Social responses without early experience: Australian brush-turkey chicks use specific visual cues to aggregate with conspecifics

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Summary

Almost all birds depend upon early experience with adults and siblings to learn recognition cues. Megapodes, such as the Australian brush-turkey (*Alectura lathami*), have evolved a very different life history. Eggs are incubated in mounds of decaying organic material. Chicks hatch asynchronously and receive no parental care, so imprinting cannot occur. Nevertheless, chicks subsequently form groups with similar-aged conspecifics. We explored the perceptual basis of this aggregation response, focussing on likely visual cues, such as pecking movements and body colour. Experiments were conducted under naturalistic conditions in a large aviary, using realistic robot models and colour filters. The robots successfully evoked a range of social responses resembling those of a live companion. Aggregation depended upon both behaviour and morphology. Simultaneous choice tests revealed that brush-turkey chicks preferred a pecking robot over either a static model or a scanning robot, suggesting that responsiveness depends upon particular movement patterns. In addition, chicks were sensitive to changes in appearance but only those that affected radiance at short wavelengths. The mechanism underlying social aggregation after hatching hence involves relatively specific cues. This perceptual bias seems to be largely experience independent and may exploit attributes to which potential predators are insensitive.

Key words: megapode, social aggregation, imprinting, species recognition, brood parasite, behavioural development.

Introduction

Understanding the mechanisms by which animals aggregate with members of their own species is a fundamental problem in the study of social behaviour (Shettleworth, 1998). In most birds and mammals, early experience plays a critical role; the young animal encounters at least one of its parents after hatching or birth and has the opportunity to imprint upon them (Spalding, 1873; Lorenz, 1937; ten Cate et al., 1993). This process is predictable because all mammals and most birds provide parental care. Imprinting is generally seen as a reliable mechanism that both ensures short-term survival and provides experience relevant to mate choice in adulthood (Ryan and Rand, 1993; Sherman et al., 1997; ten Cate and Vos, 1999).

Three groups of birds, however, reveal that other developmental pathways can evolve. Interspecific brood parasites, such as cuckoos and cowbirds (*Molothrus ater*), are incubated and raised by members of other species. Black-headed ducks (*Heteronetta atricapilla*) are incubated by heterospecifics but live independently of their foster parents soon after hatching (Weller, 1968). Megapodes also receive no parental care, but in this case the heat required for incubation is derived from inanimate sources, depriving the chicks of any potential social interactions.

The development of social attachments in brood parasites has been the focus of much study (Hamilton and Orians, 1965; West and King, 1987; Soler and Soler, 1999; Hauber et al., 2000; Payne et al., 2000; Hauber and Sherman, 2001; Hauber, 2002), but less attention has been paid to this aspect of megapode ontogeny. Megapodes leave the incubation of their eggs to solar heat, geothermal heat in burrows or the heat produced by microbial decomposition in mounds of leaf litter (Jones et al., 1995). Their highly precocial chicks dig themselves out of their underground nest and never form bonds with their parents (Jones et al., 1995; Göth, 2001b). Opportunities for imprinting thus do not occur. Wong (1999) repeated the classic experiments designed to test imprinting in other birds (Hess, 1958) and found that, in a circular runway, young chickens (*Gallus gallus domesticus*) followed a ball that was moved away from them, and thereby imprinted on it, but hatchlings of the Australian brush-turkey (*Alectura lathami* Gray; henceforth brush-turkey) showed no such response.

Recent work on brush-turkey chicks – the only megapode species studied in detail – also suggests that they are unlikely to imprint on similar-aged conspecifics during a sensitive period after hatching. Brush-turkeys hatch asynchronously and spend, on average, 40 h buried in the incubation mound before

dispersing (Göth, 2002). Thereafter, they usually live on their own while foraging in the leaf litter beneath protective thickets (Göth and Vogel, 2003). Brush-turkey chicks are capable of finding adequate food alone (Göth and Proctor, 2002) and of responding appropriately to predators without prior experience (Göth, 2001a). These attributes enable them to survive without assistance from others. In a recent radio-tracking study, free-ranging brush-turkey chicks were seen feeding near at least one other chick in 6% of all encounters (N=166 encounters with 31 chicks, aged 2 days to 4 weeks; Göth and Jones, 2003). Chicks older than 100 days are seen in groups more often (Jones, 1988). Brush-turkeys hence first aggregate with conspecifics at an unpredictable age, between two days and several weeks following emergence from the incubation mound.

A recent study in which chicks were kept in a large outdoor aviary revealed that social responses to similar-aged conspecifics were apparent from as early as two days. All of the behaviour patterns found in older chicks were present in hatchlings, and these did not change appreciably with age (Göth and Jones, 2003). In addition, hatchlings stayed close together (median distance 0.1 m while feeding and 0.34 m while resting), despite the large size (76 m^2) of the aviary (Göth and Jones, 2003). Brush-turkey chicks thus have competent social behaviour when they first encounter a conspecific, suggesting that the mechanism responsible for aggregation is largely independent of early social experience. What features of a conspecific are involved in evoking this aggregation response? The aim of this study was to evaluate the role of visual cues, including both morphology and movement.

Our general approach was based upon recent work with cowbirds (Hauber et al., 2000, 2001). These brood parasites face a similar developmental challenge in that they grow up without parents or siblings. Imprinting on the features of a heterospecific foster parent would lead to subsequent errors in species recognition and mate choice (Hauber and Sherman, 2001). Young cowbirds seem to rely instead upon self-referent phenotype matching, a mechanism in which they learn salient aspects of their own phenotype, such as calls or plumage colour, and then match the appropriate features of conspecifics to these (Hauber et al., 2000, 2001).

We tested whether two particular aspects of the brush-turkeys' phenotype affect social aggregation: 'colour' (i.e. the spectral shape of the light reflectance function) and behaviour, in particular pecking movements. Recent work has shown that plumage colour plays an important role in many avian social interactions (Hill, 1991; Bennett et al., 1997; Cuthill et al., 1999; Hunt et al., 2001). Classic studies established that galliform chicks are particularly responsive to maternal pecking (Turner, 1965), suggesting that this particular motor pattern might also be important with similar-aged companions. We did not consider vocalisations a likely cue because brush-turkey hatchlings rarely call (Göth and Jones, 2003). This is the first investigation of the way in which any megapode aggregates with conspecifics. It forms part of a series of experiments exploring whether such mechanisms are convergent across different groups with the shared life-history property of having no reliable opportunity to learn species-specific characteristics from others.

General methods

Chicks: origin and housing

Brush-turkey eggs are usually incubated by the heat produced by microbial decomposition of organic material in mounds of leaf litter. Eggs were collected from 22 such incubation mounds in the Central Coast region, north of Sydney (NSW, Australia), and incubated artificially (Brinsea Octagon 250 Incubator, temperature 34°C, humidity 80–95%). Hatchlings were isolated in individual brooders for approximately 40 h, the average time they remain in the incubation mound before reaching the surface (Göth, 2002). They did not encounter conspecifics until being observed in two-way choice tests at the age of two days. After testing, they were housed in an outdoor aviary (6×3×3 m) until release, which occurred at an age of 2–14 days. Food and water was provided *ad libitum*. All chicks were released at their place of origin.

Procedure

Tests took place in a large, T-shaped, outdoor aviary (Fig. 1), in which the chicks were presented with a simultaneous choice between two stimuli in opposite arms. The aviary was constructed in a forest (Macquarie University Fauna Park), which resembled the natural habitat of brush-turkeys. Chicks are very wary and are most likely to behave naturally in such an environment (Göth and Jones, 2003). The centre of the aviary contained a covered area (30 cm high), which was the section from which tests were begun (Fig. 1). Chicks entered the choice arms by crossing a line delineated by inconspicuous markers on the ground. A very fine green mesh 'division net' separated the central compartment from the two arms containing the stimuli (Fig. 1). The floor of the test aviary was covered with sand, pebbles and leaf litter. Observations
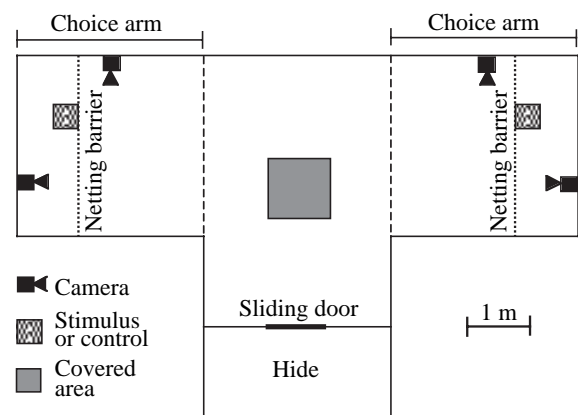

Fig. 1. Plan view of the experimental aviary, showing the position of the hide, the covered area in which chicks were placed at the beginning of the test, stimuli and cameras.

were conducted from a hide directly opposite the covered area and connected to the test arena *via* a sliding door (Fig. 1). Water and seeds were provided beneath the covered area.

Tests were begun by placing a chick under the covered area, after which the observer slowly crawled back to the hide and closed the sliding door. Chicks usually crouched during this 10–16 s-long procedure and afterward remained still for a period of up to 10 min. Such immobility is the typical response of brush-turkey chicks to predators (Göth, 2001a); it usually ended when the chick stood up and started to scan its surroundings or peck at the ground. Of the 96 chicks tested, 91 showed this behavioural sequence of crouching and scanning/pecking and it can thus be inferred that they made an active choice when finally leaving the covered area to enter one of the choice arms. Four chicks ran into a choice arm while the observer was still retreating to the hide. These were excluded from the analysis because their behaviour seemed more likely to be an antipredator response than social aggregation with the stimulus. One chick did not leave the covered area for one hour and was also excluded from the analysis. Tests were conducted in the morning (07:00 h–11:00 h) on fine days, except for three that had to be postponed until the afternoon due to rain. Each chick was tested only once and experienced a single pair of stimuli. Stimuli were assigned to the choice arms in a constrained random sequence, such that they were presented an equal number of times on the left and right side. Tests lasted for one hour.

All procedures were approved by the Macquarie University Animal Ethics Committee (Protocol no 2002/013) and the New South Wales National Parks and Wildlife Service (Licence no. S10473).

Scores and analysis

Four video cameras covered the choice arms of the aviary (Fig. 1). These were connected to a multi-channel monitor in the hide, which the observer relied upon whenever the chick was in a blind corner. At all other times, she used direct observation and recorded continuously with a stopwatch the time that the chicks spent in the centre area and in each of the two choice arms. Half of the observations were conducted by A.G., the other half by a research assistant. For analysis, we converted the time recorded in each choice arm to a percentage of the total time spent in both choice arms. Exploratory analysis revealed considerable heterogeneity of variance, and data transformation did not generate normality. We thus adopted the non-parametric Wilcoxon signed-rank test for all pairwise comparisons, as this is sensitive to both the direction and magnitude of differences (Siegel and Castellan, 1988). Tests were one-tailed because we had *a priori* predictions about chick preference in every case (see below).

Pilot test

We began with a test designed to verify that the aggregation response was expressed normally in the T-shaped aviary. Six chicks were each presented with a simultaneous choice between a conspecific in one choice arm and a box of similar

colour and dimensions ($17 \times 10 \times 13$ cm) in the other. We predicted that the box would be approached less often than the live chick. The stimulus chick was 2–3 days old and provided with food and water. Stimulus chicks were moved into the area behind the division net at least half an hour before the test. They appeared calm, moved around freely and showed the full range of natural chick behaviour. A different stimulus chick was presented in each test. Four of the five tested chicks spent 100% of their time in the choice arm containing the stimulus chick, one chick spent 97.5% of its time near the stimulus chick and the remaining time near the box. As a group, chicks approached the stimulus chick significantly more often than the box (Wilcoxon test, $z=-2.33$, $P=0.01$, one-tailed, $N=6$). This strong spontaneous preference for another chick over a size-matched object of equal novelty provides the basis for subsequent analyses designed to identify the features responsible for the aggregation response.

Behaviour as a cue evoking social aggregation

In many animals, behaviour plays an important role in social interactions. For example, courtship displays strongly influence female preference and can act synergistically with morphology (Rosenthal et al., 1996). To evaluate the importance of behavioural cues, we used chick robots. This approach provided a highly realistic stimulus under natural light conditions. The use of robots in animal behaviour is a classic technique (Simpson, 1968) that has recently been developed to reproduce quite complex avian motor patterns (Patricelli et al., 2002). Robots have the advantage that they standardise behaviour and remove social interactions between stimuli and focal animals that might otherwise complicate interpretation of the responses evoked.

We tested movement preferences using two comparisons: (1) a pecking *versus* a static robot and (2) a pecking *versus* a scanning robot. The first experiment was designed to detect a general preference for realistic movement, while the second evaluated the specificity of response by comparing pecking with a control movement of similar amplitude but in an orthogonal plane. We used one-tailed tests because we predicted that the pecking robot would be more attractive than either the static or the scanning robot. These predictions were based both upon our own previous studies of brush-turkey chicks and on published accounts of general galliform behaviour.

Brush-turkey chicks held in groups often approach a pecking companion and then fixate upon the food it is feeding on; such a response is less likely to be evoked by other types of conspecific behaviour (Göth and Jones, 2003). In addition, classic studies have established that galliform chicks in general are particularly responsive to maternal pecking (Turner, 1965), suggesting that in megapodes (which do not form bonds with their parents) this particular motor pattern might be important with similar-aged companions. There are also functional reasons for predicting that the pecking model should be more salient. Brush-turkey hatchlings face an unusual challenge:
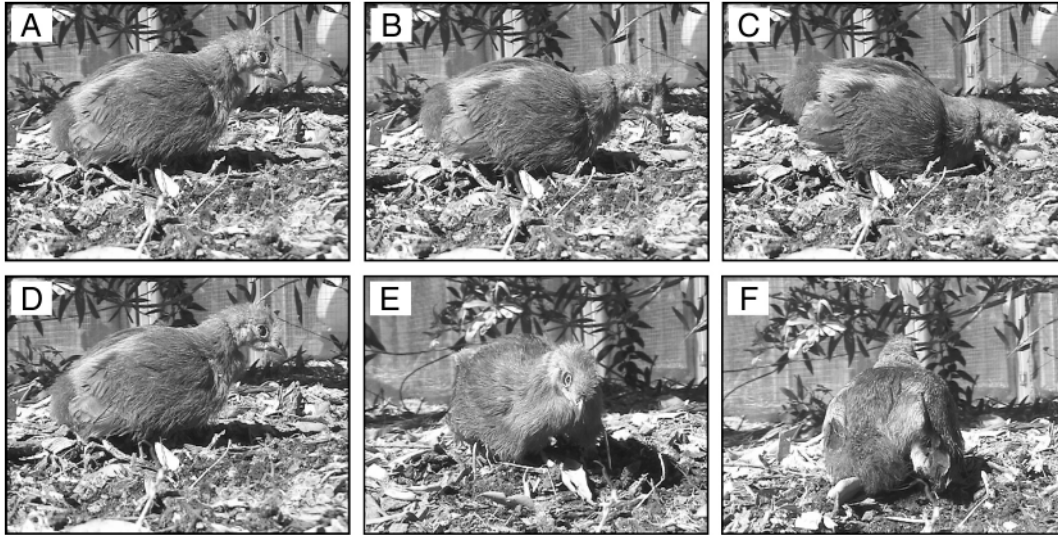
Fig. 2. Robot stimuli used to test movement preferences. Representative frames are shown to depict the two types of motor patterns presented: pecking (A–C) and scanning (D–F).

they have to find food on their own, unaided by their parents. A pecking conspecific is likely to indicate a source of food, so that preferential approach will likely enhance foraging success. Finally, sensitivity to specific motor patterns is ubiquitous in vertebrates because it helps animals to select the small sub-set of visual motion cues that are functionally important and to filter these from the many irrelevant events occurring in the environment (Nakayama and Loomis, 1974; Fleishman, 1992). We predicted that pecking movements would be responded to in this way.

Methods

The robots were constructed from taxidermally prepared mounts of 3-day-old chicks that had died naturally. They contained a servo motor ('Nagro'; Grand Wing Servo-tech, Hsichih, Taipei, Japan) that was operated by radio control ('Attack' 2-channel system; Futaba Bioengineering, Irvine, CA, USA). The motor moved the chick body in either a vertical (pecking movement) or horizontal (scanning movement) plane, while the feet remained stationary (Fig. 2). During pecking, the head moved from a static position (in which the beak was pointing forward), downward until it made contact with the ground (Fig. 2A–C). During scanning, the robot performed horizontal movements of the whole body, through an angle of approximately 45° to either side of the resting position (Fig. 2D–F). Three pecking robots were used randomly in the choice tests (including the 'filter tests' described below), and one scanning robot was presented in the pecking–scanning comparisons. The static control model was mounted in a neutral posture, with the head horizontal, the beak pointing forward and the feathers sleeked.

An assistant moved the robot *via* remote control at the beginning of each test, while the chick was being placed under the covered area by the observer. Robots were moved in bouts of 10 pecking or scanning movements with a total duration of 6.5–8.0 s, which made up a single 'stimulus event'. The intervals between stimulus events were varied between 1 min and 4 min to minimize habituation. In tests that involved the presentation of two robots, both were moved simultaneously.

Results

When given the choice between static and pecking robot models of similar-aged conspecifics, chicks spent significantly more time near the pecking robot (Fig. 3A; Wilcoxon test, $z=-1.79$, $P=0.042$, one-tailed, $N=15$). Chicks also significantly preferred the pecking robot over the scanning robot (Fig. 3B; Wilcoxon test, $z=-1.80$, $P=0.036$, one-tailed, $N=11$). This latter result suggests a degree of specificity in the
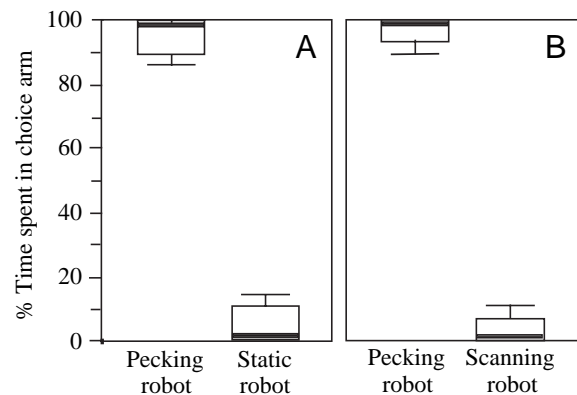

Fig. 3. Time spent by chicks in the choice arms when presented with a simultaneous choice between a pecking robot and a static model of a conspecific (A) or between pecking and scanning robots (B). Values represent percentages of the time that chicks spent in both choice arms. The median is shown by the bold line, lower bars show 1st quartiles (in this case identical to the median) and upper bars show 3rd quartiles. Whiskers indicate smallest and largest value.

aggregation response. Chicks seem to have been sensitive to the plane of movement not just to its presence or absence.

Body colour as a cue evoking social aggregation

Plumage colour has been shown to play an important role in evoking social aggregation in cowbird fledglings (Hauber et al., 2000), which have a life history that resembles, to some extent, that of brush-turkeys (see Introduction). We therefore tested whether the chicks' approach behaviour towards the pecking robot (Fig. 2A–C) changed when we manipulated its colour. We conducted simultaneous choice tests with a colour-manipulated robot in one randomly selected choice arm and a normal-looking robot, under a neutral density filter, in the other. We predicted that chicks would preferentially approach the normal-looking robot in each type of comparison and thus used one-tailed tests.

The use of colour filters allowed us to make global changes to the colour of the whole robot by altering the spectral shape of ambient light. This method of colour manipulation has been widely adopted in mate choice experiments with birds (Hill, 1991; Bennett et al., 1996, 1997; Cuthill et al., 1999; Hunt et al., 1999, 2001). Filters were mounted horizontally above the robot chicks, on a frame 35 cm high, 72 cm wide and 72 cm deep. We adopted this technique in preference to a vertically

mounted filter in front of the robot stimulus, as this would have changed the overall light conditions in the choice arm, including the background (Bright and Waas, 2002). The overhead filters only affected the light environment in a 72 cm-wide area centred upon the robot and caused no change in the light environment in the remaining area of the choice arm, which was 3 m wide.

Methods

Colour manipulation followed methods described by Hunt et al. (2001) and involved four types of filters that each blocked a different waveband of the bird-visible spectrum at rates of 95–99%. (1) UV (Rosco UV 311413) blocked UV below 390 nm; (2) SW (Rosco E 015) blocked short-wave at 380–480 nm; (3) MW (Rosco E 028) blocked medium-wave at 500–550 nm and (4) LW (Rosco E 115) blocked long-wave at 560–660 nm. The neutral density filter (Rosco E 00) provided a matched reduction in quantal flux uniformly over the range between 300 and 700 nm. The wavebands removed by the SW, MW and LW filters match as closely as possible the spectral sensitivity of the four cone types known for galliforms; the UV filter was added because some body regions were found to strongly reflect in the UV (see Results).

Tests with coloured filters were conducted outdoors under natural light. Overhead illumination was therefore not as
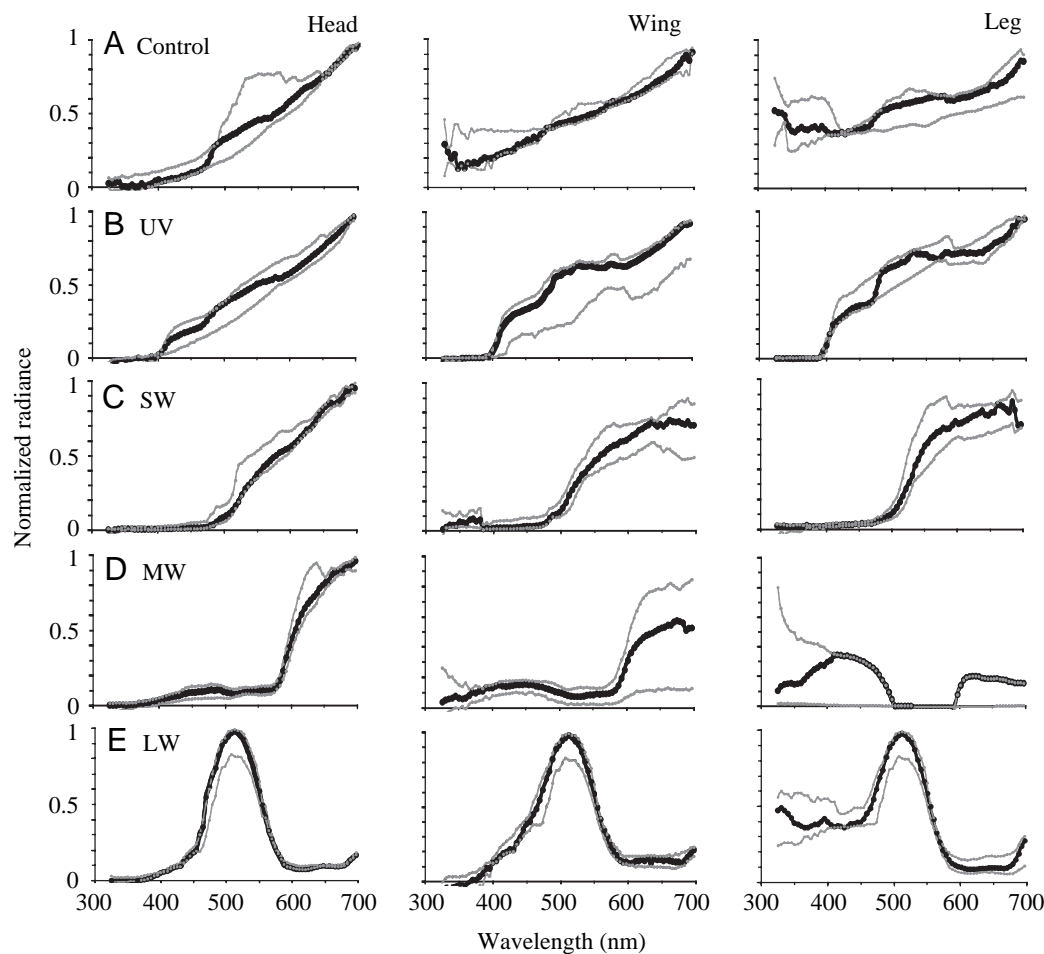

Fig. 4. Normalized radiance spectra for three body regions (head, wing and leg) of chick robots presented under five different types of filters (control, neutral density filter; UV, UV blocking; SW, short-wave blocking; MW, medium-wave blocking; LW, long-wave blocking). N_{chicks}=10; $N_{measurements}$=12 per filter and body region, taken under three different light conditions. Bold line is the median, grey lines represent 1st and 3rd quartiles. Spectra were calculated by first obtaining an individual median from four randomly located measurements within each body region and then calculating a median value for the group.

uniform and constant as in laboratory tests (e.g. Bennett et al., 1996; Hunt et al., 2001). The prevailing light environment can have profound effects on the perception of colour signals (Endler, 1993a; Bennett et al., 1997). To account for such effects, we measured the radiance spectra of three body regions of the robot chicks under each type of filter and under three different light conditions that were experienced during tests: (1) full sun, with bright sky; (2) overcast, with cloud-covered sky; (3) partly overcast and partly sunny. Measurements were conducted with a USB2000 Miniature Fibre Optic Spectrometer (Ocean Optics, Dunedin, FL, USA) and a collimating lens (74-UV; Ocean Optics). Results suggest that changing light conditions caused the expected variation in the radiance curves obtained but that the four treatments remained clearly distinct (Fig. 4).

In addition, we measured the reflectance of five body regions of 10 live chicks using a two-fibre probe, held at 45° to the sample's surface, with illumination from an internal deuterium–tungsten light (Light Mini D2T; Ocean Optics). Four randomly located measurements were taken within each body region of both robots and live chicks. The obtained spectra were the reflectance of the sample relative to that of a white WS-1 diffuse reflectance standard.

For analysis, radiance and reflectance spectra were averaged from 15 scans. Data were initially collected over the range 300–800 nm. We then calculated the median value at 5 nm intervals from 320 to 700 nm, across the four randomly located measurements. Data were normalized by dividing all values by the highest value obtained, and the median, 1st and 3rd quartiles were then calculated for each interval.

Results

The effect of filter treatments on the chicks' preference for a robot conspecific varied with spectral region (Fig. 5A–D). When UV and SW radiance were removed from the robot, chicks spent significantly more time in the choice arm containing a control robot that reflected in all wavelengths (Wilcoxon tests; UV, $z=-2.0$, $P=0.01$; SW, $z=-1.67$, $P=0.048$; both $N=15$ and one-tailed). By contrast, removal of MW and LW radiance did not have a significant detrimental effect on the attractiveness of the robot (Wilcoxon tests; MW, $z=-0.60$, $P=0.28$, $N=15$; LW, $z=-1.38$, $P=0.09$, $N=14$; both one-tailed).

Fig. 6 illustrates reflectance spectra from five body regions of live chicks. While the back, head and wing show the expected curve for brown colour, a surprisingly strong peak for UV and SW reflectance was found on the beak and especially the legs.

Behavioural responses to the robot models

In the tests described so far, a robot model was considered to be preferred when the chick spent significantly more time in the choice arm containing it. To complement these data on spatial location, we also analyzed responses to the movements of the robot in detail. This allowed us to evaluate whether approach reflected a social response.
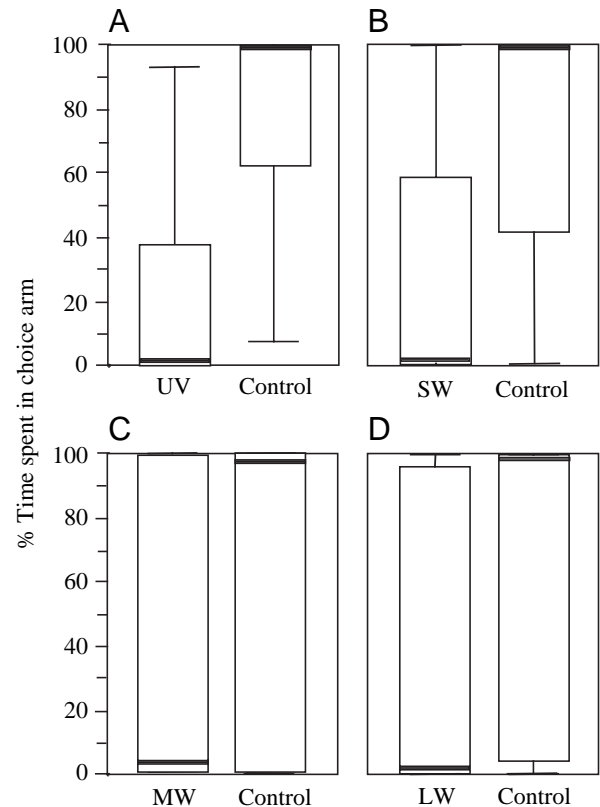

Fig. 5. Time spent by chicks in the choice arms when presented with a simultaneous choice of pecking robots under coloured filters and a pecking robot under a neutral-density filter as control (A, UV; B, SW; C, MW; D, LW). Description of values and box-whisker plots as in Fig. 3.

Methods

High-resolution footage of behaviour was obtained by tracking each chick with a digital colour video camcorder (Panasonic NV-DS 15). Subsequent analyses of recorded footage yielded frequency scores for the first behaviour that occurred in response to each stimulus event (bout of 10 robot pecking movements). Social behaviour in the choice arm was assigned to one of the following six categories:

(1) withdrawal: chick increased its distance from the robot;

(2) approach: chick moved to the division net in front of the robot, within 1 m on either side;

(3) pushing: chick pushed against the division net within 1 m on either side of the robot;

(4) pecking: chick pecked at the ground;

(5) preening: chick preened feathers or stretched a wing or leg;

(6) no response: behaviour could not be assigned to any of the above categories.

The frequency of each of these behaviours was analysed separately for each of the first 10 stimulus events. To obtain a sufficient sample size, we pooled data from all robot tests. Analyses thus reveal the extent to which pecking robots were responded to as a social companion; they do not permit fine-grained comparisons among treatments, for which we had
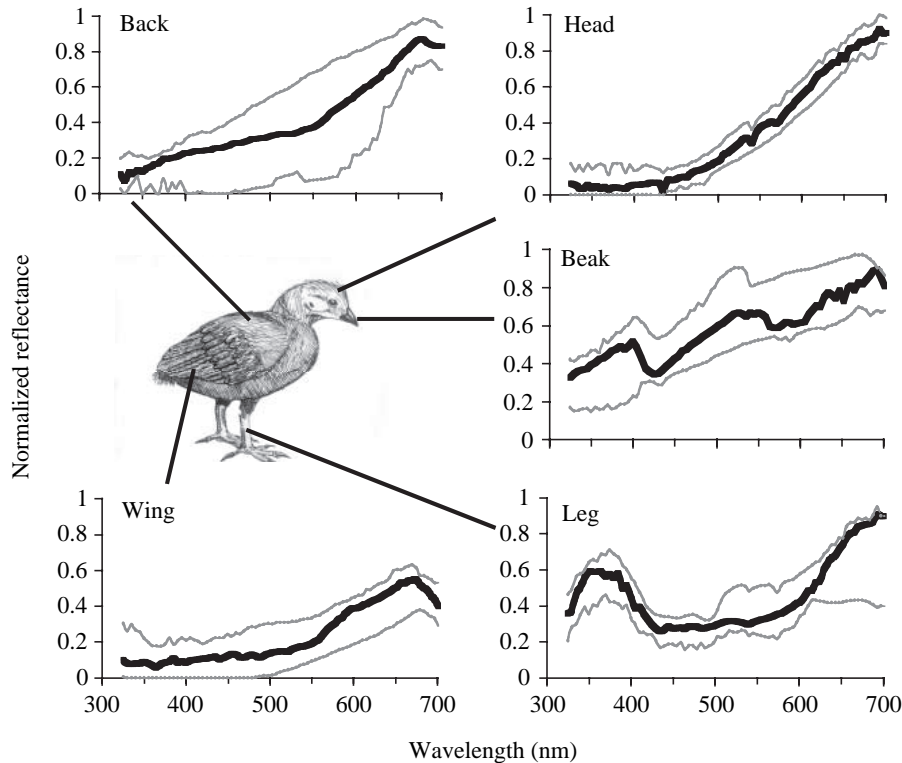
Fig. 6. Normalized reflectance spectra for five body regions of live chicks (*N*=10). Bold line shows the median, grey lines represent the 1st and 3rd quartiles. Spectra were calculated in the same way as for Fig. 4.

insufficient power. To evaluate whether chick behaviour varied over time, a Friedman non-parametric analysis of variance (ANOVA) was used for each type of response.

Results

Most chick responses to the robot were unambiguously social. Approach was the most common social behaviour (25%), followed by pecking at the ground (22%) and pushing against the division net (7%; values calculated from all responses to all stimulus events experienced by the chicks in the movement and colour experiments). Withdrawal represented only 14% of the responses, while 31% of stimulus events evoked no response.

There are some indications that the chicks' responses to the moving robot might have habituated over time, although the pattern is mixed and not all behaviours were affected (Fig. 7). The frequency of pecking decreased significantly with successive stimulus events (Friedman ANOVA, χ^2=21.85, *P*=0.009, d.f.=9), suggesting a reduction in aggregation response, but the probability of withdrawal was also reduced (Friedman ANOVA, χ^2=28.21, *P*=0.001, d.f.=9), which is consistent with some chicks becoming less fearful over time. The frequency of no response increased significantly over the test (Friedman ANOVA, χ^2=21.46, *P*=0.011, d.f.=9). However, the two remaining social behaviours, approach and pushing, occurred in response to all stimulus events, and their frequencies did not change significantly over time (Friedman

ANOVAs, approach χ^2=8.23, *P*=0.51, d.f.=9; pushing χ^2=2.87, *P*=0.97, d.f.=9).

Discussion

Brush-turkey hatchlings are attracted by the pecking movements of a conspecific (Fig. 3) and by body regions that reflect at short wavelengths (Fig. 5). This appears to be a robust effect; it is apparent despite considerable variation in lighting conditions of the type that chicks would experience in nature (Fig. 4). Detailed analyses reveal that the pecking robots (Fig. 2) evoked a range of social behaviour (Fig. 7), suggesting that they successfully engaged the same processes as a live companion. The mechanism underlying social aggregation after hatching hence involves a selective response to relatively specific behavioural and morphological characteristics. This perceptual bias seems to be largely experience independent, as chicks had absolutely no social contact prior to the choice tests.

Pecking movements may be particularly suitable cues for evoking approach behaviour. Many signals used in animal interactions are defined by movement. This is true in contexts as diverse as opponent assessment, mate choice, pursuit deterrence and alarm signalling (summary in Peters et al., 2002). Animals
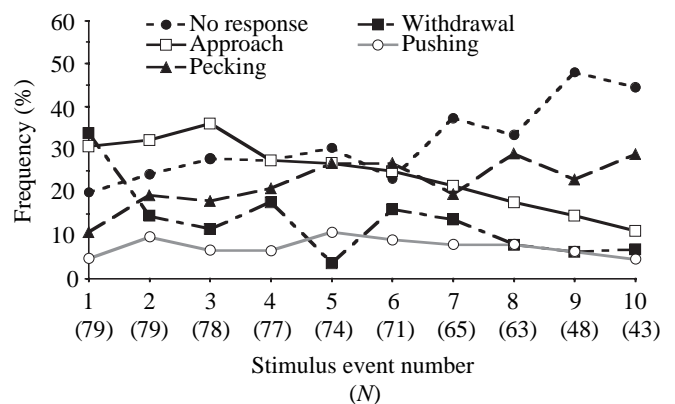

Fig. 7. Behavioural responses of brush-turkey chicks to the first 10 stimulus events in choice tests that included a pecking robot. Each stimulus event consisted of 10 robot pecking movements. Behaviours represent the initial response evoked. Numbers in parentheses show sample size (*N* chicks) per stimulus event – sample sizes vary because some chicks only spent a short time in a choice arm containing the pecking robot and experienced only few stimulus events. See Methods for detailed descriptions of behavioural categories.

have thus generally evolved high sensitivity to specific movement patterns that are functionally important (Nakayama and Loomis, 1974; Fleishman, 1992). Responding to pecking movement has a likely functional benefit, as this behaviour can indicate a potential food source. Brush-turkey chicks are omnivorous. They hatch with a general tendency to respond to some common features of food objects, such as contrast, movement and reflective surfaces, and while trial and error is initially important, they successfully aim their pecks at edible items soon after hatching (Göth and Proctor, 2002). A pecking conspecific indicating food might speed up the transition from trial and error searching to more selective pecking through social transmission of food-type preferences (Galef, 1993), or it could simply stimulate foraging more generally through social facilitation (Keeling and Hurnik, 1993). In domestic chickens, *Gallus gallus domesticus*, young chicks respond strongly to a pecking model of a hen (Turner, 1965). Megapode chicks do not form bonds with their parents but instead show this predisposition in response to conspecific chicks of similar age. These feed on similar-sized food – small invertebrates, fruit and seeds – while adults, which weigh approximately 2 kg, search for much larger items (A.G., unpublished data).

We next consider the issue of why brush-turkeys might respond selectively to a particular spectral region. In this context, it is important to note that we treat the visual attributes mediating approach and social behaviour as cues, rather than signals (review in Bradbury and Vehrencamp, 1998). Specifically, we do not yet know enough about the costs and benefits (Seeley, 1989) or the evolutionary history of these traits (Hasson, 1997) to conclude that they function as signals in the strict sense. Nevertheless, recent work on sensory processes, much of it undertaken to explore signal design, provides valuable insights concerning conspicuousness.

The relative importance of shorter wavelengths is likely to be the product of both habitat transmission and sensory tuning (Endler, 1992, 1993b; Boughman, 2002). Whether a particular colouration appears conspicuous to potential receivers depends upon the light environment and natural background against which it is usually seen (Endler, 1993a; Endler and Basolo, 1998). Brush-turkey chicks typically inhabit thickets, either in the understorey or at the rainforest edge (Göth and Vogel, 2003). In such habitats, short wavelengths are common in natural light, such as that in woodland shade, small or large gaps in the canopy, or in cloudy conditions, while they are rare in leaves and leaf litter (Endler, 1993a; Andersson et al., 1998). This latter vegetation type is the typical visual background against which chicks are viewed by conspecifics, and short wavelength reflectance is thus a good way to produce high visual contrast.

Recent studies have revealed much about the way in which the avian retina responds to visual stimuli (e.g. Endler, 1990; Bennett and Cuthill, 1994; Osorio et al., 1999; Hart, 2001; Hunt et al., 2001). The exact spectral sensitivity of brush-turkey cone cells is not known, but it most likely resembles that of other galliforms, such as the domestic chicken. This is indicated by a preliminary study of brush-turkey retinas (N.

Hart, personal communication), as well as recent findings by Odeen and Hastad (2003). In the chicken, four cone visual pigments have been identified, with mean peak absorbance at 417–420 nm (violet), 453–470 nm (short-wave), 507–540 nm (medium-wave) and 571–600 nm (long-wave) (Bowmaker et al., 1997; Osorio et al., 1999). The sensitivity of the brush-turkey's cone cells should thus have been covered by the short-, medium- and long-wave filters used in the present study. The UV filter did not precisely match the peak sensitivity of any cone type but it is likely to have filtered out wavelengths falling into the lower part of the sensitivity range of the short-wave sensitive cone. Furthermore, the violet cones can also detect long-wavelength UV, from 360 to 400 nm (Odeen and Hastad, 2003).

Signal design is influenced not only by the sensory properties of conspecifics but also by those of eavesdroppers, such as predators (Endler and Basolo, 1998). Selection for efficient communication at minimal risk has produced signals that exploit 'private channels' in some species (Cummings et al., 2003). The natural predators of brush-turkey chicks are raptors, tree goannas (*Varanus varius*), snakes and quolls (*Dasyurus* spp.) (Göth and Vogel, 2002). One remarkable finding of this study was that the chicks' legs reflected strongly in the UV and short-wave ranges (Fig. 6). Birds of prey typically have a similar spectral sensitivity to megapodes (Odeen and Hastad, 2003) but, when flying overhead, they are unlikely to spot the legs of a chick, as these will be well hidden beneath the dull brown body. Most mammalian predators are effectively blind in the UV (Jacobs, 1993), although goannas and snakes can perceive these wavelengths (Husband and Shimizu, 2001). Taken together, this pattern of results is consistent with the idea that brush-turkeys make use of a cue that is conspicuous to conspecifics – and hence effective in mediating an aggregation response – but concealed from important classes of predators, including raptors and mammals.

Legs, and to a lesser extent beaks, may be particularly suitable body regions for an aggregation cue for a second reason. Chicks grow rapidly and start replacing their brown hatching plumage with black feathers during the third week of life (Wong, 1999). Basing a cue on ephemeral plumage colour would hence seem less adaptive than using the colour of the legs, which is stable throughout development.

In summary, our results suggest that the morphological cues important in social aggregation in Australian brush-turkeys are found at short wavelengths. Future experiments will involve selective manipulation of the UV components of body coloration to determine whether this is necessary for a behavioural response. Recent studies with birds suggest that UV reflectance is important in a range of contexts, including foraging (Cuthill et al., 2000) and mate choice (Maier, 1994; Bennett et al., 1996, 1997; Andersson and Amundsen, 1997; Hunt et al., 1997, 1999), although there is some controversy over whether this spectral region should be considered 'special' (Hunt et al., 2001; Hausmann et al., 2003). Confirmation of a role for UV in the aggregation response of brush-turkey chicks would constitute the first evidence for a

new function, that of a cue mediating social responses early in life.

It will be important to establish whether the perceptual preferences described here are sufficiently specific to function as a species-isolation mechanism. In Northern Queensland and New Guinea, brush-turkeys occur sympatrically with the orange-footed megapode (*Megapodius reinwardt*). The chicks of both species look alike to humans and they behave similarly and live in the same habitat (Jones et al., 1995). A comparative study will reveal whether specific movements or morphological characteristics serve as species-recognition cues.

Our results will also allow exploration of the role of experience in the development of species recognition in megapodes. If learning occurs, perhaps triggered by specific cues that are inherently salient, then megapodes will have properties convergent with those of cowbirds, in which such processes play an important role (Hauber et al., 2000, 2001). If not, then megapodes may represent a unique solution to the challenge of species recognition without models.

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