

Flexible cuckoo chick-rejection rules in the superb fairy-wren

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Recognition of brood parasitic cuckoo nestlings poses a challenge to hosts because cues expressed by cuckoos and host young may be very similar. In theory, hosts should use flexible recognition rules that maximize the likelihood of rejecting cuckoo nestlings while minimizing the risk of rejecting their own young. Our previous work revealed that female superb fairy-wrens *Malurus cyaneus* often abandoned nestling cuckoos and that the presence of a single chick in the nest was 1 trigger for abandonment because fairy-wrens also sometimes abandoned a single fairy-wren chick. Here we use a combination of 20 years of observational data, a cross-fostering experiment, and a brood size reduction experiment to determine the basis for individual variability in the chick-rejection rules of superb fairy-wrens in response to parasitism by Horsfield's bronze-cuckoos *Chalcites basalis*. We show that the decision to abandon a single chick is based on integration of learned recognition cues and external cues. Experienced females were relatively more likely to abandon a single cuckoo chick and accept a single fairy-wren chick than naive females. Breeding experience therefore facilitates the ability to make an accurate rejection decision, perhaps through learned refinement of the recognition template. In addition, fairy-wrens modified their rejection threshold in relation to the presence of adult cuckoos in the population, becoming more likely to abandon single nestlings with increasing risk of parasitism. By using these flexible rejection rules, female superb fairy-wrens are more likely to defend themselves successfully against exploitation by the cuckoo and are less prone to mistakenly reject their own offspring. *Key words*: brood parasitism, coevolution, mimicry, recognition systems, rejection threshold, signaling. [*Behav Ecol*]

In theory, selection should favor individuals whose recognition systems identify signalers without error. However, in practice, desirable and undesirable signalers often exhibit overlapping cues (Figure 1a), and undesirable signalers may impede recognition even further by mimicking the cues of desirable signalers (Sherman et al. 1997). Thus, the central challenge to recognition systems is to optimize the balance between acceptance errors (accepting undesirable signalers) and rejection errors (rejecting desirable signalers). Exactly this challenge is faced by avian hosts of brood parasitic cuckoos. For hosts of cuckoo species that kill host young soon after hatching (evicting cuckoos), the costs of mistakenly accepting a cuckoo are especially high, both in terms of loss of their own young and the time and energy expended in rearing the cuckoo (Davies 2000). Many hosts are adept at discriminating and rejecting cuckoo eggs in their nests, even when parasitized by a cuckoo with a highly mimetic egg. The recognition processes underlying egg rejection (e.g., Davies and Brooke 1988; Lotem et al. 1992; Hauber et al. 2006; Moskát and Hauber 2007; Stokke et al. 2007; Moskát, Avilés, et al. 2008; Moskát, Székely, et al. 2008) and the factors influencing the relative costs and benefits of rejection (Davies et al. 1996; Antonov et al. 2008; Harrison and Broom 2009) have been the subject of intensive investigation.

By contrast, rejection of nestling cuckoos by hosts was unknown until recently (Grim et al. 2003; Langmore et al. 2003), and the host rules for cuckoo chick rejection are largely undescribed. Although some cuckoo hosts are known

to learn the appearance of their own eggs in their first breeding attempt and to adjust their egg-rejection decisions accordingly (e.g., Lotem et al. 1992), the possibility of equivalent learned nestling recognition among hosts of evicting cuckoos has previously been dismissed on theoretical grounds (Lotem 1993). The high cost of misimprinting on a cuckoo nestling during the first breeding attempt and subsequently rejecting all future host offspring should prevent the evolution of learned cuckoo chick recognition. Despite the theoretical improbability of the evolution of cuckoo chick recognition by hosts, 2 recent studies have revealed that some hosts can discriminate and reject cuckoo chicks (Langmore et al. 2003; Grim 2007). Here we aim to characterize the nestling recognition system exhibited by superb fairy-wren *Malurus cyaneus* hosts of the Horsfield's bronze-cuckoo *Chalcites basalis*.

Our previous work suggests that Horsfield's bronze-cuckoos have defeated host defenses at the egg stage; superb fairy-wrens rarely reject cuckoo eggs (Langmore et al. 2003). Consequently, the arms race between cuckoo and their hosts has escalated to the stage of discrimination of cuckoo nestlings, and superb fairy-wrens abandon around 38% of cuckoo chicks (Langmore et al. 2003). Females initiate abandonment, usually within a few days of hatching, and begin building a new nest nearby. Males follow suit within a few hours or days, leaving the cuckoo nestling to die in the nest (Langmore et al. 2003).

Cues used by hosts to recognize cuckoo chicks might take the form of visual or auditory cues. However, such phenotypic recognition cues may be of limited (or secondary) use to cuckoo hosts (Planque et al. 2002; Lawes and Marthews 2003; Grim 2006; Britton et al. 2007) because of constraints such as changes in nestling phenotype over time (Davies and Brooke 1988), lack of opportunity for direct comparison between host and parasitic young (Davies and Brooke 1988), and mimicry of host nestlings by young cuckoos (Davies et al. 1998;

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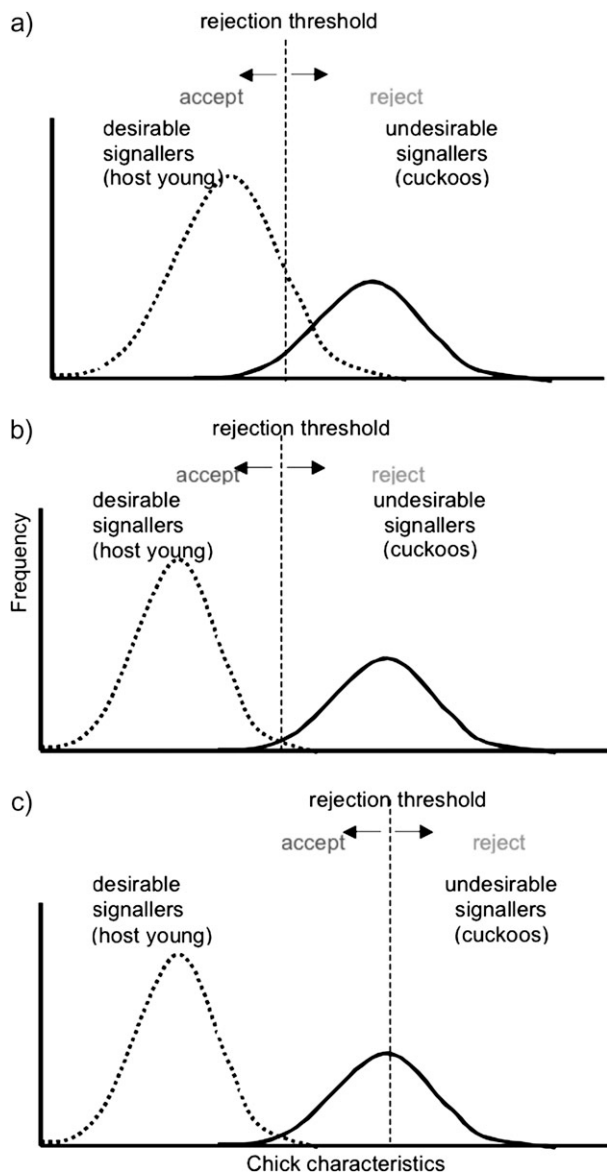


Figure 1
A theoretical recognition system used by superb fairy-wrens for discriminating between their own young and cuckoo nestlings (after Sherman et al. 1997, see also Reeve 1989; Davies et al. 1996; Rodríguez-Gironés and Lotem 1999). (a) Hosts make rejection decisions with reference to a recognition template. Mimicry by undesirable signalers (cuckoos) causes some degree of overlap between cues of identity sent by host young and cuckoo nestlings. Hosts must choose where to place their threshold for rejection to maximize their chance of correctly rejecting young cuckoos while minimizing the risk of mistakenly rejecting their own nestlings. (b) Hosts may refine their recognition template by learning characteristics associated with their own young during each breeding attempt. This will reduce the extent of overlap between cues of identity sent by host young and cuckoo nestlings and so reduce the risk of a recognition error. (c) When there are few or no adult cuckoos present, then hosts should increase their threshold for rejection because the chance of encountering a cuckoo nestling is relatively low and so is the corresponding risk of making an acceptance error.

Madden and Davies 2006). Such constraints are likely to apply to superb fairy-wrens because Horsfield's bronze-cuckoos mimic the begging call of superb fairy-wrens with a high degree of accuracy (Langmore et al. 2008).

In these circumstances, hosts may preferentially rely on non-phenotypic recognition cues (Sherman et al. 1997; also referred to as recognition-free cues, Anderson and Hauber 2007), in which recognition is possible using cues other than phenotypic attributes of the nestlings themselves. Available evidence suggests that nonphenotypic recognition cues are an important component of discrimination of cuckoo chicks by hosts. For example, the primary cue used by superb fairy-wren hosts for recognizing cuckoo nestlings is the presence of a single chick in the nest (Langmore et al. 2003). Broods parasitized by a bronze-cuckoo contain just 1 nestling because the cuckoo hatches 1–2 days before the host brood and usually completes eviction of the host eggs before they hatch (Payne RB and Payne LL 1998). By contrast, most host broods comprise multiple offspring. Superb fairy-wrens often abandon nests containing a single chick, even if it is one of their own, but never abandon broods containing multiple chicks (Langmore et al. 2003). The reed warbler *Acrocephalus scirpaceus* host of the European cuckoo *Cuculus canorus* also uses a nonphenotypic recognition cue for rejection of cuckoo nestlings; the cuckoo has a long nestling period relative to that of its host, and the reed warbler sometimes abandons nestlings that remain in the nest beyond the normal fledging date (Grim et al. 2003; Grim 2007).

Having determined in our previous work that the presence of a single chick in the nest is the primary cue for recognition (Langmore et al. 2003), our interest here lies in explaining how hosts might use this cue to maximize the chance of rejection of cuckoo nestlings while minimizing the risk of rejecting of their own young. Optimal recognition rules might vary among individual hosts in relation to their circumstances (Lotem et al. 1992; Rodríguez-Gironés and Lotem 1999), and this could explain why only about 38% of nestling Horsfield's bronze-cuckoo nestlings are rejected by their natural hosts (Langmore et al. 2003).

The first possibility we explore is whether recognition is optimized over time through learned refinement of the recognition template (Figure 1b). We suggest that learning would gradually reduce the extent of overlap between cues perceived to be unique to host young and those belonging to cuckoo nestlings, thus reducing the risk of either mistakenly accepting a cuckoo nestling or rejecting a host chick (Figure 1b). Although in theory learned recognition of cuckoo nestlings should be prevented by the high costs of misimprinting on a cuckoo nestling in the first breeding attempt (Lotem 1993), as long as there is no associated risk of misimprinting, learning could still be involved in refining rules for cuckoo nestling rejection.

In addition, we consider whether hosts adjust their rejection threshold according to context, becoming more discriminatory as the incidence of undesirable signalers increases, and the corresponding risk of making an acceptance error falls (Reeve 1989; Sherman et al. 1997; Hauber et al. 2006; Holen and Johnstone 2006; Figure 1c). Context-dependent discrimination such as this has been demonstrated in the egg-rejection decisions of several host species; when hosts see an adult cuckoo at their nest, they lower their threshold for egg rejection (Davies and Brooke 1988; Moksnes and Røskoft 1989; Moksnes et al. 1993; Davies et al. 1996; Bártol et al. 2002), making them more likely to reject eggs at times when parasitism by cuckoos is more frequent (Davies et al. 1996; Brooke et al. 1998; Stokke et al. 2008). We test whether similarly flexible rejection rules are employed in the recognition of cuckoo nestlings by using 2 experiments: a cross-fostering experiment to compare cuckoo chick-rejection decisions in parasitized and nonparasitized populations and a brood reduction experiment to compare rejection of single fairy-wren chicks in parasitized and nonparasitized populations.

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 et al. 2008). They typically lay clutches comprising 3–4 eggs between September and January and can fledge up to 3 broods in a season. Nest predation is high (66%) and usually involves the complete loss of a clutch or brood, and nestling starvation is rare. As a consequence, broods comprising a single superb fairy-wren chick only occur occasionally due to hatching failure or partial predation (~3% of broods, Langmore et al. 2003). Nestlings remain in the nest for 10–12 days. Fairy-wrens are the primary hosts of Horsfield's bronze-cuckoos throughout Australia (Brooker MG and Brooker LC 1989).

Field methods

Our study was conducted in Canberra, Australia, for 8 years in Campbell Park (1999–2007, 149°9' E, 35°16' S) and 20 years in the Australian National Botanic Gardens (ANBG, 1988–2007, 149°6' E, 35°16' S). A third site, Gungahlin Hill (149°9' E, 35°12' S), was used in 2006 and 2007 as a source of Horsfield's bronze-cuckoo eggs for the cross-fostering experiment. At Campbell Park and the ANBG, female fairy-wrens were color banded and all their nesting attempts throughout each season were monitored. ANBG experienced lower parasitism rates each year than Campbell Park and more years in which parasitism was absent altogether (8 out of 20 compared with 3 out of 9 years in Campbell Park).

To minimize loss of data due to nest depredation, we placed a large, dome-shaped cage over most of the experimental and unmanipulated nests during the incubation period, which excluded large predators such as currawongs *Strepera graculina* but had sufficiently large mesh to allow access by the fairy-wren adults. Some predators (primarily snakes) could still access nests, but overall caging reduced predation rates from 66% to 28% (Langmore et al. 2003).

Abandonment of fairy-wren or cuckoo chicks was monitored daily with minimal disturbance by observation of the nest with binoculars from ~50-m distant to confirm that the female was provisioning the chick. If feeds were delivered during this period, we did not approach the nest. If no feeds were delivered during 30 min, the nest was inspected. If the nest was empty, it was scored as depredated and excluded from the data set. If the chick was dead in the nest, it was scored as abandoned. If the chick was alive, daily nest watches continued.

Are inexperienced breeders more likely to make acceptance and rejection errors than experienced breeders?

If learning is involved in rejection decisions, we would expect that inexperienced females would be more likely to accept cuckoo chicks (acceptance error) and/or reject single fairy-wren chicks (rejection error) than experienced females. To explore the possibility that females improve their ability to detect a cuckoo through breeding experience, we scored each naturally parasitized female ($N = 20$) and each unparasitized female that reared a single fairy-wren chick due to hatching failure of the other eggs in the clutch ($N = 37$) in terms of whether they had reared superb fairy-wren nestlings previously (experienced) or whether they had never previously succeeded in hatching a brood (naive). All females were color banded, and their breeding histories were known. They were classified as "experienced" if at least 1 clutch had survived to hatching, and they had thus had an opportunity to learn the appearance of their own offspring. Some females banded as nestlings remained within their natal population ($N = 11$),

and therefore, we knew their exact age. However, due to the long-distance dispersal typical of females in their first year (Cockburn et al. 2003), most females arrived from outside the study area. When an immigrant female took up a breeding vacancy on a territory surrounded by color-banded birds, they were classified as "naive" first-year females because older females do not disperse over long distances (Cockburn et al. 2003). Unbanded females that could not be reliably classified as first years were excluded from this analysis. If a female reared a cuckoo or a single fairy-wren more than once ($N = 7$ females), we included only the first nest in the data set. None of these 7 females differed in their breeding experience classification between the first and second single chick they reared, so they could not be used for a "within-female" test of the hypothesis. Data were taken only from years when adult cuckoos were present in the population (see below), to remove any possible confounding effects of a differential response in relation to the presence or absence of adult cuckoos.

Do superb fairy-wrens abandon lone nestlings at a higher rate in the presence of adult cuckoos?

During our study, parasitism rates by Horsfield's bronze-cuckoos were variable and in some years no parasitism occurred at all (Langmore and Kilner 2007). The arrival of adult cuckoos in the population was indicated by 3 cues; 1) sightings of adult cuckoos; 2) their loud, persistent calls, which were heard repeatedly throughout the day; and 3) the appearance of cuckoo eggs in fairy-wren nests. During periods when cuckoos were laying, they were also seen and/or heard on most days. After cessation of laying, calling and sightings also ceased. Further, the field protocol at both sites involved locating every fairy-wren nest built throughout the season, so parasitism was extremely unlikely to go undetected. Thus, we could classify sites as parasitized or unparasitized with a high degree of confidence.

To test whether the probability of desertion of single nestlings was influenced by the presence of adult cuckoos required an experimental approach because cuckoo nestlings do not naturally occur in populations where adult cuckoos are absent. Between 1999 and 2007, we presented 55 fairy-wren hosts with either single Horsfield's bronze-cuckoo chicks or single nestlings of their own in populations that were either parasitized or unparasitized. The manipulations were performed during the incubation period. For the single fairy-wren treatment, we removed all but 1 egg from the clutch immediately after clutch completion and added 2 plastic, fairy-wren size eggs ($N = 30$ clutches). Most of the removed eggs were used in a parallel study on the nutritional composition of eggs ($N = 16$ clutches, Russell et al. 2007); others were discarded. The females accepted the models and continued incubating as usual. Models were removed when the nestling hatched. These experiments were conducted in Campbell Park during 4 years when cuckoos were present ($N = 13$) and 2 years in which cuckoos were absent ($N = 17$). For the cuckoo treatments, we removed a single fairy-wren egg from the clutch of an unparasitized, experimental female and replaced it with a Horsfield's bronze-cuckoo egg from a parasitized fairy-wren nest at the same stage of incubation ($N = 25$). Eight eggs were cross-fostered to females in unparasitized populations (7 to the ANBG and 1 to Campbell Park) and 17 to unparasitized females in a parasitized population (Campbell Park). When the cuckoo chicks hatched, they evicted the host eggs from the nest, so in both treatments the nest owners were left with a single chick. No female was used for the same treatment twice. Desertions of single chicks typically occurred 3–6 days after hatching (Langmore et al. 2003), and 96% of desertions between 1999 and 2007 occurred before day 8. Therefore, we used day 8 as the threshold to score "acceptance" or

“desertion,” and nests that were depredated before day 8 were excluded from the analysis.

A possible alternative explanation for desertion of single chicks is that the reproductive value of investing in a single chick varies with seasonal conditions, such that a single chick is valued more highly in drought years, when reproductive success in superb fairy-wrens is typically dramatically curtailed (Cockburn et al. 2008). The cross-fostering experiment allows us to test this hypothesis because eggs were transferred between populations that differed in parasitism rates but shared the same climatic conditions. We also tested this possibility by analyzing the rejection rates of single fairy-wren chicks in unparasitized populations in relation to breeding season rainfall (September to December, source: Australian Bureau of Meteorology). This is an appropriate measure because rainfall is both correlated with temperature in the study area and also provides the strongest climatic predictor of reproductive success in superb fairy-wrens (Cockburn et al. 2008).

Statistical methods

We first used a generalized linear mixed model (GLMM) with a binomial distribution and logit link function to test whether the probability of desertion of a single nestling (accept or reject) could be explained by 1) female breeding experience (naive or experienced) or 2) species of single chick (superb fairy-wren or Horsfield's bronze-cuckoo). We also included the interaction between these 2 variables. We tested for any potentially confounding year or study site effects by including “year” and “study site” as random terms in the model. The random effects did not explain any of the variance (estimated variance component = 0), so we eliminated these terms and reverted to a more robust generalized linear model. Previous analyses have established that there is no time-of-season effect on desertion and nor is desertion influenced by whether any host chicks hatch before they are evicted by the cuckoo (Langmore et al. 2003). For the experimental data set, we used a GLMM with a binomial distribution and logit link function to test whether the probability of desertion of a single nestling could be explained by 1) the presence of adult cuckoos in the population (present or absent), 2) species of single chick (superb fairy-wren or Horsfield's bronze-cuckoo), or 3) the interaction between them. We also included year as a random term. Again the random term failed to explain any of the variance (estimated variance component = 0), so we reverted to a generalized linear model.

To test for the possibility that the profitability of a single chick varies in relation to drought years, the rejection rates of single fairy-wren chicks in unparasitized populations in relation to breeding season rainfall were analyzed using a logistic regression, with response to a single chick (accept/desert) as the dependent variable and breeding season rainfall as the independent variable. GLMMs were performed using GenStat v. 10 (VSN International Ltd, Hemel Hempstead, UK), and other analyses were performed using JMP v. 6.0 (SAS Institute, Inc., Cary, NC).

Ethical note

Experiments were conducted under approval of the Australian National University Animal Experimentation Ethics Committee (protocol numbers F.BTZ.99.99 and F.BTZ.61.03). In experiments in which clutch size was reduced, eggs were removed at completion of egg laying so that the embryo had not yet begun to develop (fairy-wrens commence incubation after completion of laying). Although a potential end point of some experiments was the death of a fairy-wren chick, we kept sample sizes to the minimum and ultimately only 5

fairy-wren chicks were abandoned by their parents. By contrast, in these populations, about 66% of nests are depredated, and caging the experimental and observational nests improved the survival rates of single fairy-wren chicks, fairy-wren broods, and cuckoo nestlings considerably (by 38%).

RESULTS

Are inexperienced breeders more likely to make acceptance and rejection errors than experienced breeders?

The probability of desertion of a single cuckoo or fairy-wren nestling by superb fairy-wrens was predicted by female breeding experience; experienced females were both more likely to reject a cuckoo and more likely to accept a single fairy-wren than naive females (breeding experience \times species of single chick: $\chi^2_1 = 4.23$, $P = 0.04$, Figure 2). This result is notable because it means that patterns of single chick rejection can be explained by breeding experience and are not simply due to older females placing a lower value on single chicks. In addition, there was a marginally nonsignificant tendency for cuckoos to be rejected more than single fairy-wrens ($\chi^2_1 = 3.67$, $P = 0.06$). There was no significant effect of breeding experience on overall rejection rates ($\chi^2_1 = 0.29$, $P = 0.56$).

Do superb fairy-wrens abandon lone nestlings at a higher rate in the presence of adult cuckoos?

Our cross-fostering and brood reduction experiments revealed that the presence of adult cuckoos in the population was also influential in rejection decisions. Rejection of both single fairy-wren chicks and cuckoo chicks occurred almost exclusively when adult cuckoos were present in the population ($\chi^2_1 = 9.97$, $P = 0.002$, Figure 3). Cuckoo chicks were as likely to be rejected as single fairy-wren chicks (cuckoo vs. host, $\chi^2_1 = 0.28$, $P = 0.60$).

Although females apparently adjusted their rejection thresholds in relation to the presence of adult cuckoos, an alternative explanation is that fairy-wrens value a single chick less in years with good conditions, which also tended to be the years in which cuckoos were present (Langmore and Kilner 2007).

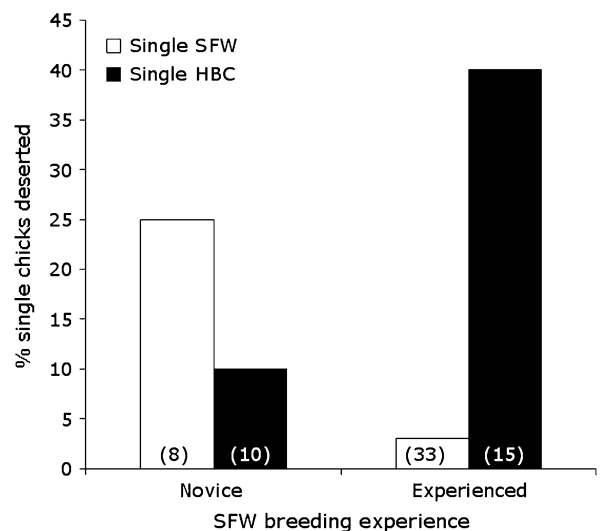


Figure 2 The percentage of single superb fairy-wren (white bars) and Horsfield's bronze-cuckoo (black bars) nestlings that were abandoned by naive versus experienced female fairy-wrens at times when adult Horsfield's bronze-cuckoos were present in the population. Sample sizes are given in parentheses at the base of the bars.

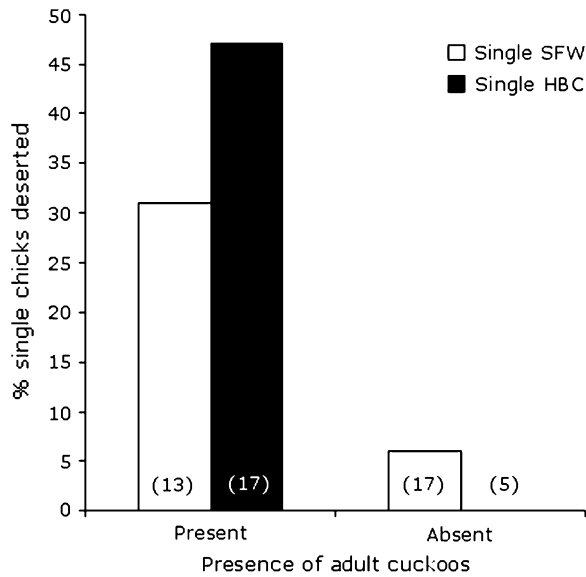


Figure 3

From experimental nests, the percentage of single superb fairy-wren (white bars) and Horsfield's bronze-cuckoo (black bars) nestlings that were abandoned during periods when adult Horsfield's bronze-cuckoos were present in the population and when they were absent. Sample sizes are given in parentheses at the base of the bars.

Thus, rejection decisions could be based on the relative value of a single fairy-wren chick in relation to seasonal conditions rather than on the likelihood of parasitism. We tested this possibility explicitly by comparing the probability of rejecting a single fairy-wren chick in relation to breeding season rainfall, using data from unparasitized populations only ($N = 39$). There was no significant effect of rainfall on the probability of deserting a single fairy-wren chick ($\chi^2_1 = 0.43$, $P = 0.5$).

DISCUSSION

Recognition theory predicts that superb fairy-wrens should flexibly adjust their recognition rules to maximize the likelihood of rejecting cuckoo nestlings while minimizing the risk of rejecting their own young (Wiley 1994; Davies et al. 1996; Sherman et al. 1997; Rodríguez-Gironés and Lotem 1999; Holen and Johnstone 2006; Figure 1). Our experimental results are consistent with theoretical predictions (Figure 1b,c) and suggest that fairy-wrens show phenotypically plastic rejection rules. First, we found that experienced females were relatively more likely to abandon a single cuckoo (avoid an acceptance error) and accept a single fairy-wren (avoid a rejection error) than naive females (Figure 2). Breeding experience therefore facilitates the ability to make an accurate chick-rejection decision, perhaps through learned refinement of the recognition template. Second, we discovered that fairy-wrens modified their rejection threshold in relation to the presence of adult Horsfield's bronze-cuckoos in the population, becoming more likely to abandon single nestlings of any species when the risk of parasitism was higher (Figure 3). By abandoning single chicks only in years when adult cuckoos were present, superb fairy-wrens are able to reduce substantially the likelihood of mistakenly abandoning one of their own young.

Phenotypic plasticity in the rejection threshold

Our findings that hosts increased rejection of single chicks when adult cuckoos were present match the results of previ-

ous work on other host species showing that the incidence of egg rejection is higher when the likelihood of parasitism is greater (Davies and Brooke 1988; Moksnes and Røskaft 1989; Moksnes et al. 1993; Davies et al. 1996; Brooke et al. 1998; Bártol et al. 2002; Hauber et al. 2006; Stokke et al. 2007, 2008). In theory, phenotypic plasticity in the positioning of the rejection threshold is especially important when parasites mimic hosts so well that there is substantial overlap in the characteristic cues produced by desirable and undesirable signalers because it provides a means of minimizing the likely ensuing recognition errors (Reeve 1989; Wiley 1994; Davies et al. 1996; Sherman et al. 1997; Holen and Johnstone 2006; Figure 1). This is exactly the case for Horsfield's bronze-cuckoos exploiting superb fairy-wrens because cuckoo mimicry of host begging calls can be highly accurate (Langmore et al. 2003, 2008) and can become even more refined during the course of the nestling period (Langmore et al. 2008).

One possible consequence of such contextual adjustment of rejection thresholds is that it may influence the parasitism strategies of the cuckoos themselves, promoting a new stage in the coevolutionary arms race between cuckoos and hosts. In theory, if discrimination is more likely when hosts perceive adult cuckoos are present, then cuckoos should aim to target victims that have not been alerted to their presence (Holen and Johnstone 2006). Thus, the longer a female cuckoo persists in exploiting a host population the less likely it will be that her nestlings are accepted because increasing numbers of hosts may become alerted to her presence and adjust their rejection threshold accordingly (Welbergen and Davies 2009). This may partly explain the transitory breeding patterns of Horsfield's bronze-cuckoos, whereby individual females breed for 2–6 weeks at a site before moving on, presumably to a new breeding site (Langmore et al. 2007).

Learned refinement of the recognition template

The most plausible explanation for the experience-related effects on rejection decisions is that females refine their recognition template through some form of learning after being exposed to their own young in the nest. Learning of the recognition template is favored when the characteristics of signalers vary over space or time (Sherman et al. 1997), and this is certainly the case with nestling birds. But what sort of learning process is likely to be involved? One possibility is that it entails some form of imprinting (e.g., Beecher et al. 1981; Soler et al. 1995; Lefevre et al. 1998), similar to the process by which egg characteristics are learned in some cuckoo hosts (e.g., Lotem et al. 1992; Moskát and Hauber 2007). The problem with imprinting, however, is that it is prone to error if individuals are exposed to an inappropriate referent (such as a cuckoo chick) during the key sensitive period (e.g., Lotem et al. 1992; Price 2008), and learned chick recognition cannot evolve if there are high costs associated with misimprinting (Lotem 1993). Perhaps, instead fairy-wrens learn to recognize their own young using a process akin to song learning in some songbirds (Marler and Peters 1977; Catchpole and Slater 1995). Here learning is innately constrained, which considerably reduces the chance of mistakenly learning from an inappropriate referent. Thus, exposure to a cuckoo nestling during a female's first breeding attempt would not cause misimprinting but would simply represent a missed opportunity to refine whatever innate recognition template of her own young she may already possess. Alternatively, the costs of misimprinting may be so rarely encountered that there is little selection against it. Misimprinting would be costly only in the doubly rare circumstances in which a female was both parasitized in her first breeding attempt and subsequently

encountered and rejected a brood comprising a single fairy-wren chick.

The possibility of learned refinement of the recognition template by hosts may also influence patterns of parasitism by the cuckoo. For example, we might expect cuckoos to target naive hosts who are unlikely to recognize a cuckoo nestling. Young females did suffer a higher parasitism rate in our study (Langmore and Kilner 2007; but see Brooker MG and Brooker LC 1996), although this may simply have reflected the better concealment of nests by older females (Sims 2002).

Alternative interpretations

We have suggested that females learn phenotypic characteristics of their own chicks through breeding experience. However, an alternative interpretation of our data is that fairy-wrens learn to recognize adult cuckoos with age or breeding experience. In other birds, including the congeneric splendid fairy-wren *Malurus splendens* (Payne et al. 1985), recognition of adult brood parasites does not appear to be dependent on learning (Robertson and Norman 1977; Briskie et al. 1992; Mark and Stutchbury 1994). This is consistent with theoretical predictions that recognition should be innate when signalers are not reliably present before discrimination is necessary or when learning might increase mortality (Sherman et al. 1997). However, there is evidence that recognition of brood parasites might improve with experience (Smith et al. 1984; Hobson and Sealy 1989; Davies and Welbergen 2009), and it would be interesting to explore this possibility further by testing responses to adult cuckoos in relation to host female age and past exposure to cuckoos.

A second alternative explanation for this result is that fairy-wrens value a single chick more highly in drought years, which also tended to be the years in which cuckoos were absent. Thus, rejection decisions could be based on the relative value of a single fairy-wren chick in relation to seasonal conditions. However, 2 lines of evidence suggest that this was not the case. First, there was no significant effect of breeding season rainfall on the probability of deserting a single fairy-wren chick in unparasitized populations. Second, we transferred cuckoo eggs between neighboring sites that shared the same climate but differed in the incidence of parasitism and found that females did not abandon single Horsfield's bronze-cuckoos that were transferred to an unparasitized population, irrespective of seasonal conditions.

Finally, the value of a single chick may vary not only with seasonal conditions but also with the breeding experience of the female. Young females have a lower probability of fledging any young in a season than older females (Cockburn et al. 2008) and may therefore value a single chick more highly than older females. However, we can dismiss this interpretation because the rejection rules used by experienced females were more sophisticated than those of naive females. Compared with naive females, experienced females were relatively less likely to reject a single fairy-wren and more likely to reject a cuckoo. This indicates that females refined their ability to avoid both acceptance errors and rejection errors with breeding experience rather than simply adjusting their decision to reject any single chick.

In summary, we have used recognition theory to describe the rules used by superb fairy-wrens for discriminating against cuckoo nestlings in their nest. Our previous work suggested that the recognition template is based on at least 2 cues that are characteristic of superb fairy-wren offspring: a nonphenotypic cue of multiple offspring in the nest and the structure of the nestling begging call (Langmore et al. 2003). Here we have shown that fairy-wrens flexibly adjust their response to these cues to decide whether or not to reject single chicks

in their nest. By refining their recognition template with breeding experience and increasing the likelihood of rejection when adult cuckoos are present in the population, superb fairy-wrens can improve their chance of successfully rejecting cuckoo chicks while minimizing the risk of rejecting their own young.

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