



# Male brush-turkeys attempt sexual coercion in unusual circumstances



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## ABSTRACT

Sexual coercion by males is generally understood to have three forms: forced copulation, harassment and intimidation. We studied Australian brush-turkeys, *Alectura lathami*, to determine whether some male behaviours towards females at incubation mounds could be classified as aggressive, whether males were attempting sexual coercion and, if so, whether the coercion was successful. We found that some male behaviours towards females were significantly more likely to be followed by the cessation of female mound activity, and hence could be classified as aggressive, while others were significantly more likely to be followed by the commencement of female mound activity, and hence could be classified as enticing. Copulation was preceded by higher rates of male enticement and by higher rates of certain types of male aggression. It therefore seemed that males were attempting sexual coercion. There was little evidence, however, that this combination of coercion and enticement was successful in obtaining copulations. While forced copulation did occur, it was infrequent, and no evidence could be found for intimidation. We conclude that harassment is the primary form of sexual coercion by male brush-turkeys. Although sexual coercion is understood to be a sub-optimal tactic, brush-turkey sexual coercion was employed as a primary tactic by dominant males who owned incubation mounds. One possible explanation for this apparent paradox is that aggression is the default solution for social conflicts in this species, and hence can be interpreted as a behavioural syndrome.

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## 1. Introduction

In most sexual organisms, males are more eager to mate than females (Trivers, 1972). This difference typically plays out as male-male conflict over mating opportunities (intrasexual competition) or as males enhancing their prospects of being chosen as mates by females (intersexual mate choice). In many circumstances, however, it can play out as males forcing females to mate, i.e. intersexual coercion or sexual coercion (Clutton-Brock and Parker, 1995; Smuts and Smuts, 1993). The term 'sexual coercion' usually refers to coercive behaviour directed specifically at obtaining copulations and does not include other male behaviour which may also involve mating-related coercion, such as sequestering females to form a harem or mate-guarding of individual females (Clutton-Brock and Parker, 1995). Although behaviours such as infanticide are included in some usages (e.g. Smuts and Smuts, 1993), three non-exclusive

forms of sexual coercion are generally recognized: forced copulation; harassment, i.e. males seeking to enhance their immediate mating success by repeatedly attempting to copulate; and intimidation, i.e. males attempting to enhance their future mating success by punishing females who refuse to mate with them (Clutton-Brock and Parker, 1995).

Sexual coercion may be employed by males of any dominance status, but it is typically a secondary or alternative mating tactic. For example, male marine turtles, *Chelonia mydas*, supplement courtship with harassment (Lee and Hays, 2004). In many species, sexual coercion is characteristically employed by subordinate males. While dominant male bighorn sheep, *Ovis canadensis*, for example, defend a single estrus ewe, subordinate rams attempt to disrupt this defense and seek forced copulations during an extended chase of the ewe. Although this tactic is much less successful for individual rams, those using it can collectively obtain up to 40% of paternities during a breeding season (Pelletier et al., 2006).

This pattern of sexual coercion being employed by subordinate males and/or opportunistically by all males suggests that the tactic is sub-optimal, probably because the male's prospects of success are usually low in relation to potential costs. Coercion involves

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a male–female contest which may be costly for the male as well as the female, and may either attract the attention of rival males, thus triggering a male–male contest (Clutton-Brock and Parker, 1995), or render both parties more vulnerable to predation (Evans et al., 2003; Griffiths et al., 2004; Magurran and Nowak, 1991). Copulation, moreover, is only a means to fertilization and without long-term influence over the female, a coercive male's fertilization prospects are more vulnerable to female counter-tactics such as copulation with alternative males (Emlen and Wrege, 1986) or sperm ejection (Pizzari and Birkhead, 2000). Coercion may, nevertheless, be the only option for subordinate males who are attempting to make the most of a bad situation.

Sexual coercion is reported less frequently in birds than in mammals (Caizergues and Lambrechts, 1999; Pradhan and Van Schaik, 2009). As in non-avian taxa, it is nevertheless likely to be adopted opportunistically by males generally or as the only available tactic by subordinates. Among waterfowl (Anatidae) paired, and hence dominant, males are sometimes able to evade the mate-guarding efforts of rival males and force extra-pair copulations (McKinney and Evarts, 1997). While Anatid males possess an intromittent organ, most birds do not (Briskie and Montgomerie, 1997), suggesting that harassment and intimidation are more likely forms of sexual coercion than forced copulation. In free-ranging feral fowl, *Gallus gallus domesticus*, mating is promiscuous with subordinate males often obtaining copulations by harassment (Lovlie and Pizzari, 2007). Harassment by non-territorial males is also common in ring-necked pheasants, *Phasianus colchicus* (Mateos, 1998). In many monogamous species, extra-pair males incur no parental care costs and hence have a strong incentive to obtain copulations by any means. The degree to which extra-pair copulations rely on coercion and the degree to which they result in extra-pair paternity, however, are both controversial questions (Westneat and Stewart, 2003).

Australian brush-turkeys, *Alectura lathami*, provide an interesting case study for avian sexual coercion because coercive male behaviour appears to be ubiquitous in the mating system. Investigation of this behaviour requires placing it in the context of reproduction in the Megapodidae (Birks and Edwards, 2002; Jones and Göth, 2008). Uniquely among birds, megapodes incubate their eggs using environmental sources of heat, usually microbial decomposition in a mound of soil and vegetation (Seymour, 1985). On the basis of this ancestral pattern, variations have evolved. In the brush-turkey system, males construct mounds, control their temperature via ongoing maintenance, defend them against rival males and are polygynous (Jones et al., 1995). Females make frequent visits to mounds, often copulate with the male and periodically dig substantial holes in which they bury their eggs. Females are not subject to mate-guarding, do not pair-bond with the male and are polyandrous (Jones et al., 1995). Males evidently use their mound as a means of attracting females interested in the incubation properties of the mound (Jones, 1992). Having attracted a female, a male typically behaves towards her in a way which suggests coercion, for example by charging at her or pecking her on the back or head (Jones, 1990b).

Male–female aggression is less extreme than that evident when male–male encounters occur near incubation mounds (Jones, 1987), but it is nevertheless substantial, as prolonged interactions can result in the female's death in captive situations where she is unable to escape (Jones et al., 1995). Aggression towards females is interspersed with non-aggressive displays possibly attempting to influence female choice. Where individual females can be confidently identified by the researcher, it is clear that males are attempting to both entice and coerce each female, rather than selectively enticing some females and driving others away. This allows us to exclude male choosiness as an explanation for the coercive behaviour in this species (for more details, see Wells, 2012). The

male's aggression probably discourages visits from females unwilling or unable to tolerate it, hence biasing the copulations which occur, but aggression is not usually a form of rejection. Expulsion of a female from the mound is almost always followed by an attempt to entice her back (Wells, 2012).

Sexual coercion is not an unusual animal mating tactic, but brush-turkey males appear to attempt it in unusual circumstances. In the discussion, we outline these circumstances, and propose that the coercion reflects a behavioural syndrome, namely a set of behaviours which is consistent across multiple different contexts, but may have little or no function when considered in one of these contexts in isolation (Sih et al., 2004).

In summary, our objectives can be expressed in the following three questions:

1. Which male behaviours are aggressive, and conversely, which are enticing?
2. If male behaviours can be distinguished as above, do males attempt to obtain copulations coercively?
3. If males are attempting to obtain copulations coercively, to what degree are they successful?

## 2. Methods

Field studies were conducted on a free-living, individually colour-banded brush-turkey population at the town of Pearl Beach in New South Wales, Australia (33.54° S, 151.30° E). Birds were captured in baited steel walk-in traps 2.4 m × 1.6 m and 1 m high. To minimize the risk of injury, traps were not left unattended. Each bird was removed for banding by entering the trap, securing its legs and placing it into a non-transparent cloth bag.

Observations were recorded remotely by five Sony HDR-SR7 video cameras mounted at active mounds and programmed to run daily for 3.5 h from first light. Previous observations have shown that nearly all reproductive behaviour occurs during these hours (Jones, 1988). Males in the study population constructed or maintained mounds between July and January. Data for Question 1 are drawn from the 2008–09 breeding season (14 males observed maintaining 17 mounds Nov–Dec 2008, there being three instances of a single male maintaining two mounds). To achieve sufficient statistical power when answering Questions 2 and 3, data from the 2009–10 season were also included (16 males, each male observed maintaining a single mound August–October 2009). With some exceptions due to access difficulties or extreme weather, each mound was observed for seven consecutive days.

When reviewing video of female visits to mounds, behaviour was recorded on an all-occurrences basis to the nearest second. All data collection and video review was conducted by a single observer. The total number of female mound visits was 144 for 2008–09 and 228 for 2009–10 (for details of how female visits were defined, see Supplementary material A). The total number of visiting females individually identifiable in the context of a mound was 46 for 2008–09 and 48 for 2009–10 (for details of how females were identified, see Supplementary material B).

Only pre-defined behaviours were recorded (Table 1). Counts were recorded for behaviours of relatively short duration, i.e. events, while the frequency and duration of bouts were recorded for behaviours of relatively long duration, i.e. states (Martin and Bateson, 2007). This distinction was in some cases influenced by context, however (for details see Supplementary material C).

### 2.1. The effect of male behaviour on female mound activity

By recording both male and female behaviour against the same timescale, it was possible to consider the effect of male behaviour

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