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Original Article

Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*

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Cuckoo hosts defend themselves against parasitism by means of mobbing, egg rejection, and chick rejection. However, each of these defenses is prone to costly recognition errors, and hosts are therefore more likely to deploy these defenses if they observe a cuckoo in the vicinity of their nest. The success of such response plasticity depends on accurate recognition of sympatric cuckoo species, but the mechanism by which hosts recognize cuckoos is largely unknown. Here, we use microgeographic variation in exposure to cuckoos in superb fairy-wren (*Malurus cyaneus*) hosts to test whether recognition of cuckoos is dependent on learning. We compare mobbing by superb fairy-wrens in response to freeze-dried specimens of a shining bronze-cuckoo (*Chalcites lucidus*) and a honeyeater control (*Lichenostomus penicillatus*) at 2 heavily parasitized sites and 2 rarely parasitized sites. Hosts at heavily parasitized sites mobbed the cuckoo intensively, including production of a distinctive whining call that appears to instigate group mobbing. By contrast, hosts at the rarely parasitized sites showed little reaction to the cuckoo, and their responses were similar to those given to the control. Furthermore, individuals with past experience of cuckoos mobbed the cuckoo specimen even when cuckoos were absent from the site, and did so significantly more than naive individuals. The extreme variation in response to cuckoos on such a small geographic scale and in relation to past exposure to cuckoos is consistent with learned recognition of cuckoos rather than local genetic adaptation. *Key words:* brood parasitism, cowbird, cuckoo, enemy recognition, referential call. *[Behav Ecol]*

INTRODUCTION

Hosts of brood parasitic cuckoos have evolved a suite of defenses against parasitism, including mobbing of adult cuckoos (Welbergen and Davies 2009), rejection of cuckoo eggs (Brooke and Davies 1988; Davies and Brooke 1989; Spottiswoode and Stevens 2011), and rejection of cuckoo chicks (Langmore et al. 2003; Sato et al. 2010; Tokue and Ueda 2010). However, each of these defenses carries potential costs to the hosts if recognition errors occur (Davies et al. 1996). Mimicry of hawks or predatory birds by some species of cuckoos can lead to cases of mistaken identity (Davies and Welbergen 2008), in which hosts mob dangerous predators. Similarly, recognition errors at the egg and chick stages can lead to the inadvertent rejection of the host's own eggs (Davies and Brooke 1988; Marchetti, 1992; Moskát and Hauber 2007) or chicks (Langmore et al. 2003). To minimize the probability of recognition errors, many host species have evolved the ability to recognize adult cuckoos (Welbergen and Davies 2008) and to adjust their rejection threshold for eggs (Davies and Brooke 1988; Moksnes and Røskaft 1989; Moksnes et al. 1993; Davies et al. 1996; Bártol et al. 2002; Guigueno and Sealy 2010) or chicks (Langmore et al. 2009) according to the probability of parasitism, as indicated by the presence of adult cuckoos in the vicinity.

The success of such response plasticity depends on accurate recognition of sympatric cuckoo species. However, the mechanism by which hosts recognize cuckoos is largely unknown. Enemy recognition may have a genetic basis, or may be learned, or may entail a combination of both, if learning is used to refine recognition skills and adjust appropriate responses (McLean and Maloney 1998). The mechanism by which cuckoo recognition occurs has important consequences for hosts in terms of preventing parasitism. If cuckoo recognition is learned, this would facilitate accurate recognition of sympatric cuckoos on a local scale, including rapid transmission of defenses through a population in response to exploitation by a new and unfamiliar brood parasite. On the other hand, young birds would be at greater risk of parasitism, due to a lower probability of successfully recognizing and mobbing cuckoos near the nest and a lower likelihood of making accurate rejection decisions about parasite eggs and chicks. Poorer discrimination of parasitic eggs and chicks by younger or naive individuals has been observed in several studies (Lotem et al. 1992, 1995; Langmore et al. 2009; but see Sealy 1995; Amundsen et al. 2002), but this has generally been attributed solely to the necessity for learned recognition of egg and chick phenotypes rather than poorer discrimination of adult cuckoos by naive birds.

Several studies suggest that learning may be important in discrimination of adult brood parasites, although the evidence is somewhat equivocal. First, reed warblers can be induced to increase mobbing of cuckoos after witnessing mobbing of cuckoos by their neighbors, suggesting either that recognition of cuckoos is learned in this species or that mobbing intensity is adjusted in relation to perceived risk of parasitism (Davies and Welbergen 2009). Similarly, reed warblers increased the intensity of their aggression toward a model cuckoo from the

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first to the second presentation, which might indicate learned recognition (Čapek et al. 2010). Second, in some species, yearlings show weaker responses to adult brood parasites than older individuals (Smith et al. 1984; Hobson and Sealy 1989), although other studies show no effect of female age (Payne et al. 1985; Mark and Stutchbury 1994). Third, some host species show a stronger aggressive response to adult brood parasites in populations that are sympatric with cuckoos than in those that are allopatric (Briskie et al. 1992; Hobson and Villard 1998; McLean and Maloney 1998; Lindholm and Thomas 2000; Røskaft et al. 2002; Honza et al. 2006; Hale and Briskie 2007). However, these behavioral differences may reflect genetic differences between populations rather than variation in the opportunity for learning (Robertson and Norman 1977; McLean and Maloney 1998). To distinguish between these possibilities, variation in responses to cuckoos should be assessed on a smaller geographic scale, such that individuals belong to the same genetic population but differ in their exposure to cuckoos.

Here, we investigate how variation in exposure to cuckoos shapes microgeographic variation in the mobbing response of an Australian cuckoo host, the superb fairy-wren *Malurus cyaneus*. Fairy-wrens are the primary hosts of Horsfield's bronze-cuckoo, *Chalcites basalis*, as well as occasional hosts of the shining bronze-cuckoo, *C. lucidus* (Brooker MG and Brooker LC). Superb fairy-wrens lack egg defenses but reject cuckoo chicks (Langmore et al. 2003). Chick rejection is a phenotypically plastic trait that is influenced both by the breeding experience of the female and by whether adult cuckoos are present in the area (Langmore et al. 2009). Naive female fairy-wrens make more recognition errors and fewer accurate rejection decisions than experienced females (who have reared at least one brood of their own), but it is not known whether this is the result of lack of recognition of adult cuckoos (and therefore, a reduced ability to adjust rejection according to the presence or absence of cuckoos in the population) or lack of experience with the phenotype of their own nestlings.

We investigated variation in responses to adult cuckoos at 4 sites that differed in levels of cuckoo parasitism. Two sites were regularly and heavily parasitized by bronze-cuckoos. Two sites with landscaped grounds and relatively high levels of human activity experienced negligible parasitism rates, but were directly adjacent to regularly parasitized woodland sites (Figure 1), so gene flow with parasitized populations was likely to be high. All sites were within a 3.5 km radius of one another (Figure 1). We predicted that if cuckoo recognition occurs independently of exposure to cuckoos, we should see mobbing of cuckoos at all 4 sites. However, if learning is necessary for cuckoo recognition, we should see 1) a higher incidence of mobbing at the sites that experience regular parasitism by cuckoos than those at which parasitism is rare and 2) within sites where cuckoos are currently absent, we would expect to see stronger aggression from birds with prior experience of cuckoos than from naive individuals.

MATERIALS AND METHODS

Study species

Superb fairy-wrens are 10 g insectivorous, facultatively cooperative-breeding passerines endemic to southeast Australia (Rowley and Russell 1997; Cockburn, Sims, et al. 2008). Groups comprise a breeding female, a dominant male, and up to 5 male helpers. Juvenile females leave their natal territory within their first year (mean dispersal distance 940 m, Mulder 1995). By contrast, males are the most philopatric bird to the natal territory thus far studied; most males never leave their natal territory and those that disperse always move to an immediately neighboring territory (Cockburn, Osmond, et al. 2008). Both Horsfield's bronze-cuckoos and shining bronze-cuckoos are breeding migrants in southeastern Australia, and annual parasitism rates on superb fairy-wrens are influenced by habitat type, host density, and rainfall (Langmore et al. 2007; Langmore and Kilner 2007). Fairy-wrens are the primary host of Horsfield's bronze-cuckoo and a secondary host of the shining bronze-cuckoo (Brooker MG and Brooker LC 1989; Langmore et al. 2008).

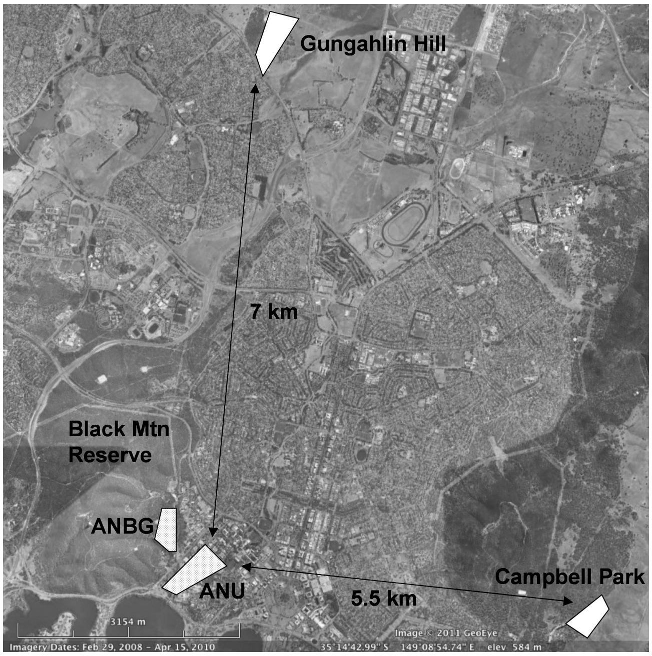

Figure 1
Map showing the 4 study sites (white areas): Campbell Park Nature Reserve, the ANBG, the Australian National University campus, and Gungahlin Hill Nature Reserve.

Study sites

We studied superb fairy-wren responses to cuckoos at 4 sites around Canberra, Australia (Figure 1); 2 sites in which bronze-cuckoos were common and 2 sites in which they were rare. Replication of treatments at 2 each of "cuckoos-present" and "cuckoos-absent" sites minimizes the possibility that the results are confounded by a habitat feature other than cuckoo presence or absence. Parasitism rates were calculated as the number of nests containing a cuckoo egg/total number of nests in which eggs were laid at that site (except at the Australian National Botanic Gardens [ANBG], where nests were not always checked for parasitism during incubation, so parasitism rates were calculated as number of cuckoo chicks that hatched/total number of nests in which any chicks hatched).

Heavily parasitized sites

(a) Gungahlin Hill (lat 149°9′E, long 35°12′S) is a nature reserve comprising open eucalypt woodland. The population of color-banded superb fairy-wrens at this site suffers high parasitism rates by Horsfield's bronze-cuckoos, with parasitism occurring in 3 of 4 years (2006–2010) and parasitism rates ranging from 0% to 45% of nests (mean for parasitized years ± standard deviation [SD] = 42.6 ± 2.5%). Experiments were conducted on 10 fairy-wren groups at this site between 24 November 2009 and 15

January 2010. Horsfield's bronze-cuckoos were observed or heard regularly during this period (35% of days on the site, $N = 20$ days) and 45% of superb fairy-wren nests ($N = 20$) were parasitized by Horsfield's bronze-cuckoos during this breeding season. The experiment was repeated on 15 groups in 2011 to compare the responses of females that had been exposed to cuckoos in 2009 with females recruited to the population in 2010 and 2011, both years in which bronze-cuckoos failed to breed at the site.

(b) Campbell Park (lat 149°9′E, long 35°16′S) is also a eucalypt woodland nature reserve. Parasitism by Horsfield's bronze-cuckoos occurred in 7/12 years (1999–2010), with rates ranging from 0% to 37% of nests/year (mean for parasitized years ± SD = 19 ± 11%). Experiments were conducted on 6 fairy-wren groups at this site between 4 October 2010 and 2 November 2010. Horsfield's bronze-cuckoos were absent during that period, but shining bronze-cuckoos were observed or heard regularly on the study site (83% of days on the site, $N = 6$ days).

Rarely parasitized sites

c) The ANBG (lat 149°6′E, long 35°16′S) is situated on the edge of Black Mountain Reserve (Figure 1). It comprises landscaped native gardens of lawns, shrubs, and trees, bordered by native eucalypt woodland around the perimeter. Although bronze-cuckoos occur regularly on Black Mountain, they avoid the landscaped core area of the ANBG. The color-banded superb fairy-wren population at this site has been monitored continuously since 1988, including complete breeding records for all females (e.g., Cockburn, Osmond, et al. 2008). Parasitism was either absent (11/23 years from 1988 to 2010), confined to the occasional laying of an egg that did not hatch (5/23 years), or occurred at low rates in the 7 years when at least some cuckoos hatched (mean ± SD = 3 ± 2% of nests, maximum = 5.7%). Cuckoo parasitism was generally restricted to the areas of natural eucalypt woodland around the perimeter of the study area. Experiments were conducted on 10 fairy-wren groups in the core area of this site between 24 November 2009 and 14 January 2010. No bronze-cuckoos were observed or heard and no superb fairy-wren nests were parasitized during this period.

(d) The Australian National University campus (lat 149°6′E, long 35°16′S) comprises landscaped lawns with native garden borders around buildings and reeds along a creek. Parasitism rates were not monitored at this site in previous years, but Horsfield's and shining bronze-cuckoos do not usually breed in highly populated urban environments. Experiments were conducted on 6 fairy-wren groups at this site between 4 October 2010 and 2 November 2010. No bronze-cuckoos were sighted or heard and none of the superb fairy-wren nests were parasitized during this period.

Experimental methods

We tested the mobbing response of superb fairy-wrens to a freeze-dried shining bronze-cuckoo, mounted in a natural posture on a short branch (Figure 2a). Although Horsfield's bronze-cuckoos are the more common parasite of superb fairy-wrens, we did not have a mount available for use. Shining bronze-cuckoos and Horsfield's bronze-cuckoos both parasitize fairy-wrens, they are morphologically similar, and an experiment by Payne et al. (1985) confirmed that mobbing responses of splendid fairy-wrens *M. splendens* to taxidermic mounts of the 2 species were equivalent. We used a freeze-dried white-plumed honeyeater *Lichenostomus penicillatus* mounted in a similar posture as a control species that does not harm fairy-wrens (Figure 2b). White-plumed honeyeaters are a common species in Canberra and are a similar size (19 g) to shining bronze-cuckoos (23 g, Brooker MG and Brooker LC). During experiments, the branch to which each mount was attached was fitted into a short stump, raising the mounts 40 cm above the ground, and placed under a dome-shaped cage (50 cm height × 50 cm diameter) of fine (1.5 cm diameter) wire mesh to protect them from damage during mobbing by fairy-wrens.

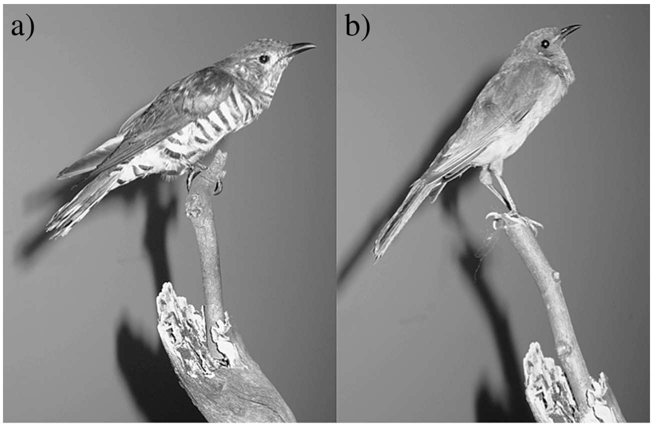

Figure 2
Freeze-dried specimens used in experiments: (a) shining bronze-cuckoo and (b) white-plumed honeyeater.

Experiments were conducted during the time frame when the focal fairy-wren nest was vulnerable to parasitism or depredation by cuckoos; either during egg laying or incubation. A small camouflage cloth hide was erected 10–25 m from the nest in a position that provided a clear view of the nest and its immediate surrounds, and the cage was pegged down 2 m from the nest. After allowing the birds to become accustomed to the hide and the cage for half hour, one of the mounts was placed inside the cage. Each fairy-wren group was presented with both the cuckoo and the control, and the order of presentation was alternated between groups. The trial commenced when one or more members of the focal fairy-wren group approached to within 2 m of the mount and then continued for 5 min. Fairy-wren responses were recorded by 2 observers in the hide. One observer recorded all vocalizations of the birds during that interval, using a Marantz PMD661 solid-state recorder, an Audio-technica condenser microphone Lo-Z and a Sennheiser MZS6 grip. A second observer used binoculars to keep a record of the distance between the mount and the nearest bird, the sex of the nearest bird, and the time at which the distance to the nearest bird changed. The number and sex of other birds present was also noted. After 5 min, the mount was removed, and the second mount was presented after an interval of at least 1 h.

Call analysis

Recordings were viewed on sonograms using Raven Pro v.1.3 (Cornell Laboratory of Ornithology). Two distinct call types were recorded, the typical superb fairy-wren alarm call (Figure 3a) and a very rapid, loud pulsed call (Figure 3b), which is probably analogous to the "whining" call produced by splendid fairy-wrens in response to a cuckoo mount (Payne et al. 1985). We counted the total number of each call type produced during each 5-min trial.

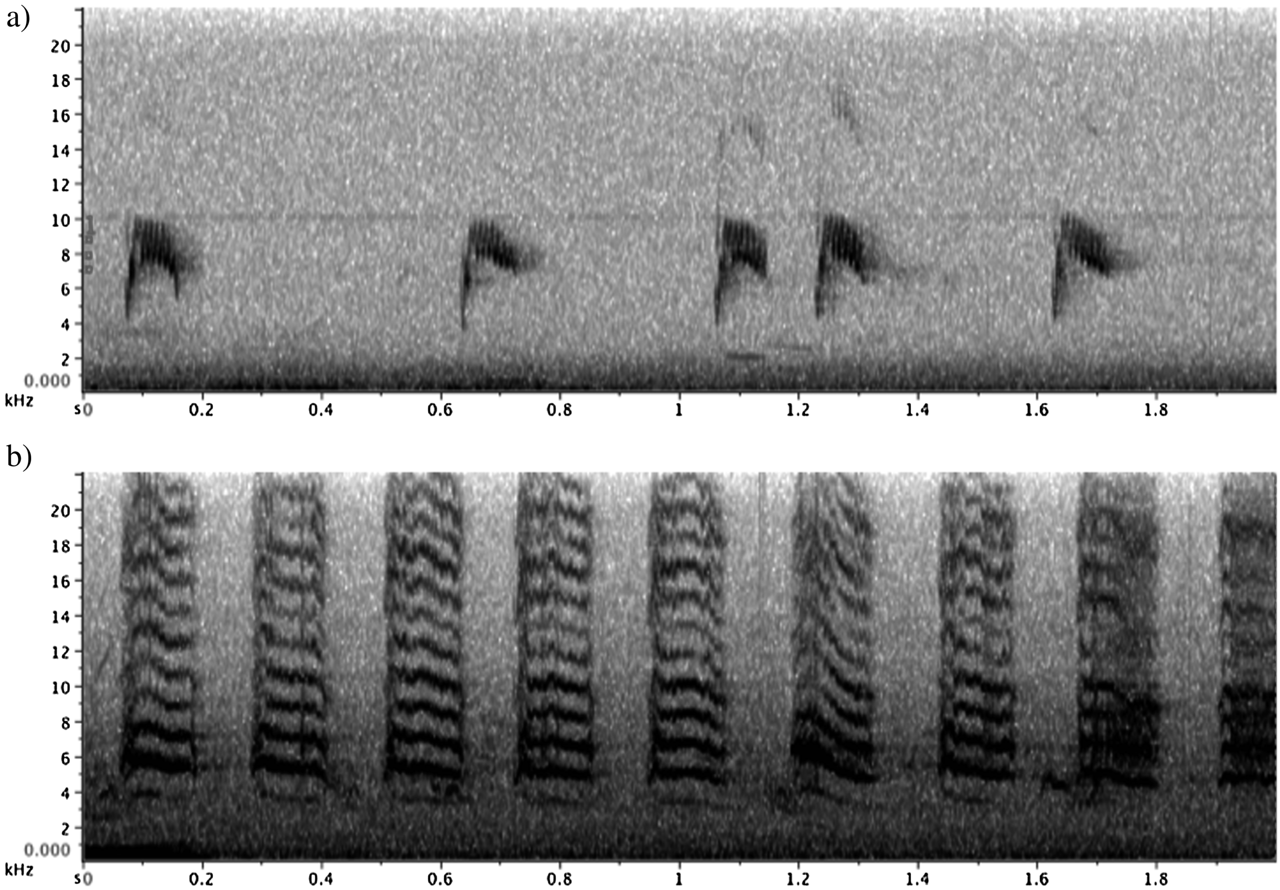

Figure 3
Vocal responses of superb fairy-wrens during experiments: (a) alarm call and (b) whining call.

Statistical analyses

We used restricted maximum-likelihood models to test whether a significant amount of variation in the data could be explained by 1) the model species (cuckoo/honeyeater) and 2) whether cuckoos occur at the study site (present/absent). We also included breeding stage of the subject (laying/incubation) and trial sequence (cuckoo or honeyeater first) as factors in the models. We included the nest identifier as a random term because 2 trials were conducted at each nest (cuckoo and honeyeater). Data were log transformed to conform to assumptions of normality. Whining calls were almost never elicited by the control (one bird that had received the cuckoo trial first subsequently approached the honeyeater producing whining calls but then switched to alarm calls as it got closer). The relative lack of whining call response to the control allowed us to restrict analyses to response to the cuckoo model for this call type, so we used a Wilcoxon–Mann–Whitney test to compare the number of whining calls produced when cuckoos were present versus absent. All analyses were performed using JMP v. 6.0 (SAS Institute, Inc., Cary, NC).

RESULTS

The responses of superb fairy-wrens differed dramatically between sites. Superb fairy-wrens called at a significantly higher rate in response to the cuckoo mount than the honeyeater mount at sites where cuckoos were regularly present, but not at sites where cuckoos were usually absent, for both total calls produced (model species × cuckoo presence, $F_{1,30} = 10.5$, $P = 0.003$, Figure 4a) and for alarm calls only ($F_{1,30} = 9.2$, $P = 0.005$, Figure 4b). Similarly, fairy-wrens produced whining calls almost exclusively in response to the cuckoo mount and at a significantly higher rate at sites where cuckoos were present than at sites where they were absent ($Z = 2.35$, $P = 0.018$, Figure 4c). The majority of whining calls were produced at the beginning of the trial, after which the group switched to alarm calls (Figure 5a). Superb fairy-wrens also spent significantly more time close to the cuckoo mount (0.5 m or less) than to the honeyeater mount at sites where cuckoos were present, but not at sites where they were absent (model species × cuckoo presence, $F_{1,29} = 10.2$, $P = 0.003$, Figure 4d). Fairy-wrens at cuckoos-present sites spent more time close to the cuckoo mount than fairy-wrens at cuckoos-absent sites (Figure 5b). Neither the breeding stage of the subject (laying/incubation) nor the trial sequence (cuckoo or honeyeater first) was significant for any analyses, so they were excluded from the final models. Grim (2005) cautioned that some control mounts may be unsuitable for use as a control because they elicit aggression due to a superficial resemblance to the cuckoo. However, the extreme contrast between the aggressive host responses to the cuckoo and the relatively relaxed response to the honeyeater indicate that the honeyeater is a suitable control in this case.

Responses in relation to sex and group size

Over all trials, the female usually approached the model first in 30 trials, a male approached first in 18 trials, and multiple group members approached together in 13 trials. An initial approach

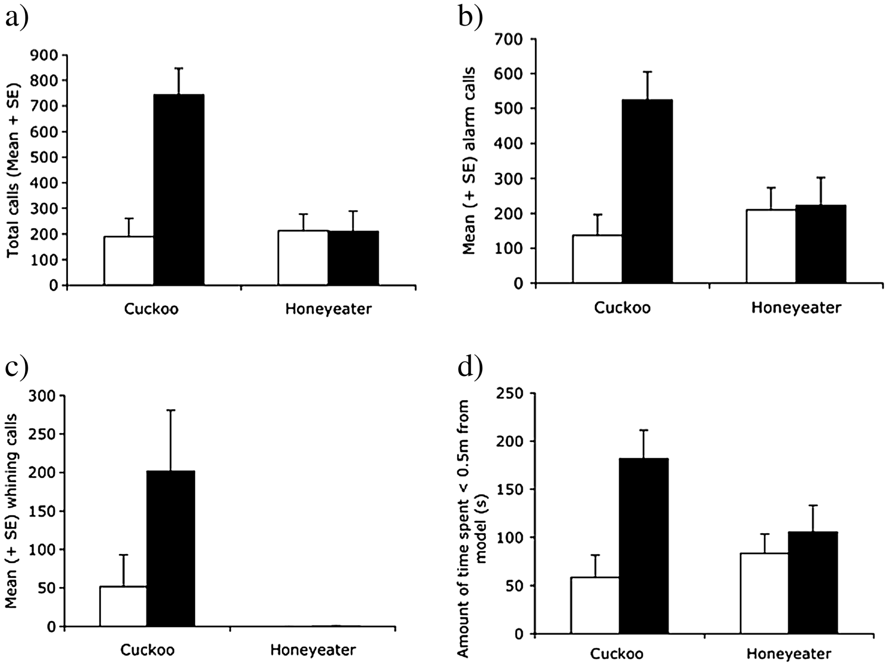

Figure 4
Mean (+standard error) (a) total calls, (b) alarm calls, (c) whining calls, and (d) amount of time spent <0.5 m from the model, during presentations of a cuckoo model and a honeyeater model at sites where cuckoos were absent (white bars, *N* = 16 fairy-wren groups) and sites where cuckoos were present (black bars, *N* = 16 fairy-wren groups).

by multiple group members was significantly more likely to occur in the cuckoos-present sites than the cuckoos-absent sites for the cuckoo trials (Fisher's Exact Test, *P* = 0.035, Figure 6a), but not for the honeyeater trials (*P* = 1, Figure 6b.).

Amongst groups with helpers (*N* = 16), one or more helper males were significantly more likely to approach within 2 m of the cuckoo mount at cuckoos-present sites than cuckoos-absent sites for the cuckoo trials (Fisher's Exact Test, *P* = 0.04), but there was no significant difference for the honeyeater trials (*P* = 0.63, Figure 6). Furthermore, within cuckoo trials, helpers only approached the cuckoo during trials in which whining calls were emitted (Fisher's Exact Test, *P* = 0.001).

Comparison of experienced versus naive females

Females with known past experience of cuckoos were significantly more likely (100%, *N* = 3) than females with no known experience of cuckoos (17%, *N* = 12) to produce whining calls in response to the cuckoo model during a year when cuckoos were absent (Fisher Exact Test, two-tailed, *P* = 0.02).

DISCUSSION

Superb fairy-wrens at regularly parasitized sites showed an intense response to the cuckoo mount; typically the entire group mobbed the cuckoo (Figure 6), crawling over the surface of the cage (Figures 4d and 5), and calling almost incessantly (Figure 4a). By contrast, most superb fairy-wren groups at the rarely parasitized sites showed little reaction to the cuckoo, and their responses were very similar to those given to the honeyeater control (Figures 4 and 6).

This microgeographic variation in response suggests that recognition of cuckoos is a learned trait in superb fairy-wrens. All 4 sites were within a 3.5 km radius and the sites at which cuckoo parasitism was rare were contiguous with parasitized habitat, so gene flow would be expected to impede any local genetic adaptation. Similar microgeographic variation has been found in superb fairy-wren recognition of heterospecific alarm calls (Magrath and Bennett 2011), and together, these studies indicate that fairy-wrens recognize and modify their responses to enemies based on learned cues.

An alternative explanation for low intensity of aggression toward cuckoos in unparasitized populations is that hosts adjust their propensity to mob in relation to perceived risk of parasitism (Davies and Welbergen 2009; Welbergen and Davies 2009). Hosts adjust their propensity to reject eggs (Davies and Brooke 1988; Moksnes and Røskaft 1989; Moksnes et al. 1993; Davies et al. 1996; Bártol et al. 2002) or chicks (Langmore et al. 2009) to minimize the risk of recognition errors, by using external cues that indicate the probability that they are cuckoo eggs or cuckoo chicks, respectively. Likewise, if there is a risk of making costly recognition errors in the identification of adult cuckoos, hosts may adjust their decision to mob according to external cues. Hosts of the common cuckoo *Cuculus canorus* face such a risk because the cuckoo mimics the appearance of the potentially lethal sparrowhawk *Accipiter nisus* (Welbergen and Davies 2011). Thus, for these hosts, it may be beneficial to adjust the decision to mob according to local cues about parasitism risk, and this has been demonstrated in reed warblers *Acrocephalus scirpaceus*, a major host of the common cuckoo (Welbergen and Davies 2009; Welbergen and Davies, 2012). This explanation is unlikely to explain our results because bronze-cuckoos are both highly distinctive in their appearance and substantially smaller than any predatory birds in the study area and are therefore unlikely to be mistaken for predatory birds. However, to test this possibility further, we compared the responses of individuals that had had prior experience of cuckoos with naive individuals (no known experience of cuckoos), during a year when cuckoos were absent. In support of our findings suggesting that cuckoo recognition is learned, all experienced birds mobbed the cuckoo, even though cuckoos were absent from the site, and they were significantly more likely to do so than naive individuals. This result contrasts with some studies that suggest that hosts might "switch off" cuckoo defenses when cuckoos are absent (e.g., Lindholm 2000; Welbergen and Davies 2009). However, mobbing a cuckoo during a year when cuckoos have not previously been present is likely to be adaptive in superb fairy-wrens for 2 reasons; 1) unlike hosts of the common cuckoo, there is no risk associated with mobbing the cuckoo and 2) bronze-cuckoos that parasitize fairy-wrens are

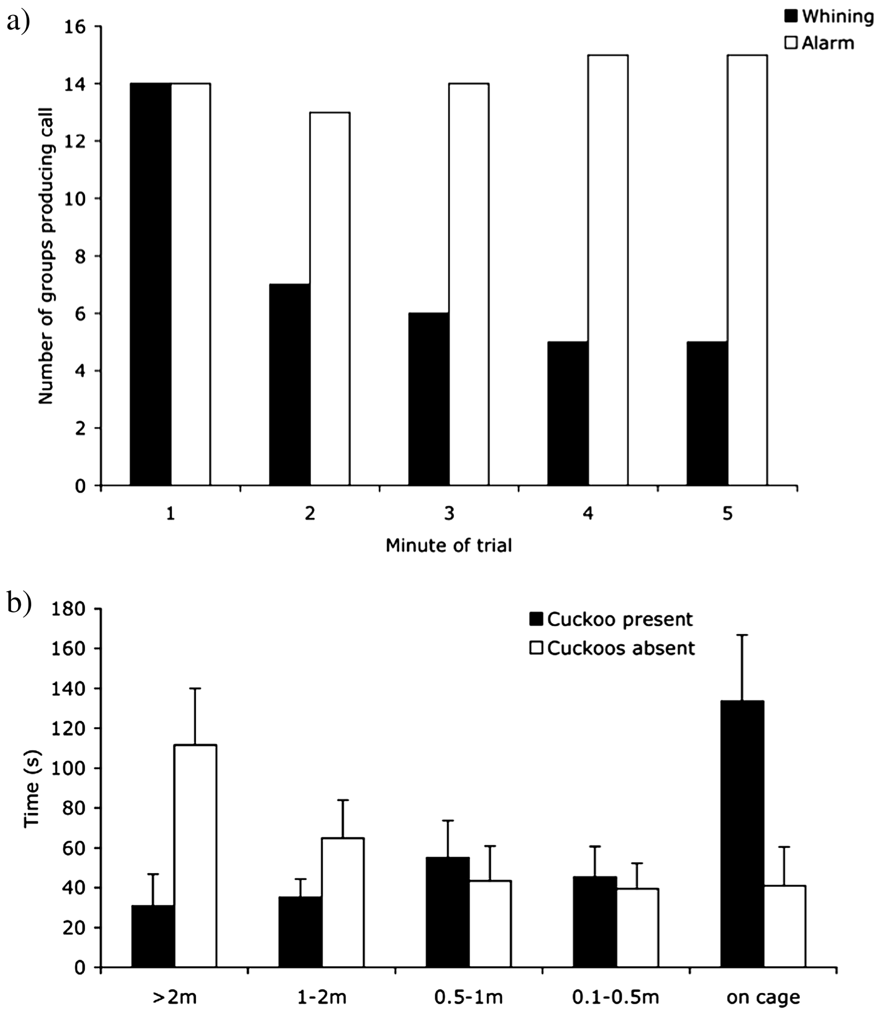

Figure 5
(a) Number of groups producing whining calls (black bars) and alarm calls (white bars) during each minute of the cuckoo presentation (data from 15 groups that produced whining calls). (b) Mean (+standard error) amount of time spent at each distance from the cuckoo mount by the nearest individual at sites in which cuckoos were present (black bars, N = 16 fairy-wren groups) versus absent (white bars, N= 16 fairy-wren groups).

transient breeders, parasitizing an area for only a few weeks before moving on to another site (Langmore et al. 2007), so a swift response to a cuckoo as soon as it is detected is likely to maximize the chances of defending the nest against parasitism.

Learned recognition of cuckoos could explain several other findings in this species. First, novice females in their first breeding attempt are more likely to suffer parasitism by cuckoos than experienced females (Langmore and Kilner 2007). Failure to recognize cuckoos could contribute to this difference, as could the lack of helpers to assist with mobbing, and poorer nest concealment by novice females (Sims 2002). Second, novice females were more likely to make recognition errors when faced with a single chick in their nest; they were both more likely to reject a single fairy-wren and more likely to accept a cuckoo chick than experienced breeders (Langmore et al. 2009). Fairy-wrens reject single chicks only when adult cuckoos are locally present, thereby minimizing the risk of recognition errors (Langmore et al. 2009). Failure to recognize adult cuckoos could therefore explain the higher error rate in recognition of cuckoo chicks by novice females.

Presentation of the cuckoo mount elicited a distinctive, loud, rapid, harmonically rich call (Figure 3b) that appears to be structurally and contextually similar to the whining call produced by splendid fairy-wrens in response to a cuckoo mount (Payne et al. 1985). Whining calls were produced almost exclusively in response to the cuckoo mount, with only one individual producing whining calls briefly in response to the honeyeater (Figure 4c). These calls appear to be analogous to the "seet" calls produced by yellow warblers *Dendroica petechia* in response to brood parasitic brown-headed cowbirds *Molothrus ater* (Hobson and Sealy 1989; Gill and Sealy 2004). However, unlike the yellow warbler call, whining calls are probably not a referential call indicating the presence of a cuckoo, because they sound the same as, and are structurally similar to, the calls sometimes produced by superb fairy-wrens, particularly fledglings, when they are caught in a mist net (Langmore NE, personal observation, Igic B, personal communication). Instead, 3 factors suggest that whining calls serve as a "rallying the troops" call, summoning group members to provide help. First, these calls occur in circumstances where the assistance of multiple group members could be beneficial. Cuckoo parasitism is highly costly to the group, and mobbing a cuckoo can provide an effective defense against parasitism (Welbergen and Davies 2009), even causing injury (Wyllie 1981; Davies and Brooke 1988; Welbergen and Davies 2008) or death (Molnar 1944; Moyer 1980) to the parasite. Furthermore, relatively higher nesting density appears to be related to reduced probability of parasitism (Robertson and Norman 1977; Brown and Lawes 2007), indirectly suggesting the group mobbing can prevent parasitism. Second, whining calls were produced at the beginning of the trial, usually immediately on sighting the cuckoo, and birds typically

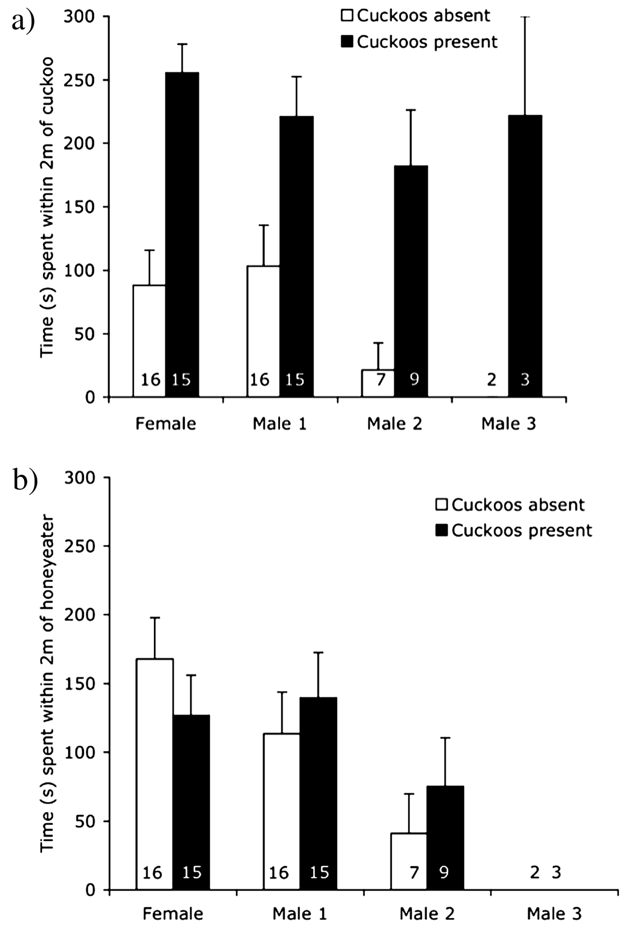

Figure 6
Mean + standard error time (s) spent within 2 m of (a) the cuckoo mount and (b) the honeyeater mount by each member of the group in sites where cuckoos were present (black bars) and sites where cuckoos were absent (white bars). Sample sizes are given at the base of the bars.

switched to alarm calls toward the end of the trial (Figure 5a). Third, in our study helpers approached within 2 m of the cuckoo only during trials in which whining calls were emitted, suggesting that whining calls are an effective means of summoning group members (Figure 6).

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