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Genetic variation for the rate of recruitment of novel insect prey into the diet of a bird

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Two lines of quail (*Coturnix coturnix japonicus*) were selected over three generations for the speed of their response to the red colour form of the two-spot ladybird beetle (*Adalia bipunctata*), an aposematic, semi-palatable prey insect. One line was bred for fast recruitment of the new prey into the diet and the other for slow recruitment. Differences between the lines suggested additive genetic variation. The birds' response to insect prey with different colour patterns and toxicities (brown beetles, green butterfly pupae, melanic two-spot ladybirds and toxic seven-spot ladybirds) demonstrated that the selection involved a specific response to novel prey. The results are discussed in relation to predator strategy and the evolution of aposematism.

ADDITIONAL KEY WORDS:–Ladybirds (Coccinellidae) – quail (Coturnix) – selection lines – warning coloration – prey recruitment.

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INTRODUCTION

The evolution of warning colour patterns in prey has been an important topic of research in evolutionary biology (see reviews by Rothschild, 1971;

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Turner, 1987; Guilford, 1988). For evolutionary change to occur, genetic variation must be present. Although such variation has frequently been studied with respect to colour patterns in prey (e.g. Turner, 1977; Sheppard *et al.*, 1985), variation in the response of predators to these signals has rarely been considered. However, the evolutionary dynamics of warning colour patterns will depend on the extent of genetic variation both in prey and in their predators. This study seeks to detect whether genetic variation exists for the response of avian predators (Japanese quail *Coturnix coturnix japonicus* L.) to warningly coloured, mildly distasteful insect prey (two-spot ladybird beetles *Adalia bipunctata* L.).

Quail were chosen because they are known to be variable in their responses to two-spot ladybirds (Marples, 1990). Captive birds tend to fall into two groups: those which take more than 10 encounters to 'recruit' the prey into their diet and those which recruit almost at once. Other workers also report a high degree of intraspecific variation in the response of birds to aposematic insect prey (Brower, 1958a,b; Rettenmeyer, 1970), although in these instances part of the cause is due to variation in the ability to distinguish models from mimics. Kovach (1987) used selection experiments to demonstrate a genetic basis for colour preference (red vs. blue) in quail chicks, but this colour preference was associated with imprinting.

The present study was designed to demonstrate whether there is genetic variation in the foraging response of quail to aposematic prey which are 'semi-palatable' (mildly distasteful but not toxic). The experiment attempted to establish, by selective breeding, lines which differed in this trait. The study consisted of two parts; a main experiment in which large numbers of birds were bred over two generations, and a subsidiary experiment which used a smaller number from the third generation.

METHODS

Feeding behaviour of quail

Captive quail are reluctant to attack novel prey. This 'neophobia' decreases as the individual gains experience with the new prey (Coppinger, 1969). The bird will then attack and taste the prey item and usually drops it uneaten a few times before either eating or rejecting it. This 'screening' may persist for several encounters, with the bird sometimes eating, and sometimes only tasting a given prey type before making a final positive or negative decision about incorporating it into its diet. I define 'screening time' as the time from first tasting the prey until it is recruited into the diet. Such recruitment will lead to the prey being eaten quickly (as defined below) on subsequent encounters. The total time from first encounter to recruitment will be termed 'prey recruitment time' (PRT) and was the trait used as a basis for selective breeding.

Insect prey

To examine variation in recruitment time it was necessary to use a prey item which was: (1) part of, or similar to, the natural diet of the quail; (2)

non-toxic, so the birds would accept it into their diet and (3) semi-palatable so that acceptance would not be immediate. Two-spot ladybirds, *Adalia bipunctata*, were used because they fulfil these requirements (Marples, Brakefield & Cowie, 1989). Of 162 captive quail tested in the present feeding experiments, 96% eventually incorporated two-spot ladybirds into their diet, although 81% showed a delay in recruitment, presumably due to the unpalatability of the prey. Being polymorphic, *A. bipunctata* also allowed two different colour patterns to be tested: a red form with two black spots ('two-spot') and a black form with four or six red spots ('melanic'). Both colour forms contain a similar level and composition of chemical defence (Pasteels *et al.*, 1973; Marples, 1993). The seven-spot ladybird *Coccinella septempunctata* L. was used as a toxic (as opposed to distasteful) insect prey (Marples *et al.*, 1989) to test the relationship between recruitment of edible prey (e.g. two-spot ladybird) and avoidance of toxic prey (seven-spot ladybird). Birds which learn to accept the semi-palatable (but edible) two-spot quickly might be generally insensitive, and so take longer to learn avoidance of the toxic seven-spot. Alternatively, fast recruiters of the two-spot ladybird might be generally fast learners, and also learn to avoid the seven-spot ladybirds quickly. Thus a comparison of recruitment and avoidance learning may give some idea of the mechanism involved.

Three palatable and non-aposematic insects were also used for comparison: light brown mealworms *Tenebrio molitor* L., dark brown lesser mealworm beetles *Alphitobius diaperinus* L. (termed the 'control beetle'), and the green pupae of a tropical satyrine butterfly *Bicyclus anynana* L.

Main experiment (F1 and F2 generations)

During the selective breeding experiment, data were collected for each bird to enable a description of: (1) the prey recruitment time (PRT) for red two-spot ladybirds; (2) the association between PRT and responses to other prey with differing colour patterns and palatability; and (3) the association between PRT and a general index of 'fearfulness' (see 'Measurement of fear' below).

The birds

A flock of Japanese quail was obtained from two suppliers in The Netherlands, 25 males from one and 25 females from the other (to minimize the initial risk of inbreeding in the flock). The birds were caged singly in $1\,m \times \frac{1}{2}\,m \times 1\,m$ high cages, and provided with food (chick crumbs) and water *ad lib.* The room was large and well ventilated and was kept at 21°C with a light : dark regime of 16 : 8 hours.

Birds of the parental stock had probably not encountered live food before the experiment. The two later generations did not encounter live food until the experiment started (when they were 2 months old).

Selection lines

In each generation of selection from the original 50 birds, the five most 'extreme' birds of each sex with the shortest and longest PRTs (see below) were selected as FAST and SLOW parents, respectively. They were then

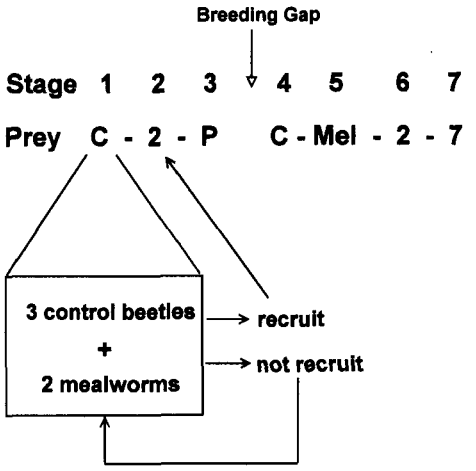

Figure 1. The sequence of prey species offered to each bird. C = control beetles; 2 = two-spot *typica* ladybirds; P = butterfly pupa; Mel = two-spot melanic ladybirds; 7 = seven-spot ladybirds. Each prey type except the seven-spot was presented with two mealworms repeatedly until recruitment occurred (see text).

paired up for breeding; the slowest male was paired with the slowest female, and the fastest male with the fastest female, until six pairings were obtained in each line. One pair in the parental generation in the slow line did not produce viable eggs, but in all other cases six families were raised. Crosses between siblings were avoided, and this appeared to be successful in preventing any inbreeding depression. The eggs from each of the pairs were hatched in an incubator. Hatchlings were colour ringed and raised together. Care was taken to distribute bright colours of rings evenly across lines to prevent differential exposure to bright colours affecting the birds' responses to brightly coloured prey.

The F1 and F2 generations were each raised to 8 weeks of age in one large communal cage. They were then individually caged and tested in the same way as the parental generation.

Treatment sequence

The sequence of prey shown in Figure 1 was offered to each bird, split into two sessions to allow an interim month for breeding. Mealworms and brown control beetles (C) are highly palatable to quail and were given mainly to widen the birds' experience and so reduce neophobia. After this, the main test-insect, the red form of the two-spot ladybird (2), was presented. This provided the values for PRT on which selection was based. With the exception of the parental generation, the birds were then offered another new prey type, a green pupa of a tropical butterfly *Bicyclus anynana* (P), which they found very palatable.

The second session began with control beetles (C), followed by the melanic form of the two-spot ladybird (Mel). The latter acted as a novel prey type, at least as far as colour pattern was concerned, but with the same degree of unpalatability as the red form (2) in the first part of the experiment. Once the melanic form had been recruited into the diet, the birds were

given a second presentation of the red two-spot ladybird (2), to examine the correlation with the measure of their earlier acceptance. Finally they were offered the seven-spot ladybird (7) to see whether those birds that were fast in recruiting prey into their diet were also fast in learning to avoid the toxic seven-spot (i.e. generally faster to learn associations), or whether they were slower (i.e. generally more tolerant of noxious prey). The duration of the seven-spot avoidance was also assessed; for method, see below.

Measurement of feeding responses

In the parental generation, each quail was given two trials per day separated by at least 3 hours. To enable the testing of more birds, in subsequent generations only one trial per day was given. Each trial lasted 5 minutes. Birds were tested in a random order and in their own cages to minimize disturbance. In each trial a bird was offered a dish containing three of the treatment prey and two mealworms. The mealworms acted as an attractant to the quail, ensuring that they saw the treatment prey in each trial.

For the non-toxic prey types (i.e. all prey except the seven-spot), the bird was offered the same species of prey in each trial until recruitment and then the next species in the sequence was offered (Fig. 1). The prey type was deemed to have been recruited if the prey had been eaten in three different trials *and* three prey had been eaten within 3 days. Thus the birds had to demonstrate a willingness over more than 48 hours to continue eating the ladybird at a higher frequency than would be expected were the birds simply forgetting to avoid it.

The criterion for completion of the toxic seven-spot stage was different. Each bird was offered seven-spot ladybirds until it failed to eat any for 3 consecutive days. Daily presentation of seven-spots was continued until the next occasion on which the bird ate one, or for seven more days, whichever was the shorter. This allowed assessment of the duration of seven-spot avoidance.

The response to each prey type (see Fig. 1) was measured both as the total number of minutes before each bird tasted the first of that prey type, and the total time from first presentation until recruitment (prey recruitment time, PRT). This also allowed a 'screening' time to be calculated which measured the period of time between the bird's first taste of the beetle and recruiting it (PRT minus the time before the first beetle was tasted).

Measurement of 'fear'

Any difference between birds of each line in their PRT could be a side-effect of general 'fearfulness', rather than a difference in specific responsiveness to novel prey. To assess this possibility, birds were tested after the first session of feeding trials in an unfamiliar 1 m × 1 m square cage. The cage contained two bright yellow corrugated plastic boards placed at an angle to each side of the cage so that they converged towards the back. At the narrow end of this passage was placed a dish containing three mealworms. The birds were placed at the wide end of the passage, one at a time, viewing the mealworms at the other end. The time taken for each bird to

approach and eat the mealworms was recorded. If the bird took more than 30 min, the trial was stopped. When offered mealworms in their home cages the birds invariably approached and ate them within a minute, so the much slower approach found under these circumstances was taken to indicate a fear of the unfamiliar surroundings.

For the F1 and F2 generations a second test was performed at the end of the second feeding session. The same cage was used, but with two large, brightly coloured plastic pompoms, one blue and one pink, in the position of the plastic boards. The correlation between this second estimate of 'fearfulness' and the first was intended to demonstrate whether the test was measuring a specific reaction to the yellow boards, or a general fear of the novel surroundings.

Subsidiary test (F3 generation)

The single most extreme fast and slow pairs from the F2 generation were bred and six offspring from each raised to form an F3 generation of 12 birds, six 'FAST' and six 'SLOW'. These were tested for their readiness to attack and eat seven-spot ladybirds when naive to them. The procedure was the same as in the Main Experiment.

RESULTS

Main experiment

Table 1 shows the differences in the above parameters across lines in each generation, and between families. The differences were in the direction of shorter PRTs in the fast line (although statistical significance was restricted

TABLE 1. Mean values for the fast and slow lines and Mann-Whitney values (W) for the FAST/SLOW comparisons. Numbers in brackets indicate the number of birds whose data was used (n) in each breeding line. Kruskal-Wallis values (H) are given for the family comparisons, and df = 10 in each case. Data are given for the total prey recruitment time (PRT) of two-spots, time before first sampling (mins. to 1st) and time between first sampling and acceptance (screening) in the F1 and F2. Significance values: * = $P < 0.05$; ** = $P < 0.01$

			F1 Mean	$W(n)$		F2 Mean	$W(n)$
FAST/SLOW	total PRT	FAST	8.77	574*	FAST	5.93	670
		SLOW	10.17	(27,24)	SLOW	6.75	(27,24)
	mins to 1st	FAST	11.80	738	FAST	7.38	706*
		SLOW	13.08	(30,24)	SLOW	11.85	(29,27)
	screening	FAST	26.67	646	FAST	22.11	730
		SLOW	37.75	(27,24)	SLOW	22.58	(27,24)
			H			H	
Family	total PRT		15.9			25.4**	
	mins to 1st		13.2			25.9**	
	screening		12.7			12.5	

to the F1 generation), and shorter times before first attack on the two-spot ladybird (significant only in the F2). In both selection lines the PRT and times before first acceptance decreased between generations, although these differences were not significant (Mann-Whitney tests NS in each case).

There were strongly significant differences between families for both these parameters (see Table 1), but in neither generation was there any difference in screening times between lines or families. When the birds from the F1 and F2 generations were pooled, the FAST and SLOW lines differed significantly both in the total PRT (means FAST = 6.17, SLOW = 8.46; W = 2434.5, $n = 54,48$, $P = 0.02$) and in the time before the first two-spot was sampled (means FAST = 9.63, SLOW = 12.43; W = 2838, $n = 59,51$, $P = 0.008$). Offspring-parent regressions based on the very small numbers of families showed positive slopes for PRT and time before the first two-spot was eaten, although they were non-significant in each generation.

The differences in screening time for both selection lines and family were non-significant, but the effect of sex was highly significant, males eating more slowly than females. This was true for both the first and second presentations of two-spot ladybirds (first presentation, $P < 0.001$; second presentation, $P < 0.001$). However, the males displayed a courtship feeding behaviour, even in the absence of a female, which slowed their consumption of the mealworms, before attacking the other food items presented. This is probably responsible for the screening difference found between the sexes.

By the F2 generation there was no significant difference in the initial time taken to attack the more effectively defended (i.e. toxic) seven-spot ladybirds (Mean FAST = 7.0, SLOW = 8.21; W = 644.5, $n = 27,24$, $P =$ NS) but the FAST line birds continued to accept seven-spots for longer than the SLOW line birds (Mean FAST = 5.67, SLOW = 3.05, W = 522.5, $n = 21,20$, $P = 0.033$).

There was no difference between FAST and SLOW birds in their response to the other treatment insects (Table 2), although there are differences between families in response to mealworms in the F1 and melanic two-spots in the F2. No differences were found between the lines in the fear experiment (Table 3). The two fear trials, one with yellow boards and one with pompoms, showed substantial variation between birds. Responses to the two tests were significantly correlated (F1: $r_s = 0.332$, df = 52, $P < 0.05$; F2: $r_s = 0.458$, df = 57, $P < 0.001$), indicating consistent individual differences in 'fearfulness'.

Analysis of the correlations between responses to different prey items for each line reveals a large number of significant ($P < 0.05$) correlations, indicating that the predation responses to the prey types were strongly interrelated.

Subsidiary test (F3)

The results of the subsidiary test on birds of the F3 generation are given in Table 4. A Mann-Whitney test comparing the number of seven-spot ladybirds eaten by birds from each line showed a significant difference, despite the small sample size (W = 53.0, $n = 6,6$, $P < 0.05$). This is clearly demonstrated by a graph of the number of seven-spot ladybirds eaten each day (Fig. 2).

TABLE 2. Mean values for the FAST (F) and SLOW (S) lines with Mann-Whitney values (W) for FAST-SLOW comparisons. Numbers in brackets indicate the number of birds whose data was used (n) in each breeding line. Kruskal-Wallis values (H) are given for the family comparisons, and df = 10 in each case. Data are given for total prey recruitment time (PRT), time before first sampling (min to 1st) of mealworms, control beetles and melanic two-spots in each generation. Significance values: * = $P < 0.05$; ** = $P < 0.01$

	Parental			F1			F2	
		Mean	$W(n)$		Mean	$W(n)$	Mean	$W(n)$
Mealworm								
F/S total PRT	F	3.33	135	F	5.30	743	F 3.41	824
	S	3.40	(12,10)	S	5.92	(30,24)	S 3.36	(29,28)
mins to 1st	F	2.08	127	F	13.30	731	F 3.90	854
	S	3.70	(12,10)	S	15.92	(30,24)	S 3.21	(29,28)
Family total PRT			–		$H = 24.9$**		$H = 10.7$	
mins to 1st			–		$H = 26.7$**		$H = 8.7$	
Control beetle								
F/S total PRT	F	3.50	104*	F	3.60	832	F 3.27	863
	S	4.10	(12,10)	S	3.38	(30,24)	S 3.46	(30,28)
mins to 1st	F	1.08	113	F	3.73	828	F 2.13	856
	S	2.30	(12,10)	S	4.04	(30,24)	S 2.75	(30,28)
Family total PRT			–		$H = 15.8$		$H = 9.2$	
mins to 1st			–		$H = 20.3$*		$H = 15.9$	
Melanic two-spot								
F/S total PRT	F	4.00	114	F	8.59	612	F 5.17	779
	S	6.63	(12,8)	S	7.04	(26,23)	S 4.71	(29,24)
mins to 1st	F	5.58	113.5	F	10.78	616	F 7.50	799
	S	22.10	(12,10)	S	11.00	(27,23)	S 4.76	(30,25)
Family total PRT			–		$H = 15.8$		$H = 20.4$*	
mins to 1st			–		$H = 11.8$		$H = 22.0$*	

TABLE 3. Mean times taken by birds in each breeding line to approach mealworms offered in a new cage near to yellow screens or brightly coloured pom-poms. Mann-Whitney values (W) are given for each FAST/SLOW comparison. Numbers in brackets indicate the number of birds whose data was used (n) in each breeding line

	Parental		F1		F2	
	Mean	$W(n)$	Mean	$W(n)$	Mean	$W(n)$
Screens						
Fast	10.50	126.5	9.73	595.5	3.82	720.5
Slow	11.29	(10,7)	9.11	(26,18)	6.88	(28,26)
Pom-poms						
Fast	–		10.79	306.5	6.62	581.5
Slow	–		11.42	(19,12)	8.88	(26,24)

DISCUSSION

The results demonstrate additive genetic variance for the speed with which quail recruit a new prey item to their diet. Selection led to a divergence between the FAST and SLOW prey recruitment lines in the main experiment (F1 and F2 generations), plus even more marked differences between lines

TABLE 4. Seven-spot ladybirds eaten by birds in the 'fast' and 'slow' selection lines on each day of the experiment, during which they were offered three ladybirds per day

Birds	Days 1	2	3	4	5	Total
Fast						
1	1	0	1	0	1	3
2	0	3	1	1	0	5
3	0	0	0	0	0	0
4	0	0	0	0	1	1
5	0	0	0	1	1	2
6	1	3	1	2	1	8
						–
						19
						–
Slow						
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	0	0	0	0	0	0
4	0	0	1	0	0	1
5	0	0	0	0	0	0
6	0	0	0	0	0	0
						–
						1
						–

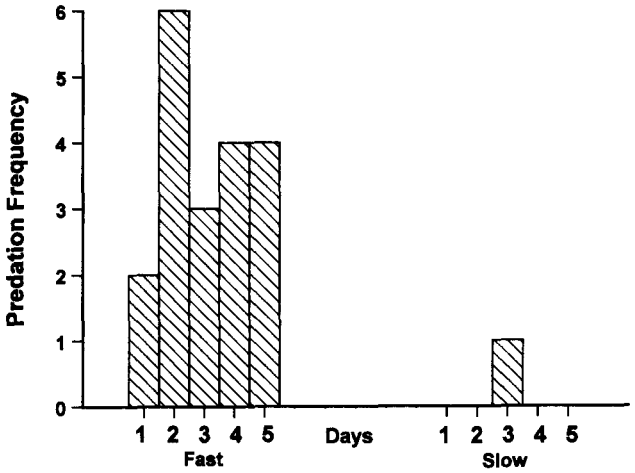

Figure 2. The total numbers of seven-spot ladybirds eaten each day by birds from the F3 generation of the FAST and SLOW selection lines.

in their avoidance behaviour, as shown in the F3 generation in the subsidiary experiment. There was also a strong family effect, siblings being more similar to one another than to the population as a whole. Such a difference between families when all birds were raised together in one 'creche' and without parental contact argues for a genetic component just as strongly as differences between the selection lines.

The results give some indication of how this difference may be mediated. The two 'fearfulness' tests revealed no correlation between selection line and the speed of eating in a new environment. Furthermore, the two tests gave correlated responses, suggesting they were testing the same attribute. These results indicate that the recruitment differences between lines are not explicable in terms of general differences in boldness or fearfulness.

The mealworms, control beetles and butterfly pupae, when first encountered, were very quickly accepted by all the birds, presumably due to their high level of palatability. This allowed little time for any difference between the lines, in response to palatable prey, to be detected. However, the results suggest that a correlation with selection line was present in the parental generation's recruitment of the brown control beetle. In the F1, both mealworms and control beetles showed significant family effects, so even for these quickly recruited insects, the foraging behaviours of the two lines were at least partially distinct.

The mildly distasteful and brightly coloured two-spot ladybird was more slowly recruited, allowing more opportunity for the detection of differences in recruitment parameters. Very little variation was found in the duration of the screening period; variation was most extreme in the time taken before first eating the beetle. This argues for the effect being based on perceptual differences, such as those related to the prey's appearance, taste or smell, rather than on differences related to the physiological effects of the prey, such as poisoning.

The responses to the melanic two-spot ladybirds showed a strong family effect in the F2, but there was no effect of selection line. Birds might be expected to show the same degree of separation in their speed of recruitment of melanic ladybirds as they showed in response to the red ones. However, experience with the taste of two-spot ladybirds, and the less conspicuous colour pattern of the melanic ladybirds may have caused the birds to recruit them before a difference between the lines could be detected. The second presentation of two-spot ladybirds also failed to demonstrate any difference between the lines as re-recruitment was too fast.

Presentation of the aversive seven-spot ladybird in the main experiment showed that the FAST birds accepted them for longer before learning to avoid them, although they did not then avoid them for longer than SLOW line birds. The subsidiary experiment confirms this finding, with far more seven-spot ladybirds eaten over a five-day period by birds from the FAST line than by SLOW line birds. Taken in conjunction with their faster acceptance of two-spot ladybirds, these observations suggest that FAST birds are either more inquisitive or more insensitive to the ladybirds' defensive chemicals. It appeared that the birds could taste the defensive chemicals present in seven-spot ladybirds, as they crushed and then abandoned them regularly, and performed beak-wiping behaviour after touching one with their beak. No difference between the lines was evident in the number of times they crushed but did not eat a ladybird, each line averaging three per bird in the F2 generation.

The exact nature of the difference between FAST and SLOW recruiting birds needs more study, but the present results show that there is additive genetic variation and that the trait in question is associated with foraging on

unfamiliar prey items, rather than with a more general fearfulness or insensitivity. The phenomenon may be widely present but undetected in other data sets, as many experiments include a selection procedure which excludes individuals failing to accept the prey used in training (Brower, 1958b; Roper & Redstone, 1987). Such studies only test animals which are more adventurous in their feeding behaviour, and which may therefore be a biased sample of the population. Workers who do not select subjects in this way may be able to reduce the variance in their data by analysing comparatively fast and slow predators separately.

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