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RESEARCH ARTICLE

Superb Fairy-wrens (*Malurus cyaneus*) increase vigilance near their nest with the perceived risk of brood parasitism

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ABSTRACT

Brood parasites typically impose costs on their hosts, which select for host defenses. However, where defenses are costly, hosts can benefit by facultative expression of defenses in relation to the risk of parasitism. The results of our model-presentation experiments show that Superb Fairy-wrens (*Malurus cyaneus*) mediate vigilance around their nest according to their perceived risk of brood parasitism; when the risk of parasitism is high, they increase the time they spend in the vicinity of their nests. In combination with previous studies, these data suggest that Superb Fairy-wrens have a plastic defense portfolio that can be acquired rapidly and deployed facultatively to prevent parasitism while minimizing wasteful investment in defenses in the absence of parasitism.

Keywords: arms race, brood parasitism, coevolution, cuckoo, nest defense, vigilance

Malurus cyaneus aumenta la vigilancia cerca de sus nidos ante el riesgo percibido de parasitismo de nidada

RESUMEN

Los parásitos de nidada típicamente imponen costos a sus hospederos, lo cual selecciona la aparición de defensas por parte del hospedador. Sin embargo, donde las defensas son costosas, los hospederos pueden beneficiarse por la expresión de defensas facultativas en relación con el riesgo de depredación. Aquí presentamos modelos experimentales a individuos de *Malurus cyaneus* para mostrar que la vigilancia alrededor del nido se relaciona con el riesgo percibido de parasitismo de nidada; cuando el riesgo de parasitismo es alto, aumenta el tiempo que pasan en la vecindad de sus nidos. En combinación con estudios previos, estos datos sugieren que *M. cyaneus* presenta una cartera variable de defensas que puede ser rápidamente adquirida y desarrollada facultativamente para prevenir el parasitismo, mientras que minimiza las inversiones excesivas en defensas en la ausencia de parasitismo.

Palabras clave: carrera de armamentos, coevolución, cuco, defensa del nido, parasitismo de nidada, vigilancia

INTRODUCTION

The interactions between brood parasites and their hosts can lead to "arms races" of adaptations and counteradaptations (Dawkins and Krebs 1979); however, the evolution, composition, and fate of adaptive portfolios—the cumulative suite of offensive or defensive adaptations—are little understood (Feeney et al. 2014b, Soler 2014). Host defensive adaptations, such as rejection of foreign eggs, persist in some species despite generations of allopatry with brood parasites (Briskie et al. 1992, Rothstein 2001, Lahti 2006, Hale and Briskie 2007, Peer et al. 2007, 2011, Soler 2014; but see Samas et al. 2014). In others, the occurrence of egg rejection in a population decreases with decreasing parasitism rates (Thorogood and Davies 2013), and individuals vary their response according to their perceived risk of parasitism (Davies and Brooke 1988, Brooke et al. 1998). Such plasticity in defenses is likely to evolve when host defenses carry costs (e.g., mistaken rejection of their own young or increased visibility to predators) or when the probability of parasitism varies over time (Tewksbury et al. 2002, Caro 2005, Welbergen and Davies 2012).

Superb Fairy-wrens (*Malurus cyaneus*) provide a good model for studying defense portfolios against brood parasitism. They are the primary host of Horsfield's Bronze-cuckoo (*Chalcites basalis*) in southeastern Australia and recognize cuckoos as a specific type of threat (Feeney et al. 2013, Kleindorfer et al. 2013). They defend against brood parasitism through aggressive group mobbing (Feeney et al. 2013) and by abandoning cuckoo chicks (Langmore et al. 2003, 2009). During mobbing, larger breeding groups of Superb Fairy-wrens attack cuckoos more vigorously and are parasitized less than smaller groups, despite there being benefits to cuckoos that successfully parasitize larger groups (Feeney et al. 2013). Unlike many other hosts of brood parasites, they very rarely reject cuckoo eggs (Langmore et al. 2005). Parasitism rates by Horsfield's Bronze-cuckoo vary dramatically between years, with 0–37% of nests in which eggs were laid being parasitized in each breeding season (parasitism occurred in 8–15 yr between 1999 and 2013 at Campbell Park, Canberra, Australia; $n = 1{,}297$ nests). Suppression of defenses during years when cuckoos are absent could therefore reduce the risk of costly recognition errors, such as misdirected mobbing or mistaken rejection of a Superb Fairy-wren chick (Langmore et al. 2009). Accordingly, Superb Fairy-wrens suppressed chick rejection behavior in years when cuckoos were absent from the population (Langmore et al. 2009).

The degree to which Superb Fairy-wren "frontline" defenses (defenses that are deployed prior to parasitism of the nest; Feeney et al. 2012) are mediated according to the perceived risk of brood parasitism is not well understood. Recognition and mobbing of adult cuckoos are learned traits in Superb Fairy-wrens (Langmore et al. 2012) that can be acquired through social transmission of information (Feeney and Langmore 2013). Once learned, an aggressive response toward a cuckoo can be elicited for several years, even without cuckoos being present in the population (Langmore et al. 2012). Superb Fairy-wrens mediate their vigilance around their nest according to their perceived risk of nest predation (Yasukawa and Cockburn 2009), and Eurasisan Reed Warblers (*Acrocephalus scirpaceus*), a host of the Common Cuckoo (*Cuculus canorus*), become more vigilant around their nest after seeing a cuckoo mount (Davies et al. 2003). Here, we investigate whether Superb Fairy-wrens adjust their nest vigilance according to their perceived risk of brood parasitism.

METHODS

Study Site and Species

Fieldwork took place in Campbell Park, a eucalypt woodland nature reserve in Canberra, Australia (149°10′E, 35°12′S), between October and December, 2012 and 2013. Superb Fairy-wrens are small (10 g), resident, facultatively cooperative-breeding passerines that are endemic to southeastern Australia and common at this study site (Rowley and Russell 1997). They build a dome-shaped, grass nest in low vegetation. Throughout their range, they are the primary host of Horsfield's Bronze-cuckoos and a secondary host of Shining Bronze-cuckoos (*C. lucidus*) (Brooker and Brooker 1989, Langmore et al. 2008). Both cuckoo species are migratory and generally arrive at the study site between August and November.

Experimental Methods

We used model-presentation experiments to test whether Superb Fairy-wrens changed the amount of time they spent close to their nest according to their perceived risk of brood parasitism. We used 2 freeze-dried Shining Bronze-cuckoos to simulate a threat of parasitism near the nest, and 2 freeze-dried White-plumed Honeyeaters (*Lichenostomus penicillatus*) as controls. All specimens for freeze-drying were obtained from the freezer stock at the Australian Wildlife Collection, Canberra. Although Horsfield's Bronze-cuckoos (*Chalcites basalis*) are the more common brood parasite of Superb Fairy-wrens, we had no models available for use. However, Shining Bronze-cuckoos are morphologically similar to Horsfield's Bronze-cuckoos, and previous study of the closely related Splendid Fairy-wren (*M. splendens*) found that these hosts attacked Horsfield's Bronze-cuckoos and Shining Bronze-cuckoos in a similar manner (Payne et al. 1985). Both of these cuckoo species have been observed being mobbed by Superb Fairy-wrens in Campbell Park (W. E. Feeney and N. E. Langmore personal observation), and previous work using Shining Bronze-cuckoo models found that they elicit a highly aggressive response from Superb Fairy-wrens (e.g., Langmore et al. 2012, Feeney and Langmore 2013, Feeney et al. 2013), which suggests that they are an adequate substitute for Horsfield's Bronze-cuckoos. White-plumed Honeyeaters are common in Campbell Park, are similar in size (19 g) to Shining Bronze-cuckoos (23 g), and present no threat to Superb Fairy-wrens (Langmore et al. 2012). Accordingly, Superb Fairy-wrens exhibit lower levels of aggression to honeyeater models than to cuckoo models (Feeney et al. 2013).

We conducted model presentations and nest watches at 30 Superb Fairy-wren nests (15 treatments and 15 controls). When a cuckoo is seen near the nest, Superb Fairy-wrens produce a cuckoo-specific vocalization that functions to "rally" other birds to quickly assist with mobbing (Feeney et al. 2013), which suggests that increased vigilance around the nest by at least 1 individual may increase the likelihood of detecting, and deterring, a cuckoo. To ensure that the Superb Fairy-wrens used in our study recognized cuckoos as a threat, we conducted experiments only on groups that contained at least 1 color-banded bird that had previously shared habitat with breeding cuckoos. Birds were not banded specifically for the present study, but as part of a long-term project investigating coevolution between Superb Fairy-wrens and Horsfield's Bronze-cuckoos (e.g., Langmore and Kilner 2007). Adult Superb Fairy-wrens were captured in mist nets, and nestlings were removed from the nest for banding, on days 6–7 of the nestling period.

Approximately half an hour before the experiment commenced, a small camouflaged hide (Advantage Timber Standard Dome Hide C30) was set up 10–25 m from the

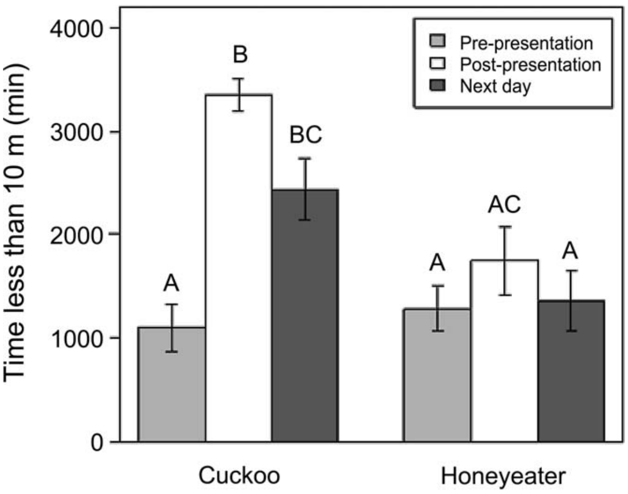

FIGURE 1. Time spent within 10 m of the nest by at least 1 Superb Fairy-wren prior to, immediately following, and the day after presentation of a cuckoo or honeyeater model ($n = 15$ cuckoo and $n = 15$ honeyeater presentations) in Campbell Park nature reserve, Canberra, Australia (October–December, 2012 and 2013). Error bars denote standard error, and letters denote results of post hoc paired *t*-tests with Holm-Bonferroni *P*-value adjustments (trials with the same letter showed no significant post hoc differences).

TABLE 1. Results of post hoc paired *t*-tests with Holm-Bonferroni *P*-value adjustments between trials with cuckoo and honeyeater models presented to Superb Fairy-wrens in Campbell Park nature reserve, Canberra, Australia (October–December, 2012 and 2013).

	Honeyeater		
Cuckoo	Pre-presentation	Post-presentation	Next-day
Pre-presentation	$P = 1$	$P = 0.5$	$P = 1$
Post-presentation	$P < 0.0001$	$P = 0.0004$	$P < 0.0001$
Next-day	$P = 0.02$	$P = 0.43$	$P < 0.0001$

nest of the focal group to allow for habituation. Following this, a 1-hr nest watch was conducted from the hide to establish the time spent by Superb Fairy-wren groups around their nest for comparisons with 2 equivalent (1-hr) nest watches immediately after the model presentation and the following day. The start time of the first and final nest watches were always matched. Each group was presented with either a cuckoo (experimental) or honeyeater (control) model for 5 min. Models were placed within a protective wire cage on a small experimental perch and placed ~2 m from the target Superb Fairy-wren nest (following Langmore et al. 2012, Feeney and Langmore 2013, Feeney et al. 2013). To minimize disturbance to the nest, all movement near the nest by the experimenter was restricted to times when no birds were in sight. Our previous model-presentation experiments have never caused nest abandonment (Langmore et al. 2003, Feeney and Langmore 2013, Feeney et al. 2013), and we likewise did not observe any nest abandonment as a result of the present experiments. All experiments were conducted during the final stages of nest building (while the nest was being lined), the period during which cuckoos monitor host nests and are mobbed aggressively by Superb Fairy-wrens (Feeney and Langmore 2013). All experiments were also conducted before Horsfield's Bronze-cuckoos arrived in the area.

The time spent by the closest Superb Fairy-wren in the vicinity of the nest (<10 m vs. >10 m) was recorded in a notepad by the observer in the hide as a measure of vigilance around the nest. The open eucalypt woodlands in which these experiments were conducted are generally sparse, so locating Superb Fairy-wrens within 10 m of the nest is not difficult. We predicted that the nest vigilance of Superb Fairy-wrens would increase after seeing a cuckoo near their nest, but not after seeing a honeyeater.

Statistical Analyses

We used a generalized linear mixed model (GLMM) to test whether nest vigilance changed after seeing a cuckoo or honeyeater near the nest. Our full model included treatment (cuckoo or honeyeater), model replicate, trial (pre-, post-, or the day following a presentation), date, group size, and all two-way interactions as fixed effects, and a group identifier as a random effect. Model replicate, date, group size, and their interactions were removed from the final model because they were nonsignificant. We used paired *t*-tests with Holm-Bonferroni *P*-value adjustments to identify differences between the treatments and trials.

RESULTS

Nest vigilance of Superb Fairy-wrens differed significantly between cuckoo and honeyeater trials (GLMM: treatment × trial $\chi^{6}_{3} = 22.16$, $P < 0.001$; Figure 1 and Table 1). Vigilance around the nest did not differ between experimental and control groups prior to presentation of the cuckoo or honeyeater model and did not change significantly in the control groups following presentation of the honeyeater model (Figure 1 and Table 1). By contrast, vigilance around the nest increased dramatically in the experimental groups following presentation of a cuckoo model, and this increase persisted until the following day (Figure 1 and Table 2).

DISCUSSION

Superb Fairy-wrens spent more time in the vicinity of their nests in the hour following presentation of a cuckoo model than in the hour before, and this increase was still evident the following day. By contrast, there was no significant change in the amount of time spent near their nest

TABLE 2. Results of post hoc paired *t*-tests with Holm-Bonferroni *P*-value adjustments between trials with cuckoo models presented to Superb Fairy-wrens in Campbell Park nature reserve, Canberra, Australia (October–December, 2012 and 2013).

Cuckoo	Pre-presentation	Post-presentation	Next-day
Pre-presentation	–	$P < 0.0001$	$P = 0.007$
Post-presentation	$P < 0.0001$	–	$P = 0.01$
Next-day	$P = 0.007$	$P = 0.01$	–

following presentation of a honeyeater model. These data suggest that Superb Fairy-wrens adjust their vigilance around the nest according to the perceived risk of brood parasitism.

Together with the findings of previous work (Langmore et al. 2003, 2009, 2012, Langmore and Kilner 2007, Feeney and Langmore 2013, Feeney et al. 2013, Kleindorfer et al. 2013), these data suggest that Superb Fairy-wrens have a "defense portfolio" of adaptations centered on learning to recognize and respond to adult brood parasites, and that the strength of response varies according to their perceived risk of parasitism. Horsfield's Bronze-cuckoos are generalist brood parasites (Brooker and Brooker 1989, Joseph et al. 2002, Feeney et al. 2014a) that are not necessarily faithful to a particular site or host species during the breeding season (Langmore and Kilner 2007); host birds at a particular location may only rarely be exposed to the risk of brood parasitism. Cuckoo-naive Superb Fairy-wrens do not respond to adult cuckoos in the vicinity of their nests (Langmore et al. 2012, Feeney and Langmore 2013). However, recognition of, and response to, an adult cuckoo can be rapidly transmitted between individuals through social learning (Feeney and Langmore 2013). Once learned, a response to a cuckoo can be elicited years later despite no further contact with cuckoos (Langmore et al. 2012). Recognition is specific (Feeney et al. 2013, Kleindorfer et al. 2013), and sight of an adult cuckoo elicits a cuckoo-specific alarm call that functions to attract other birds to assist with aggressive group mobbing (Feeney et al. 2013). The findings of the present study suggest that they also mediate their vigilance around their nest to maximize the likelihood of detecting and defending against cuckoldry after seeing a cuckoo near their nest (also see Kleindorfer et al. 2013). In addition to vigilance and mobbing, Superb Fairy-wrens also defend against brood parasitism by rejection of cuckoo chicks (Langmore et al. 2003). Chick rejection is also a phenotypically plastic defense that occurs only when adult cuckoos are present in the population (Langmore et al. 2009). Thus, the principal defenses against cuckoos in this species appear to be exhibited only once the identity of a cuckoo has been learned, and defense by an individual appears to be strongly mediated according to the perceived risk of brood parasitism.

Why some adaptations against brood parasitism persist despite generations of allopatry with brood parasites, while others are mediated according to the risk of brood parasitism, is likely to be related to the relative costs and benefits of maintenance of the trait and phenotypic plasticity in trait expression. Plasticity through learning is likely to be particularly beneficial in recognition of adult brood parasites because it facilitates a rapid response to a novel brood parasite (Feeney and Langmore 2013) or brood parasite morph (Honza et al. 2006, Thorogood and Davies 2012), and defenses will be expressed specifically in response to the parasite (Gill and Sealy 2004, Feeney et al. 2013). Correspondingly, in European Reed Warblers, frontline adaptations such as nest vigilance and mobbing were mediated according to the perceived risk of brood parasitism (Davies et al. 2003, Welbergen and Davies 2009) and were expressed only in response to the local cuckoo morph (Thorogood and Davies 2012). Similarly, Common Chaffinches (*Fringilla coelebs*) that were released from parasitism after being introduced to New Zealand ≤130 yr ago did not exhibit aggressive behavior toward adult brood parasites (Hale and Briskie 2007), and host populations that were sympatric with brood parasites responded more aggressively to a model brood parasite than allopatric populations in Yellow Warblers (*Setophaga petechia*; Briskie et al. 1992), American Redstarts (*S. ruticilla*; Hobson and Villard 1998), Superb Fairy-wrens (Langmore et al. 2012), and a variety of hosts of the Common Cuckoo (Lindholm and Thomas 2000, Røskaft et al. 2002, Honza et al. 2006). Moreover, Tewksbury et al. (2002) found that an increase in nest vigilance according to the perceived risk of brood parasitism in Yellow Warblers was coupled with an increase in nest depredation rates, highlighting a cost–benefit trade-off of an antiparasite behavior that can be mediated by phenotypic plasticity.

By contrast, learning through exposure to brood parasites may not be required for effective egg rejection based on discordancy (rejection of the odd egg out; Rothstein 1975, Marchetti 2000) or template-based egg discrimination (recognition of own eggs; Rothstein 1975, Lotem et al. 1995, Lahti and Lahti 2002; but see Hauber et al. 2006). Thus, plasticity in egg rejection behavior is likely to be adaptive only when maintenance of the trait in the absence of parasitism is costly (Rothstein 2001, Peer et al. 2007, Soler 2014). Several studies support this prediction; recognition errors are common in European Reed Warblers (>30% if the nest is parasitized with a mimetic model egg; Davies and Brooke 1988) and egg rejection is phenotypically plastic (Brooke et al. 1998), whereas in species in which recognition errors are less common, such as weavers (15%; Lahti 2006) and several hosts of Brown-headed Cowbirds (*Molothrus ater*) and Common Cuckoos (e.g., Rothstein 2001, Hale and Briskie 2007, Peer et al. 2007; but see Samas et al. 2014), egg rejection is retained despite a century or more of separation from brood parasites.

Superb Fairy-wrens appear to exhibit a flexible suite of defensive adaptations that can be acquired rapidly to combat variable parasitism regimes by Horsfield's Bronze-cuckoos. Further investigation of holistic adaptive portfolios in other systems will allow a more general understanding of the processes that determine the evolution and fate of adaptations that arise from exploiter–victim interactions.

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