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## Destruction of a conspecific nest by a female Superb Lyrebird: evidence for reproductive suppression in a bird with female-only parental care

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### Abstract

Reproductive suppression, whereby individuals decrease the reproductive output of conspecific rivals, is well-studied in mammals, but while it is suspected to be widespread in birds, evidence of this phenomenon remains rare in this class. Here we provide compelling evidence of reproductive suppression in the Superb Lyrebird (*Menura novaehollandie*), with the first audio-visual documentation of the destruction of one female's nest by another. We propose that nest destruction may be a strategy that females use in protracted territorial negotiations spanning multiple breeding seasons, and discuss how reproductive suppression could explain puzzling nesting behaviours in this species, such as the construction of multiple unfinished nests in each breeding season. More broadly, these results reveal high intra-sexual competition among female lyrebirds, and thus may provide an explanation for their elaborate vocal displays.

### Keywords

birds, female song, intra-sexual competition, nest destruction, ovicide.

## 1. Introduction

‘Reproductive suppression’, whereby individuals decrease the reproductive output of conspecific rivals, is a severe form of competitive behaviour that may involve continued harassment, eviction of subordinates, ovicide or infanticide (Clutton-Brock & Huchard, 2013). Reproductive suppression of rivals is thought to increase an individual’s own reproductive potential by decreasing competition (Wasser & Barash, 1983; Clutton-Brock & Huchard, 2013) when reproductive efforts are improved beyond the expected costs of the suppression (Wasser & Barash, 1983). Whereas, males are thought to benefit from reproductive suppression when it increases their access to receptive females (Clutton-Brock & Huchard, 2013); females are thought to benefit when it increases access to parental care or limited resources for offspring (West-Eberhard, 1983), or reduces the number of future competitors that their offspring could face (Wasser & Barash, 1983). Reproductive suppression occurs widely in mammals of both sexes, and classic examples include infanticide by male lions *Panthera leo* (Pusey & Packer, 1994) and decreased fecundity due to intra-sexual harassment in female Yellow Baboons *Papio cynocephalus* (Wasser & Starling, 1988). Importantly, in mammals it is thought that reproductive suppression may select for complex behaviours and signals (Kleindorfer & Wasser, 2004), such as communal nursing in rodents (Roulin & Hager, 2003) and sexual mimicry in hyenas (Muller & Wrangham, 2002). However, whether reproductive suppression drives the evolution of complex social behaviours or elaborate signals in birds remains unclear.

In birds, reproductive suppression is suspected to be underrepresented in the literature (Clutton-Brock & Huchard, 2013). Nonetheless, there are various examples of ovicide (e.g. Krieg & Getty, 2016) and infanticide (e.g., Riehl, 2016), and one isolated example of nest destruction (Heinsohn, 1988). Despite this, reproductive suppression is thought to occur predominantly in highly social species, such as cooperative breeders (Quinn et al., 2010) or colonial nesters (Brown & Brown, 1988), as in such species there is often strong competition for mates, breeding sites, or parental care (Boves et al., 2011; Clutton-Brock & Huchard, 2013). Yet, social breeders are relatively well-studied so that this hypothesis may simply reflect a research bias. Similarly, the belief that reproductive suppression occurs more frequently in male than female birds (Kattan, 2016) may be reflective of research bias towards males. Nevertheless, to our knowledge, there is no compelling evidence of

reproductive suppression in solitary breeding birds with female-only parental care; and yet, in such species competition for reproductive resources for offspring can be severe, especially in those that invest heavily in a limited number of offspring.

Here we present evidence that female Superb Lyrebirds (*Menura novaehollandiae*), a solitary breeding species with very low fecundity and uniparental care, destroy the nests of rival females. We discuss how this finding advances our understanding of female–female competition for limited resources.

## 2. Materials and methods

### 2.1. Study species

The Superb Lyrebird is a large, mainly terrestrial oscine passerine with a slow life history and a lek-like mating system, including female-only care (Lill, 1979a, 1986, 2004). During the breeding season, females build a large dome shaped nest that are only laid in once and not reused (Lill, 1979b; Maisey *et al.*, 2016). While the nest is active, females defend nesting territories from other females (Reilly, 1970; Kenyon, 1972; Lill, 1980; Robinson & Frith, 1981). Territorial behaviour includes counter singing with rival females (Dalziell & Welbergen, 2016) and may escalate to physical disputes where females are reported to fight “just as vigorously as males” (Higgins *et al.*, 2001, p. 153) by “striking each other with their legs” (Reilly, 1970, p. 78). Banded females are known to return to nesting territories in successive years (Lill, 2004). Female Superb Lyrebirds lay a single egg only per breeding attempt (Lill, 1986). The egg is incubated for approximately seven weeks (50 days), and upon hatching the altricial nestling remains in the nest for a further six weeks (Lill, 1986). Once fledged, young Lyrebirds remain dependent on their mothers and may reside in their care for up to a year. Attempts to re-nest within a breeding season are rare (Lill, 1986). Overall, breeding requires very high levels of investment by females, and the opportunity costs associated with a failed nesting attempt are substantial.

### 2.2. Study site

The incident of nest destruction that we report here occurred in Sherbrooke Forest, Dandenong Ranges National Park, located on the urban fringes of Melbourne, Victoria, Australia. Many of the birds at this site are banded as

part of an ongoing monitoring program by the Sherbrooke Lyrebird Survey Group (Maisey et al., 2018).

### 2.3. Methods

A Lyrebird nest with an egg inside was located on 7 July 2018. A Bushnell NatureView HD Essential Trail Camera (1280 × 720 pixel video with 44 kHz audio) was placed 2 m from the entrance to the nest on 22 July (Figure 1a). The camera was set to record 60-s videos (with audio) at a high shutter speed sensitivity (0.6-s trigger) and medium LED brightness. Incubation behaviour was recorded using an iButton (model DS1922L, 8K, temperature range –40 to +85°C) placed inside the lining of the nest underneath the egg. The iButton recorded temperature at 5-min intervals but due to iButton failure, the period after 25 August was not covered.

## 3. Results

Incubation had commenced when the nest was found, and video footage showed that the nest was actively attended by the female from 7 July until 31 August 2018. The videos show the female entering the nest or incubating. The camera trap varied in the amount of time taken to re-set after recording a video and thus video footage was not always recorded on consecutive days. iButton data showed that the egg was incubated at least until 25 August, after which there was no temperature record. On that day, the egg was still present and the attending female was observed by researchers to be unbanded. Based on an incubation period of 50 days (Lill, 1986), we predicted the egg should have hatched by 25 August 2018. On 20 September 2018 at 11:30 am the camera filmed a non-resident, colour-banded female (Figure 2b: Colour bands from top left leg; Dark Green/Yellow/Red, metal band right leg; No. 18682; henceforth DkGYR). Female DkGYR was banded as a nestling in Sherbrooke Forest in 2004 (14 years old). The footage shows DkGYR landing on the nest and tearing it apart using her feet (Figure 2; also see Supplementary Video 1 at 10.6084/m9.figshare.9872672). First DkGYR appears to inspect the nest closely, before moving approximately a metre away (from 0.07–0.22 minutes). At 0:23 minutes DkGYR flies onto the top of the nest and begins tearing at the nest with her feet. By the end of the 60-s clip, the top of the nest has collapsed and DkGYR is still present. The camera did not record DkGYR vocalising or entering the nest. The camera

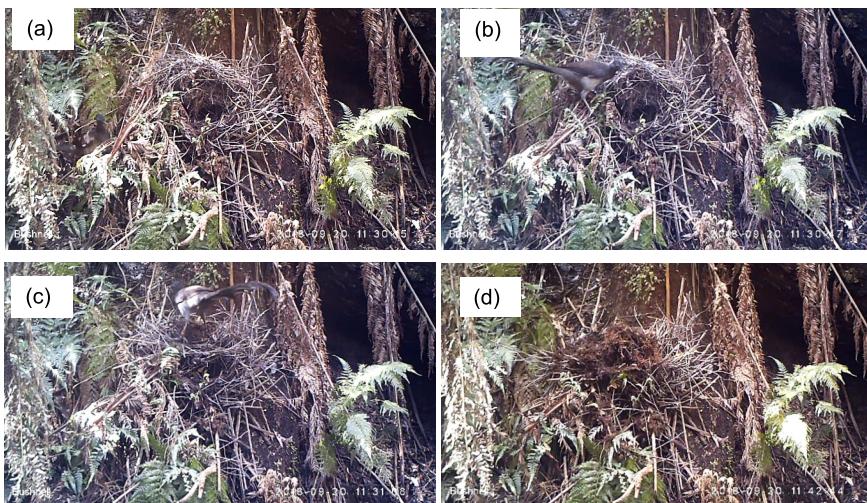


(a)



(b)

**Figure 1.** (a) The nest when found complete with egg inside on 7 July 2018. (b) The same nest on 22 September after marauding female DkGYR had destroyed the chamber.



**Figure 2.** Stills from video footage filmed on 20 September 2018 (a, b) Still shots recorded at 11:30:45 am and 11:30:47 am. Female DkGYR approaches and stands on the nest. (c) Female DkGYR begins destroying the nest using her feet. Here the nest dome is starting to collapse. (d) Still shot from video recorded 11:42:44 am. Image shows the nest after female DkGYR has left. We assume the camera was triggered on her exit.

triggers again 12 min later (Supplementary Video 2 at 10.6084/m9.figshare.9872672). In this second video DkGYR cannot be seen but the nest is completely destroyed, the top caved in (Figures 1b and 2d). Two days later when researchers checked the nest (22 September at 10:14 am) it was found in the same state as filmed by the camera (Figures 1b and 2d). There was no egg or remains of an egg inside.

At the time the nest was destroyed, it is unclear whether the nest was active. After the 31st of August, the camera is only triggered twice before the nest is destroyed — on 11 and 12 September, but no female is seen in the footage. On 12 September, there is slight damage to the entrance of the nest, indicating that a predation event may have occurred, but this cannot be confirmed.

#### 4. Discussion

In this study, we provide the first audio-visual footage of a female Superb Lyrebird destroying the nest of another female, which provides compelling evidence that female Superb Lyrebirds engage in reproductive suppression

through nest destruction. To our knowledge, this is the first evidence of reproductive suppression by a female bird with female-only parental care. Our results support early suggestions that nest destruction is a regular feature of Lyrebird breeding behaviour. While it is exceedingly difficult to observe nesting Superb Lyrebirds in the wild, Reilly (1970) described a “recognisable” (p. 70), banded female Lyrebird destroying the nest of a rival unbanded female in September of 1968 by “scratching the dome of the nest until it was completely demolished” (p. 78). Furthermore, of 525 nests monitored by the Sherbrooke Lyrebird Survey Group between 2003 and 2018, eight were found destroyed in a similar manner we report here (seven were found with the untouched egg still inside), representing 1.5% of the sample. The video shows the non-resident female engaging in a locomotion distinct from that used when foraging, thus it seems implausible that nest destruction is a by-product of foraging. Specifically, when foraging, Lyrebirds engage in repetitive digging with a motionless and fixed head position until they locate prey, at which point their head is lowered in a darting motion (Supplementary Video 3 at 10.6084/m9.figshare.9872672). By contrast, the nest destruction behaviour in the video shows a female standing on the dome of the nest and pulling it apart with her feet with her head in an upright position.

Intra-sexual competition in female Superb Lyrebirds seems a likely driver for nest destruction behaviour. We suspect that breeding resources such as food, and food-rich territories are limited. The diet of Superb Lyrebirds consists largely of invertebrates that reside just below the soil’s surface (Lill, 1986). Invertebrate based diets are considered unusual for uniparental care breeding systems due to lower abundances compared to other food sources such as fruit or nectar (Cockburn, 2006). Consequently, the effort associated with provisioning young may be especially high in Lyrebirds and reproductive suppression may be an effective means of reducing competition from rivals (Clutton-Brock & Huchard, 2013). By destroying the nest of a neighbour, female Lyrebirds are likely to secure more invertebrate-rich territory for themselves and their offspring during the breeding season. Given the extremely slow maturation rate of Lyrebird young and the high investment by females in a single reproductive attempt, the benefits of opportunistic nest destruction may outweigh the energy expenditure and risk associated with the behaviour.

Reproductive suppression involving the destruction of a nest, has very rarely been reported in birds, and it is unclear why female Lyrebirds appear to destroy nests, a physically taxing endeavour, rather than destroying

a fragile egg (ovicide). Perhaps, given the energy that needs to be expended into building a nest which can sometimes take many months (Lill, 1986), its destruction may be an extreme yet absolute method of preventing a female from re-laying in an empty nest. Nest destruction has also been recorded in White-Winged Choughs *Corcorax melanorhamphos* (Heinsohn, 1988) and, like Lyrebirds, Chough nests themselves are suspected to be extremely valuable. White-Winged Chough nests are made from mud that is only available after rainfall, and it may take quite some time to build a new nest once one is destroyed (Heinsohn, 1988). Thus, opportunities to re-nest during the breeding season may be limited for White-Winged Choughs, like for Superb Lyrebirds.

In Lyrebirds, nest destruction could explain other puzzling nesting behaviours. Female Lyrebirds often build multiple partly constructed nests in a season before one is built to completion (Reilly, 1970). This is unusual among birds (see Berg et al., 2006) and likely represent a significant investment in resources. However, if females are at high risk of having a nest destroyed by a rival, building multiple partial nests may enable females to gauge the level of threat to nests within a particular location, without risking the destruction of a complete or active nest. Indeed, given that Lyrebirds are long-lived and return to the same nesting territories year after year, nest destruction and multiple partial nest building may be a signalling strategy that females use in protracted negotiations over territorial boundaries spanning multiple breeding seasons.

While a definitive link between reproductive suppression and the evolution of complex behaviours and signals in birds has yet to be established, female–female competition may be driver of complex behaviours and signals (Tobias et al., 2012). For example, Krieg & Getty (2016) found that female House Wrens *Troglodyte aedon* that sang more were more likely to defend against ovicide by rival wrens of both sexes, suggesting that female song in this species may function, at least in part, to defend against reproductive suppression by rivals. Female Lyrebirds exhibit an impressive array of elaborate mimetic and species-specific vocalisations, suspected to play an important role in territory defence (Dalziell & Welbergen, 2016), and our finding provides important evidence that female Lyrebirds experience high intra-sexual competition. Given this competition, we suggest that reproductive suppression through nest destruction may act as a driver for elaborate vocalisations in this species.

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## Supplementary Material

**Supplementary Video 1.** Female Superb Lyrebird, DkGYR (Band colour Dark Green/Yellow/Red Left Leg, No. 18682) pulls apart a neighbouring female's nest on 20 September 2018 at 11:30.

**Supplementary Video 2.** The video triggers at 11:42 am on 20 September 2018, approximately 12 min after video 1. No Lyrebird can be seen but the nest is clearly destroyed.

**Supplementary Video 3.** A female Lyrebird foraging next to her nest. The video illustrates the locomotion of foraging.