

# Visual recognition of predators by hatchlings of the Australian brush-turkey *Alectura lathami* J.E. Gray

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The megapode hatchling receives no care or guidance from its parents and so must be able to survive by itself. This raises some basic questions about the innate abilities of megapode hatchlings, including the possibility of predator recognition. Experiments were conducted to investigate the visual predator recognition abilities of the hatchlings of the Australian brush-turkey *Alectura lathami* J.E. Gray, 1831. Two separate methods involving video images and actual stimuli were used. There were no significant differences between the behaviours observed before compared to after the presentation of each stimulus, whether it was predator or non-predator, moving or non-moving. The hatchlings did not respond with any escape or avoidance behaviours when presented with predator stimuli. Although there are a number of potential explanations for these results, it is most likely that the responses observed were genuine, indicating that brush-turkey hatchlings do not instinctively flee in response to the visual presence or movement of a predator. In the wild, they may adopt the strategy of freezing, as do hatchlings of the malleefowl *Leipoa ocellata* Gould, 1840. However, high mortality rates indicate this strategy is not very successful and their survival to sub-adult stage may be largely dependent on chance.

## Introduction

### Chick development

In avian species, chicks can hatch at vastly different levels of development and independence, ranging from totally helpless to relatively independent (Ricklefs, 1983; O'Connor, 1984). The state at hatching is related to the length of the incubation period and influences the level of parental care following hatching. In the category of least development is the altricial chick, which hatches naked with closed eyes and is totally dependent on its parents for food, warmth and protection. Examples include passerine species, some of which have incubation periods of less than two weeks (Oppenheim, 1972). At the other extreme, the most advanced, or precocial, chicks are able to walk and follow their parents soon after hatching, although they are still not totally independent. Familiar examples are the domestic chicken *Gallus gallus* (Linnaeus, 1758) and the mallard duck *Anas platyrhynchos* Linnaeus, 1758, which have incubation periods of three weeks and almost four weeks respectively (Oppenheim, 1972).

In the domestic chicken, hatchlings remain with the hen for the first 10-12 days (Bruckner, 1933, cited in Wood-Gush, 1955) and upon leaving the nest, the process of imprinting ensures that these precociously mobile chicks stay nearby (Freeman & Vince, 1974). The chicks learn appropriate responses to predators through social contact with, and by observing, the hen (McBride et al., 1969).

### Megapode hatchlings

In contrast, even to most highly precocial species, megapode hatchlings are independent from hatching and do not receive any parental care (Jones et al., 1995). Therefore, they are unable to experience the social contact and parental guidance available to most galliforms. The fact that they can walk, run, fly and feed without the help of their parents illustrates what may be regarded as superprecociality.

One of the keys to survival is managing to find food for yourself without becoming food for something else. An important factor is being able to recognise a potential predator and respond appropriately and in sufficient time to escape without injury. This is of particular interest in megapodes because of the total lack of contact between parent and hatchling. Here I describe studies of predator-hatchling interactions in the Australian brush-turkey *Alectura lathami* J.E. Gray, 1831.

### The Australian brush-turkey

The natural habitat of the Australian brush-turkey (hereafter referred to as brush-turkey) is tropical and subtropical forests (Seymour, 1991), but it is also able to survive in open forest and *Lantana* spec. scrub (Kaveney, 1958). The brush-turkey is found along the eastern coast of Australia from Cape York to the central coast of New South Wales (Blakers et al., 1984). At present, the brush-turkey is widespread and abundant throughout its distribution (Jones, 1989) and has become quite common in suburban Brisbane, particularly in suburbs near forest reserves and waterways (Jones & Everding, 1991). The fact that it is locally common in Brisbane suburbs, with eggs being readily available, makes it an ideal megapode species to use in studies of hatchling behaviour.

The brush-turkey hatchling has buff-brown to sooty-brown feathers and the area directly around the eyes is bare and dull-yellow in colour (Jones et al., 1995). The bill is black and the leg and foot dark olive-brown. A new hatchling weighs between 115-135 g (Baltin, 1969), which is comparable with the weights of other megapode species (Jones et al., 1995). Even though little is known of the brush-turkey hatchling, other aspects of the species' biology have been given considerable attention, including breeding behaviour (e.g. Jones, 1987, 1990a, 1990b), mound and egg physiology (e.g. Seymour & Rahn, 1978; Seymour, 1985; Seymour et al., 1986; Seymour & Bradford, 1992) and detailed observations in captivity (Fleay, 1937; Baltin, 1969).

As there is no hatching synchronization among the numerous eggs being incubated within a mound site, brush-turkey hatchlings may emerge from the mound independently at any time and immediately move into the surrounding forest (Jones et al., 1995). It is, therefore, virtually impossible to observe their natural behaviour in the wild during the first week after hatching. An alternative method used in this study was to conduct experiments in an artificial environment.

The behaviour of live animals is often difficult to control or predict, so video images of predators and neutral objects were initially used as stimuli in an attempt to maintain consistency between experimental sessions. The use of video techniques is becoming an increasingly acceptable and versatile tool for studies of social behaviour in animals (e.g. Evans & Marler, 1991, 1992; Evans et al., 1993a; Rowland et al., 1995). Alarm call responses to the appearance of predators have been successfully studied in

the domestic chicken using computer-generated and video images of aerial and ground predators (Evans et al., 1993b).

Hatchlings of the malleefowl *Leipoa ocellata* Gould, 1840, rely totally on their mottled camouflage by remaining motionless on the ground when approached or threatened (Priddel & Wheeler, 1994). The chance of surviving beyond one month of age was greatly increased in malleefowl only when sufficient food was available and ground-dwelling predators were removed from the habitat (Priddel & Wheeler, 1990). This suggests that the defence strategy of freezing is not effective against most predators and raises the question as to whether megapode hatchlings have the ability to recognise predators. To date, there have been no studies conducted to test the degree to which megapode hatchlings react, if at all, to the presence of ground predators.

The aims of this study were to determine whether the brush-turkey hatchling can distinguish between novel non-predators and potential predators on sight and to observe their immediate reactions, level of response and latency of reaction. A further aim was to determine whether movement of the stimulus is an important factor in eliciting a response. Two separate approaches, involving video footage and actual stimuli, were used in this study.

## Methods

### Video images

One end of a box measuring 0.8 m long  $\times$  0.5 m wide  $\times$  0.5 m high was cut to fit the screen of a Panasonic 52 cm colour television (Model TC-21E1A). Foam pieces were fitted between the screen and box to provide a seal. A clear perspex window at the opposite end to the screen allowed each session to be videotaped. A 60W light globe illuminated the subject within the arena and an elevated wooden perch was fixed diagonally across the box.

The predator images used in this experiment included 30 second sequences of each of four known predators: lace monitor *Varanus varius* (White, 1790); red fox *Vulpes vulpes* (Linnaeus, 1758); dingo *Canis familiaris dingo* Blumenbach, 1892; and domestic cat *Felis catus* Linnaeus, 1758. The non-predator images were: a plastic box, measuring 0.2  $\times$  0.1  $\times$  0.1 m; a white ceramic cup; and a black and yellow striped ball, 8 cm in diameter. The subjects did not have any prior experience or exposure to any of these stimuli.

Each stimulus tape consisted of an initial five minutes of neutral forest background (to allow the subject to adjust to the presence of a video image), followed by individual sequences of predator and non-predator images in random order and separated by 30 seconds of forest background. Three stimulus tapes were compiled, each with the images in a different random order. One of these tapes was randomly assigned to each session.

At the beginning of each session, a naive brush-turkey hatchling (up to five days old) was placed in the arena and left for one hour to become accustomed to its new environment. After this time, the video player was started remotely to play the preassigned stimulus tape. All behaviours and movements of the hatchling, as well as the

actual images being shown on the screen, were taped using a Panasonic VHS movie camera (Model NV-M40A) at a distance of 0.6 m. At the completion of the session, the hatchling was removed from the arena and returned to the aviary. Videotapes were analysed during playback. All behavioural states and events (see Table 1 for descriptions) displayed by the subject during the screening of each of the individual stimulus images and the forest footage were recorded.

A behavioural state or event was considered to be present during the session if it occurred at least once during the screening of a particular image. The events 'Foraging' (comprising of Peck and Scratch) and 'Escape' were selected as representing the two possible extremes of behaviour, with the former being displayed during periods of low stress and the latter being an indication of high stress and threat. The remaining behaviours listed in Table 1 relate to maintenance and have been grouped together as 'Other'. Statistical analysis using  $\chi^2$  contingency tables was conducted on the number of sessions (out of a total of 11) in which foraging, escape and other behaviours were observed at least once during the screening of each neutral and stimulus image for all predator stimuli combined and all non-predator stimuli combined.

#### Actual stimuli

The experimental apparatus consisted of a large outdoor enclosure measuring 3.5 m long  $\times$  2.5 m wide  $\times$  2.0 m high with a small two-way window 0.5 m wide  $\times$  0.5 m high situated at ground level at one end. The window formed one side of a box into which the stimuli were placed. The box was continuously illuminated by a 60 W light globe to make the stimuli as visible as possible. The far side of the box was also transparent, so the hatchling in the enclosure was able to see a silhouette of the stimulus as it moved around the box. Black plastic was attached to the bottom half of all four sides of the enclosure to reduce outside disturbance during the experimental sessions.

The stimuli consisted of four combinations: live predator (domestic cat); live non-predator (guinea pig *Cavia porcellus* (Linnaeus, 1758)); non-living predator (replica carpet python *Morelia spilota* (Lacépède, 1804)); and non-living non-predator (toy rabbit). None of the subjects had any previous experience with any of these stimuli.

Each subject was placed into the enclosure at the beginning of the session and left there for the duration of the experiment to reduce handling stress. The stimuli were presented individually in random order for five minutes at hourly intervals during the session. Presentation of the stimulus was made by slowly raising a black curtain behind the window. Behavioural observations were made for ten minutes prior to the presentation of each stimulus and ten minutes immediately after the stimulus was removed.

During presentation of the stimulus, observations were made of the latency to react, the level of reaction and displayed behaviours. The latency was the time elapsed until a noticeable response was made by the hatchling towards the stimulus. It was measured in seconds starting from the time the black curtain was fully raised. Displayed behaviours were recorded as a descriptive paragraph, with particular attention paid to head movements and the relative direction of locomotion. The categories for level of reaction, based on Schaller & Emlen (1962), were as follows:

| <b>Category</b> | <b>Reaction</b>  |
|-----------------|--|
| 0               | No avoidance response<br><b>a</b> - No evidence that stimulus is detected<br><b>b</b> - Looks at stimulus but does not crouch or retreat |
| 1               | Steps backwards and retreats up to 1 m   |
| 2               | Avoids stimulus by retreating up to 3 m  |
| 3               | Runs to nearest corner and pushes against the wall to get farther away   |
| 4               | Response 3, plus dashing several times from corner to corner   |
| 5               | Response 4, as well as jumping or flying against the wall  |
| 6               | Runs or flies wildly all over enclosure, sometimes directly in front of stimulus, jumps or flies repeatedly against the wall             |

For each stimulus, the mean number of 30 second intervals before and after presentation (out of a possible 20 intervals each) in which each behavioural state and event (see Table 1 for descriptions) occurred was calculated. The mean distance from the box before and after presentation was also calculated. The 'before' and 'after' values for each behavioural state and event were statistically compared using a paired t-test. Similarly, the 'before' and 'after' distances from the box were statistically compared using a paired t-test.

Table 1. Descriptions of all behavioural states and events observed during video image and actual stimuli experiments.

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|               |  |
|---------------|--|
| <b>States</b> |  |
| Walk          | Move on foot in an upright position such that one foot is always in contact with the ground          |
| Stand         | Remain stationary in an upright position with legs vertical and either one or two feet on the ground |
| Sit           | Rest breast and belly on the ground in an upright position with legs folded underneath               |
| Run           | Move on foot in an upright position such that both feet are off the ground for part of each stride   |
| <b>Events</b> |  |
| Peck*         | Use bill to pick up or strike object or food item  |
| Scratch*      | Use foot to rake the ground in a sweeping motion from front to back                                  |
| Escape        | Flap vigorously or fly in an upward direction against the wall or roof of an enclosure               |
| Preen         | Use bill to clean and maintain plumage   |
| Ruffle        | Rapidly shake body and head from side to side while fluffing out feathers                            |
| Drink         | Sip water from water dish or other water source  |
| Yawn          | Stretch neck out to the front and slowly open and close bill   |
| Scratch head  | Lower head towards ground and bring one foot forward to scratch head with claws                      |
| Wipe bill     | Lower head and wipe the end of the bill from side to side along the ground or a branch               |

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\*Peck and Scratch behaviours were combined as Foraging behaviour

Megapode hatchlings are capable of short bursts of running and flight shortly after hatching. It would be logical to assume that a hatchling would flee if it was in any doubt about the potential threat from another animal or object. To ensure the

greatest chance of escape, the hatchling should respond to any detected movement as soon as possible.

Based on the above assumptions, it could be predicted that before exposure, the hatchling would be relaxed and behaving normally, that is pecking, scratching or sitting quietly. However, during presentation of the stimulus, the hatchling should notice the movement of the live stimuli (cat or guinea pig) and respond immediately by fleeing or freezing. The hatchling may not respond to a non-moving stimuli, even though it may represent a predator (replica carpet python). When the stimulus has been removed, the hatchling should maintain its escape behaviour until it is certain any danger has passed. At this time, the hatchling should also be at the maximum distance from the stimulus box (3.5 m).

## Results

### Video images

Four subjects out of a total of 11 tested spent the majority of time pacing around the arena and attempting to escape by flying up against the walls or perspex window. Another four subjects stayed in the same position without any activity for the duration of their sessions. The three remaining subjects walked around the arena, pecking and scratching.

It was expected that the proportion of foraging behaviour (pecking and scratching) would be highest in non-threatening situations, that is when the neutral forest or non-predator stimuli were being shown on the screen. Escape behaviour (flying up against the walls) should have been displayed in higher proportions when the chick became stressed due to a predator stimulus appearing on the screen.

There were no significant differences in the number of sessions in which Foraging, Escape or Other behaviours were displayed by the subjects when non-predator stimuli were shown compared to the neutral forest footage (fig. 1). Similarly, there were no significant trends in Foraging, Escape or Other behaviours displayed for predator stimuli compared to neutral forest (fig. 2).

### Actual stimuli

For each stimulus, there were no significant differences between behavioural states and events observed before or after presentation of each of the four stimuli (fig. 3a-3d). The distance of the subject from the box was not significantly different before presentation compared to after presentation of the stimulus for each of the stimuli used (fig. 4).

Most of the immediate responses by subjects were one of the following: stayed in the same position for entire session (level of reaction 0(a)); turned its head and looked at the box (level 0(b)); peered at the box with neck outstretched (level 0(b)); or walked towards the box. The subjects generally responded to the stimuli within five seconds of presentation, or not at all. The subjects did not show any obvious escape responses to the various combinations of moving/non-moving and predator/non-predator stimuli. Most responses were neutral, involving 'curious' looking at the stimuli.

There was no indication of the hatchlings freezing, as has been observed in malleefowl hatchlings (Priddel & Wheeler, 1994). One instance of a hatchling crouch-

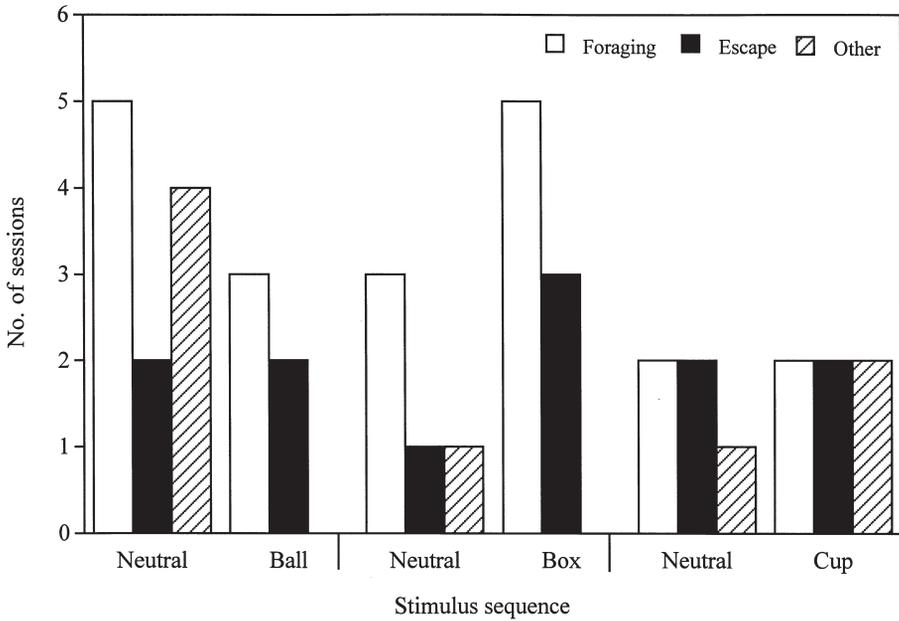


Fig. 1. Number of sessions (n = 11) in which foraging, escape and other behaviour were observed at least once when neutral and non-predator stimulus sequences were shown.

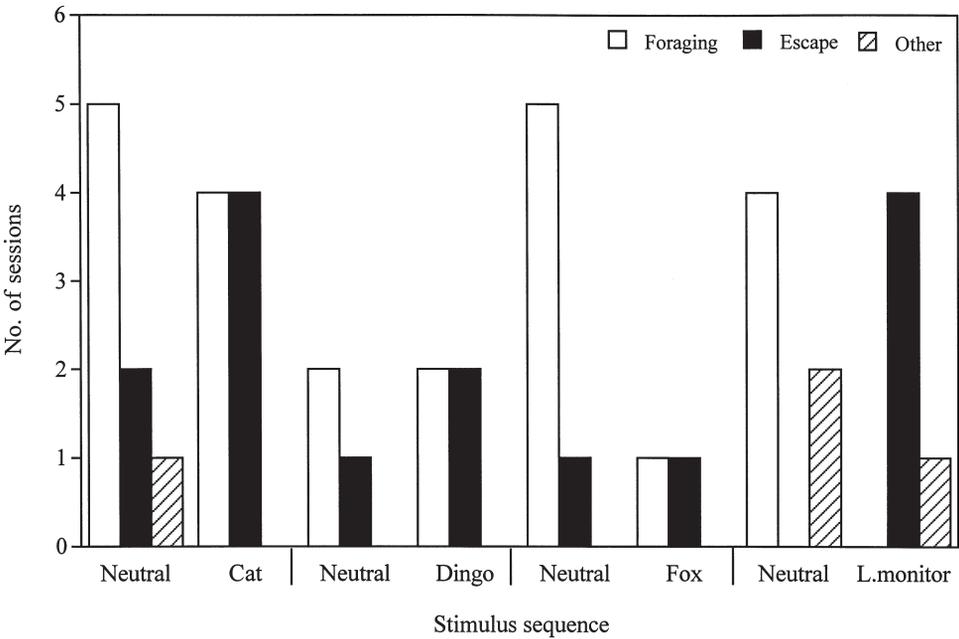


Fig. 2. Number of sessions (n = 11) in which foraging, escape and other behaviour were observed at least once when neutral and predator stimulus sequences were shown.

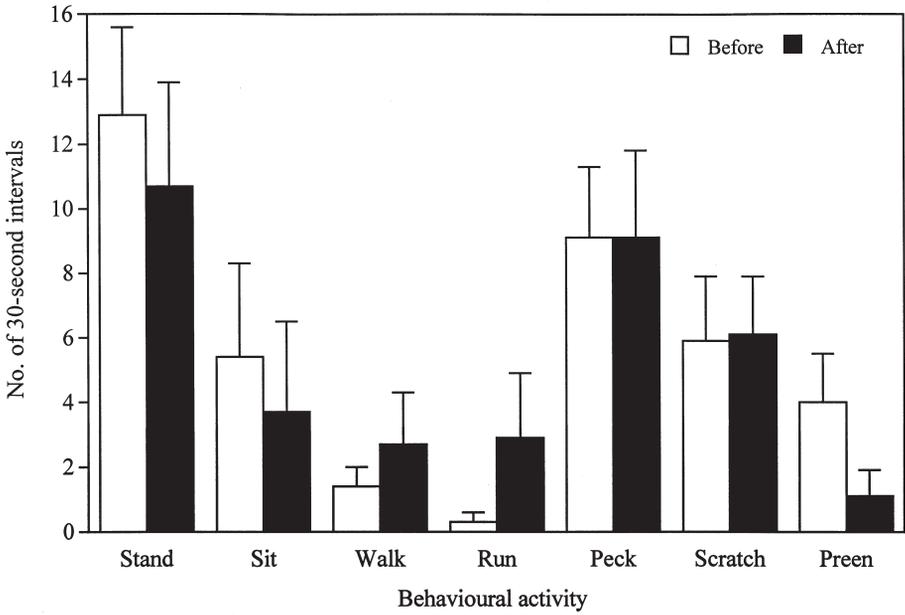


Fig. 3a. Mean number ( $\pm$  s.e.) of 30-second intervals (out of a possible 20 intervals) in which each behaviour was observed before and after presentation of a live guinea pig.

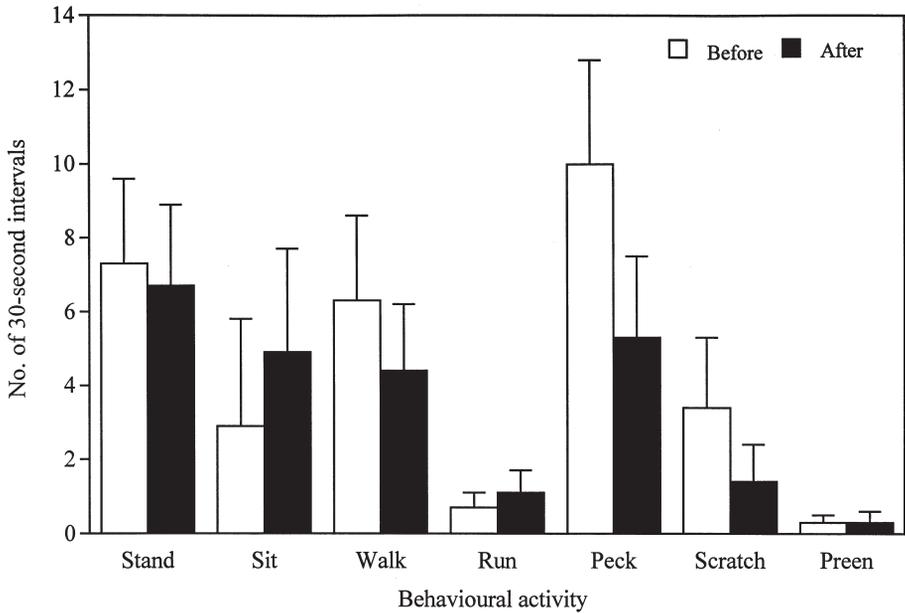


Fig. 3b. Mean number ( $\pm$  s.e.) of 30-second intervals (out of a possible 20 intervals) in which each behaviour was observed before and after presentation of a toy rabbit.

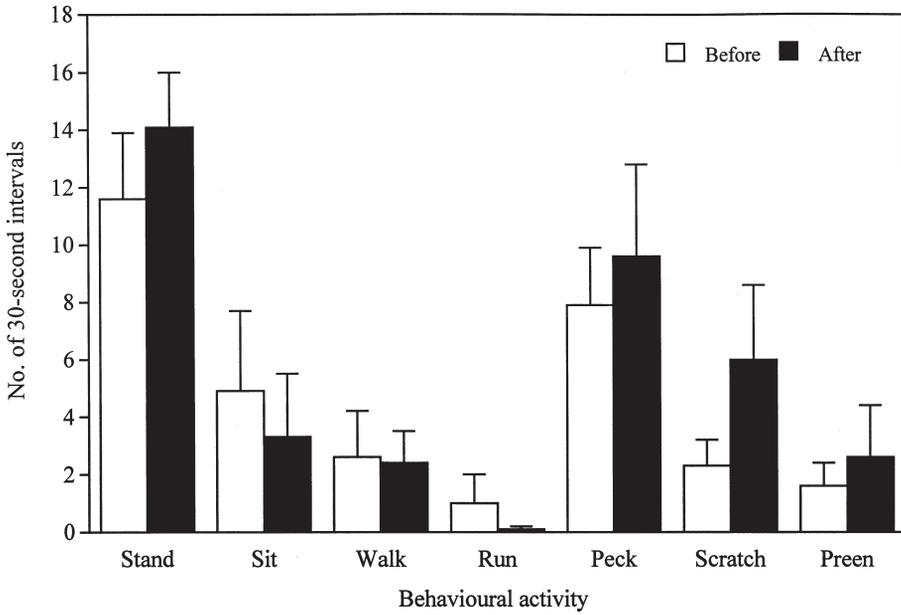


Fig. 3c. Mean number ( $\pm$  s.e.) of 30-second intervals (out of a possible 20 intervals) in which each behaviour was observed before and after presentation of the live cat.

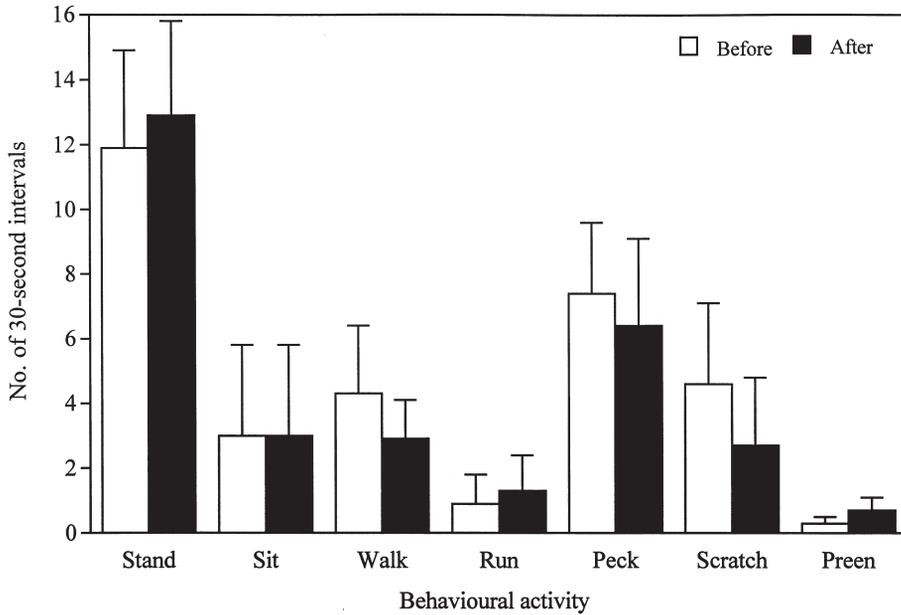


Fig. 3d. Mean number ( $\pm$  s.e.) of 30-second intervals (out of a possible 20 intervals) in which each behaviour was observed before and after presentation of the replica carpet python.

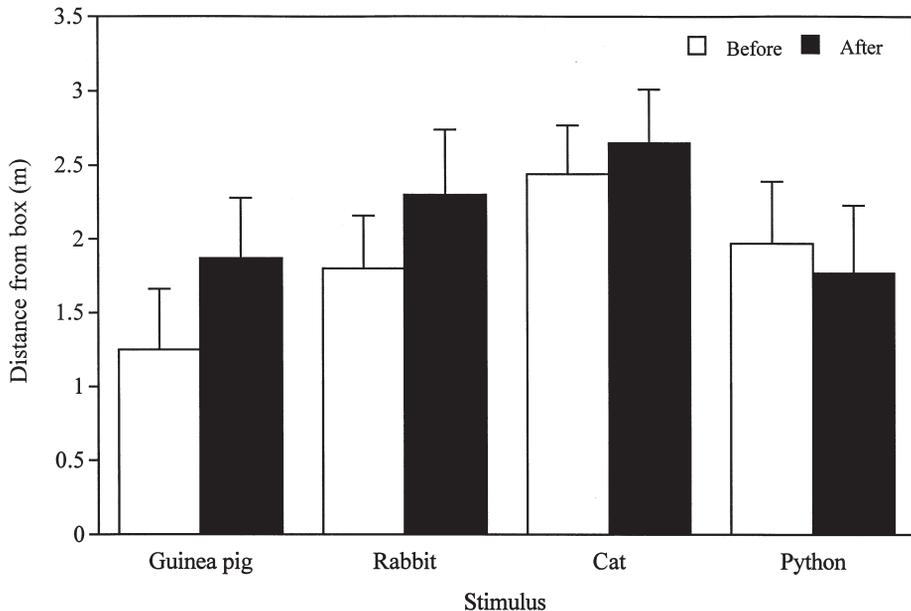


Fig. 4. Mean distance ( $\pm$  s.e.) of the subject from the box before and after presentation of each of the actual stimuli.

ing was observed on a particularly windy day when the surrounding black plastic flapped loudly and billowed. A stimulus was not in the presentation box at the time.

To observe the reaction of the brush-turkey hatchling and a live stimulus at closer range, the live guinea pig was released into the experimental enclosure at the completion of one of the test sessions. Initially, the guinea pig moved slowly around the perimeter of the enclosure and the hatchling took no notice. However, as the guinea pig started to run towards the hatchling from behind (whether intentionally or otherwise is unknown), the hatchling would run forwards for about 2 m before stopping and turning to look at the guinea pig. This continued for several minutes: the guinea pig running around the enclosure in a wide circle and the brush-turkey hatchling moving away in short bursts. The guinea pig was removed from the enclosure after five minutes.

### Discussion

This study investigated the ability of brush-turkey hatchlings to recognise various moving and non-moving predators and non-predators. The hatchlings showed no obvious reactions to the stimuli presented. There are several equally plausible explanations for these results, including: the experimental technique or apparatus may have been flawed or limiting; hatchlings may have been scared and not exhibiting normal behaviours; the hatchlings were unable to see the stimuli properly; or it was a real phenomenon and brush-turkey hatchlings do not visibly react to predators. These potential explanations will be discussed below.

### Limitations with experimental technique or apparatus

Following analysis of the videotapes, it became apparent that the use of video images as stimuli did not produce reliable results, due to the high stress levels and unnatural behaviour displayed by most of the subjects. Further, the experimental arena was a confined area that restricted any fleeing behaviour that might be important in the escape strategy of the brush-turkey hatchling.

Although the use of video stimuli has been successful with domestic chickens (Evans & Marler, 1991), it appears not to be suitable for use with brush-turkeys. It is possible that the brush-turkey hatchlings were unable to clearly see the images being presented. It is thought that the long distance vision of birds is important for identifying predators (Güntürkün et al., 1993, cited in Dawkins & Woodington, 1997), therefore the distance between the subjects in the arena and the video screen may have been shorter than that at which real predators are able to be discriminated.

The outdoor enclosure was sufficiently large to allow the hatchlings to respond properly, as there was plenty of room for the hatchlings to move and fly in any direction and there was minimal disturbance from outside the enclosure.

### Unnatural behaviours

If the hatchlings had been uncomfortable or scared in the experimental enclosure, the results would have been unreliable and not reflective of normal behaviour in the wild. This was the case in the video stimuli experiments, but it is not likely to be the case for the actual stimuli experiments. Hatchlings were regularly observed doing normal activities, such as pecking and scratching, in the outdoor enclosure, suggesting that they felt comfortable in their surroundings.

### Stimuli not sufficiently visible

As mentioned above, it is possible that the hatchlings were unable to clearly distinguish the video images. However, the stimulus box used with the actual stimuli was continually illuminated with a light globe to aid in making the stimuli visible from the outside, although the live stimuli may not have behaved in a way that would cause a reaction in the hatchlings. For example, in the wild, brush-turkey hatchlings may not react to a stimulus unless the stimulus is moving towards it and reaches a certain minimum distance. Of course, it is possible that the hatchlings rely on other cues to identify predators, such as smell or the reactions of other animals in the area.

The fact that the stimuli behaved in a similar way during all sessions meant that consistency was maintained throughout the experiment. The live cat and guinea pig remained relatively stationary in the stimulus box, although they did move sufficiently to provide a clear distinction between the moving and non-moving stimuli (replica carpet python and toy rabbit).

Domestic chickens were not used in this study, but the use of similar methods to test their reactions could, if non-significant, indicate the stimulus was poorly visible, or if highly reactive, suggest the brush-turkey hatchlings genuinely did not respond.

### Genuine response given

In the wild, most of the stimuli encountered by a newly-hatched brush-turkey hatchling would indeed be novel, which should produce a stronger escape response

due to the hatchling's lack of predator experience. The results suggest that brush-turkey hatchlings do not show an escape response when presented with a novel stimulus. The fact that some of the stimuli were also moving did not seem to have any effect on the response of the hatchlings. With regard to the aims of this study, however, it can be suggested that the brush-turkey hatchling cannot distinguish between novel non-predators and potential predators by relying on sight alone. Their immediate reactions were extremely passive, so perhaps the hatchlings have other strategies for evading predators.

The majority of megapode hatchlings emerge with dark brown or mottled plumage (Jones et al., 1995), which certainly provides excellent camouflage on the forest floor, particularly amongst poorly-lit undergrowth. If a hatchling is startled, it is able to run or fly a short distance to get out of reach. The plumage of the malleefowl hatchling is also suited to its habitat of relatively open mallee scrub and it relies upon camouflage and the strategy of freezing when approached (Priddel & Wheeler, 1994).

Four of the subjects in the video apparatus remained in the same position for the duration of their sessions. It is possible that this could have been a natural reaction of freezing in a strange environment. However, as this did not occur across all subjects, there is little that can be concluded from the observations.

Despite good camouflage, the mortality rate of hatchlings in the wild has been estimated at 90-97% for brush-turkeys (Jones, 1988) and 94% for released captive-bred malleefowl hatchlings (Priddel & Wheeler, 1994). Major causes of mortality include predation by foxes, cats, and possibly dingos, carpet pythons, and various raptors (Jones, 1988; Priddel & Wheeler, 1994). Hatchlings not able to find sufficient food or shelter upon leaving the nest weaken rapidly, increasing susceptibility to chilling after rain and vulnerability to predators (Priddel & Wheeler, 1990).

Mortality rates are likely to be high in urban areas as well, caused mainly by introduced foxes and cats. In a suburban environment, brush-turkey mounds are often located within or close to house yards thus increasing the chances of an encounter with a domestic cat by a hatchling as it moves away from the nesting site. Foxes are solitary and opportunistic hunters (Burton, 1984), while cats usually stalk and suddenly pounce upon prey, leaving little or no time for prey to escape (Wozencraft & King, 1990).

High hatchling mortality rates suggest that camouflage and remaining motionless are not very effective strategies against predators. It appears that surviving to sub-adult and adult stage depends largely on chance. However, the probability of survival is improved if the hatchling is heavier than average on hatching and is able to keep up its energy reserves during the first weeks (Priddel & Wheeler, 1990).

Predation, along with starvation, may have a significant effect on malleefowl recruitment into restricted populations (Priddel & Wheeler, 1994), but the distribution of brush-turkeys is much wider and the species more common which may reduce the immediate impacts of high hatchling mortality. However, due to the expected lifespan of the brush-turkey being at least 20 years (D. Jones, pers. comm.), a reduction in recruitment may be felt in the population at a later stage when the older adult birds begin to die off.

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### References

- Baltin, S., 1969. Zur Biologie und Ethologie des Talegalla-Huhns (*Alectura lathami* Gray) unter besonderer Berücksichtigung des Verhaltens während der Brutperiode.— Z. Tierpsychol. 26: 524-572.
- Blakers, M., S.J.J.F. Davies & P.N. Reilly, 1984. The Atlas of Australian Birds: 1-738.— Melbourne.
- Burton, R. 1984. Carnivores: 19-28.— In: J.A. Burton, ed. The National Trust Book of British Wild Animals. London.
- Dawkins, M.S. & A. Woodington, 1997. Distance and the presentation of visual stimuli to birds.— Anim. Behav. 54: 1019-1025.
- Evans, C.S., L. Evans & P. Marler, 1993a. On the meaning of alarm calls: functional reference in an avian vocal system.— Anim. Behav. 46: 23-38.
- Evans, C.S., J.M. Macedonia & P. Marler, 1993b. Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators.— Anim. Behav. 46: 1-11.
- Evans, C.S. & P. Marler, 1991. On the use of video images as social stimuli in birds: audience effects on alarm calling.— Anim. Behav. 41: 17-26.
- Evans, C.S. & P. Marler, 1992. Female appearance as a factor in the responsiveness of male chickens during anti-predator behaviour and courtship.— Anim. Behav. 43: 137-145.
- Fleay, D.H., 1937. Nesting habits of the Brush-Turkey.— Emu 36: 153-163.
- Freeman, B.M. & M.A. Vince, 1974. Development of the Avian Embryo: A Behavioural and Physiological Study: 1-362.— London.
- Jones, D.N., 1987. Behavioural ecology of reproduction in the Australian Brush-turkey *Alectura lathami*: 1-261.— Thesis, Griffith University, Brisbane.
- Jones, D.N., 1988. Hatching success of the Australian Brush-turkey *Alectura lathami* in south-east Queensland.— Emu 88: 260-263.
- Jones, D.N., 1989. Modern megapode research: a post-Frith review.— Corella 13: 145-154.
- Jones, D.N., 1990a. Male mating tactics in a promiscuous megapode: patterns of incubation mound ownership.— Behav. Ecol. 1: 107-115.
- Jones, D.N., 1990b. Social organization and sexual interactions in Australian Brush-turkeys (*Alectura lathami*): implications of promiscuity in a mound-building megapode.— Ethology 84: 89-104.
- Jones, D.N., R.W.R.J. Dekker & C.S. Roselaar, 1995. The Megapodes: 1-262.— Oxford.
- Jones, D.N. & S.E. Everding, 1991. Australian Brush-turkeys in a suburban environment: implications for conflict and conservation.— Wildl. Res. 18: 285-297.
- Kaveney, M., 1958. Notes on the Brush turkey.— Emu 58: 152-153.
- McBride, G., I.P. Parer & F. Foenander, 1969. The social organization and behaviour of the feral domestic fowl.— Anim. Behav. Monog. 2: 127-181.

- O'Connor, R.J., 1984. The Growth and Development of Birds: 1-315.— Chichester.
- Oppenheim, R.W., 1972. Prehatching and hatching behaviour in birds: a comparative study of altricial and precocial species.— *Anim. Behav.* 20: 644-655.
- Priddel, D. & R. Wheeler, 1990. Survival of Malleefowl *Leipoa ocellata* chicks in the absence of ground-dwelling predators.— *Emu* 90: 81-87.
- Priddel, D. & R. Wheeler, 1994. Mortality of captive-raised Malleefowl, *Leipoa ocellata*, released into a mallee remnant within the wheat-belt of New South Wales.— *Wildl. Res.* 21: 543-552.
- Ricklefs, R.E., 1983. Avian postnatal development: 1-83.— In: D.S. Farner, J.R. King & K.C. Parkes, eds. *Avian Biology VII*. New York.
- Rowland, W.J., K.J. Bolyard & A.D. Halpern, 1995. The dual effect of stickleback nuptial coloration on rivals: manipulation of a graded signal using video playback.— *Anim. Behav.* 50: 267-272.
- Schaller, G.B. & J.T. Emlen, 1962. The ontogeny of avoidance behaviour in some precocial birds.— *Anim. Behav.* 10: 370-381.
- Seymour, R.S., 1985. Physiology of megapode eggs and incubation mounds.— *Acta XVIII Congr. Int. Orn.* 2: 854-863.
- Seymour, R.S., 1991. The Brush turkey.— *Sci. Amer.* 265: 108-114.
- Seymour, R.S. & D.F. Bradford, 1992. Temperature regulation in the incubation mounds of the Australian Brush-turkey.— *Condor* 94: 134-150.
- Seymour, R.S. & H. Rahn, 1978. Gas conductance in the eggshell of the mound-building Brush turkey: 243-246.— In: J. Piiper, ed. *Respiratory Function in Birds: Adult and Embryonic*. Berlin.
- Seymour, R.S., D. Vleck & C.M. Vleck, 1986. Gas exchange in the incubation mounds of megapode birds.— *J. Comp. Physiol. B* 156: 773-782.
- Wood-Gush, D.G.M., 1955. The behaviour of the domestic chicken: a review of the literature.— *Brit. J. Anim. Behav.* 3: 81-110.
- Wozencraft, W.C. & J.E. King, 1990. Carnivores: 134-155.— In: E. Gould & G. McKay, eds. *Encyclopedia of Animals: Mammals*. New York.

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