to eating gregarious, but not solitary-phase, locusts, fed on the toxic plant Egyptian henbane (*Hyoscyamus muticus* L., Solanaceae). This rhizomatous plant is common throughout the Sahara and is one of the desert locust's favorite food plants (Popov *et al.* 1991). It contains tropane alkaloids that are highly toxic to vertebrates. Eating locusts that have fed on henbane causes illness in lizards, due

to the toxicity of the insect's gut contents. A lizard that has eaten a toxic black-and-yellow gregarious locust, will subsequently avoid gregarious locusts; but a lizard that has eaten a toxic green solitary locust will continue to eat solitary locusts (and to get sick). Thus, lizards learn to associate unpleasant experiences with the striking coloration of gregarious locusts, but not with the inconspicuous green of solitary locusts. The change from solitary to gregarious behavior is also consistent with this explanation, since aposematic theory shows that aggregative behavior increases the efficiency of warning coloration in deterring predators (Despland & Simpson 2005a).

Foraging behavior is another trait that has recently been shown to vary between the cryptic solitary and the aposematic gregarious phase (Despland & Simpson 2005a). This is also expected from aposematic theory, since locusts acquire defensive compounds from their diet. Although locusts have well-developed gut barriers to plant secondary compounds (Bernays & Chapman 2000), consuming these compounds, even those from well-accepted host plants, can be costly (Mainguet *et al.* 2000). Solitary locusts are therefore expected to avoid consuming plant secondary metabolites. Aposematic theory predicts that conspicuously colored prey would benefit more from consuming toxic plants than would cryptic individuals, because the former can use their coloration to advertise toxicity. Gregarious locusts are therefore expected to feed more readily on toxic plant compounds and to exhibit a wider diet breadth than solitary locusts. Transiens locusts, despite their coloration, are easily detected by predators because of their high population density. They are therefore expected to exhibit feeding behavior similar to that of gregarious locusts.

The present paper reviews recent work comparing food selection and diet breadth between solitary, transiens and gregarious locusts. First, data from laboratory experiments (Despland & Simpson 2005a) and a computer simulation (Despland & Simpson 2005b) show how feeding behavior changes during locust phase transition. Second, a review of the literature compares diet breadth in the field between solitary and gregarious locust populations. Finally, the implications of these findings in terms of antipredator strategies for both locusts and nonlocust orthopterans are considered.

Feeding behavior in desert locust phase change

Laboratory experiments.—Laboratory experiments conducted by Despland & Simpson (2005a) investigated the responses of locust nymphs, at different stages in the phase transformation process, to a plant defensive compound. As already mentioned, hyoscyamine

is a tropane alkaloid from Egyptian henbane, *H. muticus*, a plant consumed by both solitary and gregarious locusts in the field. [Henbane has a feeding index of 3, see Fig. 3 (Popov *et al.* 1991).] Hyoscyamine is highly toxic to vertebrates (Harborne *et al.* 1999) and protects locusts against predation (Sword *et al.* 2000). Gregarious and solitary-phase 4th instar nymphs were obtained by rearing locusts at high density and in isolation, respectively (Roessingh *et al.* 1993). Hyoscyamine was added to a standard chemically-defined artificial diet that supports locust development (Simpson & Abisgold 1985), at concentrations similar to those found in henbane.

The first experiment measured relative consumption of control food and food containing 2% dry weight hyoscyamine. Isolated-reared locusts were tested in isolation in small individual arenas (solitary phenotype). For the transiens and gregarious phenotypes, isolated-reared and crowd-reared nymphs were tested in groups in a larger arena. Insects were provided with a choice between a plain food and a food containing hyoscyamine [see Despland & Simpson (2005a) for further details of the experiment].

Paired t-tests were used to compare consumption of plain vs

hyoscyamine-containing food, for each phenotype (Fig. 1A). The solitary locusts discriminated against the alkaloid-containing food ($t_{14} = -2.73$, $p = 0.02$). Transiens locusts preferred the hyoscyamine-containing food ($t_8 = 2.3$, $p = 0.03$). Gregarious nymphs fed equally on both food types ($t_8 = 1.8$, $p = 0.08$).

The second experiment measured locust taste responses to hyoscyamine at first contact with this alkaloid. The most sensitive measure of a food's palatability is the duration of the first meal, since this is not confounded by post-ingestive feedbacks (Simpson & Raubenheimer 2000). Single isolated-reared locusts (solitary phenotype), grouped isolated-reared locusts (transiens phenotype) or grouped crowd-reared locusts (gregarious phenotype) were observed on either control or hyoscyamine-containing food. The mean duration of the first feeding bout was compared between treatments (see Despland & Simpson (2005a) for further details of the experiment).

For each of the 3 phenotypes, responses to the 2 food sources were compared using t-tests (Fig. 1B): solitary nymphs exhibited shorter feeding bouts at first contact with hyoscyamine-containing

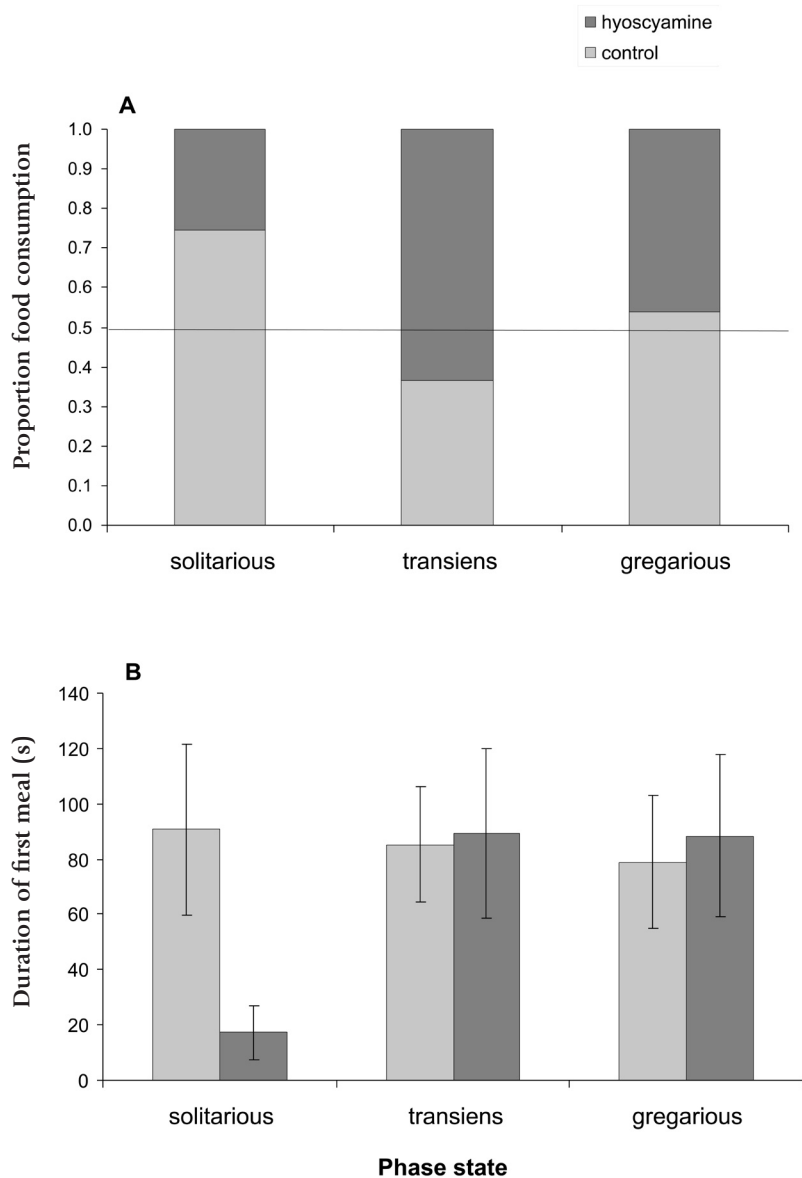


Fig. 1. A. From the first experiment, proportion of total food consumption from the hyoscyamine-containing food. The horizontal line represents the expectation if the locusts were not responding to the alkaloid and were feeding randomly from the 2 sources presented to them. **B.** From the second experiment, taste responses (indicated by the duration of the first meal) at first contact with control and hyoscyamine-containing foods. Data redrawn from Despland & Simpson (2005a).

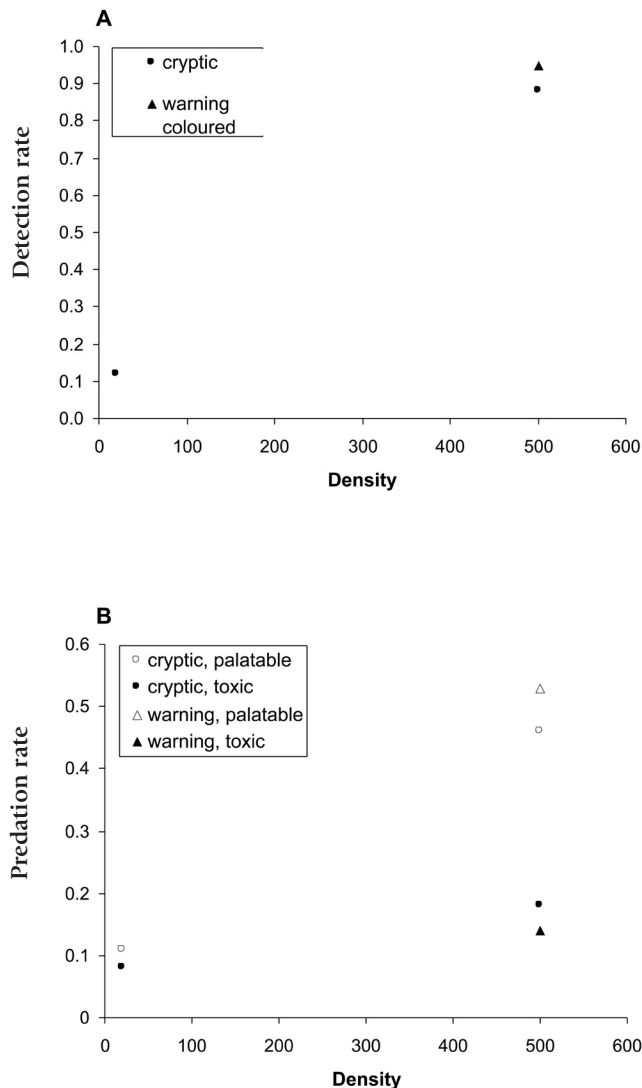


Fig. 2. Simulation output showing: **A.** the relationship between locust density and detection rate, for cryptic and warningly colored locusts; **B.** predation rate (*i.e.*, detection rate * consumption rate) for locusts with and without toxicity to predators. In both **A** and **B**, data are shown for cryptic locusts at low density (representing the solitary phenotype), cryptic locusts at high density (representing the transiens phenotype) and for warningly colored locusts at high density (representing the gregarious phenotype). Data redrawn from Despland & Simpson (2005b).

food than with control food ($t_{18} = 2.49$, $p = 0.02$). The responses of transiens and gregarious locusts did not differ between the 2 food types ($t_{21} = 0.60$, $p = 0.56$ and $t_{18} = 0.58$, $p = 0.57$ respectively).

Computer simulation.—Despland & Simpson (2005b) then built a computer simulation to investigate the role of toxicity in protecting solitary, transiens and gregarious locusts against predators. The simulation used a bounded two-dimensional environment in which model locusts and model predators were placed at random, and moved according to rules based on the observation of real locusts under both laboratory and field conditions (Roessingh *et al.* 1993,

Simpson *et al.* 1999, Despland 2001). Locust phenotype was defined in terms of color (cryptic vs warningly), palatability to predators (palatable vs toxic) and behaviour (quiet vs swarming). These traits were modelled as follows: locust color and behavior affected the distance at which the locust was detected by predators; locust color and palatability influenced the probability that the locust was consumed once detected. Predators detected immobile locusts from a greater distance if they were warningly colored than if they were cryptic. Moving locusts were detected from farther away than immobile locusts. A predator detecting a green palatable locust almost always consumed it (consumption rate, $C = 0.9$), whereas a cryptic toxic locust was less likely to be eaten ($C = 0.6$) and a warningly toxic locust even less so ($C = 0.4$). These values for consumption rate are conservative, because previous research has shown that experienced predators consume aposematic toxic locusts 40% of the time (Sword *et al.* 2000) and that adding toxic regurgitate to an acceptable cryptic prey item decreases consumption rate from 87% to 7% (Sword 2001).

Predators did not satiate or learn about prey profitability: all predators in the simulation were therefore naive. The confounding effects of predator learning are excluded from the simulation because the first aposematic animals to appear would not benefit from learned aversions in predators.

Density and phenotype of locusts in the simulated arena were varied to investigate first, the effects of locust coloration on predator detection at different population densities, and second, the effects of toxicity on predation rates for the solitary (low-density, cryptic, quiet), transiens (high-density, cryptic, swarming) and gregarious (high-density, warningly-colored, swarming) phenotypes. The model was written in Matlab Version 12 (see Despland & Simpson (2005b) for further details of the model).

The simulation showed that cryptically colored locusts had a low probability of being detected by predators at low population density, but this detection rate increased dramatically with population density (Fig. 2A). Thus crypsis ceased to be an effective antipredator strategy when population density increased. At high population density, the predator detection rate was similar, regardless of locust coloration (Fig. 2A). Fig. 2B shows that for the solitary phenotype (low density, cryptic coloration), acquiring toxicity to predators did not much alter predation rate—because these insects were cryptic and avoided predation by avoiding detection. However, for both transiens (high-density cryptically-colored) and gregarious (high-density warningly-colored) locusts, toxicity dramatically decreased predation risk—because it decreased consumption rate.

Conclusions on feeding behaviour and desert locust phase change.—Solitary locusts were repelled by the taste of the hyoscyamine food (Fig. 1B), but over a longer time period they nonetheless consumed an average of 37% of their food intake from the alkaloid-containing food (Fig. 1A), suggesting that they do not remain deterred by hyoscyamine. Indeed, desert locusts possess selective mechanisms for overcoming aversion to harmless compounds, mediated by habituation in the central nervous system (Bernays & Chapman 2000). Habituation to hyoscyamine has been demonstrated in the congeneric *Schistocerca americana*: this grasshopper rejects hyoscyamine-containing food at first contact, but after a brief period of exposure it consumes hyoscyamine-containing food as readily as plain food in no-choice tests (Glendinning & Gonzales 1995).

A laboratory feeding assay failed to detect significant costs to consuming hyoscyamine (Despland & Simpson 2005a). Hyoscyamine is a tropane alkaloid that binds with muscarinic acetylcholine

receptors. As such, it is highly toxic to vertebrates (Christie & Osborne 1999). Muscarinic acetylcholine receptors are found at low density in the insect central nervous system. These are related to, but distinct from, vertebrate receptors, and show similar affinities for antagonists, including tropane alkaloids (Trimmer 1995). Hyoscyamine is a deterrent at sublethal doses to some insects (Detzel & Wink 1993, Glendinning & Gonzales 1995, Shonle & Bergelson 2000), and is toxic to some specialist lepidopterans (*Heliothis virescens*, T. Morton pers. comm.), but not to other more generalist species [*Helicoverpa zea*, T. Morton pers. comm.; *Spodoptera littoralis* (Krug & Proksch 1993)].

The inability to detect costs associated with consuming hyoscyamine, combined with the occurrence of habituation, suggest that any such costs are slight. However, that does not necessarily mean that they are non-existent. Many of the plants that desert locusts consume in the field contain secondary metabolites that are phagodeterrent or even toxic to locusts under laboratory conditions (el Hadj 1997, Louveaux *et al.* 1998, Mainguet *et al.* 2000). For instance, *Schouwia purpurea* (Brassicaceae), one of the locust's most widely used host plants, contains very high levels of glucosinolates (Ghaout *et al.* 1991, El Sayed *et al.* 1996). When the plant tissue is crushed (*e.g.*, by locust mandibles) these compounds form breakdown products that are phagodeterrent to locusts at natural concentrations (El Sayed *et al.* 1996). Feeding on these compounds triggers the production of specific detoxifying enzymes in the midgut, similar to those found in specialist crucifer feeders (Mainguet *et al.* 2000). The locust can thus habituate to consuming this plant, but is nonetheless experiencing a cost associated with the production of detoxifying enzymes.

Although solitary locusts discriminated against the hyoscyamine-containing food, gregarious and transiens locusts readily accepted this food (Fig. 1A, B). Gregarious locusts that consume hyoscyamine are protected against predation, because predators associate the bright black-and-yellow coloration with a distasteful meal (Sword *et al.* 2000). Transiens locusts do not have this warning coloration, but they still receive some protection from consuming toxic foods, because predators can learn to associate the smell of locusts that have consumed hyoscyamine with an unpalatable meal (Sword *et al.* 2000) and because predators often quickly release prey that disgorge toxic regurgitate (Sword 2001). Why then do solitary locusts not also take advantage of this protection?

The computer simulation demonstrates how chemical defense dramatically decreases the predation risk for gregarious and transiens locusts, but does not much benefit solitary locusts (Fig. 2B). Indeed, solitary locusts avoid predation by avoiding detection, and hence the question of palatability does not even arise. This strategy becomes ineffective at high population density, when locusts are conspicuous to predators regardless of coloration (Fig. 2A). In this situation, locusts avoid predation by acquiring defensive chemicals from plants. High-density transiens locusts benefit further from switching to warning coloration that provides a stronger signal of their toxicity to predators (Despland & Simpson 2005b). Density-dependent changes in food selection thus represent a form of induced defence that is activated by the rise in predation risk that occurs when local density increases.

Diet breadth of solitary and gregarious desert locusts

Desert locusts are highly polyphagous but are nonetheless selective feeders. Indeed, locusts have remarkable abilities to regulate their food intake according to their needs (Simpson & Raubenheimer 2000). Fig. 3 demonstrates locust selective feeding on potential host

plants: among 285 native plants recorded in the Western region of the desert locust recession area, outside of outbreak periods, feeding is focussed on 28 main species (Popov *et al.* 1991). Across the entire distribution range of 400 available plant species, 127 were recorded as acceptable to the desert locust, 32 as partly palatable and 41 as never consumed (Uvarov 1977).

In the desert locust's arid habitat, most plants are chemically defended. The findings above suggest that solitary locusts should feed more selectively than gregarious locusts, avoiding novel, and potentially costly, secondary compounds. They are therefore expected to exhibit a more narrow diet breadth.

The feeding behavior of solitary locusts has received little attention; however, those studies that have compared plant use between gregarious- and solitary-phase locusts, show that solitary locusts are more specialized and exhibit a narrower diet breadth (see Table 1 and references therein). In addition, specific associations with certain host plants are documented for solitary, but not for gregarious, locusts: *e.g.*, with *Heliotropium bacciferum* (Boraginaceae) on the Red Sea coastal plain of the Sudan (Bashir *et al.* 2000, Woldewahid 2003) and *Tribulus terrestris* (Zygophyllaceae) in Mauritania (Louveaux *et al.* 1998). Within the recession area, solitary locusts are found in a more limited number of plant communities than gregarious bands (El-Bashir 1996, Popov 1997). They also show stronger discrimination between different plant species (Latchininski & Launois-Luong 1997). Solitary locusts exhibit other traits typical of more specialized feeders such as a lower number of chemosensilla (Ochieng' *et al.* 1998), a higher efficiency of conversion of consumed food (Eid *et al.* 1996) and less flexible nutrient regulation (Simpson *et al.* 2002).

Together, these observations show that solitary locusts exhibit a more narrow diet breadth than their gregarious counterparts, suggesting that the differences we observed in responses to a single plant compound are more general. Solitary locusts would thus exhibit a more discriminating feeding strategy, choosing to feed mainly on plants whose chemistry is less costly to metabolise. Gregarious locusts, like other aposematic polyphagous grasshoppers, feed on a wide range of plants and acquire toxicity to predators via a gut filled with a mix of plant defensive compounds (Despland & Simpson 2005a). Transiens locusts appear to exhibit the wide diet breadth of gregarious locusts (Popov *et al.* 1991), consistent with their need for chemical defenses against predation.

Diet breadth and antipredator strategies in other Orthopterans

Modern Orthopterans are thought to have evolved from polyphagous ancestors endowed with the ability to tolerate many plant secondary compounds and, as a result, have behavioral, anatomical and physiological adaptations to deal with plant secondary metabolites (Bernays & Chapman 2000). Orthopterans exhibit various combinations of feeding ecologies (polyphagous, grass-feeders and specialists on toxic plants) and antipredator strategies (crypsis, constitutive aposematism and density-dependent aposematism). Recent research has identified the links between food selection and antipredator strategies for several species, and has highlighted further questions to be addressed in this area.

Many orthopterans exhibit dramatic bright coloration. Some brightly colored grasshoppers are clearly aposematic (*e.g.*, *Zonocerus variegatus*, *Romalea guttata*, *Taeniopoda eques*) and their coloration warns predators of their distasteful or toxic nature. In many of these aposematic grasshoppers, toxicity to predators is obtained from

Table 1. Diet breadth of solitary and gregarious locusts in different parts of the species recession range. Each column shows the number of plant species in various families used by solitary and gregarious locusts within a study area. Data were taken from studies cited by name of first author only and date. Numbers indicate plant use; actual feeding, rather than simply perching on a plant, was not observed in all cases.

Source	Latchininsky 1997		Culmsee 1997		El-Bashir 1996		Popov 1997		Bashir 2000		Popov 1997		Woldewahid 2003	
Site	Central Asia		Mauritania		Red Sea Coast		W. Sahel		Sudan coast		Red Sea coast		Red Sea coast	
Phase	Sol.	Greg.	Sol.	Greg.	Sol.	Greg.	Sol.	Greg.	Sol.	Greg.	Sol.	Greg.	Sol.	Greg.
<i>Aizoaceae</i>				1				2						
<i>Amaranthaceae</i>	1	1		1						2		1		
<i>Asclepiadaceae</i>								1						
<i>Asteraceae</i>		1												
<i>Boraginaceae</i>				1	1	1	2		1	1		1	1	1
<i>Brassicaceae</i>				2							1			
<i>Caesalpinaceae</i>										1		1		
<i>Capparidaceae</i>				1		1		1				1		
<i>Chenopodiaceae</i>	1	2												
<i>Convolvulaceae</i>		1												
<i>Cucurbitaceae</i>		1		1							1			
<i>Eleagnaceae</i>		1												
<i>Euphorbiaceae</i>		1		3										
<i>Fabaceae</i>	2	3		1			3		1		1			1
<i>Malvaceae</i>				2										
<i>Molluginaceae</i>				1										
<i>Nyctaginaceae</i>				1				1						
<i>Poaceae</i>		2		6		1		7	1	2				2
<i>Polygonaceae</i>		1		1										
<i>Portulacaceae</i>		1												
<i>Rosaceae</i>				1										
<i>Rutaceae</i>		1												
<i>Solanaceae</i>	1	1	1									2		
<i>Tamaricaceae</i>		1												
<i>Zygophyllaceae</i>	1	1		4	1	1	1	2	1	2	1			
Total	6	19	1	27	2	4	3	17	3	9	3	7	1	4

feeding on toxic plants (Chambers *et al.* 1996, Hatle & Faragher 1998, Bernays & Chapman 2000, Fletcher *et al.* 2000). However, the feeding ecology of aposematic grasshoppers varies: some species, like *Petasida ephippiger*, specialise on particular toxic plants (Fletcher *et al.* 2000), and may either sequester compounds from their host plant in the body, or simply acquire toxicity from the presence of these compounds in the gut. Other aposematic grasshoppers, like *T. eques*, are generalists and acquire toxicity from a mix of plant compounds in the gut (Chambers *et al.* 1996). This last strategy most closely resembles that observed in gregarious locusts (Despland & Simpson 2005a).

Many other grasshoppers are brightly colored, but have not been demonstrated to be distasteful or toxic to predators. If, however, antipredator defense depends on gut contents, it might not have been detected in studies that were not explicitly designed to control for previous feeding experience. For instance, in *Schistocerca lineata* [taxonomy according to Song (2004); previously termed *S. emarginata*], populations that feed on toxic plants are distasteful to predators, whereas grasshoppers from other populations are readily consumed by predators (Sword 1999). Although the species is considered polyphagous, individual nymphs feed almost

exclusively on single plant species; variation in foraging behavior between populations is genetically controlled (Sword & Dopman 1999, Dopman *et al.* 2002). Gut-mediated chemical defense might therefore be more widespread, particularly among brightly colored grasshoppers, than is currently thought to be the case.

Density-dependent aposematism (*i.e.*, a switch from crypsis to aposematism with increasing population density) has been shown not only in the desert locust, but also in the closely related *S. lineata*. This species is not a locust, in that it does not exhibit density-dependent behavioral phase change. In *S. lineata*, density-dependent color change is only observed in a population that specializes on a toxic plant (Sword 1999, 2002): these grasshoppers are therefore always toxic, but they only acquire warning coloration at high population density.

Could density-dependent aposematism also explain phase change in other locust species? There is, as yet, insufficient evidence to provide a meaningful answer to this question. The suite of traits involved in phase change differs between locust species [*e.g.*, solitary adults larger than gregarious in *S. gregaria* and *Locusta migratoria*, but smaller in *Locustana pardalina* (Uvarov 1977)], suggesting that the selection pressures responsible for shaping density-

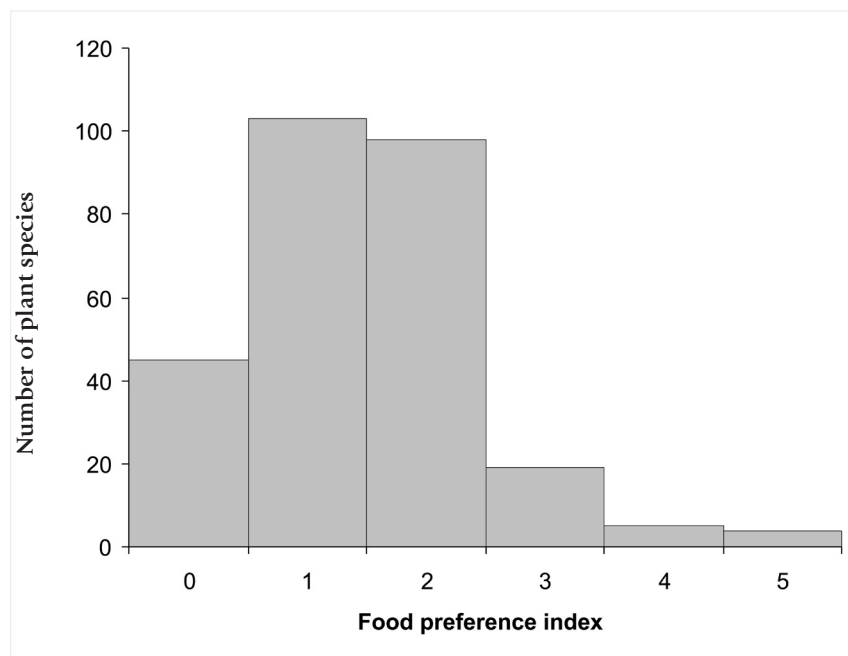


Fig. 3. Food selection behaviour of locusts in the Western area of their recession distribution range (the Sahara and Sahel zones West of Egypt). Food preference index is shown for 285 potential host plants, where 0 indicates that the plant is never eaten and 5 indicates that the plant is very frequently eaten. Data redrawn from Popov *et al.* (1991).

dependent polyphenism differ between species. Feeding ecology also differs between locust species: *L. migratoria*, for instance, is a grass specialist, and therefore the range of plant secondary metabolites available for chemical defense is less than for *S. gregaria*. However, some grasses, like *Cynodon dactylon*, are cyanogenic and could thus confer antipredator chemical defense (Wilson 2000). Solitary *L. migratoria*, like solitary *S. gregaria*, exhibit fewer chemical sensilla than their gregarious counterparts (Greenwood & Chapman 1984) and appear to have a narrower diet breadth. However, there is no *a priori* reason to expect the same adaptive function of phase change in different locust species, given that they represent independent evolutionary events.

Gut-mediated antipredator defense acquired by feeding on toxic plants appears to be an important factor in the feeding ecology of several orthopteran species, and warrants further investigation. In particular, it might provide an explanation for the bright coloration of species that do not appear to exhibit aposematism based on sequestration. Furthermore, density-dependent aposematism has so far been demonstrated in one polyphagous locust and one specialist non-locust orthopteran (Sword 1999, Sword *et al.* 2000). It remains to be seen whether density-dependent aposematism also plays a role in phase change in other locust species, and whether it is accompanied by a change in food selection toward consuming more defensive plant compounds.

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