Australian Field Ornithology 2018, **35**, 8–12
http://dx.doi.org/10.20938/afo35008012

A photographic guide for ageing nestlings of two Australian brood-parasitic cuckoo species: Horsfield's Bronze-Cuckoo *Chalcites basalis* and the Fan-tailed Cuckoo *Cacomantis flabelliformis*

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Abstract. Accurate ageing of nestling birds is important for a variety of ecological, evolutionary and ornithological research. However, this can be difficult when nests are found after the eggs have hatched, especially for less-common species such as brood-parasitic cuckoos. Here we present a photographic guide for ageing nestlings of two species of Australian cuckoo: Horsfield's Bronze-Cuckoo *Chalcites basalis* and the Fan-tailed Cuckoo *Cacomantis flabelliformis*. Evidence of chick rejection by several hosts of bronze-cuckoos *Chalcites* spp. and counter-adaptations in cuckoo nestlings has prompted increased research attention in this subject. This guide will help facilitate these efforts as well as research into the ecologies of other unstudied cuckoos.

Introduction

The nestling period presents a critical life-history stage in altricial birds and a useful model for studying a variety of biological questions. Recent emphasis has been on exploring the ecological and evolutionary importance of antagonistic interactions at the nest, such as those incited by nest-predators (reviewed in Ibáñez-Álamo *et al.* 2015) and brood-parasites (reviewed in Feeney *et al*. 2014a). These studies are generally conducted in the field (e.g. Langmore *et al.* 2003, 2008; Haff & Magrath 2010, 2011) and rely on locating and monitoring active nests. Ideally, nests are found while they are being built and are then monitored for as long as required, but some nests are inevitably found after the chicks have hatched.

The ability to accurately age nestling birds can prove critical for collecting meaningful data (e.g. Langmore *et al.* 2008; Haff & Magrath 2010; Colombelli-Négrel *et al.* 2012), but estimating nestling age can be difficult in species whose nestling phenotypes are not well documented. Australia hosts approximately 20% of the world's brood-parasitic cuckoo species (Feeney *et al.* 2013), but little is known about their natural history and ecology (see Brooker & Brooker 1989 and Langmore & Kilner 2010 for notable reviews on this topic). Unlike well-studied brood-parasite–host systems throughout the Americas and Europe, rejection of cuckoo nestlings by hosts is an important defence in at least several hosts of Australia's bronze-cuckoos *Chalcites* spp. (e.g. Langmore *et al.* 2003, 2008, 2011; Sato *et al.* 2010, 2015; see Kilner *et al.* 2004 and Grim 2007 for notable exceptions in the United States of America and Europe, respectively). These defences have selected counter-adaptations in nestling cuckoos, such as visual (Langmore *et al.* 2003, 2011; Sato *et al.* 2015) and vocal (Langmore *et al.* 2008) mimicry of host nestlings, which has led to increased research efforts into understanding these interactions. However, despite this, descriptive notes on cuckoo nestling phenotypes through ontogeny do not exist for any Australian cuckoo species (though see Gill 1982 for notes on the Shining Bronze-Cuckoo *Chalcites lucidus lucidus* in New Zealand). Here, we provide a photographic guide for ageing nestlings of two Australian brood-parasitic Cuckoos: Horsfield's Bronze-Cuckoo *Chalcites basalis* and the Fan-tailed Cuckoo *Cacomantis flabelliformis*, as well as baseline data on parasitism from our study site near Brisbane, Queensland.

Materials and methods

Study species

The two cuckoo species in this study comprise one that has received the overwhelming majority of research attention within Australia (Horsfield's Bronze-Cuckoo) and another that has not yet been the focus of any substantial research (Fan-tailed Cuckoo). Horsfield's Bronze-Cuckoos are generalist parasites of small Australian passerines (primarily malurid fairy-wrens), producing eggs that resemble those produced by numerous hosts (Feeney *et al.* 2014b) and chicks that produce begging calls that can rapidly be refined to resemble those of at least a few of their recorded hosts (Langmore *et al.* 2003, 2008; De Geest & Leitão 2017). Defences in Superb Fairy-wrens *Malurus cyaneus* (the best-studied host) appear to hinge primarily on minimising the likelihood of parasitism through aggressive cooperative mobbing (Langmore *et al.* 2012; Feeney & Langmore 2013, 2015; Feeney *et al.* 2013), and minimising the cost of parasitism, if it does occur, by abandoning nests that contain Horsfield's Bronze-Cuckoo chicks (Langmore *et al.* 2003, 2008, 2009, 2011; Colombelli-Négrel *et al.* 2012). They have also been recorded to reject eggs (e.g. Langmore *et al.* 2005), but this appears rare. By contrast, little previous research has investigated the interactions between Fan-tailed Cuckoos and their hosts (see Brooker & Brooker 1989; Marchant 1992; Guppy *et al.* 2017 for records of parasitism and notes on Fan-tailed Cuckoo behaviour), but preliminary observations at our study site suggest that White-browed Scrubwren *Sericornis frontalis* hosts might also reject Fan-tailed Cuckoo chicks under some circumstances (WEF unpubl. data).

Study site and parasitism rates

This study was conducted while monitoring the breeding ecology of colour-banded Red-backed Fairy-wren *Malurus melanocephalus*, Superb Fairy-wren and White-browed Scrubwren populations around Lake Samsonvale (27°16′S, 152°51′E) near Brisbane in Queensland, between August and January in 2015–2016 and 2016–2017.

When calculating parasitism rates, we included only nests that survived through to at least the start of incubation to ensure that our data were as accurate as possible. We also excluded White-browed Scrubwren nests found with fewer than three eggs or chicks from our calculations of parasitism rate to account for the possibility that the adults had ejected a cuckoo egg or chick before we found the nest, as it is not yet known whether this species rejects cuckoo eggs or chicks (three eggs is the typical clutch-size for White-browed Scrubwrens at this site: WEF unpubl. data). We did not use the same criteria for calculating parasitism rates for the fairy-wrens as previous studies have demonstrated that these species rarely eject cuckoo eggs (Langmore *et al.* 2005) or abandon nests with cuckoo chicks (rather than ejecting the cuckoo chicks) (Langmore *et al.* 2003).

Photographs of nestling cuckoos

Photographs of nestling cuckoos were taken opportunistically while other data were being collected. Following data collection (e.g. chick colour, size and weight), photographs were taken and the nestling was returned to the nest as quickly as possible (<1 minute). No instances of nest abandonment were recorded following the handling of nestlings. The Horsfield's Bronze-Cuckoo photograph sequence comprises photographs of Horsfield's Bronze-Cuckoos found in both Red-backed (*n* = 3) and Superb Fairy-wren (*n* = 2) nests. This should not be an issue as both these species are recorded as common hosts of this bronze-cuckoo species (Brooker & Brooker 1989) and no previous study has found evidence of genetic (Joseph *et al.* 2002) or phenotypic (Feeney *et al.* 2014b) host-specialisation in this species. The Fan-tailed Cuckoo photograph sequence comprises photographs of Fan-tailed Cuckoos from three White-browed Scrubwren nests. No photographs were taken on expected fledging dates to minimise the risk of premature fledging, photographs were included only from individuals where the date of hatching was known, and photograph sequences comprise photographs of multiple cuckoo individuals. This was because we did not visit each nest daily in order to reduce disturbance at any one nest.

Results

Parasitism rates

Parasitism of the two fairy-wren species by Horsfield's Bronze-Cuckoos occurred in ~7% (6 of 90 nests) and 13% (12 of 96 nests) of Red-backed Fairy-wren nests, and 6% (2 of 33) and 6% (2 of 32) of Superb Fairy-wren nests in 2015–2016 and 2016–2017, respectively. Brood-parasitism of White-browed Scrubwrens by Fan-tailed Cuckoos occurred in 36% (10 of 28) and 37% (11 of 30) of nests in 2015–2016 and 2016–2017, respectively.

Photograph sequences

Although the newly hatched Horsfield's Bronze-Cuckoos spanned from light pink (not shown) to a darkish purple in colour (Figure 1), which has been noted in previous studies (see Langmore *et al.* 2011 for further discussion of this phenomenon), all newly hatched Fan-tailed Cuckoos were darkish purple (Figure 2).

Horsfield's Bronze-Cuckoos showed the first stippling of feather pins along their alar tract on Days 0–2 (Day 0 = day of hatching), whereas similar development in Fan-tailed Cuckoos was more evident on Days 1–3. At around Day 3, the alar pins started breaking the skin in both species, while pin beginnings started becoming noticeable along the humeral tract around Day 3 in Horsfield's Bronze-Cuckoos and Day 4 in Fan-tailed Cuckoos. In both species, the eyes began to open and pin-feathers started to become noticeable around the caudal and femoral tracts around Day 4. The beginnings of pin-feathers along the capital and ventral tracts also started becoming noticeable around Day 4 in Horsfield's Bronze-Cuckoos, but this was more evident around Day 5 in Fan-tailed Cuckoos. Pins were clearly breaking the skin along all tracts around Day 5 in Horsfield's Bronze-Cuckoos and around Day 6 in Fan-tailed Cuckoos. Feathers started emerging from their sheaths along the dorsal, humeral and ventral tracts around Days 6–8 in Fan-tailed Cuckoos (copper and black tinge) and Days 7–9 in Horsfield's Bronze-Cuckoos (dull-green tinge). The remaining feathers began emerging from their sheaths around Days 9–10 in both species and progressively filled out until the nestlings were fully feathered around Day 14 in Horsfield's Bronze-Cuckoos and Day 15 in Fan-tailed Cuckoos. Our monitoring data suggest that both Fan-tailed Cuckoos and Horsfield's Bronze-Cuckoos fledged around 17–18 days after hatching.

Discussion

Although nestling development varies with a variety of factors, the results of this study suggest that some developmental milestones can be reliable indicators of age in nestlings of these two cuckoo species. Notably, this includes when pins start breaking the skin (*c.* Day 3 in both species), when the nestlings begin opening their eyes (*c.* Day 4 in both species) and when feathers start emerging from their sheaths along the dorsal, humeral and ventral tracts (*c.* Days 6–8 in Fan-tailed Cuckoos and *c.* Days 7–9 in Horsfield's Bronze-Cuckoos). These milestones may be conserved across breeding locations in Horsfield's Bronze-Cuckoos, as evidence suggests that this species has not diverged into host- or location-specific races (or 'gentes') (Joseph *et al.* 2002; Langmore *et al.* 2008; Feeney *et al.* 2014b). One Fan-tailed Cuckoo subspecies (*C. f. flabelliformis*) is currently recognised as breeding throughout Australia (with others breeding across New Caledonia, New Guinea, the Solomon Islands and Vanuatu: Payne 2017), so nestling development might also be conserved across breeding locations in this species within Australia.

Figure 1. Daily photographs of Horsfield's Bronze-Cuckoo nestlings from Day 0 (date of hatching) to Day 15 (day before fledging). Numbers indicate day since hatching. Photos: WEF, JAK, TAR, CP, LC & MS

Figure 2. Daily photographs of Fan-tailed Cuckoo nestlings from Day 0 (date of hatching) to Day 16 (day before fledging). Numbers indicate day since hatching. Photos: WEF, JAK, TAR, CP, LC & MS

These results provide a standard guide for ageing nestlings of these two cuckoo species. However, it must be recognised that finding cuckoo eggs before hatching and monitoring cuckoo nestlings through to fledging is difficult, and therefore these photograph series are based on relatively few individuals (*n* = 5 and *n* = 3 for Horsfield's Bronze-Cuckoo and Fan-tailed Cuckoo, respectively). Nonetheless, this guide is the first to provide a photographic key for ageing nestlings of these two cuckoo species, and we hope that it will facilitate further studies into the life histories of other unstudied cuckoos as well as interactions between nestling cuckoos and hosts.

Acknowledgements

We thank C. Brock, L. Dargis, B. Donnelly, M. Freeby, A. Miller, D.J. Thrasher and A. Werrell for support in the field, J.F. Welkin for assistance extracting data on natural history of the Red-backed Fairy-wren and M. Guppy and an anonymous reviewer for helpful comments. We also thank Seqwater for access to the field site and support of our research. It was funded by the Hermon Slade Foundation and the University of Queensland (WEF), as well as the National Science Foundation, USA (MSW). This research was conducted with approval from the University of Queensland's Animal Ethics Unit (SPS/200/15/UQPF), the Queensland Department of Environment and Heritage Protection (WISP16200615) and Seqwater (NPD20160331, NPD20170331).

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Received 8 June 2017, accepted 27 July 2017, published online 7 February 2018

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