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Aposematism in a soft-bodied insect: a case for kin selection

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Summary. This paper describes the influence on predator behaviour, and the survival of an aposematic aphid, *Aphis nerii*, in comparison with a palatable, cryptic aphid, *Acyrthosiphon pisum*, when offered to two predators with different foraging tactics. The experiments were designed to test Fisher's (1930) suggestion that aposematism could evolve by kin selection, since aposematic animals often occur in aggregations of relatives. Initially, spiders (*Zygiella x-notata*) and birds (*Parus major*) killed high proportions of distasteful *A. nerii* (60% and 54% respectively). With experience, the predators killed and ate fewer *A. nerii.* The decreasing mortality of *A. nerii* after initial encounters with predators, coupled with its apparently obligate parthenogenesis, indicate that the evolution of aposematism in this soft-bodied insect is consistent with kin selection.

Introduction

Aposematism represents a combination of distasteful and conspicuous traits in prey. Distastefulness may either evolve before conspicuousness, or the two traits coevolve (Harvey and Paxton 1981; Guilford 1985). In both cases conspicuousness facilitates predator recognition of unprofitable, distasteful prey (Gittleman and Harvey 1980; Gittleman et al. 1980; Schuler and Hesse 1985). The classical view is that aposematism evolves through individual selection in which aposematic prey individuals survive predator encounters because they are tough-bodied (Trimen 1869; Poulton 1908; Edmunds 1974; Järvi et al. 1981; Wiklund and Järvi 1982; Sillén-Tullberg and Bryant 1983). In 1930 Fisher suggested that aposematism could evolve by kin-selection since aposematic animals often occur in sibling groups, in which individuals may be sacrificed to predator education because the family group shares a genotype and aposematism enhances its fitness (Harvey and Greenwood 1978; Harvey and Paxton 1981; Harvey et al. 1982; Harvey 1983).

Both indirect and direct evidence show that high proportions of at least some kinds of aposematic prey survive predator encounters. There is indirect evidence for interactions between butterflies and their avian predators (Brower and Glazier 1975; Jeffords et al. 1979; Schoener 1979; Vermeij 1982). The direct evidence of Järvi et al. (1981), Sillén-Tullberg et al. (1982) and Wiklund and Järvi (1982) shows more convincingly that six species of tough-bodied, aposematic insects can survive bird attacks.

No direct evidence has been published to indicate that the sacrifice of some aposematic prey protects their relatives in the remainder of the group. This paper examines the survival of a potentially vulnerable, soft-bodied, aposematic insect during encounters with generalist predators. My experiments investigate the detection, pursuit, subjugation and acceptance of prey by an actively foraging passerine bird, the great tit (*Parus major* L.), and a prey-trapping araneid spider (*Zygiella x-notata* (Clerck)), to a distasteful, brightly coloured aphid (*Aphis nerii* B de F), compared with their responses to a palatable aphid (*Acyrthosiphon pisum* Harris).

Methods

Aphid prey

The bright yellow aphid, *A. nerii* is an apocynale specialist that occurs in highly aggregated colonies on oleander and milk-

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weeds, both of which contain toxic cardenolides (Rothschild et al. 1970; Roeske et al. 1976). On the milkweed *Asclepias curassavica* L., the aphid contains two host-derived cardenolides (Rothschild et al. 1970; Malcolm 1981). Using the colorimetric method of Brower and Glazier (1975) the cardenolide concentration of *A. nerii* was 246 μg/0.1 g dry aphid, with 0.5 μg cardenolide in each aphid. Cardenolides were absent from *A. pisum*. Since Brower and Glazier (1975) have shown the toxicity of cardenolides in monarch butterflies to bird predators, bitter-tasting cardenolides are the likely distasteful basis of aposematism in *A. nerii*. Its bright yellow colouration and contrastingly black legs, antennae, cauda and cornicles make *A. nerii* conspicuous. For these experiments *A. nerii* was reared on cardenolide-rich *A. curassavica* (Roeske et al. 1976). The green, cryptic, pea aphid, *Acyrthosiphon pisum* Harris, reared on broad bean plants, *Vicia faba* L. cv aquadulce, was used as palatable control prey.

Although winged aphids are more likely to be trapped by spider webs than wingless aphids, apterous aphids were used because *A. pisum* alates are approximately four times larger than those of *A. nerii*, so size could not be controlled. There were no differences between the cardenolide concentrations of apterous and alate *A. nerii*.

Predators

Since the effectiveness of prey defences is in large part determined by predator foraging success, two kinds of predators, with very different foraging tactics (visually hunting and largely indiscriminate trapping), were used because the costs of each phase of different foraging tactics are likely to vary. Three phases of predation have been recognised during prey encounters, *detection, pursuit* and *subjugation* (Schoener 1971; Vermeij 1982), and Vermeij suggested that prey defences should operate most effectively at whichever phase the predator is least effective. A fourth *acceptance* phase completes the response since predators need to accept or reject subjugated prey.

Spiders that emerged from a single egg sac of *Z. x-notata* collected in late March near Oxford, were fed on whitefly and small *A. pisum*. After two months, nine female spiderlings were each placed in a 120 × 120 mm square balsa wood frame suspended in a constant environment room at 15° C. Immature spiders weighed a mean of 1.01 mg (0.19 SE) at the start of the experiment and increased to a mean of 1.37 mg (0.17 SE) at the end of the experiment, 70 days later. During the tests each spider constructed webs with a spiral-free sector characteristic of the species (Barth 1982) and the number of new webs each spider built over 70 days was noted. Six "experimental" spiders were each fed one fifth instar (adult apterous) *A. nerii* (mean weight 0.61 mg ± 0.03 SE) followed after 30 min by one similar sized, third instar *A. pisum* (mean weight 0.66 mg ± 0.03 SE). Three "control" spiders were each fed only one third instar *A. pisum* (mean weight 0.65 ± 0.09 SE). Prey were presented to spiders at 10-day intervals, which precluded significant growth or developmental changes in spider behaviour during the 70-day period.

During the first three feeding trials with each spider (10 days apart), each aphid was weighed and placed near the web centre. Each prey presentation was observed for 30 min and the times of the following spider behaviours were measured: "bite", "bite and withdraw", "take the aphid to the retreat" and "no response". Since attacked aphids of both species can produce a rapidly hardening liquid from their cornicles, aphid response to spider attack was also noted as "cornicle secretion after a bite". After the timed observation aphids were left in the webs and once each day for ten days following the initial prey presentation, whole aphids or prey remains were picked carefully from the webs, weighed and replaced until the prey were either eaten or rejected. Mortality of these aphids was determined under a binocular microscope. Killed *A. pisum* usually appeared as a crumpled or chewed exoskeleton and killed *A. nerii* remained intact, but rapidly turned from bright yellow to dark brown.

The weights and mortalities of twenty 5th instar apterous *A. nerii* and twenty 3rd instar *A. pisum*, that were not exposed to predators, were measured daily over six days for comparison with prey aphids.

Four male great tits, *P. major*, caught near Oxford, were observed in an indoor, 4.3 × 3.7 × 2.5 m aviary. Each bird was offered aphids in two prey patches, 15 cm apart, held in 5 cm diameter plastic Petri dishes with Fluon-painted sides to prevent aphid escape. These small dishes were glued to the lids of larger 9-cm Petri dishes, painted white so that both prey types were equally conspicuous. As in the spider experiments, aphid prey were either fifth instar yellow and black, apterous *A. nerii* or, equal-sized third instar, green *A. pisum*. Aphids were offered to the birds in four consecutive, twin-patch treatments of, (1) 40 + 40 *A. pisum*, (2) 40 + 40 *A. nerii*, (3) 20/20 + 20/20 *A. nerii*/*A. pisum* mixtures, and (4) 40 + 40 *A. pisum*. Thus birds were given 40 aphids in each patch and 80 aphids in each treatment so that each bird had to move from one dish to the other to exploit both prey patches. Each of the four treatments was presented for 5 minutes at 15 minute intervals. In order to measure changes in predation with experience, the same prey sequence was offered in a second trial one day later.

The prey presentation sequence in two trials was designed to test, (1) acceptance of aphids as prey, (2) taste discrimination and rejection of distasteful aphids, (3) learned avoidance of distasteful prey, (4) visual discrimination of distasteful from palatable prey, and (5) predator satiation.

Bird behaviour was observed for five minutes through a one-way mirror and was recorded with a computer-compatible event recorder (Dawkins 1971). The behavioural events were scored as, "look", "arrive", "peck", or "leave" activities associated with the prey presentations. Birds were deprived of food for one hour before each trial of prey treatments. The number of aphids eaten from each patch was counted during the 15-min break between each of the four prey presentations. The profitability of each aphid species to great tits was measured by the number of aphids eaten divided by the time of summed pecking bouts, assuming that the aphids were equally available and nutritionally similar.

Both predators prey on aphids (Gibb and Betts 1963; Nyffeler and Benz 1981) and could naturally encounter *A. nerii* in southern Europe.

Results

Prey mortality and consumption by spiders

Experimental spiders killed 52% distasteful *A. nerii*, and control spiders killed 90% palatable *A. pisum* placed in their webs (Fig. 1). Analyses of covariance between regressions of mortality with time in Fig. 1 show that both prey *A. nerii* and prey *A. pisum* given to experimental spiders died significantly earlier than non-prey aphids (*A. nerii* prey $y = 5.63 + 0.77x$, non-prey $y = -45.54 + 0.85x$, $F_{elev(1,14)} = 41.04$, $P < 0.005$; *A. pisum* prey $y = 17.28 + 0.75x$, non-prey $y = -27.52 + 0.80x$, $F_{elev(1,18)} = 33.61$, $P < 0.005$) but at similar

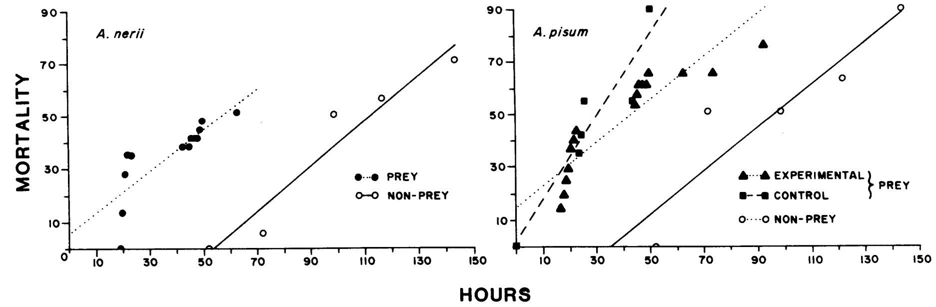

Fig. 1. Regressions of mortality (arcsine transformed) against time (h) for, prey *A. nerii* and *A. pisum* placed in the webs of experimental and control *Z. x-notata,* and for similar sized non-prey aphids

rates ($F_{\text{slopes}} = \text{NS}$). Similarly, *A. pisum* given to control spiders ($y = 1.95 + 1.55x$) died earlier than non-prey aphids ($F_{\text{elev}(1,8)} = 15.99$, $P < 0.005$) at the same rate ($F_{\text{slopes}} = \text{NS}$). This agrees with observations that the spiders killed both aphid species. However palatable aphids were killed by control spiders significantly faster than by experimental spiders ($F_{\text{slope}(1,18)} = 9.71$, $0.025 > P > 0.005$) but at the same time ($F_{\text{elev}} = \text{NS}$), suggesting that predation of palatable aphids was suppressed after contact with distasteful aphids. Palatable *A. pisum* fed to control spiders also died both earlier and at a faster rate than *A. nerii* given to experimental spiders ($F_{\text{slope}(1,15)} = 6.79$, $0.025 > P > 0.005$; $F_{\text{elev}(1,16)} = 14.13$, $P < 0.005$).

Although spiders killed 60% of *A. nerii* placed in their webs in the first two prey trials and 40% in the third trial, comparison of weight regressions with time (Table 1) suggests that too little of the *A. nerii* offered as prey in the combined experiments was eaten to give a significant weight difference from non-prey *A. nerii*. However, if the results are considered separately for each trial, and the weights of individual aphids are corrected for weight loss with time, then the proportions of *A. nerii* ingested by spiders decreased from a mean of 0.42 ± 0.09 SE in the first trial to means of 0.21 ± 0.07 SE in trial 2 and 0.23 ± 0.11 SE in trial 3. In contrast, the proportions of attacked *A. pisum* that were eaten remained consistently high at overall means of 0.84 ± 0.07 SE for experimental spiders and 0.88 ± 0.07 SE for control spiders; both sets of spiders almost always leaving a crumpled or chewed ball of exoskeleton. Compared regressions of pooled trial data also show significant weight differences between prey and non-prey *A. pisum* (Table 1). Thus spiders killed, but ate very little of the distasteful aphids, whereas they killed and ate palatable aphids.

Spider foraging behaviour

Spiders seemed unable to distinguish between aphid species before encounters, and attacked and bit similar proportions of the distasteful and palatable aphids presented (Table 2). However on touching or biting the aphids the spiders markedly rejected *A. nerii* and accepted *A. pisum* by holding on to fewer *A. nerii* or withdrawing from this distasteful aphid immediately. Distasteful aphids also produced cornicle secretions in response to spider attacks more frequently than palatable aphids. On contact with this yellow secretion a spider would behave agitatedly, dashing back to its retreat to

Table 1. Regression coefficients (b_{yx}) of weight change (mg) against time (h) for *A. nerii* (aposematic) and *A. pisum* (palatable) prey aphids given to the spider *Z. x-notata*, compared by *t*-tests with those of similar sized non-prey aphids

Treatment		Weight change				
		n	*a*	b_{yx}	*r*	*P*
6 Experimental spiders						
Prey	*A. nerii*	38	0.54	−0.0024	0.54	NS
Non-prey	*A. nerii*	160	0.53	−0.002	0.63	
Prey	*A. pisum*	26	0.65	−0.03	0.86	0.001
Non-prey	*A. pisum*	80	0.53	−0.003	0.78	
3 Control spiders						
Prey	*A. pisum*	14	0.65	−0.03	0.82	0.001
Non-prey	*A. pisum*	80	0.53	−0.003	0.78	

Table 2. Treatment of *A. nerii* or *A. pisum* placed in webs of *Z. x-notata* (numbers with percentage in parentheses)

Response to aphid	6 Experimental spiders		3 Control spiders
	A. nerii	*A. pisum*	*A. pisum*
Attack + bite	17/25 (68)	8/16 (50)	11/15 (73)
Bite + aphid held	3/25 (12)	5/16 (31)	7/15 (47)
Aphid taken to retreat	4/25 (16)	2/16 (13)	4/15 (27)
Bide + withdraw	14/25 (56)	3/16 (19)	4/15 (27)
Bite + cornicle secretion	16/25 (64)	1/16 (6)	0/15 (0)
Ignored	6/25 (24)	8/16 (50)	4/15 (27)

vigorously manipulate fore tarsi, palps and mouthparts. One of the six experimental spiders died five days after attacking an *A. nerii* which left cornicle secretion on the spider's palps and front legs. Distasteful aphids that were attacked were either left in the web, cut out, or left hanging intact from a thread when a new web was constructed. Attacked palatable aphids were either held or taken to the retreat more often than *A. nerii* (Table 2), although fewer palatable aphids were attacked by experimental spiders after encounters with *A. nerii.*

Spiders ingested palatable prey at a consistently high rate through the first three trials with means of 0.47 ± 0.09 SE for control spiders and 0.42 ± 0.07 SE for experimental spiders (weight of aphid ingested, corrected for non-prey weight loss in Table 1, divided by time in days to reach that weight). Thus, since distasteful aphids were eaten at a low overall mean rate of 0.12 ± 0.03 SE, palatable aphids were almost four times more profitable (between *A. nerii* and *A. pisum* eaten by experimental spiders, Wilcoxon matched-pairs signed-ranks test, $P < 0.005$). The low ingestion rates of *A. nerii* by spiders also decreased with experience from a mean of 0.20 ± 0.06 SE in the first trial, through a mean of 0.10 ± 0.06 SE in trial 2, to a mean of 0.07 ± 0.03 SE in the third trial.

The number of webs built by spiders also differed between prey treatments. Spiders given *A. nerii* built a mean of 6.74 ± 1.29 SE webs/70 days with an average web duration of 9.72 days, whereas control spiders fed the profitable, palatable aphids made 11.33 ± 1.20 SE webs/70 days with an average web duration of 6.18 days.

Prey mortality and consumption by birds

The four great tits usually ate all of the palatable aphids from both separate (Table 3a) and mixed aphid presentations (Table 3b). However the birds ate only 28–30% of the distasteful aphids from separate (Table 3a), and only 18–54% from mixed (Table 3b), presentations. Thus significantly fewer distasteful than palatable aphids were eaten from both separate and mixed aphid presentations. There was no evidence that birds ate fewer aposematic aphids in their second encounter with just these aphids, or with mixtures, than in their first encounter (Table 3). Although the number of *A. nerii* eaten from mixed presentations was reduced by a third between trials 1 and 2 from a mean of 21.6 to a mean of 7.2.

If the results of prey treatments in both trials are pooled, the birds ate 29% of the first presentation of *A. nerii*, 99% *A. pisum*, 39% and 95% of the *A. nerii* and *A. pisum* respectively when mixed, and 100% of the second *A. pisum* offered. Thus the birds ate 3.42 times more *A. pisum* than *A. nerii* from separate presentations and 2.44 times more *A. pisum* than *A. nerii* from mixed presentations.

Table 3a, b. Comparisons of aposematic *A. nerii* and palatable *A. pisum* eaten by great tits from separate or mixed prey patches in two trial sequences (numbers with percentage in parentheses)

Trial	Number eaten/number offered (%)		
	A. nerii	*A. pisum*	*P*
a Separate aphid presentations			
1	90/320 (28)	317/320 (99)	0.005
2	96/320 (30)	240/240 (100)	0.025
P	NS	NS	
b Mixed aphid presentations			
1	86/160 (54)	146/160 (91)	NS
2	22/120 (18)	120/120 (100)	0.001
P	NS	NS	

Unlike the spiders, the birds did not distinguish between prey subjugation and consumption since all aphids taken from prey patches were apparently swallowed. The only evidence of rejection of attacked aphids was beak-wiping and an emetic response by one bird, having preyed on *A. nerii*, much as described by Brower and Glazier (1975) for blue jays fed monarch butterflies that also contain cardenolides. This suggests that great tits may be as sensitive to cardenolides as blue jays, since if *A. nerii* contains 0.5 μg cardenolide per aphid the dose from approximately 25 *A. nerii* eaten in the first trial by a 20 g great tit would be 0.6 μg/g, compared with an emetic dose of 0.8 μg/g for blue jays (Roeske et al. 1976).

Great tit foraging behaviour

The great tits were also able to distinguish between aphid species and altered their prey response times with experience, to increase their rate of palatable prey consumption. The longest overall mean response time (the time between "look" and "leave" events) was 181.1 seconds by birds in the first trial given only *A. pisum*, and this decreased to 85 seconds in the second trial. The shortest mean response time was 56.7 seconds by birds in the second trial offered the aphid mixture. Birds in the first trial spent most time pecking at mixed aphid patches (Table 4), which may represent prey discrimination costs. But in the second trial the times of summed pecking bouts in prey patches were

Table 4. Times of summed pecking bouts (seconds) and the profitabilities of aphids (numbers eaten (from Table 3)/times of summed pecking bouts) for great tits feeding at patches of aphids presented in two trial sequences, one day apart, with four prey treatments

Treatment	Trial 1		Trial 2	
	$\bar{x}$	SE	$\bar{x}$	SE
Times of summed pecking bouts				
A. pisum	33.30	14.40	20.95	6.05
A. nerii	10.05	9.45	14.80	14.80
Aphid mixture	44.35	11.45	15.70	4.40
A. pisum	26.35	3.25	21.30	1.00
Aphid profitability				
A. pisum	2.96	1.28	3.86	0.53
A. nerii	3.22	0.76	0.98	0.98
Aphid mixture:				
A. nerii	1.00	0.25	0.54	0.01
A. pisum	2.15	1.07	2.77	0.78
A. pisum	3.08	2.18	3.77	0.18

ranked by the birds according to predicted prey profitabilities in the order, *A. pisum*$>$mixed aphids$>$*A. nerii* (Table 4).

This same rank order is even more apparent if prey profitability is measured as a rate by the numbers of aphids eaten (Table 3) divided by the time of summed pecking bouts (Table 4). Profitability of pooled *A. pisum* treatments increased significantly between trials (Wilcoxon matched-pairs signed-ranks test, $P=0.025$), whereas the profitability of pooled *A. nerii* treatments dropped significantly between trials ($P=0.025$).

Discussion

For aposematism to evolve by kin-selection in encounters between a prey species and its predators, distastefulness should reduce predator attack frequency and conspicuousness should effectively advertise low prey profitability. Subsequent prey, detected but not attacked by predators, should also be genetically related so that the shared genotype benefits from the sacrifice of one or a few relatives to predator education.

In the experiments reported here, aposematic aphids were killed in initial encounters with spiders and great tits. Because *A. nerii* did not survive these first predator attacks it cannot benefit individually from its aposematic cues, as has been reasonably claimed for the large, aposematic, tough-bodied insects that survived attacks by birds (Brower and Glazier 1975; Järvi et al. 1981; Sillén-Tullberg et al. 1982; Wiklund and Järvi 1982).

With experience the birds increased their recognition and rejection rates of distasteful *A. nerii*, whilst increasing their recognition and acceptance rates of palatable *A. pisum*. Accordingly the proportion of aposematic aphids that survived subsequent bird encounters increased.

Similarly, the numbers of aposematic aphids killed by the spiders, the proportions of aposematic aphids that the spiders ate, and the rates of predation on aposematic aphids, were all reduced between trials; whereas almost all palatable aphids were killed and eaten. However, although *A. nerii* trapped in spider webs may not be consumed this does not benefit *A. nerii*, nor can it select for aposematism of trapped individuals since they rarely escape from the web, but die there even if uneaten. Webs deal almost indiscriminately with prey detection and pursuit and also to some extent with prey subjugation. For the aphid's aposematism to be effective it must produce a change in spider foraging behaviour that increases aphid fitness. Assuming a cost to web construction, the only foraging responses available to the spider, are either to reduce the frequency of web construction until more profitable prey are caught, or to relocate its web to a more profitable trapping site. Such a reduction in foraging investment by the spider was evident since the frequency of web construction by spiders given *A. nerii* was reduced to almost half that of spiders given only palatable aphids. The spiders also built significantly disrupted and reduced webs, that recovered with time, after feeding on *A. nerii* (Malcolm 1981). With regard to web relocation, Janetos (1982), Olive (1982), and Riechert and Luczak (1982) document evaluation of web site profitability by web-building spiders. They found that spiders remained longer at more profitable than less profitable trapping sites, and the probability of relocating their web, and the distance moved, both increased with decreasing site profitability. Essentially, such spider foraging responses are equivalent to great tits foraging in one patch or foraging elsewhere according to patterns of prey profitability (Gibb and Betts 1963). A spider that builds its web near a colony of *A. nerii* will trap a high proportion of unprofitable flying alates because the aphids are highly aggregated and alate production is synchronised by exponential population growth (Malcolm and B.J. Cockrell, unpublished data). Alternative, palatable prey are unlikely to be abundant around the clumped milkweed hosts of *A. nerii* and so the spider must either wait for alate production to end or move elsewhere.

Thus it follows that aposematism of *A. nerii* must be kin selected with respect to selection by the prey trapping predator guild, since changes in spider foraging that benefit subsequent *A. nerii* cannot benefit trapped aphids.

Ultimately distastefulness is the basis by which aposematic prey profitability is assessed by predators, but a variety of proximate, conspicuous stimuli can be used to facilitate this assessment. For visually foraging predators like birds, aposematic colouration, dense aggregation and synchronised movements of natural *A. nerii* colonies are the most likely conspicuous cues. However for non-visual predators like the web spider *Z. x-notata*, specific frequencies of web-borne vibrations, tactile and olfactory cues are used to detect prey (Barth 1982; Klärner and Barth 1982). These cues should be no less a conspicuous component of aposematism than colouration (Eisner and Grant 1981). Recently, a neotropical orb-weaving spider has been shown to free trapped distasteful prey according to chemical cues and not colouration (Brown 1984; Vasconcellos-Neto and Lewinsohn 1984).

Conspicuous defences can also be enhanced by supplementing the defence with armour and retaliation (Wiklund and Järvi 1982), or by increasing group sizes (Treherne and Foster 1980; Kidd 1982). Soft-bodied, aposematic insects may even be defended against predator subjugation by becoming members of selfish herds (Hamilton 1971) where selection for individuals can operate to lower the probability of predation by reducing the distance between themselves and other individuals. Failing that, their defence operates solely at the acceptance phase of predation when it is possible that many individuals will be sacrificed and evolution may proceed by kin-selection. This sacrifice should be most evident when foraging responses to prey defence are delayed by either inexperience or by the time taken for a predator to respond to low foraging site profitability.

Not only is *A. nerii* aposematic but it is also a highly aggregated species that reproduces parthenogenetically, forming contagiously distributed clones (Hall and Ehler 1980). Thus since sexual *A. nerii* are unknown (H. Dingle, personal communication) and this aphid does not survive predator subjugation, its aposematism may be maintained by kin-selection through altruistic loss of individuals from clones to predator education.

The evolution of conspicuous adaptations through individual selection may be considerably more frequent than by kin-selection, since Vermeij (1982) found that the incidence of unsuccessful predation and sublethal damage was high between 60 predator species and their predominantly armoured prey. Nevertheless, kin-selection for the aposematism of *A. nerii* is a likely consequence of predation pressure on this small, soft-bodied, densely aggregated and parthenogenetic insect. Kin-selection of similar conspicuous, gregarious or aggressive traits is also likely to be the case for other soft-bodied animals, especially apomictic Homoptera.

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