excessive weight problem and was tolerated by the crabs. The inside-dwelling *C. plana*, however, could possibly constitute an obstacle for complete withdrawal by a crab into a shell with limited space, a possibility supported by my observations during the course of these tests. Small shells with *C. plana* would accordingly be rejected as in my tests. In the tests with larger (and heavier) than normally preferred shells *C. plana* evidently posed neither volume nor weight problems to deter the crabs. On the other hand, the presence of *C. fornicata* may have discouraged crab occupancy because its growth in size or number can raise the total weight to a level above that tolerable to the crab.

Hermit crabs prefer shells within a certain weight-range relative to their body weight, rejecting those either too heavy or too light (Reese 1962). In the present study, when tests were run with small shells (below the lower limit of preferred shell-weight), the crabs might have been expected to select shells with *C. fornicata* since the symbiont would increase the total weight closer to a preferred level. However, the results indicate that this was not the case.

Observation on naturally-existing specimens indicate that a difference in epifauna exists between empty shells and shells occupied by hermit crabs. One might assume that the difference is due merely to the selective advantages or disadvantages of being associated with a hermit crab. On the other hand, as this study

has demonstrated, the difference may result from *Pagurus* selecting shells occupied by certain symbiont species and rejecting shells occupied by others.

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THE RESPONSE TO EYE-LIKE SHAPES BY BIRDS.
I. THE EFFECT OF CONTEXT: A PREDATOR AND A STRANGE BIRD

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Abstract. Laboratory-reared 40-day-old white leghorn chicks were placed individually in an arena with a dummy bird. The dummy was either a predator (kestrel) or a strange, non-predatory species (kiwi), further distinguished by the conspicuousness of the eye region. The hawk's eyes were either left intact (conspicuous) or covered. The kiwi's eyes were untouched (inconspicuous) or accentuated. Birds approached the unaltered kiwi but strongly avoided the hawk. Obscuring the eyes diminished hawk avoidance. Enhancement increased aversion to the kiwi. These results indicate the potential importance of the eyes as a stimulus feature of non-conspecifics.

This paper reports an investigation into the potential stimulus value of eyes in causing avoidance responses in birds. More precisely just what parameters of the eyes are important in eliciting such a response? Blest's (1957) work suggests that, for several small passerine species at least, eye-recognition cues are relatively simple. In common with other authors (e.g. Coss 1970) he stresses attributes like circularity which are so general as to be possessed by almost any vertebrate eye. Coss (1972 and in preparation) identifies pairedness, horizontal orientation and circular concentricity as important 'recognition cues'. While such features may well be necessary for recognition they can scarcely be sufficient. How, for instance, might predator eyes be distinguished from those of conspecifics? Further, Scaife (1974, 1976 pp 200–206) using great tits (*Parus major*) in an extended replication of Blest's (1957) model experiments could find little avoidance to bichromatic, two-dimensional patterns incorporating the above recognition cues. There was, rather, a mild attraction towards the stimuli. Absence of strong avoidance in these experiments conflicts with claims that such ('eyespot') patterns are aversive whether because of their resemblance to predator (owl, cat) eyes (Poulton 1890; Blest 1957) or because of an aversion to any 'eye gestalt' (Coss 1972). If one allows the basic premise that (real) eyes are indeed potent stimuli it is reasonable to assume that there are a variety of other cues besides the simple configuration of two light rings enclosing a darker area which are responsible for causing a shift in response from interest or mild arousal to aversion.

It is entirely possible that the context (used here merely to indicate physical surrounds)

of the eyes is a significant contributor to their stimulus value. This suggestion would seem to be at least partly contrary to the eye-mimicry theory of eyespot function unless, of course, one assumes that context is only operative in increasing general alarm regardless of how it does so. However, the importance of specific contexts is demonstrated by the work of Curio (e.g. 1969, 1975), who showed that there is often a complex interaction between stimulus features. For the pied fly-catcher (*Ficedula hypoleuca*), the stimulus potential of the eyes of a pygmy owl (*Glaucidium passerinum*) depends heavily on plumage characteristics. Therefore it is relevant to investigate contextual determinants of response to circular and eye-like patterns. It was thought convenient to do this by exposing chickens to a predator (a stuffed hawk) and a strange bird (a stuffed kiwi) both bearing the same (glass) eyes. A variety of other situations were also examined. These tests may be compared with responses to similar eye-like shapes presented in isolation and this in turn with a control stimulus of rectangular form.

Methods

Forty-five, 40-day old, male white leghorn chickens purchased at 1-day-old from a commercial hatchery and communally housed in a windowless room were maintained on a 14-hr on/10-hr off photoperiod at about 20°C. All chicks were healthy and habituated to the proximity of humans.

Testing was performed in a room different from the housing pen. Birds were transported in a box in groups of four or five to the test room and placed in a wooden holding pen of approximately 1 m³ which contained both food and water. They were then left undisturbed for 30 min to settle down.

The testing arena, constructed from 1·9-cm chipboard, measured $2 \times 1 \times 1$ m high. The floor was subdivided, using a black ink marker, into two halves 1×1 m. A small door at the midpoint of one of the long sides allowed introduction of subjects into the arena.

Tests were conducted as follows. Firstly the stimulus to be tested was placed at one end of the arena at the midpoint of one of the end walls (Fig. 1). Within a group of subjects given the same stimulus, half were shown the stimulus at one end, half at the other. An individual bird was removed from the holding pen and placed in the arena through the door. The bird was left for 10 min while its behaviour was recorded with an inconspicuous overhead television camera. At the end of this period the bird was removed, marked and returned to the holding pen. The arena was cleaned and the next test initiated. Each bird was tested once only, and all tests were completed within 2 days. Birds were selected randomly for inclusion within any particular group, and tests with different stimuli were also mixed up in a random manner.

The video record was analysed and the bird's position in the arena over the whole test period noted. The measure used was position with respect to the stimulus. These scores were simply indications of when the bird was in that half of
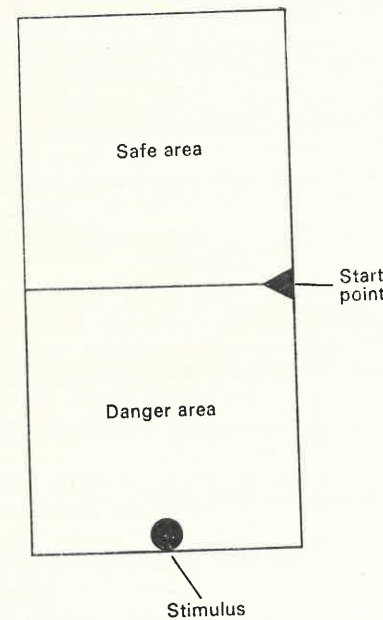

Fig. 1. Plan of test arena.

the box nearest the stimulus, called the 'danger area' or in the other half, the 'safe area'. Entry into one or the other was defined as both feet within the boundary.

In addition to locomotion other behaviour were recorded, notably escape attempts. An attempt was scored whenever the bird tried to fly or run up the wall.

Seven stimuli were used. The original aim of equal group sizes was not possible and the numbers of birds per group is given in brackets after the heading.

(i) Hawk (8). A stuffed kestrel (*Falco tinnunculus*) with 9-mm diameter glass eyes having a black pupil (4-mm diameter) and yellow iris. The kestrels' own (inconspicuous) eye ring was left intact.

(ii) 'Blind' hawk (8). As (i) but with the eyes obscured by feathers matching those of the eye surrounds,

(iii) Hawk longbeak (4). As (i) but with the beak obscured and replaced by one like that of a starling, 25-mm long, painted black.

(iv) Kiwi altered (8). A stuffed kiwi (*Apteryx* spp.), much bulkier than the hawk, given the same type of eyes as the hawk but otherwise intact.

(v) Kiwi normal (4). As (iv) but with plain brown glass eyes, 9-mm diameter with no obvious pupil. The eyes did not contrast with the head as much as those of (iv) but were still clearly visible.

(vi) Round eyes alone (8). A pair of 15-mm diameter glass eyes, patterned as those of the hawk but proportionally larger. These were mounted on a piece of brown card similar in colour to the arena walls at the same height as the hawk and kiwi.

(vii) Square eyes alone (5). A pair of rectangular Perspex blocks, 20×30 mm, arranged side by side as a horizontal pair with a black 'pupil' 15×10 mm and a surrounding yellow iris. These were displayed in a similar fashion to (vi). Patterns of both (vi) and (vii) were painted on the front surface with gloss paints. Total area and contour of (vii) was greater than (vi).

In all cases the stimuli were aligned so that they appeared to look down the midline (long axis) of the arena, i.e. towards the end wall.

Results and Discussion

Several specific questions were asked comparing different stimulus conditions. However, only one of the measures, position with respect to the stimulus, proved useful in separating the

conditions and the questions are, therefore, reserved for the data in that section.

(i) Escape behaviour. There were no noticeable differences between the scores. Almost all birds attempted at least one escape. The location of the attempt was always in the area of the box where the birds were standing for most of the time (although landings could be some distance away) and therefore provides no additional information to the other scores.

(ii) Other behavioural measures. Notes were taken of the postures adopted but there did not seem to be any systematic correlation with stimulus type. Birds in all groups would stand or sit with equal frequency when immobile or, more rarely, would crouch (as they do to the alarm call). There was a strong impression that the subjects with the hawk remained very attentive to the stimulus over the whole 10 min, frequently standing and monocularly fixating the hawk from the other end of the arena. This was less marked in the blind hawk group where for at least three birds hardly any prolonged fixation occurred after a short initial bout. In other groups there tended to be less obvious fixation. In the two kiwi groups, however, the initial 2 min were characterized by a long scrutiny of the stimulus with only occasional movement. Subsequent to this the kiwi altered birds continuously monitored the stimulus while remaining immobile at the other end of the arena. The kiwi normal birds also showed great interest, with one of the subjects attacking the stimulus eight times in 20 s and another making several pecks at its eye. This type of behaviour was not seen in any of the other groups.

Finally, the aversiveness of the three hawk conditions was underlined by the behaviour of birds which made rushes at the wall in attempting to escape and fell back close to the stimulus. In all of these cases (seven subjects in all from the three groups) the birds' immediate reaction was to run to the other end of the arena. In one case the bird actually leapt a metre away. The violence of this response was not matched in any of the other groups, retreat being conducted at walking pace should the bird land near the stimulus.

(iv) Position with respect to the stimulus. The data are presented in Table I. This shows the median time per group in the safe area over the 10-min test period. Mann–Whitney U-tests on required comparisons are shown in Table II. These comparisons may now be discussed.

Table I. Median Time in Seconds Per Group in the Safe Area for Total Test Period (600 s)

Group	Median time
Hawk	581·5
Blind hawk	513·5
Longbeak hawk	547
Kiwi altered	517
Kiwi normal	153
Round eyes alone	412
Square eyes alone	359

Table II. Selected Comparisons of Median Total Times in the Safe Area

Comparison	U	Two-tail P
Hawk & blind hawk	13	0·05
Hawk & longbeak hawk	12·5	NS
Hawk & kiwi normal	0	0·01
Kiwi altered & kiwi normal	2	0·025
Round eyes alone and square eyes alone	16	NS

(Where one group of chicks features in more than one comparison this must increase the chances of falsely rejecting the null hypothesis. This has to be borne in mind when assessing the results.)

(a) Do naïve chickens avoid a resting avian predator more than an equally strange, but non-predatory bird? If this is so they should avoid the hawk (stimulus i) more strongly than the kiwi normal (stimulus v). Subjects avoided the hawk but approached the kiwi normal, birds spending significantly longer in the safe area with the former stimulus, Table II. The violence of the response to proximity to the hawk confirms the aversive nature of the stimulus. Thus there seems to be an avoidance response independent of experience with the predator.

(b) What features of the hawk are important in eliciting an avoidance response? Are the eyes important, hawk (stimulus i) versus blind hawk (stimulus ii)? Is the beak important, hawk (stimulus i) versus longbeak hawk (stimulus iii)? It is of course, impossible to specify the

basis for avoidance, i.e. whether the stimulus, or parts thereof, are merely maximally novel or whether there is an 'innate schema' for recognition, without the sorts of detailed investigation that Curio (1975) reports for pied flycatchers. However, the data (hawk versus blind hawk), Table II clearly show that loss of the eyes reduces the aversive properties of the stimulus although alteration of beak shape was not shown to (hawk versus longbeak hawk, Table II). These results are interesting. Von St Paul (1948, cited in Curio 1975) found that covering the model's eyes interferes with recognition of owls but not hawks in naïve shrikes. However, alteration of beak shape had the reverse effect. reducing the releasing value of a hawk although not an owl. Curio (1975) reports alteration of beak shape, by addition of a wooden snipe beak, similarly ineffective in altering responses to owls, in this case using pied flycatchers. Gallup et al. (1971) describe experiments where covering the eyes of a Cooper's hawk (*Accipter cooperri*) with black tape significantly reduces (experimenter-induced) immobility when the bird is held down in front of the predator compared to an intact dummy situation. The chicken, then, seems to use the eyes as cues for avoidance responses. Further speculation about the relative importance of each feature cannot be made on the basis of these hawk groups comparison alone.

(c) Does alteration of the conspicuousness of the eyes affect the response to a non-predatory bird: kiwi normal (stimulus v) versus kiwi altered (stimulus iv)? The alteration to the eye region of the kiwi produced qualitatively the most dramatic change in response observed in the experiment. While the conspicuously eyed stimulus was avoided the intact one was something attacked. The reasons for attack might be that the kiwi has features similar enough to those of the subjects to cause it to be classified as an outlandish chicken. For instance the large feet and general shape might function in this fashion. This partial similarity might stimulate approach in an analogous fashion to the 'discrepancy-principle' (Kagan 1970) postulated to explain why objects mildly dissimilar from the familiar should elicit more attention than completely novel ones, which tend, on the whole, to cause avoidance. Another parallel might be with the apparent curiosity component of mobbing behaviour in small passerines. Andrew (1972) speaks of 'extended recognition comparison' as a possible reason for the great length of mobbing observed in many birds, suggesting

that perhaps the partially familiar (in his case vis-à-vis an internal predator schema) causing approach to the eliciting stimulus.

In the case of the kiwi altered, the stimulus is avoided significantly more than the kiwi normal, Table II. There are various possible reasons for the difference. Firstly, it might be argued that by enhancing the eye region the stimulus situation is made more complex and that this alone is sufficient to 'tip the scale' and turn approach into avoidance. However, such a small area of the total stimulus is involved that this seems unlikely. Secondly, it may be that the eye pattern is part of a predator recognition mechanism which can be abstracted or is effective in different contexts, i.e. what Curio (1975) terms 'donor-related'. Thirdly, it might be that enhancement of the eyes is sufficient to cause avoidance if the kiwi has been classified as some sort of chicken. This might work because details of the eyes are normally only seen at close quarters, which often means a threatening situation or aggressive encounter, birds tending to withdraw under such circumstances. McBride, James & Shoffner (1963) note that chickens tend to avoid frontal views but turn to face as bird–bird distance decreases.

(d) How much of the effectiveness of the eye as a stimulus in causing avoidance is due to the specific features of circularity? Comparison between round eyes alone (stimulus vi) and square eyes alone (stimulus vii) should give an indication of this. It was not possible to show significant differences between the two isolated patterns used, Table II. However, this result, utilizing static patterns, can be no more than indicative and rather more experimentation is necessary to understand the problem of eye recognition. This is reported elsewhere (Scaife 1975, 1976 pp 200–206).

In conclusion, while the cues involved are by no means certain, the experiment demonstrates that alteration of the eye region affects the aversive properties of a bird stimulus. Conversely, the stimulus value of eye-like shapes is markedly affected by the context of their presentation.

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