

Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators

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Abstract. Male chickens, *Gallus gallus*, produce aerial alarm calls in response to a broad range of stimuli moving overhead, including both predators and innocuous objects. Computer-generated animations of raptor-shaped images were presented on an overhead video monitor to explore the stimulus characteristics necessary for eliciting both aerial alarm calls and non-vocal anti-predator behaviour (e.g. crouching and visual fixation). In experiment 1, apparent size (angle subtended at the bird's eye) was varied from 1° to 8°. Stimuli subtending more than 4° elicited qualitatively more alarm calls than smaller stimuli. The magnitude of non-vocal responses also increased significantly with stimulus size. In experiment 2, apparent speed was varied over a range extending from values characteristic of soaring raptors at one end (1.875 lengths/s), to values near the highest recorded (30 lengths/s) at the other. Stimuli moving faster than 7.5 lengths/s evoked significantly more alarm calling than slower-moving stimuli. Increases in apparent speed also caused a small but significant increase in the magnitude of non-vocal responses. Hence, the non-vocal anti-predator behaviour elicited by overhead stimuli is strongly influenced by apparent size. In natural encounters, this cue varies with object altitude and is likely to be a good predictor of the probability of detection and attack by a raptor. The data on vocal responses suggest that, at least when shape is constant, the probability of alarm calling is dependent on whether stimuli exceed threshold values for apparent size and speed. This perceptual strategy has the advantage of requiring minimal processing and may be adaptive for species, like the jungle fowl, that have evolved in habitats where visibility is limited and reaction times must therefore be brief.

Recognizing predators and discriminating them from similar species that do not present a danger are problems of primary importance for all prey species. The perceptual strategy employed is likely to reflect factors such as detection distance, determined by both habitat characteristics and visual acuity (Walters 1990), discriminability of predator species from non-predators, and predation risk. Species with distinctive alarm calls are particularly suitable for studies of the perceptual basis of recognition, since call type and number provide sensitive indices of the way in which complex visual stimuli are categorized (e.g. Leger et al. 1979; Seyfarth et al. 1980; Gyger et al. 1987; Macedonia 1990).

Male domestic chickens, *Gallus gallus*, like the red jungle fowl from which they are thought to be derived (Collias & Collias 1967), give qualitatively different vocalizations in response to aerial and

terrestrial predators (Konishi 1963; Collias 1987; Gyger et al. 1987). Potential predators approaching on the ground, such as dogs, elicit a series of high-amplitude broad-band pulsatile calls, while aerial predators evoke calls of much longer duration, made up of at least two units: an initial short pulse and a subsequent element, which may be quite broad-band (i.e. scream-like) or relatively tonal (i.e. whistle-like; see Fig. 1 in Gyger et al. 1987). While both cocks and hens give ground alarm calls, there is pronounced sexual dimorphism in aerial alarm calling, with almost all calls being produced by males (e.g. Gyger et al. 1987; Karakashian et al. 1988). Aerial alarm calls can be elicited readily in the laboratory by presenting simple raptor-shaped models such as those employed in the classic studies of Lorenz, Tinbergen and Schleidt (see Schleidt 1961). Experiments of this type have revealed that aerial alarm calling is sensitive to social context; cocks rarely call when alone, but call readily in the presence of a conspecific 'audience' bird (Gyger

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et al. 1986; Karakashian et al. 1988; Evans & Marler 1991).

Current evidence suggests that, unlike some mammals (e.g. vervet monkeys, *Cercopithecus aethiops*, Seyfarth & Cheney 1990, 1986) and other birds (e.g. lapwings, *Vanellus* spp., Walters 1990), expression of anti-predator behaviour in galliforms is not principally dependent on the fine structure of aerial objects. Schleidt (1961) has demonstrated that apparent size (i.e. the angle subtended at the bird's eye) and speed (i.e. image lengths/s) largely determine the response of turkeys, *Meleagris gallopavo*, to models presented overhead. Similarly, under natural conditions, chickens produce aerial alarm calls in response to a broad array of airborne objects (Gyger et al. 1987). Eliciting events include potential predators, such as raptors, but calls are also occasionally evoked by non-predators, such as small passerines. Detailed analyses of call structure reveal that spectral characteristics vary consistently with the apparent size of the eliciting stimulus (Gyger et al. 1987).

Our aim in the present study was to explore further the stimulus characteristics required to elicit both aerial alarm calling and non-vocal anti-predator behaviour in chickens. In these initial experiments, we have focused on the roles of apparent size and speed, while holding other attributes, such as shape and pattern of flight, constant. We decided to exploit the recent finding that chickens are responsive to visual images not only of conspecifics (Evans & Marler 1991), but also of predators (Evans & Marler 1992), presented on a large video monitor. Simple black silhouettes, shaped approximately like raptors as seen from below, are sufficient to elicit responses qualitatively similar to those observed during natural interactions with potential avian predators. Cocks crouch and visually fixate on such images as soon as they appear overhead; when hens are present, males also produce aerial alarm calls (Evans & Marler 1992).

We report here on two experiments in which computer-generated animations were used to elicit aerial alarm calls. This approach allows great flexibility in defining stimulus characteristics, and permits manipulations that would be difficult with traditional techniques, such as varying speed while holding stimulus duration constant. In experiment 1 we presented a range of stimuli differing in apparent size, while in experiment 2 we examined the importance of apparent speed.

GENERAL METHODS

Subjects

Subjects were male golden Sebright bantam chickens, drawn from a colony housed on a diurnal 1525:0875 h light:dark cycle (experiment 1) or a 12:12 h light:dark cycle (experiment 2). Each male was housed either with a single female, in a cage measuring 75 × 50 × 44 cm deep, or with two females, in a cage 120 × 70 × 120 cm deep. All cages were fitted with perches. Water, oyster shell and food (West-Nesbitt 'Pure-Feed' crumble or Purina 'Layena') were continuously available.

Test Apparatus and Stimuli

Experiments were conducted in chambers measuring 1.2 × 2.6 × 2.3 m high (experiment 1) or 2.13 × 2.29 × 2.13 m high (Acoustic Systems model RE 143; experiment 2). Both test chambers were lined with 10 cm 'Sonex' echo-attenuating foam (Illbruck Inc.). Each subject was confined in a wire cage, measuring 0.6 × 0.6 × 1.0 m, in the centre of the floor. Since cocks rarely produce alarm calls when alone (Gyger et al. 1986; Karakashian et al. 1988; Evans & Marler 1991), we provided an 'audience' by confining a conspecific hen in an identical cage abutting the subject's cage.

An NEC model PM-2571A video monitor (screen size 61.25 cm measured diagonally) was mounted, with the screen facing downward, directly above the subject's cage and supported on a metal frame (Evans & Marler 1992; Fig. 1). Animated stimulus sequences generated by a Commodore Amiga 2000 microcomputer were used to elicit alarm calling (see below). The chamber was lit by incandescent lights, which were mounted on retort stands and angled so that the face of the video monitor was not illuminated.

During testing, we observed males continuously through a Panasonic WV-3230 video camera mounted at floor level in the chamber. Elapsed time was displayed continuously at the bottom of the video image, on a Panasonic CT-110MA colour monitor. All test sessions were video-recorded using a Panasonic NV-8420 VHS-format VCR. Vocalizations were recorded with a Realistic model 33-1070 microphone and a Marantz PMD420 recorder (experiment 1) or a Sony TC-D5M recorder (experiment 2).

We analysed test session videotapes using a Panasonic AG-7510 video recorder, together with

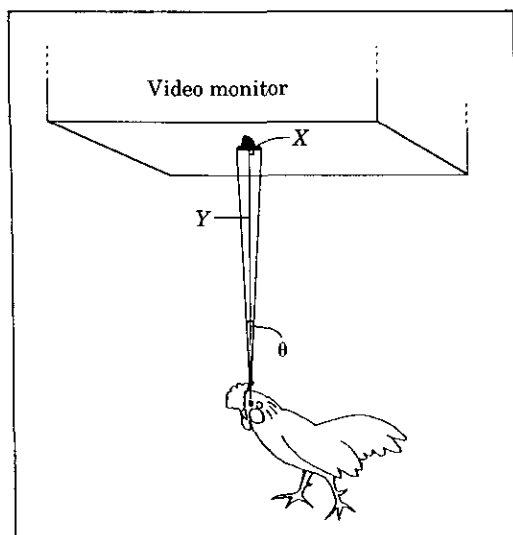


Figure 1. Method for calculating the size of hawk-shaped stimuli. The body length of the raptor-shaped image forms one side of an inverted isosceles triangle. Since both mean chicken eye-height and the distance between the video monitor and the floor were known, the typical distance between the bird's eye and the screen (Y) could be estimated. The angle that stimuli were required to subtend at the subject's eye (θ) was then used to calculate the required size of the screen image (X) (see text for details). Stimulus size exaggerated for clarity.

a Panasonic AG-A7510 edit controller and a Panasonic CT-1331Y colour monitor. This equipment allowed us to review test videotapes with single-frame accuracy and to make measurements of duration by comparing the time codes recorded on each frame.

Alarm calls were elicited by presenting computer-generated animation sequences on the overhead video monitor. Raptor-shaped images were created and animated using commercial 'paint' and video-effects software. To avoid the rapid response habituation associated with repeated identical stimulus presentations (e.g. Hirsch et al. 1955; Melzack 1961; Melvin & Cloar 1969), two versions of each stimulus were produced, allowing us to vary the X and Y coordinates at which the raptor shapes appeared and disappeared. All of the animations presented a black 'hawk' silhouette moving against a featureless white background and were double-buffered for smooth movement. The background was displayed constantly. During test sessions, stimulus sequences were generated in real time, triggered from the computer keyboard.

Analysis of Recorded Vocal and Non-vocal Responses

All calls elicited within 30 s of a stimulus presentation were examined using 'SoundEdit', a Macintosh-based sound analysis system which generated spectrograms from a series of overlapping 128 point FFTs (frequency resolution 172 Hz, bandwidth 11 kHz). Aerial alarm calls were readily recognized by their characteristic acoustic structure (see Fig. 1 in Gyger et al. 1987).

Non-vocal responses to 'hawk' stimuli were scored 'blind' from test session videotapes (i.e. by an observer who was unaware of the stimulus sequence that the bird had received). An ordinal scale was developed to describe anti-predator behaviour. This was designed to accommodate the full range of responses observed both in natural interactions and in previous laboratory experiments. Response categories were as follows.

- (0) No visible response
- (1) Looking upwards (typically by rolling the head to fixate with one eye)
- (2) Looking upward and flexing the neck, so as to draw the head towards the body
- (3) Responses 1 and 2, together with perceptible crouching.
- (4) Responses 1 and 2, together with pronounced crouching, so that the body makes contact with the floor
- (5) Responses 1, 2 and 4, together with running in a crouched posture

Ratings were obtained for a 10-s period following the appearance of 'hawk' stimuli and from a 10-s 'baseline' interval 1 min earlier. Hence, we were able to assess both the absolute effectiveness of stimuli (by comparing the response to presentations with the baseline score) and their relative effectiveness (by comparing responses to different stimulus types).

Data Analysis

The number of alarm calls produced by each male in the two test trials of each stimulus type was first averaged. These means were then subjected to a log ($X+1$) transform (Winer 1971) to eliminate positive skew and a repeated-measures ANOVA was performed on the entire data set. If a significant treatment effect was obtained, then further comparisons were conducted with paired t -tests (Carmar & Swanson 1973).

Table 1. Experiment 1 stimulus characteristics

| Stimulus | 1° | 2° | 4° | 8° |
|---------------------------|-------|-------|-------|-------|
| Length (pixels) | 2 | 4 | 8 | 16 |
| Wingspan (pixels) | 8 | 16 | 32 | 64 |
| Angle subtended (degrees) | 1.014 | 2.029 | 4.056 | 8.102 |
| Track length (pixels) | 38 | 76 | 152 | 304 |
| Apparent speed (length/s) | 7.50 | 7.50 | 7.50 | 7.50 |
| Total duration (s) | 5.066 | 5.066 | 5.066 | 5.066 |

Analyses of non-vocal responses were similar, except that analogous non-parametric statistics were employed. Overall comparisons with the Friedman ANOVA were followed, when appropriate, by pair-wise Wilcoxon matched-pairs signed-rank tests. All statistical comparisons were two-tailed, with an alpha level of 0.05.

EXPERIMENT 1

Measurement of Eye Height

In order to generate a series of stimuli with known apparent sizes, it was first necessary to obtain an estimate of chicken eye-height. This was accomplished by superimposing computer-generated cross-hairs over still video images, using the Amiga 2000, together with a Digital Creations 'SuperGen' broadcast-quality genlock (a device which synchronizes the signals produced by a microcomputer and a video-recorder so that they can be combined) and an RCA model VPT 695 HF video-recorder with digital freeze-frame. For each video frame, we measured eye position and the location of each foot. Eye-height was then calculated as the vertical distance between the eye and the average of the two foot positions. Measurements of screen position (vertical resolution 200 pixels) were converted into actual distances by using the cage wire (vertical separation 25.4 mm) as a reference. In order to sample variation resulting from movement and changes in posture, we made 10 measurements, at 60-s intervals, from each of eight males. Whenever one of the measurement points was invisible (e.g. head obscured during preening) the next clear frame was used. Mean eye height was calculated for each bird, and an overall mean was then derived from these individual scores. We estimate mean (\pm SE) eye height for our subjects to be 232 ± 16.5 mm.

'Hawk' Stimuli

Stimulus properties were calculated based upon our estimate of subject eye height, the size of the overhead video monitor and the height of the screen above the floor. In order to generate a series of hawk silhouettes varying in apparent size (i.e. in θ , the angle subtended at the bird's eye), we treated the eye as the apex of an inverted isosceles triangle (Fig. 1).

It is convenient to calculate image size by dividing this triangle into two right-angle triangles, each of which has an opposite side equal to half the length of the raptor shape (X) and an adjacent side equal to the distance from the bird's eye to the screen (Y). X can then simply be calculated

$$X = (\tan\theta/2)Y$$

The total length of the raptor shape is twice this value. This distance (mm) is then converted into screen units (pixels).

Our goal was to create a series of stimuli with lengths subtending 1, 2, 4 and 8° at the chicken's eye. Since pixels are discrete, we were constrained to choose the values that best approximated these apparent sizes (Table 1). The maximum difference between actual and target values was less than 1.5%. We created raptor silhouettes using a commercial graphics program ('Deluxe Paint II'; Electronic Arts) and varied size so that both body length and wingspan doubled in successive stimuli (Fig. 2). These shapes were then animated using a program ('Deluxe Video II'; Electronic Arts) that required us to specify starting and ending positions for a trajectory and then interpolated all intervening frames.

All of the stimuli moved across the screen at the midpoint of the Y -axis. We varied trajectory length in order to hold stimulus duration and apparent speed constant. For example, while the 8° stimulus

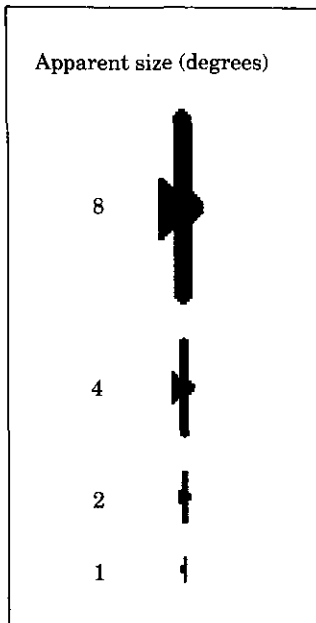


Figure 2. Raptor-shaped silhouettes used in experiment 1. Apparent sizes range from 1° to 8°. Each stimulus in this series has a body length and wingspan twice that of the one before.

moved from one edge of the screen to the other, the 4° stimulus moved along a track that was also centred on the middle of the screen, but was only half as long. Each of the four stimuli moved a total distance proportional to its size (Table I). Stimulus presentations were made up of two transits; hawk images moved across the video screen, reversed direction and orientation (remaining visible), re-crossed the screen, and disappeared at their point of origin. Two versions of each stimulus type were created, one appearing on the left side of the monitor screen, the other on the right. Subjects were randomly assigned one of these versions in each of the two test sessions, so that stimulus characteristics were never precisely repeated.

Subjects

Twenty-four cocks were tested; 20 housed with a single hen and four with two hens.

Test Procedure

Prior to the first test day, males were adapted to the test situation by placing them in the chamber

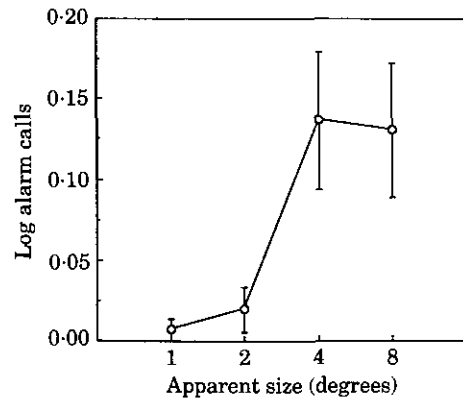


Figure 3. Effect of stimulus apparent size on alarm calling. Values shown are group means (\pm SE).

for two 15-min intervals, separated by a minimum of 24 h, without any stimulus presentation.

A test session was begun by placing the subject male in the chamber, with an audience hen already present in the adjacent cage, and with the white background displayed on the overhead video monitor. The first 'hawk' animation was presented 15 min later, followed by the remaining three stimuli at 15-min intervals. Both audio- and video-recordings were made of the period extending from 1 min prior to each stimulus presentation to 2 min post-stimulus.

Subjects experienced two such test sessions, separated by a mean (\pm SE) of 14.7 \pm 0.65 days. Each male was assigned a unique random sequence of the four stimuli for the first session and was re-tested with the sequence reversed.

RESULTS

Alarm Calling

The silhouettes subtending 4° and 8° evoked the most alarm calls, while relatively few calls were elicited by the two smallest stimuli (Fig. 3). The overall ANOVA revealed a robust treatment (image size) effect ($F_{3,95} = 6.56$, $P = 0.0006$). Subsequent pair-wise comparisons demonstrated that the two smallest stimuli (1° and 2°) both elicited significantly fewer alarm calls than the two largest stimuli (4° and 8°) (smallest $t = 2.85$, $df = 23$, $P = 0.009$). The two small stimuli did not differ significantly in effectiveness ($t = 0.76$, $df = 23$, $P = 0.453$). Similarly, there was no reliable difference in the number of alarm

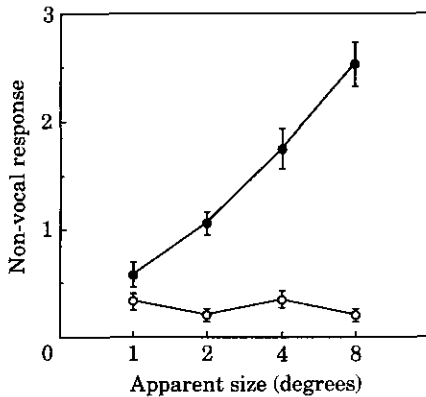


Figure 4. Effect of stimulus apparent size on non-vocal responses. Values shown are group means (\pm SE). Behaviour was scored frame-by-frame for the 10 s following stimulus presentations (●) and during an equivalent 'baseline' period one minute prior to each stimulus (○).

calls elicited by the two largest stimuli ($t=0.15$, $df=23$, $P=0.885$).

Non-vocal Responses

All of the stimuli elicited non-vocal behaviour, such as crouching and visual fixation (see Methods). Unlike alarm-call production, the magnitude of these responses increased monotonically with increases in apparent size (Fig. 4). Small images typically elicited monocular fixation, together with tracking movements of the head. Larger stimuli (4° and 8°) also evoked crouching. Responses to the 8° stimulus also included pronounced 'scuttling' movements, during which the cocks ran a few steps across the cage with head and neck lowered and legs bent, so that their bodies were almost touching the floor.

Friedman non-parametric ANOVAs revealed a significant treatment effect for stimulus presentations ($\chi^2=41.23$, $df=3$, $P=0.0001$), but no significant variation in baseline (pre-stimulus) behaviour ($\chi^2=4.11$, $df=3$, $P=0.25$). Subsequent pair-wise comparisons of responses to stimuli demonstrated that every increment in image size was associated with a significant increase in non-vocal response (Wilcoxon matched-pairs signed-rank test; smallest $z=2.82$, $N=24$, $P=0.005$).

Finally, all of the stimuli elicited significantly greater non-vocal responses than were observed during the pre-stimulus baseline periods (smallest $z=2.49$, $N=24$, $P=0.013$).

DISCUSSION

The results of experiment 1 demonstrate that production of aerial alarm calls is sensitive to variation in the apparent size of raptor-shaped stimuli. Large silhouettes were significantly more effective in eliciting alarm calls than small ones. Although we specified stimulus size in terms of silhouette length, it is possible that the males were attending to features that co-varied with this parameter, such as wingspan or total area, or to a combination of such cues. These features would all be highly correlated in natural aerial predators, and, so long as wing position were constant, would be determined by a combination of altitude and body size.

Since very few calls were elicited by stimuli subtending less than 4°, it was not possible to compare their acoustic characteristics with those of calls elicited by larger stimuli. We cannot therefore determine whether the relationship between apparent size and call bandwidth described under natural conditions (Gyger et al. 1987) is also apparent in the laboratory.

The alarm call data might be taken to imply that some pairs of stimuli (1° and 2°, 4° and 8°) were indiscriminable. The non-vocal response data show clearly that this was not the case; frame-by-frame analysis demonstrates that cocks discriminated between all of the stimuli. For example, increases in size from 1° to 2° and from 4° to 8° were both associated with significant increments in non-vocal response, but there was no significant change in alarm calling in either case. This comparison provides an example of a relatively loose coupling between production of vocalizations and other behavioural responses to a stimulus, a phenomenon that is also apparent in 'audience' effects, where social context affects calling but not other anti-predator behaviour (e.g. Karakashian et al. 1988; Evans & Marler 1991).

Finally, the comparisons of stimulus and baseline non-vocal response scores demonstrate that all of the stimuli had reliable effects on male behaviour, always including a high probability of visual fixation. Consequently, we can be confident that the very low levels of alarm calling observed with smaller images were not simply a consequence of the greater visibility of large stimuli.

Table II. Experiment 2 stimulus characteristics

| Stimulus | 1.875 | 3.75 | 7.5 | 15 | 30 |
|---------------------------|-------|-------|-------|-------|-------|
| Length (pixels) | 8 | 8 | 8 | 8 | 8 |
| Wingspan (pixels) | 32 | 32 | 32 | 32 | 32 |
| Angle subtended (degrees) | 4.056 | 4.056 | 4.056 | 4.056 | 4.056 |
| Track length (pixels) | 38 | 76 | 152 | 304 | 608 |
| Apparent speed (length/s) | 1.875 | 3.75 | 7.5 | 15 | 30 |
| Total duration (s) | 5.20 | 5.20 | 5.20 | 5.20 | 5.20 |

EXPERIMENT 2

Our aim in this experiment was to assess the importance of a stimulus-attribute orthogonal to size, namely apparent speed (Schleidt 1961). In the first experiment, we held apparent speed constant and manipulated size. In experiment 2, we held size constant and varied speed.

'Hawk' Stimuli

We examined the response of chickens to five stimuli moving at a range of apparent speeds which included values characteristic of soaring raptors at one end (1.875 lengths/s) and near the maximum reported (30 lengths/s; Meinertzhagen 1955) at the other (Table II). Each stimulus in the series moved at double the apparent speed of the one before. By design, this series included one stimulus (7.5 lengths/s) used in the previous study. All stimuli were constructed using the 4° silhouette. Track length varied with apparent speed so as to keep total stimulus duration constant (Table II).

To obtain adequate stimulus durations, the 'hawk' image moved across the screen, reversed direction and orientation to return to the point of origin, and then repeated this sequence, crossing the screen a total of four times. As in experiment 1, two versions of each of the five stimuli were created, one for each of the two test sessions, in order to avoid re-presenting stimuli.

In experiment 1, the animation software had calculated image positions, in real time, during stimulus presentations. To achieve the high speeds required in the second experiment, without sacrificing smoothness of movement, it was necessary to employ a slightly different animation technique. Each stimulus frame was first created and saved as a still image (a total of 312 frames per stimulus). These static images were then compiled into an

animation using a 'pageflipping' algorithm (Page-flipper plus FX; Mindware) which calculates the differences between successive screen displays and then saves this information for later playback. The resulting files not only require much less memory than the images from which they have been derived, thus allowing quite long sequences, but can also be displayed at a sufficiently high speed (60 frames/s). The image quality obtained with this approach was indistinguishable from that of the experiment 1 stimuli.

Subjects

Twenty-eight cocks were tested; 19 housed with one hen and nine housed with two hens. Seven of these birds had also participated in experiment 1.

Test Procedure

Subjects were first habituated to the test situation as in experiment 1. They then experienced two test sessions, each containing five 'hawk' stimulus presentations. Test sessions were separated by a mean (\pm SE) of 36.7 ± 0.96 days. Each male was assigned a unique random sequence of the five stimuli for the first sessions and was re-tested with the sequence reversed.

RESULTS

Alarm Calling

There was marked variation in the number of alarm calls produced as apparent speed was manipulated. Raptor-shaped silhouettes moving slowly (1.875 and 3.75 lengths/s) elicited relatively few calls. Stimuli moving at 7.5 lengths/s were more effective, and the fastest stimuli, moving at 15 and 30 lengths/s, evoked calling at high rates (Fig. 5).

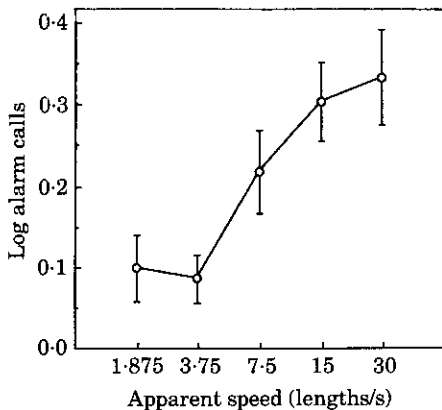


Figure 5. Effect of stimulus apparent speed on alarm calling. Values shown are group means (\pm SE).

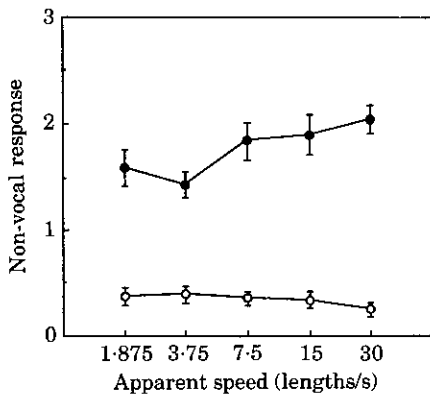


Figure 6. Effect of stimulus apparent speed on non-vocal responses. Values shown are group means (\pm SE). Stimulus presentations (●) baseline periods (○).

The overall ANOVA confirmed that the effects on alarm calling of variation in apparent speed were statistically reliable ($F_{4,139} = 13.29$, $P = 0.0001$). Subsequent pair-wise comparisons revealed that the two slowest stimuli (1.875 and 3.75 lengths/s) did not differ significantly in effectiveness ($t = 0.35$, $df = 27$, $P = 0.727$) and that they each elicited significantly fewer alarm calls than the three faster stimuli (7.5, 15 and 30 lengths/s; smallest $t = 2.96$, $df = 27$, $P = 0.006$). The response to the stimulus moving at 7.5 lengths/s did not differ reliably from that evoked by the 15 lengths/s stimulus ($t = 2.02$, $df = 27$, $P = 0.054$), but was significantly less than that evoked by the 30 lengths/s stimulus ($t = 2.93$, $df = 27$, $P = 0.007$). Finally, the 15 lengths/s and 30

lengths/s stimuli did not differ in effectiveness ($t = 0.64$, $df = 27$, $P = 0.529$).

Non-vocal Responses

While all of the stimuli elicited visual fixation and tracking movements of the head, together with occasional crouching, the effect of stimulus speed on these responses was more subtle than that on call production (Fig. 6). Apparent speed did, nevertheless, significantly affect non-vocal anti-predator behaviour associated with stimulus presentations ($\chi^2 = 12.71$, $df = 4$, $P = 0.013$). There was no significant variation in pre-stimulus (baseline) behaviour ($\chi^2 = 4.51$, $df = 4$, $P = 0.34$).

Comparisons of non-vocal responses to each of the stimuli revealed fewer significant differences than the analogous comparisons of alarm calling. The slowest stimulus (1.875 lengths/s) elicited significantly weaker responses than the fastest (30 lengths/s; $z = 2.34$, $N = 28$, $P = 0.02$). Similarly, the stimulus moving at 3.75 lengths/s was significantly less effective than the two fastest stimuli (15 and 30 lengths/s; smaller $z = 2.07$, $N = 28$, $P = 0.039$). None of the other pair-wise comparisons was significant.

Finally, responses to stimuli were compared with the baseline scores obtained 60 s prior to each stimulus presentation. All five comparisons yielded highly significant differences (smallest $z = 4.25$, $N = 28$, $P = 0.0001$).

DISCUSSION

The apparent speed of a raptor-shaped silhouette clearly affected the probability of aerial alarm calling by cocks. Fast-moving stimuli, with apparent speeds exceeding 7.5 lengths/s, elicited large numbers of calls, while slow-moving stimuli were relatively ineffective. In contrast, the variation in non-vocal response was relatively small; statistically significant differences were obtained only in comparisons between stimuli drawn from opposite ends of the speed continuum.

The comparisons of stimulus and baseline non-vocal responses yielded robust differences in every case; all of the stimuli had reliable effects, eliciting obvious fixation and tracking movements. Consequently, it is clear that variation in the number of alarm calls produced is not attributable to differential visibility.

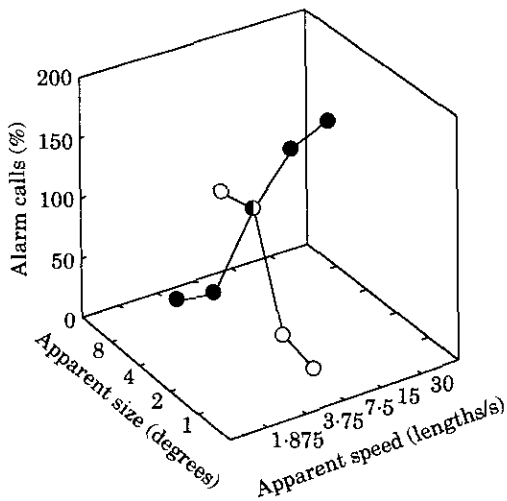


Figure 7. Summary of the results from experiment 1 (apparent size) and experiment 2 (apparent speed). In order to align the two response functions, alarm calling has been expressed as a percentage of the response evoked by the stimulus subtending 4° and moving at 7.5 lengths/s, which was found in both series.

GENERAL DISCUSSION

The results of these two experiments suggest that production of aerial alarm calls by male chickens is strongly affected by the apparent size and speed of eliciting stimuli. This is perhaps most clearly seen when data from both experiments are combined (Fig. 7). In order to represent in the same figure two response functions in which the absolute levels of alarm calling were somewhat different (compare Figs 3 and 5), call rates have been expressed as a percentage of those elicited by the stimulus subtending 4° and moving at 7.5 lengths/s, which was used in both series. The largest numbers of alarm calls were evoked by large stimuli moving at relatively high apparent speeds; silhouettes subtending less than 4° or moving at less than 7.5 lengths/s were much less effective. It should ultimately be possible to generate a surface, built up of a number of such response functions, that would describe exhaustively the relationship between alarm calling and stimulus characteristics.

The non-vocal response to hawk silhouettes was more dependent upon apparent size than on apparent speed. Since predator altitude is inversely proportional to apparent size, this suggests that the probability of responses that function to reduce the likelihood of detection, including crouching and

prolonged immobility, is well matched to predator behaviour. Hence, these laboratory data predict that, in natural interactions, low-flying raptors will elicit the most pronounced vocal and non-vocal responses.

The results obtained in experiments 1 and 2 demonstrate that cocks glean sufficient information from a video display to allow quite subtle discriminations, and thus extend our previous finding that computer-generated animations are effective in eliciting alarm calls and other anti-predator behaviour (Evans & Marler 1992). Males are also known to distinguish videotaped images of conspecific and heterospecific hens, presented as 'audiences' for production of aerial alarm calls (Evans & Marler 1991). Thus, both recorded and synthetic video images have proved useful for exploring perception of visual stimuli in chickens. The finding that images presented in this way are effective in contexts as different as response to a predator and social behaviour encourages the further use of these techniques.

Our results are consistent with Schleidt's (1961) demonstration that alarm calling in turkeys is principally dependent on the apparent size and speed of models presented overhead. Similarly, blue tits, *Parus caeruleus*, have been shown to change alarm call type as model size is varied (Klump & Curio 1983) and Mexican chickadees, *Parus sclateri*, tend to give higher pitched calls in response to low-flying sharp-shinned hawks, *Accipiter striatus*, than to high-flying hawks or non-predators (Ficken 1990). In contrast, Alatalo & Helle (1990) report that willow tits, *Parus montanus*, gave significantly more alarm calls to a small raptor-shaped model than to a larger one. Although apparent speed was constant in these experiments, the small model was visible for four times as long as the large model. It is consequently difficult to determine whether or not the lack of agreement with our results and those of Schleidt (1961) is due to species differences in anti-predator behaviour.

There is an apparent lack of specificity in chicken aerial alarm calling under natural conditions (Gyger et al. 1987). Surprisingly, although chickens gave aerial alarm calls almost exclusively to objects moving overhead, only a small percentage of these calls were found to be associated with the appearance of potential predators, such as red-tailed hawks, *Buteo jamaicensis*, or kestrels, *Falco sparverius*. Alarm calls appeared to be elicited by a number of non-predators, such as small passerines,

and occasionally by innocuous objects such as insects and falling leaves. The responses that we have obtained in the laboratory, with artificial raptor-like images, suggest that chickens employ a 'rule of thumb', calling to stimuli that exceed threshold values for apparent size and speed. Hence, small, low-flying, passerines may sometimes elicit alarm calls because they have properties that place them in the same region of stimulus space as a much larger raptor, flying at a greater altitude. Such a perceptual strategy may reflect a property of the chicken visual system, which is characterized by laterally placed eyes that provide an extremely wide angle of view at the cost of reduced resolution and distance estimating ability (Gyger et al. 1987).

Further experiments will be necessary to determine the role played by other stimulus attributes that potentially facilitate discrimination of predators and non-predators. For example, the relative importance of shape remains to be examined. Recent improvements in the processing speed of microcomputers and in the sophistication of commercial animation software now allow us to compare more complex and realistic stimuli. Digitized images of raptors, which preserve information present in colour and underwing patterns, can be substituted for the simple silhouettes employed in the present study. A further step toward creation of fully naturalistic stimuli involves the addition of head, wing and tail movements, all possibly salient to chickens and providing further potential cues for discriminating the movement patterns of soaring raptors from those of non-predator species.

Predator-recognition strategies have almost certainly also been shaped by ecological conditions. Red jungle fowl, *Gallus gallus*, which are thought to be the ancestral species for all domesticated chicken strains, live in forest and dense brush (Collias & Collias 1967). Simple criteria for call production have the advantage of requiring minimal processing and may consequently be highly adaptive in such habitats, since visibility is limited and reaction times must therefore be brief. It is intriguing that cock-of-the-rock, *Rupicola rupicola*, which inhabit dense forest, also have a high frequency of responses to non-predators (Trail 1987). In contrast, Walters (1990) has demonstrated that three species of lapwings (*Vanellus* spp.), which live in relatively open habitats, seem to discriminate among even quite similar species of potential predators. For example, long-toed lapwings, *Vanellus crassirostris*, never gave alarm calls to vultures, even though these were

abundant, and called more often to harriers (*Circus* spp.) than to fish eagles, *Haliaeetus vocifer*.

As Walters (1990) points out, while limited detection distances constrain response time, long detection distances not only allow more careful evaluation of predator characteristics, but also increase the cost of false alarms; predator-like birds will probably be visible much of the time and the frequency of alarms, and of consequent interruptions of behaviour, is potentially high. It seems probable that criteria for predator recognition have evolved in response to the relative costs of false alarms on one hand and of failing to respond on the other. Further comparative study of the way in which predators are recognized and categorized may well reveal that perceptual strategies have reliable ecological correlates.

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