# Mate choice in Australian brush-turkeys *Alectura lathami*: a preliminary report

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Female brush-turkeys respond to several factors when choosing with whom they will mate and where they will lay their eggs. The most important factors seem to be mound condition (especially incubation stage and digging effort required), male presence at mounds (though not necessarily male quality), and perhaps competition with other females for access to mounds. Most visits by females to mounds are for the purpose of copulation and mound "assessment" rather than egg laying. Females visit several mounds/males during the breeding season. Once they make a choice, most remain loyal to the chosen mound/male for several weeks, and are rarely seen at other mounds during this time. When switching to new mounds, females always choose more recently built ones even if older mounds with proper incubation conditions are available. Occasionally females lay eggs in the mound of one male while simultaneously seeking further copulations with another. Paternity analyses, quantification of mound characteristics, and experiments that manipulate mounds and males should lead to a better understanding of female mate choice in the future.

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## Introduction

Non-random mating patterns that result in sexual selection can arise through either intrasexual competition between males or mating preferences of females (Darwin, 1871), and both processes may operate simultaneously. Competition between males for females is well documented (Waage, 1973; Cox & Le Boeuf, 1977) and may determine those males to which females have access (Heisler et al., 1987). However, the importance of female mate choice as a component of sexual selection is less well understood, partly because few data are available on how females choose mates in nature (however, see Arak, 1988; Trail & Adams, 1989). Field data on female behaviour during mate choice are needed to resolve several issues, including: a) what decision rules or tactics are used by females when sampling potential mates (Wittenberger, 1983), and b) among males sampled, what factors are important in determining with whom a female will mate.

In general, females of any species are thought to choose mates based on: a) non-genetic benefits or resources provided by the male (e.g. nuptial gifts, territories, parental care) or b) genetic benefits (e.g. "good genes" or attractive sons). There is little controversy over the existence of female choice for non-genetic benefits (resources) provided by the male, and there is convincing evidence that some females choose mates based on such resources (e.g. Thornhill, 1981; Pleszczynska, 1978).

Empirical evidence for female mate choice based solely on male quality is rare in the literature and much more controversial (Partridge & Halliday, 1984). Two general types of benefits have been proposed for female choice based on male quality: a)

increased viability for both sexes of offspring (Kodric-Brown & Brown, 1984; Nur & Hasson, 1984), and b) increased mating success for their sons due to the sons' "attractiveness" (defined by a potentially arbitrary female preference for some male trait (Fisher, 1930; Lande, 1981)).

In the former case, females should choose males that indicate their viability in some way (such as maintaining bright plumage when this is costly (Hamilton & Zuk, 1982). Both hypotheses may help explain extreme male traits (e.g. plumages and displays), and in practice are difficult to differentiate. Few studies have explored mate choice in systems where both male quality and resources may be important to females (Bradbury & Davies, 1987). In the few that have, resources have usually been the most important factor in determining mate choice (Searcy, 1979).

Mate choice has yet to be explored in any detail in the megapodes (Galliformes; Megapodiidae), although they exhibit an intriguing diversity of mating systems: some provide no parental care and are probably monogamous (e.g. the maleo, *Macrocephalon maleo*, Dekker, 1990) whereas those that build large incubation mounds can be either promiscuous (e.g. the Australian brush-turkey, *Alectura lathami*, Jones, 1990) or apparently monogamous (e.g. the orange-footed scrubfowl, *Megapodius reinwardt*, Crome & Brown, 1979, and the malleefowl, *Leipoa ocellata*, Frith, 1959).

The use of external heat sources (geothermal heat, solar heat, or heat produced during decomposition of organic material) by megapodes has several consequences that may affect mate choice. Megapode females are free from incubating and caring for young, and lay their unusually large eggs asynchronously over a period of several months. This pattern of egg laying may provide non-monogamous megapode females with the potential to make many mate choice decisions throughout the breeding season. In addition, the use of diverse incubation sources by different megapode species may have resulted in widely varied selection pressure on megapodes in the past. Comparative mate choice studies may help clarify how ecological pressures, and specifically the source of incubation heat, have helped shape reproductive behaviour and mating systems in this family.

Of the megapodes, Australian brush-turkeys in particular provide an intriguing mating system in which to study female choice. In this species, males invest large amounts of time and energy in large incubation mounds which they build, defend, and tend regularly. They are territorial and may usurp each other's mounds. Many males cannot successfully maintain and defend a mound. Even among males with mounds, mating success is highly variable (Jones, 1987; Birks, unpubl. data). Female brush-turkeys provide no parental care; instead, they lay their eggs in the mounds tended by males, depositing eggs singly in chosen mounds. Males usually copulate two to four times with females at the time of laying, but no pair bond is established, and males have no direct means of ensuring their paternity.

A unique aspect of mate choice in brush-turkeys is that females can potentially make a separate mate choice for each egg, rather than just one for each reproductive attempt. Captive studies of brush-turkeys show they are capable of laying up to 30 eggs over a period of several months (Fleay, 1937; Baltin, 1969). My observations indicate most females lay an egg every three to five days during favourable conditions. Because females lay over such a long period of time, they could potentially make a *series* of mate choices rather than just one, as is the case with most birds that lay discreet clutches. In effect, each egg can be thought of as a separate clutch, that requires a

separate decision by the female. Since the number and condition of potential mates and their incubation mounds changes throughout the breeding season, the array of choices availabe to females is highly temporally variable.

Female brush-turkeys are unusually rewarding subjects for studying mate choice because of both the dynamic availability of potential mates and the number of decisions females must make during each breeding season. In addition, because all known sexual behaviour occurs at mounds, females can be observed directly as they visit and compare males, and their interaction with each visited male and his mound can be described. Here, I report preliminary observations of female mate choice tactics and potential factors that determine mate choice in Australian brush-turkeys.

## Study site and methods

A population of 52 individually marked adult brush-turkeys were observed in North Tamborine Environmental Park, Southeast Queensland from June - December, 1989 and 1990. This park comprises 7.5 ha of rainforest containing 10-15 active brush-turkey mounds each year. Birds were caught in drop grain-traps and marked with numbered steel leg-bands and sex-specific, coloured patagial wing-tags. Observations were made during the morning hours (dawn - 0900 hrs.) from hides at incubation mounds; the vast majority (±95%) of breeding activity takes place at this time (Jones, 1987). Usually two to three incubation mounds were watched simultaneously, with the most active mounds receiving the majority of observations. Detailed behavioural data were collected on all male and female interactions at mounds including copulation, egg-laying, inter- and intrasexual aggression, and mound "assessment" behaviour (described below).

## Results

Data on the behaviour of 25 females were collected during 261 female visits to 27 mounds, and 77 eggs were laid. Females brush-turkeys moved freely among the active incubation mounds in the forest, and any mound within the study site was easily accessible to a female within a morning - most were only a few minutes' walk away (several hundred meters between mounds). Males exerted no control over female movement, never denied females access to their mounds unless another female was already present, and did not guard females away from mounds. Females made frequent visits to different mounds throughout the season, occasionally visiting more than one mound per morning (n = 3). In the majority of cases (71%), females visited the mound for purposes other than laying (Fig 12). Instead, females showed interest in and seemed to "assess" the mound, and they often copulated with the attending male.

During mound "assessment", females behaved in two ways: 1) they stood on or near the mound observing male behaviour and/or watching the area around the mound. These "observation" bouts could be prolonged (up to an hour) and sometimes included observing the behaviour of other females who had previously arrived at the mound. 2) they dug and "probed" in the mound. Probing behaviour in brush-turkeys

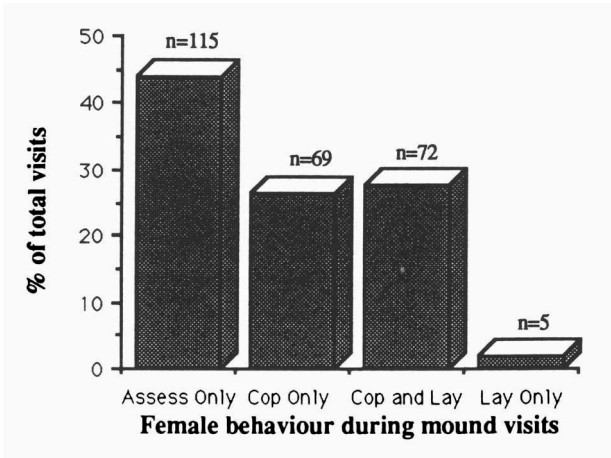


Figure 12. Female visits to mounds. Behaviour of 29 females during 261 visits of females to incubation mounds. The first column includes visits in which females assessed the mound without copulating with the attending male or laying an egg. The remaining columns include visits in which females engaged in sexual behaviour (copulation only, copulation accompanied by egg laying, and egg laying without copulation) as well as assessment behaviour. Numbers above the columns indicate sample sizes.

has been discussed in detail in several previous papers, and involves taking a beak full of mound material and manipulating it (Fleay, 1937; Baltin, 1969). Digging could also be prolonged (> 1 h), and was often accompanied by observation and/or copulation with the male. Females also probed in the mound repeatedly when digging during egg-laying visits. Copulation nearly always accompanied egg laying (Fig. 12).

Female brush-turkeys fulfill one important criterion for active mate choice: they reject some males in favour of others. Females copulated with attending males at fewer mounds (X = 1.9, range 1-3) than they visited (X = 3.4 , range 1-6). They were often seen on mounds when males were absent (e.g. late morning or afternoon) and ran away if the male approached, indicating an interest in assessing the mound without the males' presence.

Females were never observed mating with males that did not own mounds. Since only ±40% of the males in the population were able to maintain and defend a mound, females only chose from a subset of sexually available males.

Females showed a distinct pattern of mound use; though they usually visited several mounds during the season, females did not visit many mounds at the same time. Instead, they returned repeatedly (often daily) to the same mound to solicit copulations, "assess" mound condition, or lay eggs. They remained "loyal" to this mound for an extended period, usually three to six weeks (Fig. 13). If they did visit other mounds, they usually did not copulate with the attending male (±80% of visits to other mounds). After several weeks tenure with one male, females switched to a new mound/male and repeated this behaviour. When switching to a new mound, females always chose a more recent mound (Fig. 13).

Mounds did not receive steady use throughout these months. Instead, they showed a distinct pattern of use, receiving many female visits during the first few weeks after they had attained incubation temperature, followed by a sharp decrease in female visits after one-two months (Fig. 14).

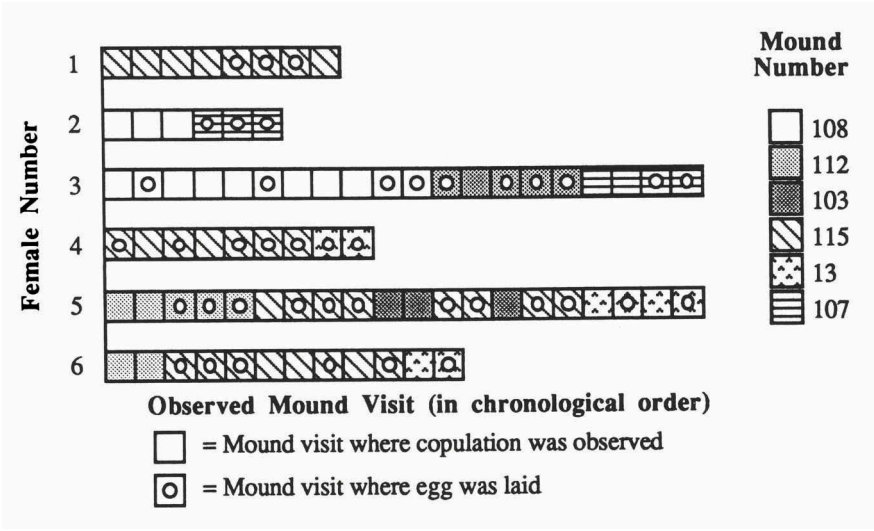


Figure 13. Pattern of female visits to incubation mounds. The patterns of mound visitation for six individual females that were seen more than ten times during the 1990 field season. For each female, mound visits are given in chronological order. Only sexual visits (involving copulation or egg-laying) are included. Mounds are listed in the order in which they were built.

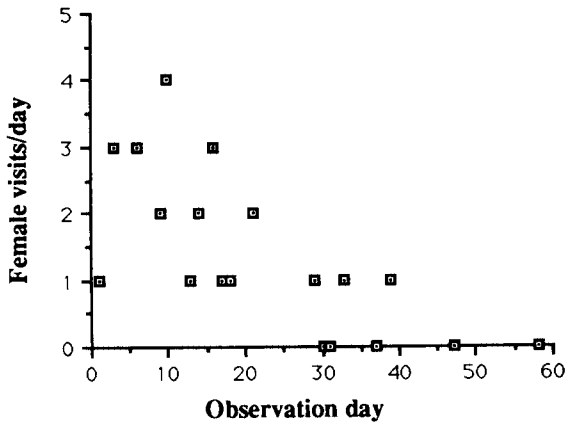


Figure 14. Number of female visits at mound 36 (1989). Pattern of female visits at one mound over a period of 58 days. This mound is representative of most mounds. Day 1 corresponds roughly to the day when the mound reached a proper incubation temperature (>30 °C). Each point represents the number of females visiting the mound on a given observation day (mounds were not observed every day). The decrease in female visits over time was significant (Spearman Rank Correlation $r = -.74$; $p < .0008$).

## Discussion

Unlike many other birds, where close pair-bonds and mate-guarding limit extra pair copulations to some extent (Westneat et al., 1990), brush-turkey females are free

to mate with additional males while laying eggs in the mound of one male, and in a small number of cases this was observed. However, the general tendency of females to remain "loyal" to males is surprising because there appears to be no *a priori* reason why an exclusive mating relationship with one male would be a superior strategy to more promiscuous mating. This tenure with one male, coupled with additional copulations solicited between egg-laying visits, indicates that females mated most often with the male whose mound they were currently using. With the exception of eggs laid soon after females switched to new mounds, paternity levels may be quite high for mound-holding males.

## Mounds or males?

Male-male competition in brush-turkeys determines the subset of males in the population that have mounds and are thus available to females. However, after initial "screening" of the population by male-male competition, female choice is important in determining with whom females mate.

Based on observational data so far, it seems likely that female brush-turkeys assess both mound and male quality during mate selection. Although theoretically a female's choice of mate and choice of mound need not be identical, it often seems to be the same in this species, because: a) mound-tending males usually "force" (try to copulate with females that do not solicit) copulations at the time of laying and b) the female visiting behaviour described above results in additional copulations for males in whose mounds females are currently laying.

Exactly how a female brush-turkey makes her choice is still unclear, but several results from this study indicate that mound quality is more important to females than male quality:

a) females switch mounds within a season.

b) females show no loyalty to males from year to year. All eight females that were observed both years mated the second year with males they had rejected the first, and vice versa.

c) in one case where a relatively popular male disappeared (assumed predated), his mound was immediately usurped by a male who had beforehand received no known female visits. The female visiting this mound did not switch and continued using the mound as before.

d) by 1990, I was able to predict roughly which mounds would be popular and which would not, based solely on casually observed features of the mound.

e) the male whose mound received the most eggs in 1990 was a very young male who was subordinate to most others away from his mound and could not produce a mature booming vocalization (used in male-male interactions) due to his underdeveloped wattle.

## Mound characteristics

Incubation mounds are obviously important resources for female brush-turkeys, and must certainly play an important role in mate choice. A well-functioning mound

is essential to egg incubation (Booth, 1987), and it is not surprising that females spend much time assessing mound condition. What is not as obvious is what constitutes a "good" versus "bad" mound. What mound characteristics determine where females will lay? Several differences between mounds are easily perceptible to humans and could be measured quantitatively: temperature, moisture level, ease of digging, ecto-parasite load of mound, time of building, location, and male presence. Of these, location seemed to have very little impact on female choice, at least on a large scale. Females visited mounds from every area of the study site.

Temperature is an important factor for successful egg incubation, but may play a more active role in egg placement decisions within a mound than in mate choice decisions. Though females were never seen laying in mounds that had not reached a stable incubation temperature of about 33 °C, all actively tended mounds eventually reached this temperature, and there was more temperature variation within areas of one mound than between similar areas of different mounds.

Neither parasite load nor moisture level were measured quantitatively, but casual observations suggested that these parameters vary considerably between mounds. Moisture levels can dramatically affect oxygen available to eggs (Seymour et al., 1986) but seemed to depend more on the time of year and recent weather than on the mound; females laying at any one time would likely choose among mounds of very similar moisture levels. Parasite level (e.g. ticks) varied dramatically between mounds (as measured by how many we picked up while digging in the mounds). However, several mounds active simultaneously and differing in their parasite load seemed to be equally popular with females. One factor that may mitigate parasite importance is that most parasites seem confined to the upper insulation layer of mounds, and chicks would probably spend relatively little time exposed to parasites after they hatch. However, females would be vulnerable to parasites whenever they dug in affected mounds.

Three mound characteristics that seem important to females are the ease in which one could dig in a mound ("digging effort"), the date a mound had been started, which reflects its incubation stage ("mound stage"), and male presence at the mound. Mounds differed greatly in digging effort: some required arduous toil through masses of heavy sticks and invading roots, while others had a soft, fine-grained, well-mixed interior that required very little effort to dig down to a level where incubation temperature was adequate. Females usually take 45-60 minutes to dig egg-laying holes, and the process appears strenuous. Using mounds that require less effort could save females time, energy and possible injury, and also ensures that: a) the mound material has been thoroughly and repeatedly mixed by the male, which may be important in regulating $CO_2$ and $O_2$ levels in the mound, and b) the chicks will be more likely to succeed in digging their way out of the mound after hatching - a difficult process that not all survive.

Mounds take several weeks to reach a proper incubation temperature, but after this may maintain an adequate temperature for several months (Jones, 1987). However, mounds were not visited steadily throughout these months; instead, female visits declined sharply approximately 40-50 days after mounds reached the incubation temperature (Fig. 14). Females showed strong preferences for mounds at early stages of incubation, even though mounds could maintain a good incubation

environment for several months longer.

There was evidence that male presence (if not identity) was important to females when deciding where to lay. In several cases, males were absent from their mounds while females were visiting. When the male did not appear, the female invariably left, showing no interest in the mound. Females quickly (within two to three days) stopped visiting mounds where males were frequently or permanently absent.

Male tenure with mounds is variable due to disappearance (assumed death), eviction from the mound by other males, and abandonment by the mound-owning male. Females laying in mounds have no guarantee that males will continue to tend those mounds during the lengthy time (42-51 days; Birks, unpubl. data) required for incubation. In several cases, eggs were still incubating in mounds when they were abandoned. Temperatures of abandoned mounds drop after several weeks (Jones, 1987), and mounds become cratored from the digging activity of bandicoots and other animals. Deteriorating conditions could make eggs more vulnerable to weather conditions and physical damage, and may reduce their viability.

By preferentially laying in mounds during their earliest stages, females may optimize their chances of maintaining eggs in a safe, temperature-controlled environment during incubation.

## Male characteristics

The other major factor females may take into account when deciding where to mate and lay their eggs is the genetic quality of the mound-holding male. Even if females pursue copulations away from mounds in which they lay, forced copulations by the mound-holding male at the time of laying will probably ensure that some of their eggs are fertilized by tending males.

Australian brush-turkeys are sexually dimorphic: males are slightly larger than females, and have large brightly coloured yellow wattles that contrast with their bright red heads and black plumage (females have much smaller and duller coloured wattles). Males extend their wattles when displaying toward females, moving their heads up and down slowly in a ritualized "stalking" display as females approach the mound. Wattles are also used to produce a low "booming" sound used both in aggressive interactions with other males and occasionally in displays toward females. Using only behavioural observations, it is difficult to tell whether or not a female is evaluating a male (as opposed to the mound, area, etc.), though the dimorphism and display indicate that this may be an important factor. Wattles become enlarged as males age, and wattle colour and size could be good indicators of male viability. Experiments altering these characteristics are needed to determine to what extent females use male appearance and/or displays to select a mate.

## Other factors

An additional factor that may influence female mate selection is competition between females for access to mounds. Because males can tend a number of eggs equally well, and eggs exposed during digging by other females were carefully

avoided and immediately re-covered, brush-turkey females do not pay a noticeable cost in sharing male parental care with other females. However, females may pay a cost in time and energy wasted trying to lay eggs in popular mounds. Some mounds had several females visiting simultaneously in the morning. Only one female laid at a time, and laying females often fought repeatedly and vigorously with other females that tried to approach. On several occasions females were kept waiting until they were apparently desperate to lay their eggs, and in three cases laid in under 15 minutes - less than a third of the time normally taken. At other times females were denied access by others, and eventually left, presumably to go to lay in another mound.

## Paternity

In two cases (e.g. Female 2, Fig. 13), females copulated with one male while laying in the mound of another, and at least some of these copulations were solicited by the female. During 1990 all eggs observed being laid were collected and incubated for the purpose of studying paternity. Fifty-eight eggs from ten mounds were marked at the time of laying, and removed from mounds approximately one month later to complete incubation in heated incubators. Blood samples were collected from chicks that hatched out, as well as all adults in the population. Paternity is being analyzed using DNA fingerprinting techniques (Wetton et al., 1987) at Cornell University. Results from DNA fingerprinting analyses using blood samples from chicks, from females, and from putative fathers, should clarify both paternity and mate choice, since they will help indicate when and how often females mated with other males.

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