

Surviving the change to warning colouration: density-dependent polyphenism suggests a route for the evolution of aposematism

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Summary. How warning colouration first appeared remains a disputed question in evolutionary biology. A density-dependent transition from crypsis to aposematism that occurs during phase change in the desert locust (*Schistocerca gregaria*) provides insight into the conditions under which acquiring warning colouration is adaptive. When crowded for only a few hours, solitary locusts cease avoiding each other and actively aggregate. This occurs well before they acquire warning colouration. We show that accompanying this early behavioural gregarisation is a remarkable shift in feeding behaviour, in which solitary insects switch from being deterred by a toxic plant alkaloid to feeding avidly upon foods containing it. A computer simulation shows how crypsis ceases to be effective as an anti-predator strategy when solitary locusts are crowded, how chemical defence becomes essential as conspicuousness increases with local density, and how warning colouration becomes advantageous under these conditions. These findings provide empirical evidence for an adaptive route for the change from a cryptic edible phenotype to a brightly coloured toxic one.

Key words. *Schistocerca gregaria* – phase polymorphism – induced defences – anti-predator strategies – phenotypic plasticity – individual-based modelling.

Introduction

Charles Darwin was puzzled by the bright colouration of many immature insects and put the question to Alfred Russell Wallace in a letter. In his reply, Wallace suggested that the colouration could be a signal to advertise toxicity (Marchant 1975). Since then, the functional role of warning colouration has been well demonstrated (Guilford 1990). However, the route by which aposematism evolved still poses an enigma (Lindström 1999; Lindström *et al.* 1999; Mallet & Joron 1999; Brodie & Agrawal 2001; Sherratt 2002; Speed & Ruxton 2002; Santos *et al.* 2003). The first

brightly coloured individual in a population is likely to be detected by a predator and is therefore at greater risk than are its cryptic neighbours. What then are the conditions under which switching from inconspicuous to showy colouration confers a survival advantage?

Locusts and certain grasshoppers change from a green solitary phase to a brightly patterned gregarious phase in response to increased population density (Uvarov 1977). In these species, the transition from crypsis to aposematism occurs within the lifespan of an individual rather than over evolutionary time (Sword 1999; Sword *et al.* 2000; Despland & Simpson 2005). Since the same individual can switch from one phenotype to the other during its development, the phenotypes can be compared without the confounding effects of different genotypes. Density-dependent phenotypic plasticity in colouration is common among insects (Applebaum & Heifetz 1999) and could be an evolutionary precursor to constitutive aposematism: because plasticity per se is variable and subject to natural selection, density-dependent colour change could lead to constitutive expression of warning colouration via reaction norm evolution (Schlichting & Pigliucci 1998; Sword 2002). Locust phase change, unlike evolutionary processes, can be observed in the laboratory; density-dependent phase polyphenism therefore permits empirical investigation of the process of change from a cryptic to an aposematic phenotype, and of the conditions under which it occurs.

At low population density, desert locusts (*Schistocerca gregaria*, Forskål (Orthoptera: Acrididae)) are solitary, cryptic and timid, but when density increases, they switch to the aposematic, black-and-yellow, swarming gregarious phase. When crowded, solitary locusts begin behaving gregariously within hours, but colour change can only occur during the moult to the next nymphal stadium (Roessingh & Simpson 1994). Phase change therefore includes a transitional period of several days, in which the locust behaves gregariously, but retains the cryptic solitary colour. Solitary locusts in transition to the gregarious phase, henceforth termed transiens locusts, are aggregated and very active, and are therefore conspicuous to predators despite their cryptic colouration (Pitt & Ritchie 2002).

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We hypothesise that, for locusts, increased predator detection risk at high population density provides the conditions under which switching to aposematism is adaptive, and that the first step in this transition is a change in feeding behaviour leading to chemical defense. Although they have no capacity to sequester or synthesise toxins, desert locusts are protected against predation if toxic compounds from host plants are present in the gut (Sword *et al.* 2000). Chemical defence is therefore under behavioural control, as the insect chooses which plants to consume. Chemical defense provides some protection to locusts regardless of their colouration, because predators sometimes release locusts that disgorge toxic regurgitate (Sword 2001). However, predators learn to avoid toxic locusts faster when they are black-and-yellow than when they are cryptically coloured (Sword *et al.* 2000). In addition, many naïve predators avoid novel brightly coloured prey (Lindström *et al.* 1999; Lindström *et al.* 2001). Therefore, conspicuous transiens locusts would profit from acquiring toxicity, and would benefit further from switching to warning colouration, even in a situation where all predators are naïve.

In order to test the hypothesis outlined above, we conducted a laboratory experiment to determine whether solitary, gregarious and transiens locusts regulate chemical defence behaviourally. We predict that gregarious and transiens locusts will feed more readily on a toxic compound than do solitary individuals. We also built a simple computer simulation that formalizes the verbal hypothesis to examine how phase-related changes in colouration and chemical defence can influence predation risk for solitary, gregarious and transiens phenotypes at different population sizes.

Taste experiment: Materials and methods

We investigated the taste responses of locust nymphs at different stages in the phase transformation process to hyoscyamine, a tropane alkaloid from a plant *Hyoscyamus muticus* L. (Solanaceae) consumed by both solitary and gregarious locusts in the field (Popov *et al.* 1991; Culmsee 2002). Hyoscyamine is highly toxic to vertebrates (Harborne *et al.* 1999) and protects locusts against predation (Sword *et al.* 2000).

The most sensitive measure of a food's palatability is the probability of commencing a meal at first contact, since this is not confounded by post-ingestive feedbacks (Simpson & Raubenheimer 2000). We therefore conducted short-term behavioural observations of locusts' responses to synthetic foods, either plain or containing hyoscyamine. Chemically defined artificial foods were standard cellulose-based preparations (Simpson & Abisgold 1985), formulated on the basis of previous work to be nutritionally balanced (Simpson *et al.* 2002). Foods contained equal amounts of protein and digestible carbohydrate (21% of each). *L*-hyoscyamine (free base, Sigma-Aldrich Inc.) was dissolved in ethanol and added to the diet at 2% dry weight, which is similar to the concentration found in *Hyoscyamus muticus* (El-Shazly *et al.* 1997).

Gregarious- and solitary-phase insects were obtained by rearing locusts at high density and in isolation, respectively (Roessingh *et al.* 1993). Fourth instar nymphs were removed from the culture on the day of the moult, maintained at rearing densities and fed plain synthetic food for 2 days prior to the experiment.

Nymphs were then marked with a spot of poster paint on the pronotum: this distinguished the focal individual from the stimulus insects in the crowded treatments (see below).

For the experiment, each insect was transferred to a clear plastic box (17 × 11 × 7 cm) with a water bottle and a single food dish containing either the control or the alkaloid-containing food. Each insect's behaviour was observed for a period of 4 h, recording every 10 s whether the insect was quiescent, walking, in contact with the food, or feeding. From these data, we calculated the following variables for each treatment: the frequency of meal initiation at first contact with the food (a meal was defined as a feeding bout lasting more than 50 s, based on detailed analyses of feeding bout distributions in previous experiments (Simpson & Raubenheimer 2000)), the mean duration of the first feeding bout (defined as the time up to the first non-feeding gap > 4 min (Simpson & Raubenheimer 2000)), the mean amount of food eaten and the mean proportion of the trial time spent feeding. Each individual was only tested once, with one of the two food types.

We compared taste responses between plain and alkaloid containing food for locusts at different stages in the transition from nymphs to aposematism. Ten to 12 replicates of the following treatments were tested with each of the two experimental foods: a) gregarious insects pre-treated for 4 h in a group (i.e., with five gregarious nymphs) and tested in a group – this treatment represented the baseline gregarious phase; b) gregarious insects pre-treated in a group and tested alone – this treatment was included to control for possible effects of crowding during the test; c) solitary nymphs pre-treated alone and tested alone – this treatment represented the baseline solitary phase; d) solitary nymphs pre-treated alone and tested in a group; e) solitary nymphs pre-treated in a group (i.e., with five gregarious nymphs) and tested alone. The solitary locusts in treatments d) and e) had begun to gregarise due to contact with other locusts (Roessingh & Simpson 1994) – they are therefore in the transiens phase. Recordings of activity level during the test show that the insects in treatments d) and e) were behaving like gregarious, not like solitary, locusts. Phenotype treatments were specifically chosen to test for effects of phase state while controlling for possible effects of crowding during the test.

The three measures of readiness to feed which met the assumption of ANOVA (duration of first feeding bout, proportion of assay time spent feeding and total amount of food eaten) were combined in multiple analyses of variance to test for overall differences in behaviour between the phenotype treatments. Differences between responses to plain and alkaloid-containing food were then examined using *t*-tests for the three above variables and a χ^2 test for the proportion of insects initiating a meal.

Results

The MANOVAs show that phenotype did not influence behaviour of the insects on control food (Wilk's λ : multivariate $F_{12,111} = 1.71$; $P = 0.07$) but that it did affect feeding on hyoscyamine containing food (Wilk's λ : multivariate $F_{12,127} = 4.62$; $P < 0.001$). *T*-tests comparing responses to the two food types for each of the phenotype treatments showed that solitary nymphs tested alone had shorter first feeding bouts, ate smaller amounts and spent less of the total assay time feeding on hyoscyamine containing food than they did on plain food ($t_{18} = 2.49$, $p = 0.02$, $t_{18} = 4.07$, $p = 0.01$ and $t_{18} = 3.45$, $p = 0.003$ respectively). No significant differences between food types were observed for the other phenotype treatments (see Fig. 1).

Similar results were found for the probability of meal initiation: solitary-phase locusts tested alone consumed the plain food but were deterred at first contact with the hyoscyamine-containing food (Pearson's $\chi^2_1 = 3.88$, $p = 0.04$). Gregarious-phase locusts initiated meals as readily

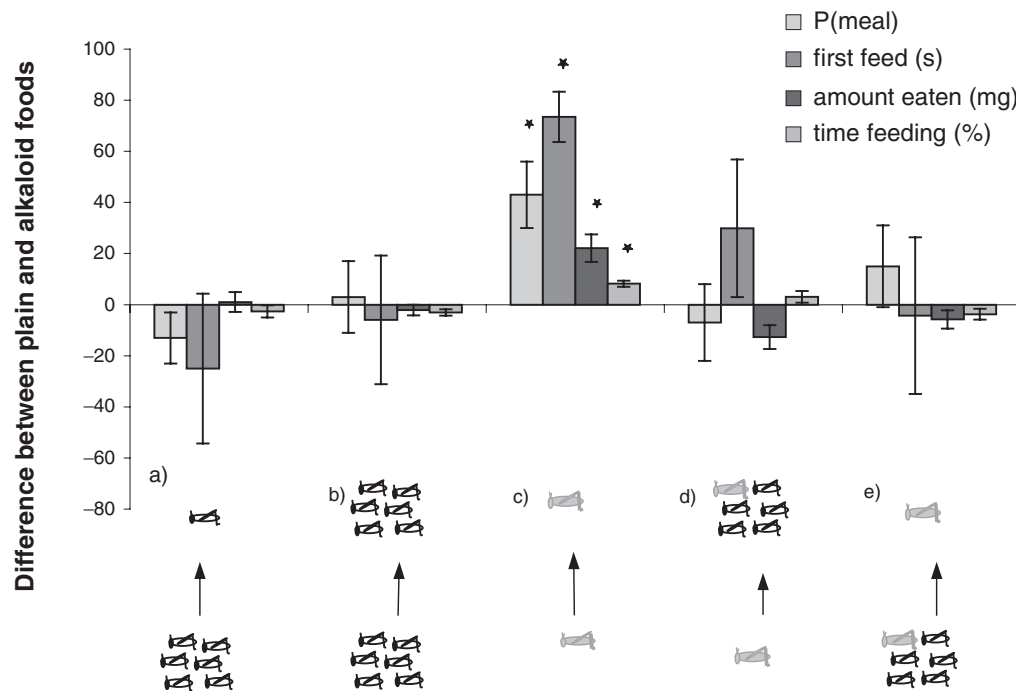


Fig. 1 Bars indicate differences between locust feeding behaviour on plain food vs that on hyoscyamine-containing food. The variables are: frequency of meal initiation at first contact with the food (in %), mean duration of the first feeding bout (in s), total amount of food eaten during the trial (in mg) and mean proportion of assay time spent feeding (in %). Icons on the x-axis depict locust phenotype treatments as explained in the methods section. Error bars are standard errors. Stars indicate significant results in the t-test comparing the two food types (i.e., difference between foods is non-zero)

on the hyoscyamine-containing food as they did on the plain food, whether tested alone (Pearson's $\chi^2_1 = 0.61$, $p = 0.44$) or in a group (Pearson's $\chi^2_1 = 0.34$, $p = 0.55$). The two transiens treatments fed readily on the alkaloid food – Pearson's $\chi^2_1 = 0$, $p = 1$ and Pearson's $\chi^2_1 = 0.40$, $p = 0.53$, respectively.

Computer simulation: Methods

The computer simulation used a bounded two-dimensional environment (1000 × 1000 grid) 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 (Simpson *et al.* 1999). Model locusts were characterized by colour (cryptic vs conspicuous), palatability to predators (palatable vs toxic) and behaviour (quiet vs swarming). Locust behaviour was defined by the probability of spontaneous movement per time step (0.05 for quiet, 0.1 for swarming locusts), the distance moved per time step (locusts move in a straight line, distance is random but bounded by the following maxima: 2 for quiet and 16 for swarming locusts), and response to neighbours. Locusts responded to the movement of their nearest neighbour if it was closer than 64 units: quiet locusts jumped in an escape response (distance < 64), whereas a swarming locust followed the movement walking normally (i.e., distance < 16). This behaviour led to aggregation of swarming locusts. Parameter values for locust movement were calculated from data showing that gregarious locusts are twice as likely to spontaneously begin walking than are solitary locusts and walk eight times farther (Roessingh *et al.* 1993), and that solitary locusts show stronger responses to stimuli from conspecifics than do gregarious locusts (Despland 2001).

Combinations of these three traits defined the solitary, gregarious and transiens phenotypes, based on previous research and on the results of the taste experiment above. Solitary locusts were cryptic, quiet and palatable, gregarious locusts were conspicuous, swarming and toxic, and transiens locusts were cryptic, swarming and toxic.

Locust colour and movement affected the distance at which predators detected locusts; locust colour and palatability influenced the probability that the locust was consumed once detected. Differences in consumption rate were based on previous research showing that lizards often release locusts with toxic regurgitate (Sword 2001) and that many naïve predators avoid novel conspicuous prey (Lindström *et al.* 1999; Lindström *et al.* 2001). The parameter values for predator detection and consumption were varied through the ranges indicated below and the model was found to be robust. Predators detected immobile locusts from a greater distance if they were conspicuously coloured ($L = 4$, range 16–32) than if they were cryptic ($L = 4$, range 2–8). Moving locusts were detected from farther away than immobile locusts ($L = 48$ regardless of colour, range 32–64). A predator detecting a green palatable locust almost always consumed it (consumption rate, $C = 0.9$, range 0.8–0.99), whereas a green toxic locust was less likely to be eaten ($C = 0.6$, range 0.5–0.8) and a conspicuous toxic locust even less so ($C = 0.4$, range 0.3–0.5). 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 accepted prey item decreases consumption rate from 87 % to 7 % (Sword 2001). If a predator did not detect a locust during a given time step, it moved at random; the distance travelled per time step by a predator was greater than that travelled by a locust (distance < 256). Predators did not satiate or learn about prey profitability: all predators in the simulation were therefore naïve. 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. Consumed locusts were not replaced. The model was written in Matlab Version 12 (The MathWorks Inc).

Each trial contained 5 predators. Trials were run with locusts of a single phenotype, varying the population size from 20 to 300 locusts. This range of population sizes is conservative as field densities can range between a few individuals per ha to thousands per m² (Uvarov 1977). Simulations were run for 50 iterations, and each phenotype treatment was replicated 100 times. First, rates of both predator detection and of predation were compared for the three phenotypes (solitary, gregarious and transiens) at different population sizes. Second, predation rates were evaluated with and

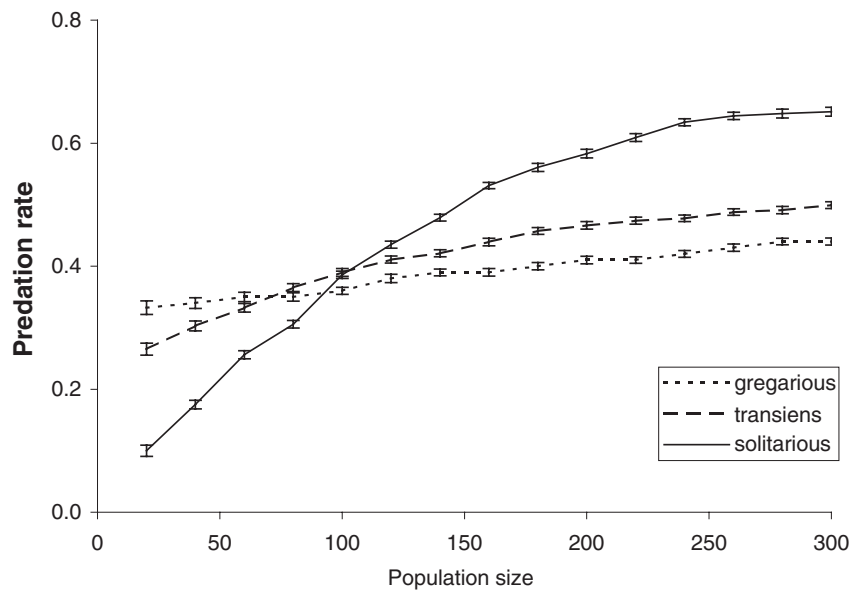


Fig. 2 Simulation results of predation rate (proportion of individuals consumed at the end of the run) on solitarius, gregarious and transiens locusts at a range of population sizes. Error bars are standard errors

without chemical defence (i.e., palatable vs toxic trait) for solitarius locusts at low population size ($n = 20$), and for gregarious and transiens locusts at high population size ($n = 300$).

Results

At low population size, predation rate was lowest for the solitarius phenotype (see Fig. 2). As population size increased, predation on solitarius locusts rose dramatically. The gregarious phenotype experienced the highest predation at low population size, but became the most advantageous strategy as population increased. The transiens phenotype was intermediate between the extreme phenotypes: it outperformed the gregarious, but not the solitarius, at low population density, and was more advantageous than the solitarius, yet less so than the gregarious, at high density.

Predation rate (proportion of individuals consumed at the end of the simulation) is a function of the detection rate, D = proportion of locusts detected per time step, and the consumption rate, C = proportion of locusts detected in a given time step that are consumed. C was fixed a priori for each phenotype (see methods section above) because the predators do not learn about the profitability of the prey they consume. However, the value for D emerges out of the dynamics of the simulation. This is because the distance at which a predator detects a locust (L) depends not only on its phenotype, but on its motion. D is therefore a function of M , the proportion of locusts moving per time step, which arises out of the locusts' behavioural rules. As population increases from 20–300, M changes from $0.11 (\pm 0.002 \text{ S.E.})$ to $0.67 (\pm 0.003 \text{ S.E.})$ for solitarius locusts, from $0.48 (\pm 0.004 \text{ S.E.})$ to $0.57 (\pm 0.0009 \text{ S.E.})$ for transiens locusts, and from $0.50 (0.003 \text{ S.E.})$ to $0.58 (0.001 \text{ S.E.})$ for gregarious locusts. Fig. 3 shows that D increases with population size for all phenotypes, but much more so for

solitarius locusts. For the solitarius phenotype, D is very sensitive to population size because M increases rapidly with increasing crowding, due to solitarius locusts' strong response to neighbours. The interaction between C and D controls the relationship between population size and predation rate for each of the three phenotypes.

At low population size, solitarius locusts escape predation by avoiding detection (i.e., low D). But when population grows and locomotion, and hence conspicuousness, increase, D increases as well. For gregarious locusts, detection rate is high due to conspicuous colouration and does not vary much with population density: therefore predation rate doesn't change much either. However, consumption rate is low due to both toxicity and warning colouration, and the gregarious phenotype outperforms the other two at high population density. Transiens locusts are more conspicuous than solitarius locusts (because of their high activity rate) but less so than gregarious locusts (because of their cryptic colouration) – this explains their intermediate predation rate at low population density. At high density, D increases, and transiens locusts perform better than the solitarius, but less well than the gregarious, phenotype because of their intermediate C value. Thus, at low population density, differences in predation rate reflect differences in D associated with colouration and behaviour; however, at high density, D becomes similar for all three phenotypes and therefore differences in C become critical in determining predation risk.

The benefits associated with toxicity to predators differ between the three phenotypes. For solitarius locusts at low population size, palatability has very little effect on predation rate (see Fig. 4). Palatability influences consumption rate but not detection rate; since D is low for solitarius locusts at low population size, a decrease in C has little

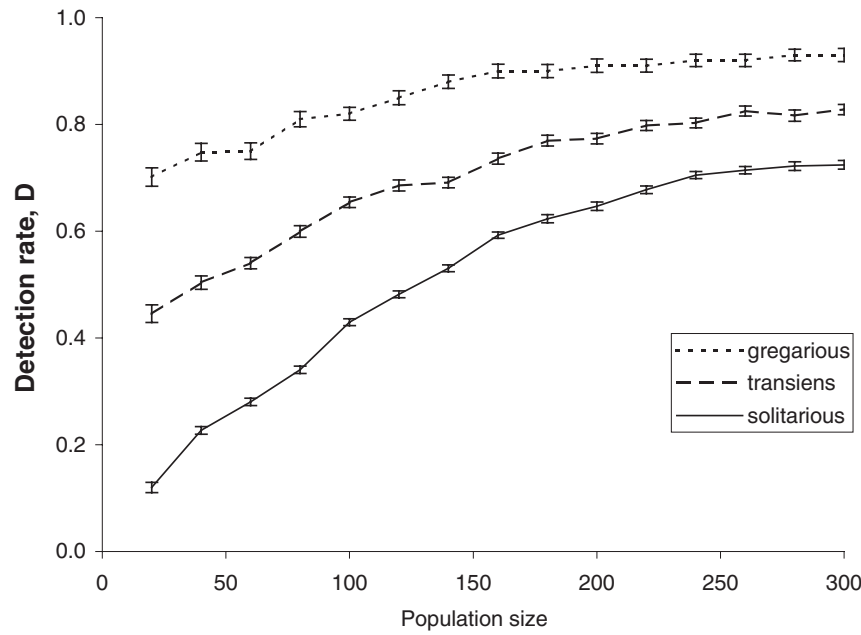


Fig. 3 Predator detection rate, D , for the three phenotypes at different population sizes (proportion of individuals detected per time step). Error bars show standard errors

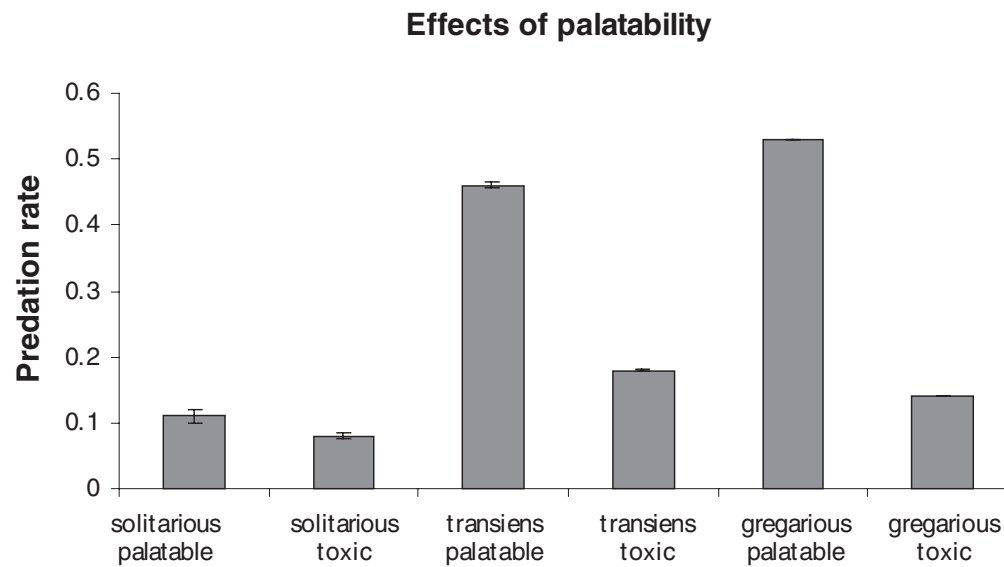


Fig. 4 Comparison of predation rate with and without the toxicity trait, for solitary locusts at low population sizes (20 individuals) and gregarious and transiens locusts at high population sizes (300 individuals). Error bars are standard errors – invisible error bars represent very small standard errors

effect. However, for both gregarious and transiens locusts in large populations, toxicity confers a significant advantage. In this case, D is high and therefore decreasing C leads to a significant decrease in predation.

Discussion

The taste experiment shows that although solitary locusts are deterred by a toxic plant chemical, neither gregarious nor transiens locusts show this aversive response. Previous research has shown that solitary locusts avoid toxic compounds but that gregarious locusts mix chemically

defended foods (Despland & Simpson 2005). Locusts appear to incur physiological costs when consuming toxic plants (Mainguet *et al.* 2000). In the field, gregarious locusts exhibit greater dietary breadth than do their solitary counterparts (El-Bashir 1996); this suggests that the phase differences we demonstrated here in response to hyoscyamine might also apply to a wide range of plant defensive compounds.

The computer simulation demonstrates how chemical defense is essential in protecting gregarious and transiens locusts against predators, but would be of little benefit to solitary locusts. The advantage of gregarious over transiens locusts at high, but not at low, population density suggests

that the benefits of warning colouration outweigh the costs when conspicuousness to predators is already high. This occurs at high population density, not only because the large group is more conspicuous (Pitt & Ritchie 2002) but also because crowded locusts are more active (Despland *et al.* 2000). Although warning colouration increases predator detection rate, it also decreases attack rate. Indeed, inexperienced predators often avoid novel brightly coloured prey, either through innate preferences (Lindström *et al.* 1999) or neophobia (Lindström *et al.* 2001). Thus, warning colouration can be advantageous even for the first aposematic individuals, who, as in our simulation, are faced with only naïve predators. As more aposematic individuals appear in the population, additional benefits accrue due to predator avoidance learning (Guilford 1990).

These findings thus suggest an answer to the question posed in the introduction: when it is advantageous for a member of a cryptic population to acquire warning colouration? When population density is so high that escaping predator detection is impossible, and cryptic colouration is therefore effectively useless. In this situation, locusts adopt an anti-predator strategy that involves acquiring toxicity to increase the probability of surviving an attack, and subsequently developing warning colouration to decrease the chance of being attacked. Since the development of warning colouration takes time (until the next moult), the switch to toxic foods helps bridge the gap between the two colour forms. The sequence of density-dependent plastic changes during locust phase transition is as follows: normally, desert locusts live in the cryptic, solitary phase at low population densities. Under favorable conditions following rain, populations build up. As conditions then degrade, locusts become concentrated on available patches of vegetation (Despland *et al.* 2000). Now crypsis is no longer a viable strategy. Predation risk increases because high population density implies greater conspicuousness to predators but does not confer any protection per se (Gamberale & Tullberg 1998). Solitary-phase locusts respond to this increased population density with rapid changes in behaviour: within hours of crowding, the insects start to aggregate (Roessingh & Simpson 1994) and, as we have demonstrated here, to feed on a toxic plant compound. At this stage, transients locusts are high-density, aggregated, chemically protected prey, and thus constitute a system where warning colouration would be beneficial. Indeed, according to one current scenario, these represent precisely the sort of conditions under which aposematism evolved (Alatalo & Mappes 1996; Riipi *et al.* 2001). If crowded conditions continue, the locusts acquire the gregarious-phase warning colouration at their next moult.

The sequence of changes outlined above minimizes predation risk at all stages because, when the detection rate, D , increases due to high population density (caused by environmental factors), the consumption rate, C , decreases via a change first in feeding behaviour and second in colouration. The fitness trough between the low-density, cryptic and

solitary phenotype (high C , low D) and the high-density, aposematic, gregarious one (high D , low C) is lessened by a change in feeding behaviour leading to chemical defence which lowers C . For high-density transients locusts, the cost of acquiring warning colouration is low because D is already high; the switch to aposematism is thus adaptive because it further decreases C .

Like the desert locust, many species combine aposematism with gregariousness. However, the evolutionary relationship between warning colouration and aggregative behaviour remains controversial (Sillen-Tullberg 1988, Alatalo & Mappes 1996; Gamberale & Tullberg 1998; Hunter 2000; Tullberg *et al.* 2000; Riipi *et al.* 2001). We have shown that an environmentally-driven increase in population density, and hence conspicuousness to predators, followed by induction of chemical defence via changes in food selection generate conditions where the costs of acquiring warning colouration are minimised. The sequence of changes documented in locusts provides empirical evidence to explain how the successful combination of toxicity, gregariousness and bright colouration can arise.

Acknowledgements

Thanks go to Tim Dodgson and Steve Roberts for maintaining the locust cultures and assisting in the experiments. We are grateful to the anonymous reviewers who greatly improved this manuscript. This study was funded by a Natural Sciences and Engineering Research Council (Canada) – Royal Society (UK) Millennium Fellowship.

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Received 21 July 2004; accepted 10 September 2004.



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