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STARTLE AND HABITUATION RESPONSES OF BLUE JAYS (CYANOCITTA CRISTATA) IN A LABORATORY SIMULATION OF ANTI-PREDATOR DEFENSES OF CATOCALA MOTHS (LEPIDOPTERA: NOCTUIDAE)

by

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(With 5 Figures)
(Acc. 9-VII-1993)

Summary

Blue jays were used in laboratory experiments to determine what visual characteristics of *Catocala* hindwings are important in eliciting and maintaining startle reactions in avian predators. Hand-reared blue jays, inexperienced with warningly coloured, inedible prey, took significantly longer to touch novel colours that possessed bold, black bands than to touch novel, unbanded colours when these discs covered a food reward. Thus, being conspicuous (as opposed to simply being novel) appears to enhance startle reactions. Bold patterns are commonly found on aposematic prey and *Catocala* hindwings. These same hand-reared birds also tended to take longer to touch novel coloured discs of yellow and red hues as opposed to discs of blue, green, or purple hues. The colours that produced the greatest hesitation are similar to the colours found on *Catocala* hindwings. Red-yellow colours are also characteristic of aposematic prey. Wild-caught birds took longer to habituate to startling stimuli when presented with several different startling disc types during the habituation process. Thus, predator pressure may explain why several different *Catocala* species with different hindwing colours occur sympatrically.

Introduction

The relationships between predators and their prey can be analyzed as a series of strategies and counterstrategies. Prey are under selective pres-

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sure to evolve mechanisms that help them avoid predation, and predators are under pressure to evolve more effective methods of obtaining prey. The relationship between *Catocala* moths and birds is a classic example of such predator-prey interactions. Since the moths of this genus are palatable (JONES, 1932; SARGENT, 1973b, 1990), they are under presure to evolve adaptations that help them avoid detection and capture.

Catocala are night flying insects that rest by day on tree trunks (SARGENT, 1976). The forewings of most species resemble the bark of the trees on which they rest, and experimental studies have demonstrated that these moths will choose appropriate backgrounds and orient on these backgrounds to maximize crypsis (SARGENT, 1966, 1968, 1969a & b, 1973a; KEIPER, 1968; SARGENT & KEIPER, 1969).

Catocala moths also have a startle device that they can use when crypsis fails. When disturbed, these moths spread their cryptic forewings to expose hindwings which have either bright colours with black bands or are solid black. Evidence from field and laboratory studies indicates that the sudden presentation of *Catocala* hindwings will startle birds (SARGENT, 1973b; VAUGHAN, 1983; SCHLENOFF, 1985).

Exactly why these hindwings startle birds is not completely understood, although there are a number of factors that may be involved (SARGENT, 1990). The hindwings may mimic some characters of noxious prey, causing birds to avoid them through association with prior negative experiences (BROWER, 1958; BROWER & BROWER, 1962). The hindwings may also elicit innate avoidance because they mimic characteristics of noxious or dangerous animals that can be found in the same environment (SMITH, 1975, 1977; CALDWELL & RUBINOFF, 1983). On the other hand, the hindwings may produce startle reactions in birds simply because they are novel. It is well established that many animals are reluctant to take novel food items (BARNETT, 1958; COPPINGER, 1969, 1970; CARROLL *et al.*, 1975; DOMJAN & GILLIAN, 1976; DOMJAN, 1977; VAUGHAN, 1983).

Recent research, however, has shown that novelty alone may not be enough to startle blue jays that are trained to take food in a controlled laboratory setting. Working with blue jays and moth models, SCHLENOFF (1985) found that the sudden appearance of novel grey hindwings did not elicit startle, whereas the sudden appearance of hindwings that had novel colours with black bands did. These results suggest that brightly coloured and patterned hindwings may startle birds because they are "conspicuous" (*i.e.* intense, with strong contrasts – see SARGENT, 1990). On the other hand, if birds were habituated to the brightly coloured and patterned startling hindwing models, presentation of grey hindwing models did cause them to startle (SCHLENOFF, 1985). This result supports the hypothesis that animals may startle to stimuli that are unexpected or out-of-context (SARGENT, 1973b, 1978, 1990).

The adaptive predator response to a startle display is habituation (THORPE, 1963; SCHLENOFF, 1985; SARGENT, 1990). From what we know of habituation, we can generate several predictions regarding the appearance and/or behaviour of prey whose successful avoidance of attack depends upon prolonging or negating the habituation process in predators (see THOMPSON & SPENCER, 1966 for a review of the characteristics of habituation). Startle displays should involve sudden movements, strange or unusual stimulus characteristics, or stimuli of a very intense nature. One would also expect startling prey to be rare (*i.e.* encountered infrequently) or found in association with other types of frightening prey so that predators would rarely see a succession of any one type of startle stimulus (SARGENT, 1990).

In view of this last point, it is not surprising that many *Catocala* species displaying a diverse array of hindwing types often occur together in nature (SARGENT, 1976), but it is not clear why there are no hindwing polymorphisms in the genus. In all members of a species, not only is the colour of the hindwings the same, but the banding patterns are nearly identical (SARGENT, 1973b, 1976).

It is possible that there is a limit to the effectiveness of diversity as an interfering factor in the habituation process. For example, with a limited number of hindwing types, birds may attempt to form predictions concerning the type of hindwing that is concealed by a *Catocala* moth, causing birds to startle if their expectations are not met (SCHLENOFF, 1985). If, however, diversity were so great that successive encounters with any one stimulus rarely occurred, then novelty might become the rule and the phenomenon to which habituation occurs. If this were true, predators might take longer to habituate to two or three different hindwing types than to a larger array of different hindwing types.

Given the evidence that *Catocala* hindwings do startle blue jays and that these birds do habituate to simulated startle displays, the following experiments were designed to investigate various aspects of the relationship between startle and habituation. Specifically, experiments were designed to address the following questions: (1) does the presence of a banding pattern enhance the startle reaction to novel coloured stimuli, and (2) does the number of different stimulus types affect the rate of habituation such that increasing the diversity of stimulus types may either increase or possibly decrease the number of stimulus encounters necessary to produce habituation.

General methods

The experimental apparatus was a rectangular wooden board (115.0 cm × 25.5 cm) which had 24 feeding stations where blue jays could carry out a behavioural sequence in order to obtain a food reward (Fig. 1). Each feading station consisted of an 11 mm diameter well covered by a 21 mm diameter disc that was in turn covered by a masonite flap. Birds had to push the masone flap aside in order to expose the disc and then remove the disc to gain access to the food reward (one-half of a mealworm, *Tenebrio* larvae).

The masonite flaps were braced against each other such that the subject had to trigger each flap in order (*i.e.* the bird had to trigger flap one before it could trigger flap two and flap two before flap three). Each flap was attached to a rubber band that was anchored to the bottom of the board (Fig. 1). Thus, once a bird gave a flap a strong push, it would quickly snap aside to reveal the underlying disc. Although the masonite flaps had to be pushed aside in sequence (from right to left), it was not necessary for a bird to remove a disc or take a food reward in order to proceed to the next flap.

The patterns and colours on the discs were the experimental variable in this study and were varied as required by each experiment. Birds manipulated the discs by grasping a

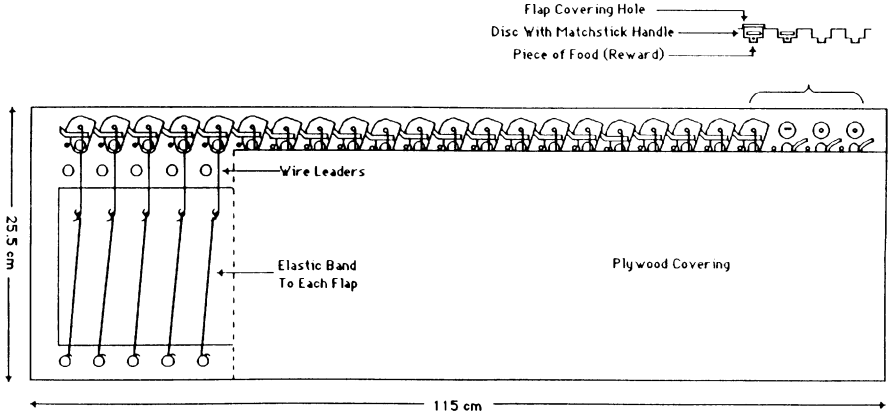

Fig. 1. The experimental apparatus was a wooden board with 24 wells cut into it; each well was covered by a cardboard disc that was in turn covered by a masonite flap. The flaps could only be opened in sequence from right to left. In this illustration, the bird has pushed aside the first three flaps, removed the first two discs, and eaten the food that was located behind these discs.

piece of matchstick that was glued to each disc. These handles were not coloured or treated in any way.

A computer was used as a timing device to measure how long it took a bird to touch each disc once the disc had been exposed. Data were manually recorded by pushing the one button located on a joystick each time the bird pushed a flap aside and again when it touched the disc beneath. If the bird did not take a disc, pushing the joystick in any direction would reset the system.

These experiments were conducted at the University of Massachusetts in Amherst between 1981 and 1985. Locally obtained blue jays (*Cyanocitta cristata*) were the subjects in all experiments. During experiments, birds were maintained at 90% of free feeding weight and were always fed at the end of the day. Water was available at all times in the home cage. Birds were kept on a 14:10 hour daily light-dark schedule (800 hours to 2200 hours light, EST).

During the experiments, the birds were housed individually in 61 × 61 × 46 cm cages. An opening with a sliding door was located at one end of each cage, and a traveling cage could be attached there to facilitate transport of the bird to the experimental cage. Birds were weighed while in the traveling cage just prior to the first experimental session of the day. A sliding door controlled by a string regulated the bird's entrance into the experimental cage. At the end of an experimental session, the bird was returned to its home cage via the traveling cage.

Experiment I

Procedure.

Given that visually novel food items will startle birds, Experiment I was designed to determine whether blue jays would take significantly longer to touch novel coloured discs that possess a bold, black banding pattern as opposed to unbanded coloured discs when these discs covered a food reward. Although this experiment was not specifically designed to compare the startling effects of different novel colours, some evaluation was possible.

Hand-reared birds were used in this experiment. In order to investigate the response of naive birds to novel stimuli, it was necessary to use birds that had never encountered warmingly-coloured (aposematic) prey or any other kind of unpalatable food.

The blue jays were trained to use the experimental board with control discs that were painted grey. These discs had a white base coat and then two coats of grey made from a 3:1 white to black mixture of glossy paint. The experimental discs were made using nine

TABLE 1. The values designated by the Munsell Color Company to identify the nine colours used in Experiment I

Hue	Symbol	Value/Chroma
blue	B 5	6/6
purple-blue	PB 7.5	6/10
purple	P 5	6/8
red-purple	RP 7.5	6/10
red	R 5	6/10
yellow-red	YR 2.5	6/14
yellow	Y 2.5	6/8
green-yellow	GY 7.5	6/10
green	G 7.5	6/6

"Value" indicates the reflectance and "Chroma" indicates the saturation of each colour.

coloured papers that were obtained from the Munsell Book of Color (Neighboring Hues Edition, matte surface samples, 1963) (Table 1). Colours of equal brightness were selected, but it was impossible to obtain both equal brightness and equal saturation for many different colours. Each coloured paper was cut and glued onto cardboard discs to make the experimental stimuli. Three vertical bands, 3.2 mm wide and spaced approximately 3.2 mm apart, were added to some discs by marking them with a black colouring pencil, roughly mimicking the banding pattern found on some *Catocala* hindwings.

The experiment proper lasted nine days. The birds were tested once a day between 1600 and 1800 hours, EST. On each day, a bird encountered 21 control discs and three experimental discs in the experimental board. The three experimental discs were always of the same type on any one day (*e.g.* all solid yellow or all solid blue or all banded red). The three experimental discs were placed randomly in the board, with the following constraint: the board was divided into three equal regions of eight consecutive stations each, and each of these regions contained one randomly placed experimental disc. There were no external markers to indicate which flaps hid the experimental discs. An experimental session began when the first disc was exposed and ended when the bird had exposed all 24 discs.

The birds were divided into two groups, each of which consisted of four birds. Birds in group 1 received solid-coloured experimental discs each day for nine days. Birds in group 2 received solid colours for four days and colours with black bands for the next five days. All birds were presented with a different colour on each day of the experiment. Each bird in group 1 was paired with a bird in group 2, and paired birds received the same sequence of colours during the experiment (Fig. 2). The colour sequences for each pair were randomly determined.

After running the first four birds (two from the banded group and two from the solid group), the equipment was upgraded. Thus, the timing device for birds 2, BL, 6, and 10 was accurate to 0.1 second. All other measurements were made using a timing device that was accurate to approximately 0.017 second. The median response time to touch control discs for the eight birds ranged from 0.26 to 1.00 second.

In order to quantitatively compare the colours shown to the birds with those found on *Catocala* hindwings, discs composed of the coloured portions of the hindwings of three different species of *Catocala* moths were made. Then, the spectral characteristics of these *Catocala* hindwing discs, along with the discs made from the Munsell colours were analyzed using a GE Recording Spectophotometer (Table 2). The three species which were selected to represent the three basic colours found on *Catocala* hindwings were *C. concumbens* (pink), *C. ultronia* (red), and *C. gracilis* (yellow). A minimum of five individuals was used to construct the hindwing disc for each species. The relationships of the hues of the hindwing colours and the coloured papers are illustrated in Fig. 3. The values for the *Catocala* hindwings are an average of two separate readings done on each sample.

Analysis and results.

I compared each bird's latency to touch the experimental discs with its latency to touch its own control discs on each day of the experiment in order to compensate for differences in individual birds' reactions to the experimental board. Each bird's latency to touch experimental discs was converted into a ratio percent (percent latency to touch control discs) for each day of the experiment. This value was obtained by dividing a bird's mean latency to touch the experimental discs by its mean latency to touch control discs for each day of the experiment and multiplying this number

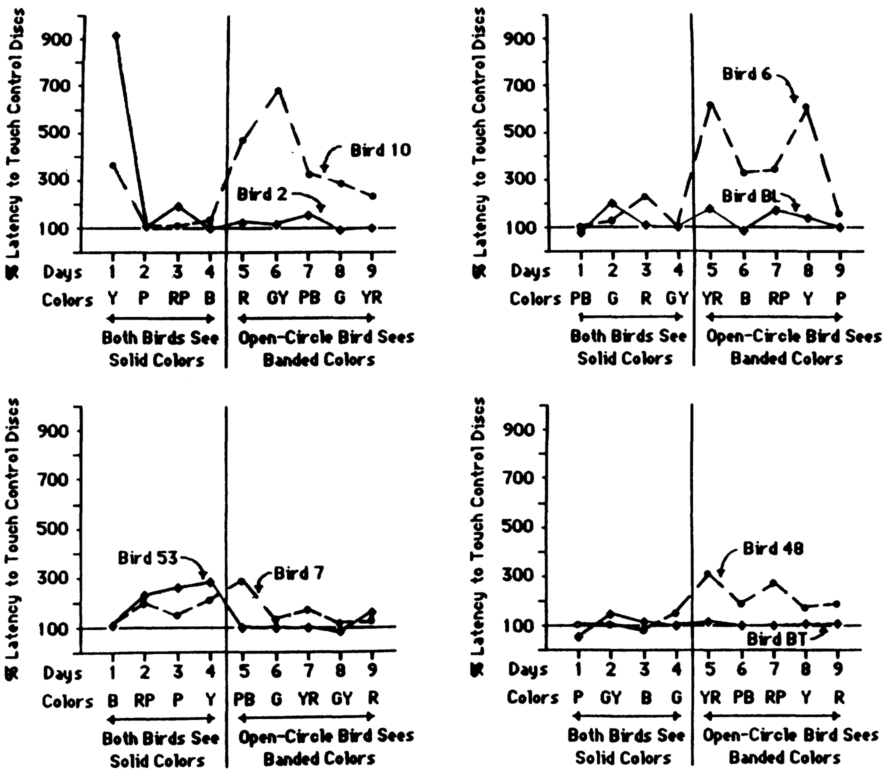

Fig. 2. The latencies of individual birds to touch the Experimental discs in experiment I. Latencies are expressed as percentages of the latency to touch control discs. If a bird's response to the experimental discs was equal to its response to the control discs on a particular day, the percent latency would be 100. This is indicated by a line on each graph. Solid dots connected by solid lines represent birds that saw only solid colours throughout the experiment; open dots connected by dashed lines represent birds that saw banded colours beginning on the fifth day of the experiment. Colour codes are listed in Table 1.

by 100. Thus, if a bird's responses to the experimental discs were the same as its responses to the control discs on a given day, the ratio percent would equal 100. If the bird touched the experimental discs more quickly than the controls, the ratio percent would be less than 100. If a bird failed to touch a disc, the latency was scored as 10 seconds. This was longer than the longest latency for any disc that was touched in this experiment, 7.96 seconds. The ratio percents were used in ranking each bird's reactions to the various colours and to determine if birds reacted differently to solid versus banded novel colours.

TABLE 2. Spectrophotometer readings of the nine coloured papers used in Experiment I and of the coloured portions taken from the hindwings of three species of *Catocala* moths

Papers/Moths	L	A	B
Papers			
Blue (B)	54.1	-16.3	-16.7
Purple-Blue (PB)	53.6	6.9	-39.0
Purple (P)	53.6	18.2	-23.4
Red-Purple (RP)	54.0	38.2	1.2
Red (R)	53.3	38.7	13.9
Yellow-Red (YR)	53.8	39.9	30.7
Yellow (Y)	54.5	6.7	29.2
Green-Yellow (GY)	54.1	-26.2	28.8
Green (G)	54.2	-24.4	6.7
Moths			
C. concumbens (pink)	44.2	26.1	14.0
C. ultronia (red)	41.5	21.3	17.7
C. gracilis (yellow)	52.4	9.8	23.8

"L" represents a light-dark (brightness) value; "A" represents a reading along the red-green spectrum (red is positive and green is negative); and "B" represents a reading along the yellow-blue spectrum (yellow is positive and blue is negative).

The data are not normally distributed and all attempts to transform the data to allow the use of parametric statistics were unsuccessful. The Friedman's two-way analysis of variance by ranks (SIEGEL, 1956) was used to determine if birds responded differently to banded, as opposed to solid novel colours. The ratio percent for each bird in group 2 (the banded group) was subtraced from the ratio percent of the bird from group 1 (the solid group) that was paired with it. This was done for each pair for each day of the experiment, and these values were used to test for a day effect. A comparison of the birds' responses to solid colours and banded colours is presented in Fig. 4. There was no day effect during the first four days of the experiment when all birds saw solid colours (Friedman two-way analysis of variance by ranks, $N=4$, $k=4$, $p \leq .158$), and there was also no day effect for the second five days of the experiment when the birds in group 2 saw banded colours (Friedman two-way analysis of variance, $N=4$, $k=5$, $p \leq .10$). There was, however, a day effect across the entire nine days of the experiment (Friedman two-way analysis of variance, $N=4$, $k=9$, $p \leq .0.1$). Thus, the day effect occurred between days four and five, and inspection of the data show that this effect was produced when the

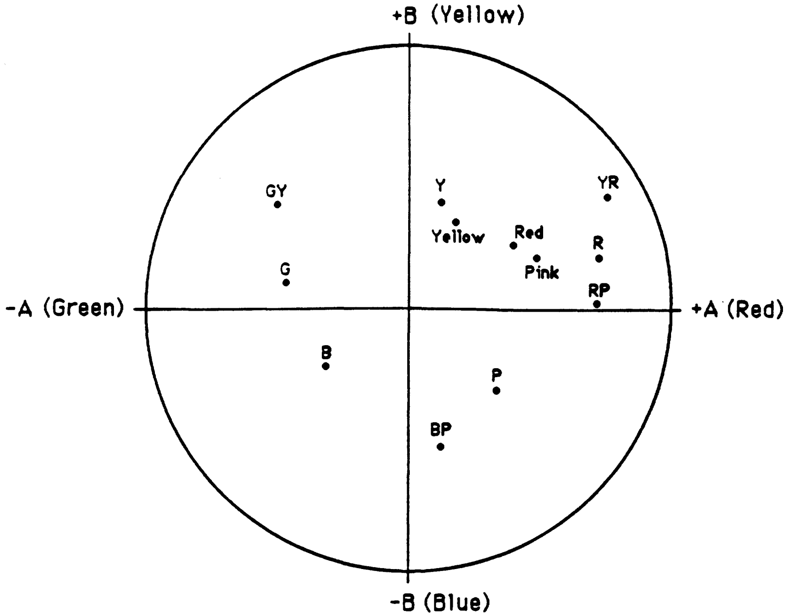

Fig. 3. A "colour wheel" illustrating the relationships among the colours used in Experiment I and selected *Catocala* hindwings. The A and B values of each colour were plotted. Coloured papers are represented by letters, and the hindwing colours by "pink", "red" and "yellow" (see Table 2).

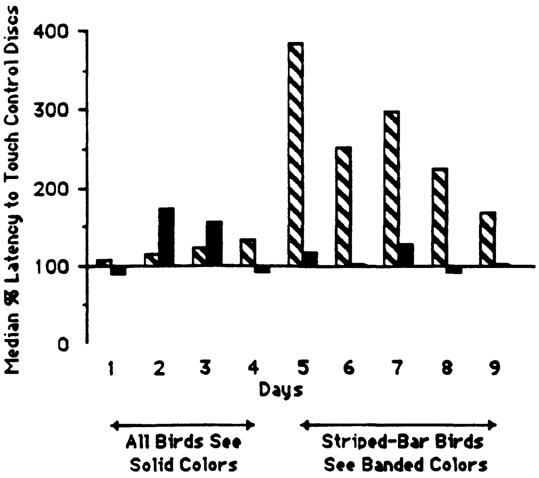

Fig. 4. The median percent latency of responses to control discs for the four birds in each of the two experimental groups in Experiment I. When the birds' responses to the experimental discs are equal to the control discs, the percent latency is 100. The black bars represent the birds that saw solid colours for the entire experiment, and the striped bars represent the birds that saw banded colours beginning on the fifth day of the experiment.

birds in group 2 were switched from solid to banded colours. Thus, birds took longer to touch novel colours that had black bands than they did to touch solid novel colours.

In order to compare the effects of the solid colours on the birds, the reaction time of each bird to each of the nine colours was ranked. These rankings were calculated for the birds that saw only solid colours throughout the experiment in order to control for differences between birds and the tendency to habituate to the stimuli over the nine days of the experiment. Then, a mean rank was calculated (Table 3). The birds showed the greatest hesitation to touch yellow discs. The four highest ranking colours (yellow, red-purple, red, and yellow-red) are located in the red-yellow quadrant of the colour wheel. This quadrant also contains the three *Catocala* hindwing colours (Fig. 3). The colours that lie in the red-blue quadrant (purple-blue and purple) produced the shortest latencies.

Experiment II

Procedure.

This experiment was designed to determine how the number of different novel stimuli (or the diversity of the startling stimuli) encountered during the habituation process might affect the number of stimulus presentations necessary to produce a significant decrease in the birds' hesitancy to touch startling discs.

All of the birds in this experiment were obtained as adults from the wild (wild-caught). Thus, these blue jays would have had various experiences in their natural habitat (*e.g.*

TABLE 3. Mean ranks of the birds' responses and colour quadrants for the nine colours used in Experiment I

Colour	Mean rank	Quadrant
yellow	7.25	+A+B
red-purple	6.25	+A+B
red	5.75	+A+B
yellow-red	5.25	+A+B
green-yellow	4.75	−A+B
blue	4.50	−A−B
green	4.00	−A+B
purple-blue	3.75	+A−B
purple	3.50	+A−B

The "quadrant" refers to the area of the "colour wheel" in Fig. 3 where each colour is located.
+A+B=red-yellow quadrant, −A+B=green-yellow quadrant.
+A−B=red-blue quadrant, and −A−B=green-blue quadrant.

encounters with noxious prey and predators) that might effect their reactions to potentially startling stimuli. Using wild-caught birds should give one more confidence when attempting to generalize from laboratory results to field situations.

The birds were trained to operate the experimental board using unpainted grey-brown cardboard discs (made from the cardboard backing of writing tablets). During the experiment, all birds received three experimental discs per session. While training wild-caught birds in a pilot study, it was noted that certain individuals adopted body postures that made pushing aside flaps 23 and 24 very difficult. Given this problem, a decision was made to not place experimental discs under these flaps. Since this left 22 flaps under which to place three experimental discs, flap 1 was also deleted in order to create three equal regions across the board (flaps 2-8, 9-15, and 16-22). Thus, the three experimental discs were distributed in the experimental board with the following constraints: 1) stations 1, 23, and 24 never contained an experimental disc, 2) the rest of the board (stations 2-22) was divided into three equal regions with one experimental disc randomly placed within each of the three regions, and 3) experimental discs were never placed in adjacent stations.

All flaps that covered an experimental disc were marked with a triangular piece of grey tape. Since a bird's expectations can effect startle responses (SCHLENOFF, 1985), this created a situation in which the birds could form expectations concerning what type of experimental stimulus lay beneath a marked flap.

Experimental stimuli consisted of the following disc types: 1) orange with black band, 2) yellow with black bands, 3) pink with black bands, 4) white with black bands, and 5) solid black. These stimuli correspond to the five different *Catocala* hindwing types described by SARGENT & OWEN (1975). Disc were coloured by painting them with Testor's gloss enamel paints. Each colour was equivalent to the colour designated by the Testor's paint company except that pink was made by mixing equal amounts of red and white paint. All patterned discs had three vertical black bands, 3.2 mm wide, made from glossy black Chartpak pressure-sensative graphic tapes.

The 17 subjects in this experiment were divided into five groups. Group 1 consisted of five birds, and each bird was presented with one of the five disc types. Groups 2 through 5 consisted of three birds each. Birds in group 2 received equal numbers of two disc types over the course of the experiment. Similarly, birds in group 3 received three discs types, birds in group 4 received four disc types, and birds in group 5 received five disc types (Table 4). All birds were run in the apparatus until their hesitancy to touch the experimental discs had declined to an equivalent level.

Birds were tested twice a day. The first session began between 1000 and 1300 hours EST, and the second session occurred three hours after the first. If at any time after the beginning of a session the bird stopped pushing barriers aside for a period of two minutes, the session was terminated and the subject was returned to its home cage. All of the subjects' responses were timed using the upgraded equipment described in Experiment I. The median response time to touch control discs for the 17 wild-caught birds ranged from 0.26 to 0.55 seconds.

As outlined above, birds in all groups were presented with three experimental discs per session and had two sessions per day. Thus, the birds in groups 4 and 5 did not see all of their possible disc types in one session, but could see their entire collection of disc types in one day. Birds that were presented with a variety of experimental stimuli received equal numbers of the different disc types. This was accomplished by presenting the bird with its collection of disc types over and over again, with the order of the stimuli that made up that collection randomly arranged each time. Thus, it was possible for a bird to see a particular disc type twice, but never three or more times in a row.

It was necessary to select a method to decide when all of the birds' responses to the experimental discs had decreased to an equivalent level. The Mann-Whitney U-test (SIEGEL, 1956) was used to evaluate the reaction of each bird to the experimental stimuli at the end of each session, and a bird was considered habituated when its latency to touch experimental discs did not differ significantly from its latency to touch control discs (Mann-

TABLE 4. The specific stimuli presented to the birds in Experiment II

Diversity group	Bird	Colour array
1	F	Orange
	K	Black
	B	White
	R	Yellow
	Z	Pink
2	L	Yellow, Pink
	P	Orange, Black
	N	Orange, White
3	I	Yellow, Pink, White
	D	Yellow, Pink, Black
	M	Orange, White, Black
4	O	Orange, White, Pink, Yellow
	H	Orange, White, Pink, Yellow
	A	Orange, White, Black, Yellow
5	G	Orange, White, Pink, Yellow, Black
	C	Orange, White, Pink, Yellow, Black
	J	Orange, White, Pink, Yellow, Black

"Diversity group" is the number of different stimuli presented to each bird during the habituation process. All discs, except black, had three black vertical bands.

Whitney U-test, p≤.01, one-tailed test) for five consecutive experimental sessions. If the bird elected to skip a disc once it was exposed, that disc was ranked as if it had the highest latency.

Occasionally, a bird would not see all three experimental stimuli during a session because the bird would be removed if, after two minutes, it failed a push a barrier aside. Sessions in which a bird saw only one experimental stimulus were disregarded when attempting to determine if a bird had habituated to the stimuli.

Analysis and results.

The number of experimental stimuli seen prior to habituation was taken as the value establishing habituation rate. This number does not include the number of experimental stimuli seen over the five consecutive sessions when the bird did not respond significantly to the experimental discs. This value (the number of experimental discs seen prior to habituation), and the one based on the diversity of stimuli seen (one-five), were then ranked in order to obtain a Spearman rank correlation coefficient (SIEGEL, 1956). There was a significant positive correlation between the number of stimulus types presented to blue jays (Fig. 5) and the number of stimulus presentations required to achieve habituation (Spearman rank

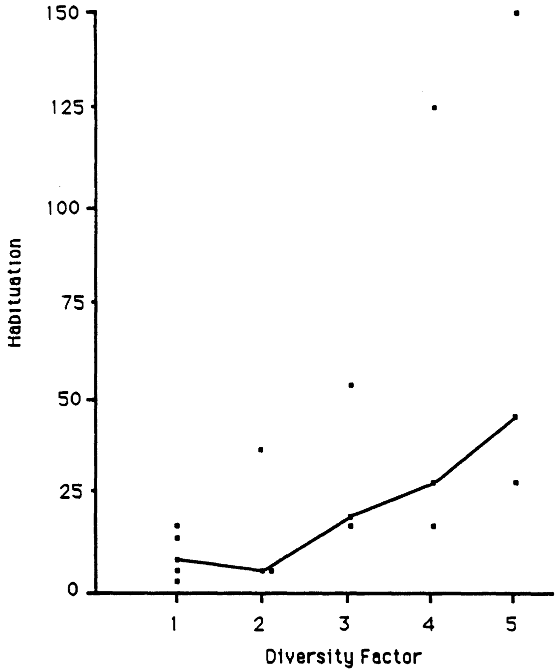

Fig. 5. Habituation versus the number of different startling disc types seen during the habituation process in Experiment II. Each point on the graph represents an individual bird. "Habituation" represents the number of experimental stimuli seen prior to habituation. "Diversity Factor" represents the number of different disc types seen during the habituation process. The highest point for diversity group 5 represents a minimal value for the bird that never habituated (Bird G). The points connected by the line represent the median value for all birds with the same diversity factor.

correlation coefficient, N=17, r=.7474, p≤.002, two-tailed test). Thus, an increase in the diversity of the startling stimuli extended the habituation process. The data do not, however, show a significant increase in the number of any one individual disc type seen prior to habituation as the overall diversity of the experimental stimuli increased (Spearman rank correlation coefficient, N=17, r=.182, p>.10, one-tailed test) (Table 5).

Certain birds reacted very strongly to the experimental discs. One bird in group 5 (bird G) had not habituated after 149 presentations of the stimuli (requiring 59 sessions). At this point, the bird was still electing to skip experimental discs. On rare occasions during the experiment, bird G would take an experimental disc and consume the food behind it. Despite these instances in which the bird could learn that the food was palatable,

TABLE 5. Median number of each individual disc type seen prior to habituation in each diversity group in Experiment II

	Diversity group				
Birds	1	2	3	4	5
1	3	3	5	4	5
2	6	3	6	7	9
3	8	19.5	18	31	>30
4	12				
5	15				
Median for each group	8	3	6	7	9

such experiences did not appear to alter the bird's general reaction of extreme avoidance to the experimental stimuli. This bird was given the highest rank for habituation rate when the Spearman rank correlation coefficient was calculated.

Discussion

Colours and patterns.

Warningly coloured prey often have bold patterns (*e.g.* black bands that have sharp boundaries against lighter colours). These bold patterns may make aposematic prey especially conspicuous, making it easier for predators to learn to avoid them (GITTLEMAN & HARVEY, 1980; GITTLEMAN *et al.*, 1980; SILLEN-TULLBERG, 1985; ROPER & REDSTON, 1987). But will being conspicuous also enhance innate avoidance or startle responses?

The present research suggests that bold black banding patterns (similar to those found on *Catocala* hindwings) will increase the startling effect that novel colours have on birds, even though these birds have had no experience with aposematic prey. Recently, others have shown that stimuli possessing striking visual characteristics, particularly abrupt visual boundaries, may elicit reflex-like avoidance reactions in avian predators (CALDWELL & RUBINOFF, 1983; SCHULER & HESSE, 1985).

Given the design of Experiment I, it is possible that the reaction of the birds to the banded discs was not due to the presence of the bands; it could be argued that the birds would have startled to any change in the experimental stimuli. This seems unlikely given the following two observations. First, initial reactions of the naive, hand-reared birds to the solid, novel colours were quite mild (except for yellow), and they often treated the solid-coloured discs as if they were control discs. Thus, a change from all control discs to solid-coloured discs did not cause hesitation to touch these discs in most cases. For example, on the first day of the experiment, six of the eight birds did not hesitate to touch their coloured discs; again, the two birds that did hesitate to touch the experimental discs were the two that saw yellow. On the second day of the experiment, the two birds that had hesitated to touch yellow did not hesitate to touch purple discs (Fig. 2). Thus, the bird did not hesitate to touch the novel colours in general, but they had very strong responses to the banded colours. Second, in Experiment II, the birds that received banded discs as their first novel disc type were very reluctant to touch these discs (see discussion of diversity and habituation); whereas, birds that were first presented with solid black discs did not show the extreme avoidance observed with banded discs even though black has been found to be an aversive stimulus for blue jays (VAUGHAN, 1983).

As noted by SARGENT (1990), most experiments studying startle reactions have confounded conspicuousness and novelty. The present research, however, certainly suggests that unbanded novel colours are far less effective at producing avoicance reactions then are novel coloured stimuli that have bold black patterns. Thus, it is likely that these bold patterns help make *Catocala* hindwings more conspicuous and therefore more effective as startling stimuli.

Differences in the birds' reactions to the various colours were not expected since VAUGHAN (1983) had found no colour effects when he tested blue jays in the same apparatus using novel colours of blue, yellow, green, red, and white. It was observed, however, that some colours produced more hesitation then others. These results probably differed from VAUGHAN's (1983) because different background colours were used during the experiments; Experiment I used grey as the background colour, and VAUGHAN used either red or blue. Other research indicates that different control colours (or background colours) influence a bird's reactions to novel stimuli of other colours (GITTLEMAN & HARVEY, 1980; GITTLEMAN *et al.*, 1980; ROPER & REDSTON, 1987; ROPER, 1990).

The colours found on chromatic *Catocala* hindwings (yellow, red-orange, and pink) are similar to the colours that produced the greatest hesitancy in the hand-reared blue jays used in Experiment I. Red and yellow are also the colours that are most commonly found on aposematic prey (*e.g.* WICKLER, 1968; RETTENMEYER, 1970; EDMUNDS, 1972).

Diversity and habituation.

According to THOMPSON & SPENCER (1966), habituation to a variety of stimuli that are perceived as different should take longer than habituation to one stimulus, assuming that all other factors (such as the frequency of stimulus presentations) are equal. Given that each *Catocala* species has only one hindwing type and that the expectations birds form may affect startle responses, the goal of Experiment II was to determine how the variety of startling stimuli would affect the rate at which birds habituate. There was the possibility that birds might habituate more rapidly when presented with many different disc types because such diversity might prevent the formation of expectations. The present results, however, demonstrated a positive correlation between stimulus diversity and the number of stimulus presentations necessary to habituate blue jays to a set of startling stimuli. The data were not detailed enough, however, to indicate whether any one species with a particular hindwing type would benefit from being found in nature with other species possessing different hindwing types.

Whether or not *Catocala* species with different hindwing types would benefit one another would depend in part on the rate at which they are encountered by predators. If this encounter rate is extended for any one species, then some mutual benefit seems likely. Resolution of this question awaits further research efforts.

If *Catocala* species do benefit by coexistence, one would expect to find extensive sympatry of species with different hindwing types. Field data show that many *Catocala* can be found in the same habitats at the same time of year, often feeding on the same food plants. For example, *C. coccinata*, *C. cerogama* and *C. retecta* often occur together during July and August (SARGENT, 1977). These moths possess red and black, yellow and black, and solid black hindwings, respectively. Similarly, *C. concumbens* (pink and black), *C. habilis* (orange and black), and *C. robinsoni* (black) all have uniform pale grey forewings and occur sympatrically in the late summer (SARGENT, 1977). Indeed, SARGENT (1978) found a number of remarkable ecological pairings among Juglandaceae-feeding *Catocala* in southern New England. These pairs consisted of one member with orange-banded (chromatic) and one with black (achromatic) hindwings. Normally, one would expect that competition between such closely related species would result in some divergence in niche utilization, but predation, in this case, might favor the co-occurrence of species with different hindwing types.

Experiment II also provided some behavioural observations to suggest that patterned hindwings represent powerful avoidance stimuli. While observing the birds, some common reactions to the initial experimental stimulus were noted. When the first experimental disc was banded, birds often recoiled from the disc and shook their heads. Many birds jumped to the opposite side of the cage and seemed reluctant to come close to the exposed experimental disc. They frequently spent time trying (unsuccessfully) to push the flaps at the far end of the board. These responses are similar to the ones COPPINGER (1969, 1970) noted when he presented birds with boldly patterned, novel butterflies, that SCHLENOFF (1983) observed when she presented blue jays with models of banded *Catocala* hindwings, and that CALDWELL & RUBINOFF (1983) saw when they presented egrets and herons with dead yellow and black sea snakes.

Not only were some birds' initial responses to the experimental stimuli dramatic, but certain birds reacted very strongly to the experimental stimuli by refusing to touch them over prolonged periods. One bird never habituated to the stimuli and almost always elected not to touch the experimental discs; this bird was in the highest diversity group. Others have found that especially strong stimuli may result in little or no habituation, and examples of startle responses that do not habituate can be found in both the ethological (THORPE, 1963) and psychological (OLDFIELD, 1937) literature.

In conclusion, it would seem reasonable to suggest that the behavioural tendencies described above would create a selective pressure on the *Catocala* moths favoring 1) bold patterns on the hindwings, 2) bright colours on the hindwings, and 3) species complexes that bring together individuals with similar forewings but dramatically different hindwings.

References

BARNETT, S.A. (1958). Experiments on "neophobia" in wild and laboratory rats. — British J. of Psychol. 49, p. 195-201.

BROWER, J.V.Z. (1958). Experimental studies of mimicry in some North American butterflies. Part 1. The monarch, *Danaus plexippus*, and the viceroy, *Limenitis archippus archippus*. — Evolution 12, p. 32-47.

—— & BROWER, L.P. (1962). Experimental studies of mimicry. 6. The reaction of toads (*Bufo terrestris*) to honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis vinetorum*). — Am. Nat. 96, p. 297-307.

CALDWELL, G.S. & RUBINOFF, R.W. (1983). Avoidance of venomous sea snakes by naive herons and egrets. — Auk 100, p. 195-198.

CARROLL, M.E., DINC, H.I., LEVY, C.J. & SMITH, J.C. (1975). Demonstrations of neophobia and enhanced neophobia in the albino rat. — J. Comp. Physiol. Psychol. 89, p. 457-467.

COPPINGER, R.P. (1969). The effect of experience and novelty on avian feeding behaviour with reference to the evolution of warning coloration in butterflies. Part I: Reactions of wild-caught adult blue jays to novel insects. — Behaviour 35, p. 45-60.

—— (1970). The effect of experience and novelty on avian feeding behaviour with reference to the evolution of warning coloration in butterflies. II. Reactions of naive birds to novel insects. — Am. Nat. 104, p. 323-335.

DOMJAN, M. (1977). Attenuation and enhancement of neophobia for edible substances. — In: Learning mechanisms in food selection (L.M. BARKER, M.R. BEST & M. DOMJAN, eds). Baylor University Press, Waco, p. 151-179.

—— & GILLIAN, D. (1976). Role of novelty in the aversion for increasingly concentrated saccharin solutions. — Physiol. Behav. 16, p. 537-542.

EDMUNDS, M. (1972). Defensive behavior in Ghanaian praying mantids. —J. Zool. J. Linn. Soc. 51, p. 1-32.

GITTLEMAN, J.L. & HARVEY, P.H. (1980). Why are distasteful prey not cryptic? — Nature (London) 286, p. 149-150.

—— & GREENWOOD, P.J. (1980). The evolution of conspicuous coloration: some experiments in bad taste. — Anim. Behav. 28, p. 897-899.

JONES, F.M. (1932). Insect coloration and the relative adaptability of insects to birds. — Trans. R. Ent. Soc. Lond. 80, p. 345-386.

KEIPER, R.R. (1968). Field studies of *Catocala* behavior. — J. Res. Lepid. 7, p. 113-121.

OLDFIELD, R.E. (1937). Some experiments bearing on "internal inhibition". — British J. Psychol. 28, p. 28-42.

RETTENMEYER, C.W. (1970). Insect mimicry. — Ann. Rev. Entomol. 15, p. 43-74.

ROPER, T.J. (1990). Responses of domestic chicks to artificially coloured insect prey: effects of previous experience and background colour. — Anim. Behav. 39, p. 466-473.

—— & REDSTON, S. (1987). Conspicuousness of distasteful prey affects the strength and durability of one-trial avoidance learning. — Anim. Behav. 35, p. 739-747.

SARGENT, T.D. (1966). Background selections of geometrid and noctuid moths. — Science 154, p. 1674-1675.

—— (1968). Cryptic moths: effects on background selections of painting the circumocular scales. — Science 159, p. 100-101.

—— (1969a). Behavioral adaptations of cryptic moths. II. Experimental studies on bark-like species. — J. N.Y. Ent. Soc. 77, p. 75-79.

—— (1969b). Behavioral adaptations of cryptic moths. IV. Preliminary studies on an anthophilous species, *Schinia florida* (Noctuidae). — J. N.Y. Ent. Soc. 77, p. 123-128.

—— (1973a). Behavioural adaptations of cryptic moths. VI. Further experimental studies on bark-like species. — J. Lepid. Soc. 27, p. 8-12.

—— (1973b). Studies on the *Catocala* (Noctuidae) of southern New England. IV. A preliminary analysis of beak-damaged specimens, with discussion of anomally as a potential anti-predator function of hindwing diversity. — J. Lepid. Soc. 27, p. 175-192.

—— (1976). Legion of night: the underwing moths. — University of Massachusetts Press, Amherst.

—— (1977). Studies on the *Catocala* (Noctuidae) of southern New England. V. The records of Sidney A. Hessel from Washington, Connecticut, 1961-1973. —J. Lepid. Soc. 31, p. 1-15.

—— (1978). On the maintenance of stability in hindwing diversity among moths of the genus *Catocala* (Lepidoptera: Noctuidae). — Evolution 32, p. 424-434.

—— (1990). Startle as an anti-predator mechanism, with special reference to the underwing moths, (*Catocala*). — In: Insect defenses: adaptive mechanisms and strategies of prey and predators (D.L. Evans & J.O. Schmidt, eds). SUNY Press, Albany, p. 229-250.

—— & Keiper, R.R. (1969). Behavioral adaptations of cryptic moths. I. Preliminary studies on bark-like species. —J. Lepid. Soc. 23, p. 1-9.

— & Owen, D.F. (1975). Apparent stability in hindwing diversity in samples of moths of varying species composition. — Oikos 26, p. 205-210.

Schlenoff, D.H. (1985). The startle responses of blue jays to *Catocala* (Lepidoptera: Noctuidae) prey models. — Anim. Behav. 33, p. 1057-1067.

Schuler, W. & Hesse, E. (1985). On the function of warning coloration: a black and yellow pattern inhibits prey attack by naive domestic chicks. — Behav. Ecol. Sociobiol. 16, p. 249-255.

Siegel, S. (1956). Nonparametric statistics for the behavioral sciences. — McGraw-Hill, New York.

—— & Castellan, N.J. (1988). Nonparametric statistics for the behavioral sciences. 2nd edn. — McGraw-Hill, New York.

Sillen-Tullberg, B. (1985). The significance of coloration *per se*, independent of background, for predator avoidance of aposematic prey. — Anim. Behav. 33, p. 1382-1384.

Smith, S.M. (1975). Innate recognition of coral snake pattern by a possible avian predator. — Science 187, p. 759-760.

—— (1977). Coral-snake pattern recognition and stimulus generalization by naive great kiskadees (Aves: Tyrannidae). — Nature (London) 265, p. 535-536.

Thompson, R.F. & Spencer, W.A. (1966). Habituation: A model phenomenon of the study of neuronal substrates of behavior. — Psychol. Rev. 73, p. 16-43.

Thorpe, W.H. (1963). Learning and instinct in animals. 3rd edn. — Methuen, London.

Vaughan, F.A. (1983). Startle responses of blue jays to visual stimuli presented during feeding. — Anim. Behav. 31, p. 385-396.

Wickler, W. (1968). Mimicry in plants and animals. — World University Library, London.

Résumé

Les geais bleus, dans les expériences de laboratoire, ont servi comme sujets pour déterminer quelles caractéristiques des ailes arrière des *Catocala* étaient importantes pour obtenir et maintenir des réactions surprises dans des prédateurs aviaires. Les geais blues élevés à la main, inexpérimentés avec les proies immangeables et à couleurs alertantes, ont pris, d'une manière significative, plus de temps à toucher de nouvelles couleurs qui possédaient d'éclatantes bandes noires verticales qu'à toucher de nouvelles couleurs sans bandes quand ces disques recouvraient une récompense mangeable. Donc, être visible (plutôt que d'être tout simplement nouveau) semble bien rehausser les réactions surprises. On trouve communément des patrons éclatants sur la proie aposématique et sur les ailes arrières des *Catocala*. Ces mêmes oiseaux élevés à la main tendent aussi à prendre plus de temps à toucher de nouveaux disques teintés jaune et rouge, comparés aux disques teintés blue, vert, ou pourpre. Les couleurs qui ont produit la plus grande hésitation sont semblables aux couleurs qu'on trouve sur les ailes arrières des *Catocala*. Les couleurs rouge-jaune sont aussi

caractéristiques de la proie aposématique. Les oiseaux attrapés dans la nature ont pris plus de temps à s'habituer aux stimulus effrayants quand on leur a présenté plusieurs types différents de disques effrayants pendant le processus d'habitation. Donc, la pression des prédateurs pourrait expliquer pourquoi plusieurs espèces différentes de *Catocala* à couleurs d'ailes arrière différentes se trouvent symaptricalement.