Predator exaptations and defensive adaptations in evolutionary balance: No defence is perfect

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Predator exaptations and defensive adaptations in evolutionary balance: no defence is perfect

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Summary

The lubber grasshopper, *Romalea guttata*, is large, aposematic, and extremely toxic. In feeding trials with 21 bird and lizard species, none were able to consume this chemically defended prey. Predators that attempted to eat lubbers, often gagged, regurgitated, and sometimes died. Loggerhead shrikes, *Lanius ludovicianus*, regularly impale this toxic prey in peninsular Florida. They, like other bird species, are unable to consume fresh lubbers. However, our tests show that they are able to consume lubbers if the prey are allowed to 'age' for 1–2 days. This suggests that lubber toxins degrade following death and that shrike impaling behaviour serves as a preadaptation for overcoming the toxic defences of this large and abundant prey. These results also imply that counter adaptations against chemical defences need not involve major morphological or metabolic specializations, but that simple behavioural traits can enable a predator to utilize toxic prey.

Keywords: *Romalea guttata*; *Lanius ludovicianus*; chemical defences; predation; impaling; defensive behaviour

Introduction

Phenotypic adaptations are maintained in populations when their fitness-related benefits exceed their costs. When there is no longer a selective advantage for a trait, that is when fitness-related costs exceed benefits, that trait will be eliminated. Examples supporting this axiom include the loss of eyes and colour in cave-dwelling animals (e.g. Burr, 1968; Poulson and White, 1969; Culver, 1982), the loss of flight and defensive behaviour in island-dwelling birds (e.g. MacArthur and Wilson, 1967), and the correlation of high defence chemical titres with predator sympatry, but not allopatry (Jones, 1974; Jones *et al.*, 1978).

Likewise, natural selection should act to increase the effectiveness of a given adaptation, but only if the fitness benefits gained outweigh the costs. As the effectiveness of a given adaptation reaches 100%, the shunting of additional resources to that adaptation is counterproductive (additional costs would not be balanced by additional benefits). The result of this trade-off is that adaptations should be less than 100% effective. This hypothesis leads to the prediction that no

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Figure 1. *R. guttata* performing warning display. Note raised wings, twisting abdominal tip, and black and yellow striped abdomen. A gland just above the middle leg expels the defensive secretion.

defence is perfect. Examples supporting this prediction include cases of predation on organisms widely regarded as 'without predators', such as lions, elephants, rhinos, large crocodilians (Schaller, 1972), cardenolide-containing monarch butterflies (Calvert *et al.*, 1979; Fink and Brower, 1981), and ecdysone-containing ferns (Lawton, 1976; Balick *et al.*, 1978; Hendrix, 1980).

In this paper we provide an example of a predator that has overcome the defences of 'well-defended' prey. This system involves the chemically-defended lubber grasshopper *Romalea guttata* and its avian predator, the loggerhead shrike, *Lanius ludovicianus*.

R. guttata exemplifies the chemical defence syndrome (Fig. 1) (Pasteels *et al.*, 1983; Whitman *et al.*, 1985). These grasshoppers are large (up to 7 cm and 9 g), conspicuous, diurnal, flightless, and slow-moving, and they aggregate in groups of up to several hundred (Watson, 1941; Rehn and Grant, 1959; Whitman, 1988). Being large, conspicuous, and flightless, and occurring in clumps, these grasshoppers should be easy prey for birds. However, during ca 38 h of field observations in Georgia and Florida, during which 102 insectivorous birds from 17 species foraged in or adjacent to *Romalea* aggregations, only one attack was observed. In additional laboratory tests, 119 individual birds and lizards (ranging across 21 species) were individually tested for their ability to feed on *Romalea*. In all but one case, birds rejected the grasshopper either before or after sampling (Whitman, 1988, 1990; Whitman, unpublished data). Birds and lizards that consumed *Romalea* often vomited showing that *Romalea* possesses potent internal toxins (Whitman *et al.*, 1990). Only one captive eastern meadowlark (*Sturnella magna*) failed to be deterred by *Romalea*: on day 1 it consumed 15 larvae, on day 2 it consumed 10, and on day 3 it died (Whitman, unpublished data). These observations strongly suggest that birds and reptiles are unable to utilize *Romalea* as a food item.

Like many chemically defended insects, *Romalea* advertises its unpalatability to potential predators. It combines bright, aposematic colours with a volatile, pungent defensive secretion that is squirted out with a hissing noise during predator encounters (Eisner, 1970; Eisner *et al.*, 1971; Whitman *et al.*, 1990). The secretion is stored in a gland in the thorax and contains a mixture of phenols, quinones, and sequestered plant allelochemicals (Eisner *et al.*, 1971; Jones *et al.*, 1986, 1988, 1989; Blum *et al.*, 1990; Whitman *et al.*, 1991). The animals' colouring, sound production, smell, and taste all function as warning signals, and, in addition, the secretion by itself has been shown to deter predators (Eisner *et al.*, 1971; Jones *et al.*, 1989; Whitman, unpublished).

Loggerhead shrikes are large, active predators, often found in the same habitat as *Romalea*. These birds exhibit a characteristic behaviour: they regularly impale insects and small vertebrate prey conspicuously on thorns or barbed wire. Birds later return to this 'cache' to consume the impaled prey. Impaled items also serve a courtship function. During the breeding season, male shrikes impale not only food but also other conspicuous materials (e.g. ribbons, paper, feathers, snails, crusts of bread) (Yosef, 1989). In northern shrikes (*Lanius excubitor*), cache size is positively correlated with male mating success (Yosef and Pinshow, 1989).

In 1990 we observed loggerhead shrikes impaling large numbers of adult *Romalea* grasshoppers in central Florida. There are several possible explanations for this behaviour. Shrikes may discriminate during feeding but not while capturing and impaling lubbers, or perhaps shrikes have overcome the toxic defences of *Romalea*. Alternatively, impaling of the brightly coloured lubbers may serve a non-nutritional purpose (e.g. intra-specific communication). In this paper we test three hypotheses and provide evidence that loggerhead shrikes have developed a behaviour that allows them to overcome the toxic defences of *Romalea*.

Methods and materials

All observations and experiments were conducted at or near the MacArthur Agro-ecology Research Center of the Archbold Biological Station, Lake Placid, Florida. For laboratory experiments, loggerhead shrikes were trapped with composite bal-chatri-treadle traps (Yosef and Lohrer, 1992), placed into 3 m^3 screen cages (one bird per cage), tested, and then released at the site of capture. Cages contained strands of barbed wire for impaling prey. Shrikes had food and water *ad libitum*, and their feeding behaviour toward palatable prey was recorded.

R. guttata grasshoppers were collected each day at dawn, transferred to the laboratory, weighed on an Acculab Electronic balance (Model 333, accuracy ± 0.00 g), and then presented to shrikes. Each insect was used once. Grasshoppers that were alive post-trial were released in the field. Grasshoppers were always handled gently so that none expelled the defensive secretion prior to the feeding tests.

Field observations were made between June and September 1990 at the MacArthur Agro-ecology Research Center, a 4120 ha cattle ranch containing 36 resident loggerhead shrike pairs. Colour banding allowed identification of individual birds and their territories. Grasshopper and shrike densities, the frequency and manner of impaling, and the fate of impaled prey items were recorded. We also observed other predators that kleptoparasitized caches of loggerhead shrikes, and other potentially poisonous animals that shrikes impaled.

Experiment 1

To determine if shrikes consumed live *Romalea*, 10 young shrikes (45–60 days old) were trapped in their natal territories and maintained in the laboratory. Birds were held in individual cages; on the first 3 days of the experiment, they were offered freshly killed laboratory mice (*Mus musculus*) daily. Food was always presented at the same time of day (ca 07:00 h), in the same manner, in the same dish, and in the same area of the cage, in order to condition the birds to the feeding regime. At night, no food was available to the birds. On days 4, 5 and 6, five live adult *Romalea* (three males and two females) were offered every morning (instead of mice). The following data were recorded: time of attack, mode of attack, feeding or rejection, prey parts consumed and impaled, and sex and behaviour of attacked grasshoppers. Observations were recorded from a blind 7 m distant, and continued as long as birds interacted with lubbers. If a lubber remained unattacked for 30 min, all grasshoppers were removed and a freshly killed mouse was placed in the cage.

Experiment 2

Ten adult shrikes (sexes unknown) were collected, maintained, and tested once, in a similar manner as the juveniles (above), except that any impaled grasshoppers were left in the cage, and surviving grasshoppers were removed and replaced by mice 3–4 h after the last shrike attack.

Experiment 3

To test if dead *Romalea* become less distasteful over time, 33 shrikes of various ages were trapped in October 1990, maintained in the laboratory in individual wire screen cages, and conditioned to feed on mice, lizards, and palatable insects from a dish placed in their cage. The birds were allowed to habituate to captivity for 3 days and then were offered live adult *Romalea*. Six individuals that aggressively attacked grasshoppers were selected for further testing.

Each of the six shrikes was offered six grasshoppers that had been frozen and then thawed. Three of the grasshoppers had been thawed 48 h previously and had been held at room temperature, and their colour had changed from yellow to brown. The other three grasshoppers had been thawed 2 h prior to the test and retained their aposematic colours.

Results

Field observations

From June to August 1990, we observed the attack and impaling behaviour of loggerhead shrikes towards adult *R. guttata*. Nine shrike territories contained one or more impaled lubber grasshoppers (territories averaged 7.1 ± 4.2 SD ha and 2 adults per territory). The absence of impaled *Romalea* from 14 other shrike territories, could be explained by the population boundaries of the grasshopper: shrike territories devoid of impaled *Romalea* were also devoid of live lubbers.

In territories containing impaled *Romalea*, this grasshopper comprised 17.6% of all impaled prey items. Up to 20 carcasses were strung along a single length of barbed wire (Fig. 2). Other orthopteroids (palatable grasshoppers, katydids, mantids, and cockroachs) comprised an additional 44.1% of impaled items. Shrikes were observed to impale a wide range of prey which included other organisms with toxic properties such as monarch butterflies (*Danaus plexippus*) and the eastern narrow-mouthed toad (*gastrophyne carolinensis*).

All lubbers were impaled with the wire barb piercing the thorax (Fig. 2). After 24–48 h, impaled grasshoppers disappeared, and in almost all cases, grasshopper legs, wings, and thoraces were found on the ground nearby, suggesting that only the head and abdomen had been consumed. This agreed with the procedure the shrikes normally employ when dealing with impaled Orthoptera, except that with palatable grasshoppers, the thorax was also eaten.

In two instances shrikes were observed to attack *Romalea* in the wild. In both cases the bird

Figure 2. Barbed wire fence with impaled *R. guttata*. Note that all lubbers are impaled such that the barbs pierce the thorax.

detected the prey from a perch on a fence post, alighted alongside it, picked it up in its beak, and, holding the grasshopper by its head, flew to a nearby stretch of barbed wire fence and immediately impaled the prey on a barb. In both cases, the handling time (landing to impaling) was shorter than 4 s.

Audubon's crested caracaras (*Polyborus plancus*) and burrowing owls (*Athene cunicularia*) were observed to kleptoparasitize caches of loggerhead shrikes. Prey remains at burrowing owl burrows contained thoraces of *Romalea*. The owls appeared to swallow the prey whole.

Experiment 1 – response of juvenile shrikes to R. guttata

When 10 juvenile shrikes were offered live *Romalea* grasshoppers, seven attacked within 64 s (Table 1). Three shrikes failed to attack and appeared agitated, flying back and forth across their cages while eyeing the grasshoppers. During attacks, grasshoppers were quickly seized with the beak (range: 1–4 s after landing), manipulated such that they pointed head first into the beak, and partially swallowed. During the attack, the grasshoppers usually discharged their defensive secretion, regurgitated, kicked, and sometimes flicked their brightly coloured hind wings. All seven birds that seized a grasshopper quickly performed two or more of the following aversive behaviours: disgorged and dropped prey, gagged (held mouth open), stuck out tongue, dripped saliva, squawked, and shook head back and forth. Avoidance behaviours continued for up to 180 s by which time all shrikes had resumed normal behaviour. All grasshoppers survived the attack and moved away. Although grasshoppers remained in the cages, no further attacks occurred. After 30 min, all grasshoppers were removed and replaced by dead mice, which all birds attacked and consumed within 4 min.

Table 1. Reaction of caged juvenile loggerhead shrikes (*Lanius ludovicianus*) to live adult lubber grasshoppers (*Romalea guttata*)

Shrike no.	Prey sex	Attack latency(s)[1]	Mode of attack[2]	Shrike reaction[3]	Duration of aversive reaction (s)[4]
1	m	33	C	D,G	<60
2	f	20	C	D,G,H	180
3	f	64	C	D,G	<60
4	–	–	–	–	–
5	f	45	A	D,G,H	75
6	m	23	C	D,G	<60
7	–	–	–	–	–
8	–	–	–	–	–
9	f	20	A	D,G	<60
10	f	35	C	D,G,H	135

[1] Attack latency: interval between when bird first noticed prey and when it first attacked prey.
[2] Mode of attack: – = did not attack; c = approached prey cautiously by first landing next to it; a = attacked prey aggressively by landing directly on it.
[3] Shrike reaction: D = drop prey; G = gag by holding mouth open for greater than 2 s; H = shake head.
[4] Duration of aversive reaction: time between first and last aversive behaviours.

On days 5 and 6, *Romalea* grasshoppers were reintroduced for 60 min. Although birds inspected the prey, there were no attacks suggesting that one-trial food aversion learning had occurred.

Experiment 2 – response of adult shrikes to R. guttata

When captive adult shrikes were each offered live *Romalea*, six birds of the 10 tested failed to attack (Table 2). The other four birds immediately attacked, and in quick succession impaled all

Table 2. Reaction of caged adult shrikes (*Lanius ludovicianus*) to five live adult lubber grasshoppers (*Romalea guttata*)

Shrike no.	Sequence of prey impaled[1]	Attack latency (s)[2]	Mode of first attack[3]	Consumption latency (h)[4]	Aversive behaviours[5]
1	–	–	–	–	N
2	m,f,m,m,f	9	A	36	–
3	–	–	–	–	N
4	–	–	–	–	N
5	–	–	–	–	N
6	m,m,f,m,f	17	A	24	–
7	–	–	–	–	N
8	f,m,f,m,m,	10	A	36	–
9	m,m,f,f,m	7	A	48	–
10	–	–	–	–	N

[1] Sequence of prey impaled: m = male; f = female.
[2] Attack latency: interval between when bird first noticed prey and when it first attacked prey.
[3] Mode of first attack: – = did not attack; c = approached prey cautiously first landing next to it; a = attacked prey aggressively by landing directly on it;
[4] Consumpt latency: interval between impaling and consumption.
[5] Aversive behaviour during predation: N = no reaction; D = drop prey; G = gag by holding mouth open for greater than 2 s; H = shake head; R = disgorge prey; S = salivate and drip saliva.

five grasshoppers on the barbed wire provided in their cages. With palatable grasshoppers, shrikes normally bit the prey at the thorax and crushed it, held it with their feet, pulled off the legs, wings, and antennae, and then swallowed it head first. Shrikes given *Romalea* behaved differently; the prey was grasped and immediately impaled without removing appendages. Attacked *Romalea* expelled their defensive secretion, and some birds exhibited avoidance behaviour. However, each of the four birds that attacked, continued attacking until all prey were impaled.

The impaled *Romalea* were not consumed immediately, but only after their colour changed from bright yellow to brown (ca 24–48 h). In all cases, only the head and abdomen were eaten; legs, wings, and thoraces (containing the defensive glands) were always rejected.

Experiment 3 – palatability of fresh versus aged carcasses

Six shrikes were each given six dead *Romalea*. Three of the grasshoppers had been freshly thawed and still retained their bright yellow colouration. The other three grasshoppers had been 'aged' (thawed 48 h previous), and were brown in colour.

Five of the six shrikes quickly impaled all the aged grasshoppers. They then removed their appendages and consumed them (interval between first attack and last consumption: range = 5.33 to 11.08 min). Only after all aged grasshoppers had been eaten did the birds impale the freshly killed grasshoppers. These were consumed 23–56 h later. The sixth bird quickly impaled all the grasshoppers, and then fed on only the aged individuals. As before, only the heads and abdomens were eaten; thoraces, legs, and wings were discarded.

Discussion

Until now, *Romalea* were considered impervious to bird predation; observations on 21 bird and lizard species showed no successful predation (Whitman, 1988, 1990; Whitman unpublished). Birds and lizards that fed on *Romalea* sometimes regurgitated or died (Whitman *et al.*, 1990). Our results show that loggerhead shrikes can attack, impale, and consume *Romalea*.

Why can loggerhead shrikes consume this chemically-defended insect, while other birds cannot?

Our results suggest that shrikes are no different than other birds in that they are unable to feed on fresh *Romalea* (shrikes that attacked live *Romalea* often exhibited gagging, head-shaking, and other aversive behaviours). However, shrikes often cache food by impaling more prey than they can consume at one time. This preadaptation has allowed shrikes to successfully overcome the chemical defences of *Romalea*, because, apparently, *Romalea* toxins decline in potency with age after death. It is this 'Achilles heel' in lubber defences that has allowed shrikes to overcome them. Our data show shrikes cannot consume freshly killed *Romalea*, but will eat them if the carcass has been allowed to 'age' for 24–48 h.

In the lubber–shrike relationship, an adaptation serves as an exaptation for another function. Shrikes (Laniinae) are found throughout much of the world and all impale prey (Miller, 1931). Impaling is an adaptation that probably evolved to facilitate prey handling, but now allows shrikes to store food and communicate with conspecifics. With loggerhead shrikes, this adaptation has come to serve yet another function: impaling has fortuitously preadapted loggerhead shrikes to feeding on a toxic insect. Indeed, caching may have opened a new feeding niche for shrikes. During our field studies, we observed shrikes impaling other chemically defended organisms such as monarch butterflies (*Danaus plexippus*) and the eastern narrow-mouthed toad (*Gastrophyne carolinensis*). Perhaps, like *Romalea*, these toxic prey are consumed at a later date. The ability to broaden its feeding niche to include chemically defended prey would be advantageous to shrikes; chemically defended prey are often abundant, conspicuous, and easily caught, and hence, would be a ready food source.

The ability of shrikes to feed on *Romalea* has important evolutionary implications for the ecology and behaviour of this insect. *Romalea* is the quintessential chemically defended insect: it is large, sluggish, conspicuous, flightless, gregarious, and aposematically coloured (Whitman, 1988, 1990). These characters are common in chemically defended insects (Pasteels *et al.*, 1983), but are exactly opposite to those of palatable grasshoppers such as *Melanoplus* and *Schistocerca* which tend to be cryptic, wary, active, and quick to take flight on powerful wings. Presumably, *Romalea* has lost these escape attributes because it does not need them; its chemical defence system has been efficient in deterring predation. The conspicuous bright warning colouration and gregarious behaviour of *Romalea* may bolster the effectiveness of chemical defence by enhancing attack neophobia and food aversion conditioning in potential predators. Escape from predation through chemical defence may have allowed *Romalea* to be large; palatable insects usually need to be small in order to be able to hide. Indeed, large size and chemical defence appear to be correlated in insects (Pasteels *et al.*, 1983). *Romalea* would be an easy prey to find and catch, but for its chemical defences. Because large size makes for a greater food reward, *Romalea* represents an ideal prey for any predator that can break through its chemical defences.

In the relationship between shrikes and *Romalea*, defensive features of *Romalea* that were previously adaptive (conspicuousness, large size, bright colours, gregariousness, etc.), may now be a liability. That is, shrikes may be a countervailing selective force against lubber aposematic colours. Hence, we would predict that where *Romalea* and shrikes are sympatric, these grasshoppers might be less aposematic, gregarious, sluggish, etc., or perhaps better defended. In the future we hope to examine this prediction by comparing the intensity of selection pressure by shrikes *versus* other predators on the maintenance of aposematic colouration and gregarious behaviour in lubbers.

The relationship between shrikes and *Romalea* parallels that between monarch butterflies and their predators. Like *Romalea*, monarchs possess chemical defences (Brower *et al.*, 1982, 1984; Kelley *et al.*, 1987). In addition, both species are large, brightly coloured, and form conspicuous aggregations (Urquhart and Urquhart, 1976; Tuskes and Brower, 1978). Because of their chemical defences, monarchs were once considered fairly impervious to predation. However, it has been shown that a number of predators have been able to break through the monarch defences (Brower *et al.*, 1985; Glendinning *et al.*, 1988). Black-backed orioles (*Icterus abeillei*) sample monarchs and consume those individuals with low cardenolide titres (Fink and Brower, 1981). Black-headed grosbeaks (*Pheucticus melanocephalus* Swainson), are apparently insensitive to monarch toxins (Fink and Brower, 1981). Together, these predators take several hundred thousand monarchs from among the millions in the dense overwintering aggregations in Central Mexico each year (Brower and Calvert, 1985).

The lubber grasshopper and monarch butterfly both illustrate how traits may be acted upon by competing selective forces. Conspicuous colouration and gregariousness are probably adaptive traits in most *Romalea*–bird interactions, however, they allow shrikes to more easily find and prey upon these grasshoppers. Also, lubbers should be less valuable to shrikes than other insect prey because they cannot be consumed immediately, and may be lost to kleptoparasites during the curing process. This leads to the question of why are these aposematic-coloured grasshoppers impaled in conspicuous places? One possible answer lies in that they may play a role in the shrikes' territorial or sexual displays. Yosef and Pinshow (1989) demonstrated that colourful objects in the conspicuous caches of male northern shrikes affect mate selection by females, and that reproductive success is increased in individuals with larger caches. A possible evolutionary pathway may be that shrikes initially impaled lubbers for their eye-catching colours and latter developed the exaptation of feeding on them when discoloured.

In a broader sense, our study supports the prediction that no defence is perfect: for any defence, there will be at least one predator that can overcome that defence. Although *Romalea* appears well defended against most birds, at least one bird species, the Loggerhead Shrike, has developed the ability to successfully prey upon it.

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