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First recorded evidence of ejection of a cuckoo egg in a fairy-wren species

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Abstract. Brood-parasitic cuckoos lay their eggs in the nests of other birds, abandoning parental care to their hosts. Many host species have evolved defences to escape or reduce the costs associated with cuckoo parasitism. Superb Fairy-wrens *Malurus cyaneus*, which are a host to several cuckoo species in Australia, can distinguish cuckoo eggs based on their size or shape, or by using indirect cues such as the timing of egg laying or the presence of an adult cuckoo near the nest. They have previously been shown to reject cuckoo eggs by methods of egg burial or abandonment. These methods are likely to be costlier than ejecting the cuckoo egg from the nest (as seen in some other host species), because of the complete failure of the reproductive attempt, in addition to the costs associated with renesting. In this study, we document with photograph and video footage an incident of a Fan-tailed Cuckoo *Cacomantis flabelliformis* parasitising a nest of a Superb Fairy-wren in the Australian National Botanic Gardens, Canberra. Shortly after the parasitism event occurred, we recorded the female Fairy-wren returning to the nest and ejecting the single Cuckoo egg. To our knowledge, this footage represents the first evidence of ejection of a cuckoo egg in this species.

Introduction

Interspecific avian brood parasites lay their eggs in the nests of other species, and thus abandon parental care to their hosts (Soler 2017). In addition to the associated costs of rearing the parasite's offspring, those host species parasitised by cuckoos generally incur a total loss of reproductive success as the cuckoo nestling evicts all of the host's offspring from the nest soon after hatching (Davies 2000). Many host species have evolved defence mechanisms to escape or reduce the costs associated with cuckoo parasitism (Davies & Brooke 1989; Langmore *et al*. 2005). One of the most widespread host defences is the recognition and rejection of cuckoo eggs (Medina & Langmore 2015).

Some host species can distinguish cuckoo eggs based on their size, shape, colour and pattern (Langmore *et al.* 2003; Stokke *et al.* 2005; Taylor & Langmore 2020). In turn, this has led to the counter-adaptation of mimetic cuckoo eggs to reduce the risk of egg recognition (Davies 2000), with studies showing that cuckoo eggs that more closely mimic the size, shape, colour and pattern of their host's eggs are less likely to be rejected (Spottiswoode & Stevens 2010; Stoddard & Stevens 2011; Taylor & Langmore 2020).

When egg recognition does occur, host species can employ one of three known methods of rejection. First, if the cuckoo egg is laid before the host eggs, many hosts will bury it in the nest lining (resulting in insufficient incubation and thus failure to hatch; egg burial). However, cuckoos usually time their egg laying to coincide with the egg-laying period of the host, precluding burial of the cuckoo egg alone (although some host species may then bury the entire clutch and lay again in the same nest: Guigeno *et al.* 2014). Second, the host may reject the cuckoo egg by ejecting it from the nest by either grasping the egg between the mandibles (grasp-ejection) or by puncturing the eggshell with the bill to grip the egg (puncture-ejection: Underwood & Sealy 2006). For many small cuckoo host species, grasp-ejection is not likely to be possible because of limitations in their bill size (Rohwer & Spaw 1988). Puncture-ejection may also be impossible in some cases, as cuckoos have evolved eggshells relatively strong for the size of the egg (Spaw & Rohwer 1987; Brooker & Brooker 1991; Picman & Pribil 1997), or alternatively may increase the risk of the host damaging its own eggs whilst attempting to remove the cuckoo egg (Antonov *et al.* 2006). Third, if ejection of the egg is either not feasible or too costly, hosts may abandon the nest entirely (egg abandonment: Davies & Brooke 1989). Nevertheless, most cuckoo host species demonstrate only intermediate rates of egg rejection, and a considerable number of cuckoo eggs are still accepted (Lotem *et al.* 1995; Medina & Langmore 2015).

Superb Fairy-wrens *Malurus cyaneus* are a host to several cuckoo species in Australia. Their nests are primarily parasitised by Horsfield's Bronze-Cuckoo *Chalcites basalis* (up to 37% of nests per year: Langmore *et al.* 2003; Langmore & Kilner 2007) but they are also parasitised by the Shining Bronze-Cuckoo *Chalcites lucidus*, Fan-tailed Cuckoo *Cacomantis flabelliformis* and Brush Cuckoo *Cacomantis variolosus* (Brooker & Brooker 1989; Rowley & Russell 1997; Langmore 2013). Parasitism of Superb Fairy-wren nests by species other than Horsfield's Bronze-Cuckoo is uncommon and only occurs at low rates (Rowley & Russell 1997; Langmore & Kilner 2007), which may have important consequences for the evolution of host defences (Langmore *et al.* 2012).

Superb Fairy-wrens rarely reject Horsfield's Bronze-Cuckoo eggs (which closely resemble their own eggs: Langmore *et al.* 2003). Nor do they typically reject model cuckoo eggs of the same size but painted a different colour to their own eggs (Langmore *et al.* 2003). One possible explanation for this is that their dimly lit, dome-shaped nests constrain egg recognition via visual cues (Langmore *et al.* 2005). However, they have been found to reject larger model cuckoo eggs (Langmore *et al.* 2003), and they are also more likely to reject rounded real cuckoo eggs (Taylor & Langmore 2020), suggesting that tactile cues are important for egg recognition. Additionally, they can use indirect cues such as the timing of egg laying or the presence of an adult cuckoo near the nest to inform rejection decisions (Langmore *et al.* 2003). When egg recognition does occur, Superb Fairy-wrens have been shown to reject cuckoo eggs by methods of egg burial or abandonment (Rowley 1965; Langmore *et al.* 2003), both of which have been recorded in our study area (AC unpubl. data).

In this study, we document with photograph and video footage (hereafter, camera footage) an incident of a Fan-tailed Cuckoo parasitising the nest of a Superb Fairy-wren in the Australian National Botanic Gardens, Canberra. Shortly after the parasitism event, we recorded the female Fairy-wren returning to the nest and ejecting a single egg belonging to the Cuckoo. To our knowledge, this footage represents the first evidence of ejection of a cuckoo egg in this species.

Methods

The host

The Superb Fairy-wren is a small (~10 g: Dunning 2007) passerine endemic to south-eastern Australia. It is sedentary and lives on year-round territories, with territory boundaries maintained throughout the year. Each territorial group consists of a single breeding female and a socially dominant male. Although pairs can breed alone, about half are assisted by one to four (very rarely, five) male helpers that are usually, but not always, offspring from previous breeding seasons (Cockburn *et al*. 2008; Hajduk *et al*. 2021).

Although all males provide care to the nestlings, female Superb Fairy-wrens are solely responsible for nest building and incubating eggs (Rowley 1965; Rowley & Russell 1997). Nests are dome-shaped and often built close to the ground in dense vegetation such as shrubs or thick grass (Nias 1986; Rowley & Russell 1997; Colombelli-Négrel & Kleindorfer 2009). Because of high rates of nest predation, females can initiate up to nine clutches within one breeding season (which can span from August to March of the next calendar year: Lv *et al.* 2019). A new nest is built between each breeding attempt; only very rarely are nests re-used.

Clutch size ranges from one to five eggs, but most clutches typically consist of three eggs (Rowley & Russell 1997; Cockburn *et al.* 2016). Eggs are ~16 × 12 mm in size and tapered-oval, with one blunt pole (broader end) and one tapered pole (narrower end). They are pink/white in colour, with brown speckles, particularly towards the blunt pole (Figure 1; Beruldsen 2021). A single egg is laid per day and incubation commences once the final egg has been laid. Incubation lasts *c*. 13 days before the eggs hatch synchronously; fledging occurs *c*. 12 days later (Rowley & Russell 1997).

Parasitism of Superb Fairy-wren nests by Horsfield's Bronze-Cuckoos can be high (up to 37% of nests per year: Langmore *et al.* 2003; Langmore & Kilner 2007). However, parasitism by other cuckoo species is uncommon and occurs at only low rates (Rowley & Russell 1997; Langmore & Kilner 2007). Until the present study, only Horsfield's Bronze-Cuckoos have been confirmed parasitising Superb Fairy-wren nests in our study population (AC unpubl. data), although the Shining Bronze-Cuckoo and Fan-tailed Cuckoo are more common in the study area, with the latter being the most common (Fraser & Purdie 2020; eBird 2021).

The cuckoo

The Fan-tailed Cuckoo is a medium-sized (~50 g: Dunning 2007) cuckoo distributed throughout eastern and south-western Australia. It is partly migratory, with numbers peaking in the south of its range from late winter to early summer. It prefers well-timbered areas with well-developed understorey and is most common in sclerophyll eucalypt *Eucalyptus* spp. forests and woodlands, but it can also occur in urban areas. Fan-tailed Cuckoos preferentially parasitise host species that build dome-shaped nests close to the ground; their primary host is the White-browed Scrubwren *Sericornis frontalis* (Brooker & Brooker 1989; Beruldsen 2021) but they have also been recorded parasitising at least six species of fairy-wren, including the Superb Fairy-wren (Brooker & Brooker 1989; Higgins 1999). Their eggs are ~21 × 16 mm in size and rounded (with two blunt poles). They are a dull white colour, with moderate brown speckling, particularly towards one pole (Figure 1; Beruldsen 2021).

Fan-tailed Cuckoos generally remove one of the host's eggs from the nest before replacing it with an egg of their own (Higgins 1999). However, like most cuckoos (Davies 2000), they may often find host nests too late for successful parasitism, and thus they sometimes spoil nests by removing all of the host's eggs or nestlings (Guppy *et al.* 2017). The purpose of this strategy is thought to instigate renesting by the host species, enabling the cuckoo to synchronise her egg laying to successfully parasitise the replacement nest (Davies 2000).

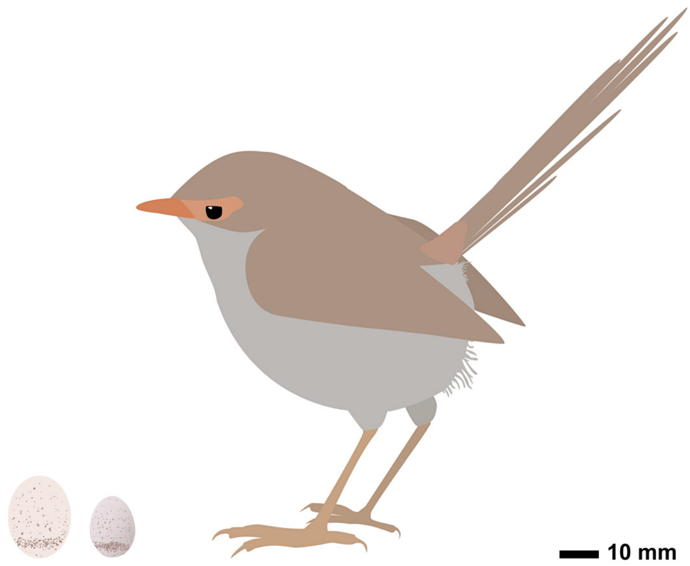

Figure 1. Example of the size, shape, colour, and pattern of a Fan-tailed Cuckoo egg (left, 21 × 16 mm) and a Superb Fairy-wren egg (right, 16 × 12 mm), in relation to the body size of a female Superb Fairy-wren. Illustration: Richard S. Turner & Ashley Latimer (egg illustrations are adapted from Beruldsen 2021).

Figure 2. Excerpts from the camera footage on 16 October 2019 (see Videos 1–2 at https://doi.org/10.6084/m9.figshare.19188026). Left: 1449 h, Fan-tailed Cuckoo perched beside nest of a Superb Fairy-wren. Right: 1457 h, Superb Fairy-wren ejecting an egg from the nest. Note the very large size of the egg relative to the body size of the Fairy-wren, indicating that the ejected egg was that of the Cuckoo. Photo: Richard S. Turner

Study area and nest monitoring

The study area is located in and adjacent to the Australian National Botanic Gardens, Canberra (35.27°S, 149.10°E), in an area encompassing ~65 ha. It contains a range of habitat types, from open lawns and densely planted gardens to native open eucalypt woodland around the periphery (Fraser & Purdie 2020). We have monitored a colour-banded population of Superb Fairy-wrens here since 1988 (Cockburn *et al.* 2016).

During the 2019–2020 breeding season [which spanned 16 September 2019 (date first nest was located) to 20 January 2020 (date when young fledged from final nest or final nest failed)], we filmed a subset of Superb Fairy-wren nests (while attempting to identify nest predators for another project) using Bushnell 119877 motion-sensing trail cameras (Bushnell Outdoor Products 2015). Each camera was positioned ~1.5 m from a nest and attached to a plastic stake. One camera was used per nest. Cameras were set to hybrid mode, capturing one image followed by 10 seconds of video for each trigger. We set the sensitivity of the passive infrared sensor to normal sensitivity, to reduce the potential of the cameras triggering falsely by motion of the surrounding vegetation (Bushnell Outdoor Products 2015). Because a camera was positioned close to a nest, we set the light-emitting diode control to low, to minimise overexposure (Bushnell Outdoor Products 2015). Cameras were able to record constantly from the time of installation. To reduce the likelihood of nest abandonment, they were positioned only once incubation was underway. None of the Fairy-wrens showed any signs of distress from the presence of a camera, and all returned to normal behaviour soon after the camera was set up.

Results

The observations reported here are based on camera footage recorded at one Superb Fairy-wren nest between 16 and 18 October 2019. The video footage (described below) is available at https://doi.org/10.6084/m9.figshare.19188026. The nest was first discovered on 23 September 2019. It was located 0.25 m above the ground and under early construction in a Spiny-head Mat-rush *Lomandra longifolia* at the time of discovery. The female Fairy-wren laid three eggs between 7 and 9 October, at which point she started incubating and a camera was positioned at the nest. On 18 October, she was observed building a new nest. Inspection of the original nest revealed it to be empty but intact. Subsequently, we reviewed all the camera footage for the original nest to identify the date, time, and probable cause of the nest failure.

On 16 October at 1449 h Australian Eastern Daylight Time, the camera footage revealed a Fan-tailed Cuckoo perched beside the Fairy-wren's nest (Figure 2, Video 1). The Cuckoo remained in this position for *c.* 6 seconds before flying off, but there was no information on camera showing the Cuckoo arriving at, or interacting with, the nest. In the next sequence at 1457 h, the camera footage revealed the female Fairy-wren entering the nest and ejecting a single egg, by a method appearing to resemble puncture-ejection (Figure 2, Video 2, Table 1). Over the next 40 h, the female Fairy-wren was recorded three more times at the nest, but there was no information on camera of her removing or incubating any remaining eggs (Videos 3–5). On 18 October, field observations and camera footage revealed the female Fairy-wren removing nesting material (Videos 6–11) and building a new nest ~2 m away. She began laying her second clutch 7 days later.

Table 1. Responses of Superb Fairy-wrens to real and model cuckoo eggs. Size: S = foreign egg is ~16 × 12 mm (i.e. similar in size to Superb Fairy-wren egg), L = foreign egg is ~21 × 16 mm (i.e. larger than Superb Fairy-wren egg); Type: M = model egg, R = real egg; Colour: M = mimetic (i.e. closely resembles colour and pattern of a Superb Fairy-wren egg), NM = non-mimetic (i.e. does not resemble colour and pattern of a Superb Fairy-wren egg); Timing: PL = pre-egg-laying, EL = egg-laying, I = incubation; Event: N = natural parasitism event, R = egg deposited into nest by researcher; Response: A = accept, AB = abandonment, EB = egg burial, PE = puncture-ejection. Sample size is the number of responses documented for each different observational or experimental manipulation of cuckoo egg size, type, colour, timing, or event (indicated by the hairlines). All data are from Langmore *et al*. (2003) except for the last entry in this table, which is from the present study.

Size	*Type*	*Colour*	*Timing*	*Event*	*Response*	*Sample Size (%)*
S	M	M	EL	R	A	14/18 nests (77.8%)
S	M	M	EL	R	AB	4/18 nests (22.2%)
S	M	NM	EL	R	A	22/27 nests (81.5%)
S	M	NM	EL	R	AB	5/27 nests (18.5%)
S	R	M	PL	N	A	2/15 nests (13.3%)
S	R	M	PL	N	EB	13/15 nests (86.7%)
S	R	M	EL	N	A	52/53 nests (98.1%)
S	R	M	EL	N	AB	1/53 nests (1.9%)
S	R	M	I	N	A	1/8 nests (12.5%)
S	R	M	I	N	AB	7/8 nests (87.5%)
S	R	M	I	R	A	26/27 nests (96.3%)
S	R	M	I	R	AB	1/27 nests (3.7%)
S	R	NM	EL	R	A	7/7 nests (100%)
L	M	NM	EL	R	A	8/15 nests (53.3%)
L	M	NM	EL	R	AB	7/15 nests (46.7%)
L	R	NM	I	N	PE	1/1 nest (100%)

Discussion

Fan-tailed Cuckoos generally remove one of the host's eggs from the nest before replacing it with an egg of their own (Higgins 1999). However, a previous study has shown that they will sometimes spoil nests that they find too late for successful parasitism by either eating or ejecting all of the host's eggs or nestlings (Guppy *et al.* 2017). The purpose of this strategy is thought to instigate renesting by the host species, enabling the cuckoo to synchronise her egg laying to successfully parasitise the replacement nest (Davies 2000).

Based on a combination of the Fan-tailed Cuckoo's presence at the nest, the subsequent ejection by the Superb Fairy-wren of a single egg (which was considerably larger in size than any eggs she could feasibly lay herself: Figures 1–2), the absence of any eggs or egg fragments in the vicinity of the nest following a nest check (2 days later), and the absence of any information on camera to suggest that any, or all, of the eggs might have been depredated at a different time by something other than the Cuckoo, the most plausible scenario is that:

1. The Fan-tailed Cuckoo spoiled the Superb Fairy-wren nest before laying her own egg. Although it may seem counter-adaptive to lay in the nest after spoiling it, it is unlikely that the Cuckoo would be able to delay laying once her own egg was fully developed (Seel 1973).
2. After the parasitism event, the camera triggered when the Cuckoo left the nest and perched in the open. Although there is no information on camera of the Cuckoo interacting with the Fairy-wren nest, it is possible that the dense vegetation surrounding the nest (Figure 2) prevented the camera from triggering when the Cuckoo first approached the nest (see Newey *et al*. 2015 for more on the limitations of using motion-sensing trail cameras in animal research).
3. The female Fairy-wren entered the nest and ejected the single Cuckoo egg before ultimately abandoning her now-empty nest.

Despite the apparent benefits of egg rejection, there is substantial variation both between and within host species in their responses to cuckoo eggs (Langmore *et al.* 2005; Stokke *et al.* 2005; Campobello *et al.* 2017). One of the most widespread responses to cuckoo parasitism is the rejection of the cuckoo egg, by either ejection or nest abandonment (Davies 2000), though some host species, of which the Superb Fairy-wren is one, also reject cuckoo eggs that are laid before their own eggs by burying them within the nest lining (Rowley 1965; Langmore *et al.* 2003; Table 1). Egg ejection involves costs associated with recognition errors, such as when the host's own eggs are mistakenly ejected (Davies & Brooke 1989; Antonov *et al.* 2006). Additionally, inadvertent damage to the host's own eggs can occur during the ejection process (Lotem *et al.* 1995), which is more likely when the cuckoo egg has a thicker eggshell; many cuckoo species, including *Cacomantis* species (Picman & Pribil 1997), have evolved eggshells that are thicker and stronger than in their hosts, relative to their body size, which is thought to be a defence against puncture-ejection by hosts (Spaw & Rohwer 1987; Antonov *et al.* 2006). Nevertheless, nest abandonment is likely to incur higher costs because of the complete failure of the reproductive attempt, in addition to the costs associated with renesting (Hauber & Montenegro 2002; Hoover 2003). Thus, it is paradoxical that nest abandonment, and not egg ejection, is more frequently recorded in some host species.

There are two possible explanations for this paradox. First, in observational studies of brood parasitism, researchers rarely visit nests daily. Thus, rates of parasitism (and subsequent estimates of egg recognition and rejection) may go largely undetected, particularly if hosts are good at recognising cuckoo eggs and are able to quickly respond to them before researchers ever find out. Second, in experimental studies of brood parasitism, researchers have often used model cuckoo eggs to simulate real brood parasitism, and these model cuckoo eggs are often made of harder materials (such as plaster, plastic or clay) than the shell of real cuckoo eggs (Davies & Brooke 1989; Lotem *et al.* 1995; Langmore *et al.* 2003; Roncalli *et al.* 2017). However, many small host species are unable to grasp-eject the relatively large cuckoo eggs from their nests because of limitations in their bill size (Moksnes *et al.* 1991). Rather, they are likely to naturally rely on puncture-ejection to eject cuckoo eggs from their nests. Therefore, it is possible that the frequency of rejection has often been underestimated because the difficulty of puncturing model cuckoo eggs is likely to be much higher than that of puncturing a real cuckoo egg (Moksnes *et al.* 1991; Roncalli *et al.* 2017).

Previous studies have shown that Superb Fairy-wrens generally accepted both model and real cuckoo eggs that were a different colour, as long as they were similar in size to their own eggs (Table 1; Langmore *et al.* 2003). However, when tested with large model cuckoo eggs, they frequently abandoned the nest (Table 1; Langmore *et al.* 2003). In addition, they were shown to be more likely to reject rounded real cuckoo eggs (Taylor & Langmore 2020). These studies indicate that failure to reject small model cuckoo eggs was not related to an inability to puncture the egg, and that egg discrimination was based on egg size and shape rather than colour. Our findings confirm these results, showing that Superb Fairy-wrens can also discriminate and eject real cuckoo eggs that are larger in size and different in shape to their own eggs.

Conclusions

Our findings provide new insights into the interactions between Superb Fairy-wrens and their cuckoo parasites, showing for the first time that Superb Fairy-wrens are capable of ejection of a cuckoo egg. Additionally, they add to a growing body of literature that suggests that tactile cues are important for egg recognition in this species. Future studies are required to determine how prevalent ejection of a cuckoo egg is in Superb Fairy-wrens, with natural observations or the use of real eggs recommended whenever possible.

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