

Inflated clutch size in the Superb Lyrebird *Menura novaehollandiae*

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The factors that determine clutch size in birds are a widely-debated topic in ornithology (Ricklefs 1980; Hořák *et al.* 2015). Many factors that potentially influence clutch size have been suggested, including those that are intrinsic to a species (e.g. body size, mode of development; Zammuto 1986) and those of extrinsic origin (e.g. food resources, predation risk; Jetz *et al.* 2008). Pioneering work by Lack (1947) linked clutch size with resource availability, proposing that the optimal number of eggs in a clutch represents, on average, the greatest number of offspring that the parents can raise in a breeding attempt in a given environment. This paradigm provides an explanation for the positive relationship between clutch size and latitude (Ashmole 1963; Cody 1966), because longer daylight hours in summer in temperate latitudes allow for an increased daily duration of foraging and thus greater resource provisioning to offspring. An alternative hypothesis suggests that perceived vulnerability to nest predation may influence clutch size (Slagsvold 1982; Martin 2014). In environments with a high perceived risk of predation, nesting birds may undertake less frequent visits to nests, resulting in restricted provision of food to nestlings, irrespective of the resources available within the breeders' home range (Eggers *et al.* 2005).

Such extrinsic factors undoubtedly interact with intrinsic influences on clutch size, making generalisations about clutch size determination problematic. In precocial species, clutch size tends to be larger, which is consistent with their relatively small parental investment after laying, whilst in altricial species, clutch size tends to be smaller and associated with a higher parental investment after laying (Jetz *et al.* 2008). The type of nest used has also been related to clutch size; cavity nesters generally lay larger clutches than open nest users, and birds that build domed nests lay an intermediate number of eggs (Jetz *et al.* 2008). Even diet has been linked with clutch size, with granivores and omnivores producing larger clutches than species with other types of diet (Jetz *et al.* 2008).

Whilst many bird species exhibit variation in clutch size as an adaptive response to environmental cues, such variation can sometimes become maladaptive. The Lesser Grey Shrike *Lanius minor* in Slovakia produces inflated clutches during years of high cockchafer *Melolontha melolontha*, Coleoptera abundance, yet fledging success is no greater than in years when cockchafer are scarce, allegedly due to the inability of parents to successfully incubate larger clutches (Hoi *et al.* 2004).

The Superb Lyrebird *Menura novaehollandiae* is a polygamous passerine that inhabits wet forests of the Great Dividing Range in south-eastern Australia. It is well known for its elaborate courtship displays in which loud mimicry and species-specific vocalisations are accompanied by rhythmic dance-like motions (Dalziel *et al.* 2013). Male lyrebirds are not involved in incubation or brooding or feeding young (Lill 1986). The female constructs a large, domed nest in autumn or early winter in preparation for laying in mid-June or early July (Maisey *et al.* 2016). Relative to the body mass of a female lyrebird, the egg mass (mean fresh weight = 62 g; Lill 1987) is close to twice that expected for a passerine (Rahn *et al.* 1985), and the incubation period (43–53 days; Lill 1987) is three times longer than would be expected for a passerine species of comparable size (Rahn *et al.* 1985). Thus, lyrebirds have a slow life-history strategy, with uniparental care of the young, a clutch size of one and a single clutch annually (Lill 1987).

The Sherbrooke Lyrebird Survey Group (SLSG), a volunteer organisation, has been monitoring the movements, breeding and behaviour of Superb Lyrebirds in Sherbrooke Forest (37°53' S, 145°21' E), an 800ha section of the Dandenong Ranges National Park, since 1958. The vegetation of Sherbrooke Forest is primarily wet forest dominated by Mountain Ash *Eucalyptus regnans*, with a diverse understorey of small trees and shrubs. First-order streams are flanked by narrow strips of cool temperate rainforest, where Southern Sassafras *Atherosperma moschatum* and Blackwood *Acacia melanoxylon* are the dominant canopy trees.

Members of the SLSG have recorded single-egg clutches as being the norm for the Superb Lyrebird in Sherbrooke Forest, but occasionally there are two eggs present in a single nest. Overall, of 495 clutches recorded from 2002 to 2016, only five contained two eggs (i.e. 0.8% of all clutches). In two-egg nests, close monitoring (nest visited pre-dawn or post-dusk) suggested that incubation was either not initiated or not completed to hatching (SLSG, unpubl. data). In contrast, in a multi-year study undertaken on the southern slopes of Victoria's Central Highlands (including Sherbrooke Forest), Lill (1986) reported twin-egg clutches in 3 out of 43 nests (7%), none of which progressed to hatching.

Here, we report the first record of a three-egg clutch for the Superb Lyrebird. On 20 August 2016, we discovered a lyrebird nest containing three eggs, located approximately 20 m north-west of a tributary to Sherbrooke Creek, south of Wattle Track



Figure 1. Five abandoned lyrebird eggs collected from five separate nests in Sherbrooke Forest, Dandenong Ranges National Park, Victoria, during the winter breeding season of 2002 (image depicts all eggs collected by the SLSG during 2002).

in Sherbrooke Forest (37°52'56" S, 145°21'10" E). The eggs and the feathers lining the nest were saturated with condensation, indicating prolonged exposure to the atmosphere and that the nest had been abandoned some time before its discovery. One of the eggs had a small, pin-sized hole through the shell, causing the contents to become rancid. The eggs were of similar size, measuring (length x maximum breadth) 58.3 x 42.6mm, 60.9 x 40.2mm and 59.2 x 38.0mm.

We think it likely that the three eggs in this nest were laid by the same individual. Female lyrebirds vigorously defend their territory and have been implicated in the destruction of the nests of neighbouring lyrebirds (Reilly 1970). Furthermore, the colour of lyrebird eggs is highly variable among individuals (Fig. 1). The three eggs in this nest were similar in colour and pattern (Fig. 2), suggesting that all were produced by the same female lyrebird.

Inflated clutch size (beyond a single egg) in the Superb Lyrebird appears to be a rare occurrence that is apparently detrimental to fecundity. Successful incubation of more than one egg has never been recorded. It is doubtful that this paternally emancipated species would be able to rear a brood of more than one young, because the food requirements of two or more offspring would probably be greater than could be met by a single parent (Lill, 1986). We do not know whether the trio of eggs were fertile, nor was this known for any of the twin-egg clutches that have been reported. The cause of laying multiple eggs in a clutch in this species may be a hormonal malfunction (Ouyang *et al.* 2011). In normal circumstances, hormonal factors should lead to disruption of ovarian follicular growth and thus cessation of clutch development during a breeding attempt (Haywood 1993). It is interesting to note that in all cases observed or reported, breeders were believed to have abandoned the clutch before initiating, or in the early stages of, incubation, therefore avoiding further detrimental effects on individual fitness.

It is unknown whether inflated clutch size in the Superb Lyrebird is heritable. Given the probably strong deleterious effect on potential offspring in an enlarged brood, inflated clutch-size appears to be either dysfunctional or maladaptive. This is suggested by the rarity of such events in lyrebird populations. Research investigating whether clutch size can be linked to environmental conditions would be valuable in further developing our understanding of inflated clutch sizes in lyrebirds.



Figure 2. Image detailing the colour and pattern of the three eggs collected from a single lyrebird nest in Sherbrooke Forest, Dandenong Ranges National Park, Victoria, on 20 August 2016.

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