Females that experience threat are better teachers

Sonia Kleindorfer, Christine Evans and Diane Colombelli-Négrel

School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia

Superb fairy-wren (Malurus cyaneus) females use an incubation call to teach their embryos a vocal password to solicit parental feeding care after hatching. We previously showed that high call rate by the female was correlated with high call similarity in fairy-wren chicks, but not in cuckoo chicks, and that parent birds more often fed chicks with high call similarity. Hosts should be selected to increase their defence behaviour when the risk of brood parasitism is highest, such as when cuckoos are present in the area. Therefore, we experimentally test whether hosts increase call rate to embryos in the presence of a singing Horsfield’s bronze-cuckoo (Chalcites basalii). Female fairy-wrens increased incubation call rate when we experimentally broadcast cuckoo song near the nest. Embryos had higher call similarity when females had higher incubation call rate. We interpret the findings of increased call rate as increased teaching effort in response to a signal of threat.

1. Introduction

Animals that learn, and hence generate new motor patterns in response to currently perceived information, can rapidly embark on altered evolutionary trajectories [1]. Brood parasites and their hosts are model systems to test different evolutionary trajectories that arise from learning because of strong selection on hosts to avoid cuckoo recognition errors in their nest, and selection on cuckoos to locate suitable host nests. For example, reproductive isolation between indigobird (Vidua spp.) brood parasites is maintained because young males learn to mimic their host species’ song and young females learn to prefer attributes of the host species nest and the learned song of the conspecific male [2]. Naive juvenile superb fairy-wrens (Malurus cyaneus) use social learning to recognize a brood parasite after observing experienced birds mob the cuckoo mount [3]. Recently, Colombelli-Négrel et al. [4] showed that learning begins inside the egg; female superb fairy-wrens teach their embryos a vocal password that chicks produce as a begging call after hatching to elicit parental food provisioning [4]. Chicks that had learned the call well, as evidenced by high call similarity after hatching, received more parental provisioning [4]. On the contrary, Horsfield’s bronze-cuckoo (Chalcites basalii) chicks had low call similarity after hatching, perhaps because the embryos are exposed to the female incubation calls for fewer days or because they use call matching after hatching to elicit food from their foster parents [4,5].

In Australia, high annual fluctuation in brood parasite prevalence in host nests (0–43% across years and study sites [6]) creates selection for risk assessment and dynamic response to changing threat levels [7]. When hosts express defences towards brood parasites, the costs can be high because of recognition errors; hosts may incorrectly identify the eggs and chicks of cuckoos versus their offspring [8–11]. Therefore, hosts should be selected to modify the expression of defence in relation to the risk of parasitism [7,12]. For example, Acrocephalus hosts increase mobbing behaviour at the nest when the risk of parasitism is high [13]. But when brood parasite risk is low, hosts accept more foreign eggs into their nest, thereby lowering the rejection threshold for eggs and chicks [12,14]. Here, we test whether incubating female fairy-wrens
increase their incubation call rate when they hear the broadcast of a cuckoo near their nest. Cuckoo chicks do not learn as embryos (no evidence to date), whereas fairy-wren embryos do; the presence of a well-learned begging call element is a signal to feed or abandon the brood in this system [4]. This study tests for an early frontline defence mechanism (in this case, teaching embryos) that would thwart the successful fledging of a cuckoo chick [7,8,15].

2. Material and methods

Superb fairy-wrens are common hosts of Horsfield’s bronze-cuckoo [6,16]. In South Australia, annual parasite intensity varied from 0 to 37% in 233 nests studied since 2006 (D. Colombelli-Négrel 2014, unpublished data). This study was done during 2007–2013 at Cleland Wildlife Sanctuary (34° 58′ S, 138° 41′ E) and Newland Head Conservation Park (35° 37′ S, 138° 29′ E).

We recorded in-nest vocalizations from 17 nests as follows: 2 h of incubation call recordings day 10–11 of incubation and 2 h of chick begging call vocalizations day 4–6 post-hatching. During 2007–2011, the nest recordings were done as described in [4]. In 2012–2013, the recordings were made using a Zoom handy recorder H4n (Zoom Corporation, Australia). We recorded all sound files as broadcast wave files (44.1 kHz sampling rate, 16-bit depth). We edited the recordings with AMADEUS PRO v. 1.5 (Hairer-soft Inc., Switzerland) and analysed them with RAVENPRO v. 1.3 (for methods, see [4]). We noted the number of incubation calls per hour for each female on the basis of acoustical and visual records (spectrograms). An incubation call contains a unique element per female termed the signature element, which is the same element as the chick begging call element after hatching. We calculated call similarity scores per nest for five signature elements per female and five chick begging calls per nest using spectrographic cross-correlation in RAVEN PRO v. 1.3 and principal coordinates analysis (PCoA); we used R-package software to create PCoA coordinate values (similarity values) [4] and regression analysis to test for number of calls per hour and mean similarity values (‘call similarity’).

To test whether females adjust incubation call rate to the threat of cuckoo parasitism, we conducted playback trials at 22 nests in 2012 and seven nests in 2013 during the incubation phase (day 10 or 11). We used only one stimulus per nest and broadcast the song of either Horsfield’s bronze-cuckoo (at 16 host nests) or striated thornbill (Acanthiza lineata; control; at 13 host nests). The playback stimuli (five different Horsfield’s bronze-cuckoo, five different striated thornbill) were normalized at −15 dB and saved as uncompressed 16-bit 44.1 kHz broadcast wave files (AMADEUS PRO v. 1.5). The playback stimuli consisted of 15 s of song repeated every minute for 1 h. The stimulus track had 1 h of pre-playback silence (pre-trial) followed by 1 h of playback (trial). We broadcast the playback stimuli as uncompressed files from an Apple iPod (Apple Inc., USA) connected to a yo-yo speaker placed 5 m from the nest. We recorded the nest again for 1 h on the following day; all recordings were made using a Zoom handy recorder H4n.

3. Results

Call similarity between female signature element and chick begging call was predicted by the number of incubation calls per hour (linear regression: $r = 0.58$, $t = 2.21$, $p = 0.046$), which we tested in 17 observational nests without exposure to playback stimuli. If females had high incubation call rate, then the call similarity between female signature element (during incubation) and chick begging call element (after hatching) was higher.

4. Discussion

Female superb fairy-wrens increased the number of incubation calls under conditions of perceived threat of brood parasitism. The similarity between begging call and female signature element (call similarity), which is a proxy for embryonic learning outcome and which predicts parental food provisioning of chicks, was higher when females produced more incubation calls [4,17].

Cuckoo call to attract a mate [18]. Upon hearing a cuckoo call, a host should increase vigilance and other anti-parasite behaviours to thwart the cuckoo from successfully fledging [7,15]. Here, we showed that female fairy-wrens that heard a cuckoo near their nest increased call rate to embryos,
which increased call similarity after hatching, and hence—as we previously showed—increased detectability of an intruder cuckoo chick after hatching. Assuming that cuckoo embryos could learn (for which there is no evidence to date [5]), increased female incubation call rate (which begins late in the incubation phase [4]) would have a lesser effect on cuckoo embryos that hatch days earlier than host embryos (early cuckoo hatching is favoured to evict host eggs). This study provides a mechanistic explanation for how ‘experience’ with a brood parasite near the territory can lead to increased cuckoo abandonment [19], which is a pattern found across numerous studies [6].

Most studies of host–parasite coevolution focus on visual arms races [20,21]. Our research has shown that acoustical cues are sufficient for fairy-wren hosts to perceive the threat of brood parasitism [6]. Acoustical cues may be more reliable than visual cues to detect the presence of cuckoos. First, visual detection of cuckoos could fail, because cuckoos are discreet while tracking egg-laying hosts, given that hosts will likely mob a detected cuckoo. Second, cuckoos can be similar in appearance to Accipiter hawks, thereby creating potential for a costly recognition error [22]. The use of acoustical cues could therefore reduce the chance of mistaking a hawk for a cuckoo while mobbing a bird close to the nest [23]. The use of visual cues can also be misleading for cuckoo detection in the nest. While host nests with a single chick are more likely to be abandoned by fairy-wren parents, it is not always the case that nests with a single chick are cuckoo chicks. Usually, a Horsfield’s bronze-cuckoo egg hatches earlier than the host eggs and the newly hatched cuckoo evicts all host eggs in the nest, leaving a single chick [12]. But sometimes a cuckoo egg may hatch after the host chicks have hatched; in these cases, the newly hatched cuckoo chick evicts the somewhat older fairy-wren chicks. Low reproductive success is not uncommon in fairy-wrens (especially during drought years), and may result in a nest with a single fairy-wren chick. While fairy-wren parents are more likely to abandon a single chick, this is an unreliable cue for cuckoo presence in the nest; using a simple visual cue such as ‘single chick’ increases the risk of mistakenly abandoning one’s own sole surviving offspring [6]. Notably, superb fairy-wren parents are more likely to reject a single chick (cuckoo, fairy-wren) when there are cuckoos in the study area [12]—which is evidence that fairy-wrens alter their rejection rules. Here, we show that female fairy-wrens increase incubation call rate when there are cuckoos in the area, which we argue would lower the probability of committing an acceptance error for a cuckoo, or a rejection error for a fairy-wren chick.

The so-called frontline of defence in host and brood parasite systems is well supported by evidence [15], including cuckoo mobbing [8], egg mimicry [24] and begging call learning [25]. This study shows that female fairy-wrens increased teaching effort to embryos after receiving acoustical information about the threat of brood parasitism during incubation. In a separate study, we showed increased predation risk at nests with high incubation call rate [26], which likely explains why female fairy-wrens only increase call rate when the risk of cuckoo parasitism is high. The benefits to the embryos of learning could be numerous, including a lifelong trajectory of learning in unpredictable environments [27]. These findings add to a growing body of empirical evidence that animals teach naive individuals, such as offspring [28–32], and that hosts modify the expression of defence in relation to risk, including risk of parasitism [11]. What is novel about this study is that we show changes in host teaching effort (call rate) and host learning outcome (call similarity) under conditions of brood parasite threat.

Acknowledgements. We thank the Hermon Slade Foundation, the Australian Research Council and the Australian Geographical Society for financial support. Special thanks to Katharina Mahr for field assistance and nest recordings and to Jeremy Robertson for song recordings used for the playback stimuli. All data are available from the online Flinders University data repository at http://researchdata.ands.org.au/incubation-calls-and-playback-data-of-female-superb-fairy-wrens-recorded-at-newland-head-conservation-park-and-cleland-wildlife-park-south-australia-between-2007-and-2013.

References


