Review

The coevolutionary arms race between Horsfield's Bronze-Cuckoos and Superb Fairy-wrens

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Abstract. Brood parasitism by cuckoos imposes high reproductive costs on hosts, selecting for the evolution of host defences. Cuckoos retaliate by evolving counter-adaptations to host defences, giving rise to a coevolutionary arms race between cuckoos and their hosts. Here we review the observational and experimental evidence for a coevolutionary arms race between Horsfield's Bronze-Cuckoos (*Chalcites basalis*) and Superb Fairy-wrens (*Malurus cyaneus*). We present evidence that the arms race has reached a uniquely advanced stage in this cuckoo–host pair; mimicry of host chicks by cuckoos has evolved in response to rejection of cuckoo chicks by hosts. We discuss the escalation of the arms race between these species in relation to the evolution of defence portfolios. Defences evolved by hosts are not only dependent on attributes of the cuckoo, but are also dependent on the success of other behaviours in host-defence portfolios. Thus, Superb Fairy-wrens rely heavily on rejection of cuckoo chicks, even though it is the costliest possible line of defence, because Horsfield's Bronze-Cuckoos can usually breach the cheaper defences against parasitism mounted earlier in the breeding attempt.

Introduction

The theme of this special issue, *Avian Biodiversity: Evolution in Action*, is dramatically illustrated by the interactions between cuckoos and their hosts. Parasitism by cuckoos imposes high reproductive costs on hosts and consequently hosts are selected to evolve defences against cuckoos. However, for every defence evolved by hosts, cuckoos retaliate by evolving ever-better means of fooling their hosts into rearing their young. This process of reciprocal adaptation between cuckoos and their hosts gives rise to a coevolutionary arms race (Rothstein 1990; Rothstein and Robinson 1998; Davies 2000; Payne 2005). In this paper we review the adaptations and counter-adaptations of Australian Horsfield's Bronze-Cuckoos (*Chalcites basalis*) and their hosts, the Superb Fairy-wren (*Malurus cyaneus*), and illustrate how the arms race between them has reached a uniquely advanced stage.

Superb Fairy-wrens and Horsfield's Bronze-Cuckoos

Superb Fairy-wrens are small (~10 g), facultatively cooperatively-breeding insectivores endemic to south-eastern Australia. Breeding pairs may be assisted by from one to four non-breeding helpers, who are commonly sons from previous broods. Breeding usually occurs between September and February, during which time the female may rear up to three broods of young. Starvation of broods is rare, but predation is high and females may build as many as eight nests in a season (Cockburn *et al*. 2008). The female constructs the dome-shaped nest and incubates the eggs alone, but she is assisted in defence of the nest and provisioning of young by other group members.

Horsfield's Bronze-Cuckoos parasitise a range of host species, but fairy-wrens (*Malurus* spp.) are the primary hosts throughout their range (Brooker and Brooker 1989*a*, 1989*b*; Langmore and Kilner 2007). They are small (~22 g; Brooker and Brooker 1989*a*), nomadic, insectivorous cuckoos that occupy temporary breeding territories as monogamous pairs (Langmore *et al*. 2007). Partnerships are short-lived; females leave the breeding territory after only a few weeks, and are often replaced by a new female, creating a pattern of sequential monogamy (Langmore *et al*. 2007). Parasitism usually takes place in the morning after the host lays her own egg and the Bronze-Cuckoo removes one host egg before laying her own (Brooker *et al*. 1988). Parasitism of a nest by more than one Horsfield's Bronze-Cuckoo is rare (Langmore and Kilner 2009), and is probably largely prevented by territoriality (Langmore *et al*. 2007). The nestling Bronze-Cuckoo usually hatches 1–2 days before the young of the host and evicts all eggs and nestlings of the host from the nest within 2 days of hatching (Payne and Payne 1998). Thus the hosts lose all their own offspring and, from the start of incubation, they invest around 50 days in rearing the Bronze-Cuckoo. Parasitism is therefore costly for Superb Fairy-wrens.

The first line of host defence: prevention of parasitism

The most successful defence against parasitism by cuckoos is to prevent the cuckoo from laying in the nest, because this preserves the host's own reproductive attempt intact. Most hosts have evolved means of deterring parasitism by cuckoos. For example, hosts typically mob adult cuckoos and this can successfully reduce parasitism (Welbergen and Davies 2009).

Some host species improve the success of this strategy by breeding in large colonies, which facilitates cooperative nest-defence (Brown and Lawes 2007). Group living can also reduce rates of parasitism in cooperative breeders, if provisioning of the breeding female by helpers increases nest-attendance by the female (Canestrari *et al.* 2009).

Like most cuckoo hosts, fairy-wrens mob Horsfield's Bronze-Cuckoos (Payne *et al.* 1985; N. E. Langmore and R. M. Kilner, pers. obs.), but the effectiveness of this defence against cuckoo parasitism and the potential benefits of the assistance of helpers in mobbing remain untested. Cooperative nest-defence successfully reduces rates of parasitism in the colonial Red Bishop (*Euplectes orix*) (Brown and Lawes 2007). A similar helper benefit also seems possible in Superb Fairy-wrens, because sentinel behaviour and vigilance increase with group size (Yasukawa and Cockburn 2009), and in the closely related Splendid Fairy-wren (*M. splendens*) helpers assisted the breeding pair in vigorous physical attacks on both wild Horsfield's Bronze-Cuckoos and mounted Shining Bronze-Cuckoo specimens (Payne *et al.* 1985). A previous analysis failed to find a significant effect of Superb Fairy-wren group size on rates of parasitism (Langmore and Kilner 2007) but this may reflect the scarcity of large groups during the study. Most groups of Fairy-wrens in our study comprised two or three individuals, and the rates of parasitism suffered by these two sizes of group were similar (Fig. 1). However, a few groups comprised four or more individuals, and in these groups parasitism was rare (1 of 21 nests in eight groups; Fig. 1). Therefore, further investigation of whether large groups provide a benefit against brood parasites in this species may be warranted.

Counter-adaptations by the Horsfield's Bronze-Cuckoo

Although these first lines of host defence against cuckoo parasitism are often successful, cuckoos have evolved counter-adaptations, such as fast and secretive parasitism at times when the host is likely to be absent from the nest (Davies and Brooke 1988), and in some cases cuckoos may even have evolved visual mimicry of predators to deter mobbing (Davies and Welbergen 2008).
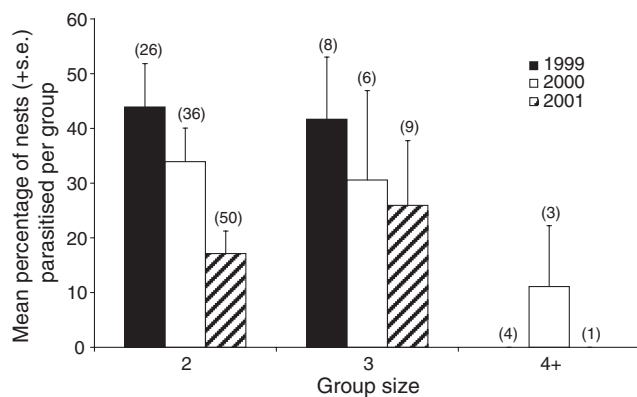

Fig. 1. Mean percentage of nests (+s.e.) parasitised per group for Superb Fairy-wren groups comprising two, three or four or more individuals in 1999, 2000 and 2001. Number of groups in each category is indicated in parentheses above the bars.

Horsfield's Bronze-Cuckoos lay their eggs very rapidly (in ~6 s) and at a time when the hosts are typically absent from the nest – shortly after the host female has laid her own egg (Brooker *et al.* 1988). Thus most parasitism events appear to be undetected by the host (Brooker *et al.* 1988). Circumstantial evidence suggests that studying cuckoo counter-adaptations to host mobbing could be a profitable line of future research. We know, for example, that novice female Superb Fairy-wrens are more likely to be victimised by Horsfield's Bronze-Cuckoos than older birds (Langmore and Kilner 2007). It would be interesting to investigate whether this is the result of specific counter-adaptations in the Cuckoo.

The next line of host defence: rejection of eggs

Protecting the nest from adult cuckoos is the most effective defence against cuckoo parasitism, but cuckoos often evade this defence and succeed in parasitising the nest. This carries an immediate cost for hosts, because most cuckoos remove one host egg from the nest before laying their own. However, further costs of parasitism might be prevented if the host succeeds in detecting and rejecting the cuckoo egg. Hosts of other cuckoo species have evolved various direct and indirect means of improving their chances of detecting a cuckoo egg. Direct discrimination of eggs is facilitated through learned or inherited recognition of their own egg-type (Rothstein 1974; Lotem *et al.* 1992), the ability to compare eggs in the nest (Lahti and Lahti 2002) and the evolution of decreased variation within a clutch and increased variation in colour and pattern of eggs between clutches laid by different females in a population (Davies and Brooke 1989*b*; Øien *et al.* 1995; Moskát *et al.* 2008; also see review in Kilner 2006). Indirect cues include the presence of an adult cuckoo near the nest, which may lead to increased rates of egg rejection or abandonment of clutches (Davies and Brooke 1988; Moksnes *et al.* 1993; Bártol *et al.* 2002; Langmore *et al.* 2003). Hosts may also use the timing of parasitism as a cue, because some hosts will bury eggs that appear in their nest before they have begun laying their own eggs (e.g. Brooker and Brooker 1996; Langmore *et al.* 2003).

Egg-rejection defences deployed by Superb Fairy-wrens

At the egg-stage, the defences mounted against cuckoos by Superb Fairy-wrens seem rather poor when compared with those of other cuckoo hosts, and they rely primarily on indirect cues associated with brood parasitism. At our study site in Canberra, for example, Cuckoo eggs that were laid during the laying period of the host were never rejected (Langmore *et al.* 2003). When we experimentally added to the Fairy-wren clutch either a Zebra Finch (*Taeniopygia guttata*) egg or a Superb Fairy-wren egg that had been painted to look different from the host's own eggs, we found some indication of recognition and rejection of eggs by the Fairy-wrens (5 of 34 non-mimetic eggs were rejected; Langmore *et al.* 2003) but it did not match the high degree of rejection seen in other cuckoo hosts (e.g. Davies and Brooke 1989*a*; Moksnes *et al.* 1991; Lahti and Lahti 2002). However, Fairy-wrens were significantly more likely to reject model eggs that were larger than their own, perhaps through the use of tactile cues in the dim interior of their dome-shaped nests, and they did so by abandoning the entire clutch (Langmore *et al.*

2003). But by far the best predictors of egg-rejection were the indirect cues connected with brood parasitism. The timing of laying was one such cue. Cuckoo eggs laid before the Fairy-wren host had started her own clutch were routinely rejected because they were sewn into the nest-lining, which results in insufficient incubation and failure to hatch (Langmore *et al.* 2003). The presence of an adult cuckoo at the nest was another indirect cue. When we experimentally added a foreign egg to the nest after the onset of incubation, the egg was nearly always accepted. But when the cuckoo herself added an egg after incubation had begun, it was nearly always rejected (Langmore *et al.* 2003).

Counter-adaptations by Horsfield's Bronze-Cuckoos

Horsfield's Bronze-Cuckoos lay eggs that closely match the speckled eggs of Superb Fairy-wrens in both colour and size (Langmore *et al.* 2003). Their eggs are small for their body size (Krüger and Davies 2004) and this is likely to have evolved in response to host discrimination of eggs (Langmore *et al.* 2003). However, the mimetic colouring and patterning of the eggs is more of a mystery, given the Superb Fairy-wren's weak rejection response when odd-looking eggs are added to their clutch (Langmore *et al.* 2003). It seems unlikely that the current egg-rejection behaviour of Superb Fairy-wrens is responsible for the Cuckoo's mimetic egg.

An alternative explanation is that Horsfield's Bronze-Cuckoos have evolved mimetic eggs for disguise from other cuckoos (Davies and Brooke 1988; Brooker and Brooker 1989*a*, 1990; Brooker *et al.* 1990; Davies 1999). Female cuckoos remove one egg from the nest during parasitism and they would benefit by selectively removing any cuckoo egg that had already been laid in the nest, thereby preventing another cuckoo chick from evicting their own egg along with the host clutch. However, this hypothesis was not supported by our genetic analyses showing that Horsfield's Bronze-Cuckoos defend a cluster of host territories from rivals (Langmore *et al.* 2007). As a result of this territorial behaviour, a second Horsfield's Bronze-Cuckoo female is unlikely to visit an already parasitised nest. Even if she did, recent experimental work suggests that she is unlikely to remove an odd-looking egg preferentially before adding her own. When faced with a clutch comprising host eggs and one non-mimetic model egg, Horsfield's Bronze-Cuckoos selected the non-mimetic egg no more frequently than would be expected by chance (Langmore and Kilner 2009). Nor do we have any evidence of interspecific competition for host nests between cuckoos, as none of the other four cuckoo species at our study site – Shining Bronze-Cuckoo (*Chalcites lucidus*), Fan-tailed Cuckoo (*Cacomantis flabelliformis*), Brush Cuckoo (*Cacomantis variolosus*), and Pallid Cuckoo (*Cacomantis pallidus*) – parasitised Superb Fairy-wren nests (Langmore and Kilner 2009). Therefore we conclude it is unlikely that Horsfield's Bronze-Cuckoos have evolved mimetic eggs in response to competition with other cuckoos.

A final possibility, which is most consistent with the evidence to date, is that egg-mimicry by cuckoos was selected by hosts at some point in their evolutionary history, but that egg rejection has since ceased to be adaptive owing to high recognition costs (Davies and Brooke 1988; Marchetti 1992; Davies *et al.* 1996; Takasu 1998*a*). This seems particularly plausible given the

constraints on egg discrimination in the dark interiors of the Fairy-wren's dome-shaped nest. Poor visibility in the nest is one of the most significant factors explaining low rates of egg rejection in hosts of Australian and European cuckoos (Langmore *et al.* 2005). When combined with highly accurate egg-mimicry, the chances of successfully detecting a cuckoo egg are likely to be low, and the chance of mistakenly removing a host egg would be correspondingly high. It will be difficult to find evidence that tests this hypothesis critically, but it does generate a prediction for future work. If the Horsfield's Bronze-Cuckoo's mimetic egg is the result of selection by hosts (and is not simply owing to an accident of evolutionary ancestry), then it should look different from the ancestral cuckoo egg in its lineage.

To summarise this section on egg-stage defences, we have shown that although Superb Fairy-wrens can recognise cuckoo eggs if they are too large or if they are laid at the wrong time, cuckoos, for the most part, evade their host's second line of defence. Horsfield's Bronze-Cuckoos have evolved a small egg for their body size (Brooker and Brooker 1989*b*; Krüger and Davies 2004) and most cuckoo eggs are laid during the laying period of the host (Langmore *et al.* 2003).

The final line of host defence: rejection of the chick

Until recently, it was believed that defences against cuckoos did not extend any further into the breeding attempt than the laying or early incubation stage; once a cuckoo egg was accepted it was generally reared as though it was the host's own young (Davies and Brooke 1989*b*; Rothstein and Robinson 1998). This was somewhat surprising considering that hosts have much to gain by abandoning a cuckoo chick, and the differences between parasite and host young often appear to far exceed those between parasite and host eggs. Consequently the absence of cuckoo chick rejection by hosts was held up as one of the major remaining puzzles in the study of avian brood parasitism (Rothstein and Robinson 1998). A convincing explanation was put forward for cuckoos that evict the host young by Lotem (1993), who argued that learned recognition of cuckoo chicks would be prevented by the high cost of mis-imprinting on a cuckoo nestling during the first breeding attempt, and subsequently rejecting all future host offspring. Despite the theoretical elegance and plausibility of this argument, our research revealed that Superb Fairy-wrens do detect and reject cuckoo chicks (Langmore *et al.* 2003).

Rejection of Cuckoo chicks by Superb Fairy-wrens

During our study in Canberra, Australia, ~38% of Horsfield's Bronze-Cuckoo chicks were abandoned by their foster parents (Langmore *et al.* 2003, 2009). Females initiated abandonment, usually within 2–6 days of hatching, by starting to build a new nest nearby. Males followed suit within a few hours or days, leaving the cuckoo nestling to die in the nest, and its corpse to be consumed by meat ants (*Iridomyrmex purpureus*) within a few hours (Langmore *et al.* 2003). It is interesting to note that Horsfield's Bronze-Cuckoos have also been reported to die in the nests of Splendid Fairy-wrens (8 of 71 hatchlings; Brooker and Brooker 1989*b*), though the cause of these deaths was not known. More recently, other studies have also found observational evidence (Grim *et al.* 2003; Sato *et al.* 2009; N. E. Langmore, G. Maurer and R. M. Kilner, pers. obs.) and

experimental evidence (Grim 2007) of rejection of cuckoo chicks in other host species, suggesting that this host defence may not be uncommon under certain conditions (Lawes and Marthews 2003; Grim 2006).

Defences of Superb Fairy-wrens against mimetic cuckoo chicks

How do female Fairy-wrens tell that the cuckoo chick in their nest is an imposter? One direct cue for recognition used to inform rejection decisions appears to be the degree to which the chick's begging calls sound like those uttered by young Superb Fairy-wrens. A close relative of the Horsfield's Bronze-Cuckoo is the Shining Bronze-Cuckoo, which primarily parasitises thornbills (*Acanthiza* spp.) and produces a rasping thornbill-type begging call, quite unlike the purer sounding notes produced by the Superb Fairy-wren nestlings. When Superb Fairy-wrens were given Shining Bronze-Cuckoos to rear, every Cuckoo nestling was abandoned within 1 week of hatching (Langmore *et al*. 2003).

However, Fairy-wrens also use indirect cues to recognise cuckoo chicks. For example, the presence of a single chick in the nest is used as a cue to identify cuckoos. Broods parasitised by a Bronze-cuckoo contain just one nestling, because the Cuckoo usually completes eviction of the host eggs before they hatch (Payne and Payne 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 they never abandon broods containing multiple chicks (Langmore *et al*. 2003). This simple rule-of-thumb is a fairly reliable means of detecting Cuckoo chicks because broods comprising a single chick are rare in fairy-wrens (Langmore *et al*. 2003). However, Fairy-wrens can further refine their decision about whether to reject a single chick in two ways. First, rejection decisions are dependent on the presence of adult cuckoos in the breeding area; abandonment of single Cuckoo chicks and single Fairy-wren chicks occurs almost exclusively during years in which Cuckoos are present (Langmore *et al*. 2009). Second, females are relatively more likely than inexperienced breeders to reject a single cuckoo and accept a single Fairy-wren chick if they are experienced breeders (Langmore *et al*. 2009). This suggests that females refine their nestling recognition template following exposure to their own young, or improve their ability to recognise adult cuckoos through experience, or both. The combination of these recognition rules prevents the possibility of mis-imprinting on a cuckoo in the first breeding attempt and thereafter rejecting entire broods of Fairy-wren chicks in later breeding attempts (Langmore *et al*. 2009). Hence it explains why Lotem's (1993) theoretical argument for the general absence of rejection of cuckoo chicks does not apply in the case of Superb Fairy-wrens and Horsfield's Bronze-Cuckoos.

Counter-adaptations by the cuckoos

Just as other cuckoo species have evolved egg-mimicry to prevent rejection of eggs by hosts (Davies and Brooke 1989*a*; Rothstein and Robinson 1998; Davies 2000), nestling Horsfield's Bronze-Cuckoos have evolved mimicry of begging calls of host chicks to evade detection by their hosts (Langmore *et al*. 2003). A study by Payne and Payne (1998) revealed that the begging calls of nestling Horsfield's Bronze-Cuckoos in Fairy-wren nests and thornbill nests differed because they resembled those of their respective hosts. To test whether these mimetic calls were learned, or instead represented genetically distinct, host-specific lineages (e.g. Gibbs *et al*. 2000), we cross-fostered Cuckoo eggs from Fairy-wren nests to either a different Fairy-wren nest or a thornbill nest and recorded the calls produced by the nestling Cuckoos (Langmore *et al*. 2008). We found that all hatchlings initially produced a Fairy-wren type call, but the chicks that had been cross-fostered to thornbill nests rapidly modified their begging calls to resemble those of thornbill nestlings, even though they had never heard thornbill begging calls (Langmore *et al*. 2008; Fig. 2). Modification of calls probably occurs through reinforcement by host parents, by selective provisioning in response to the more mimetic calls. Although mimicry of begging calls has been described for other species of cuckoo (e.g. McLean and Waas 1987), this study provides the first evidence that mimicry of begging calls has evolved in response to rejection by hosts, and thus represents a new stage in the coevolutionary arms race between cuckoos and hosts.

Two other possible counter-adaptations may have evolved in Horsfield's Bronze-Cuckoos to facilitate evasion of detection by hosts. First, Horsfield's Bronze-Cuckoos show transitory breeding patterns. Pairs typically establish breeding territories in late August or early September, but females depart after only a few weeks of breeding, and are sometimes subsequently replaced by new females (Langmore *et al*. 2007). One possible explanation for this transitory breeding pattern is that females maximise the number of nests they parasitise while minimising the amount of time they spend in any one area. This reduces their conspicuousness to hosts and consequently minimises the likelihood of host rejection of their offspring (Langmore *et al*. 2009). Second, Horsfield's Bronze-Cuckoos parasitise novice female fairy-wrens at a higher rate than experienced females (Langmore and Kilner 2007). This could reflect the lower vigilance and greater nest-conspicuousness of novice females (Sims 2002), but might also indicate preferential parasitism by Cuckoos of hosts that are less likely to have experience of both adult cuckoos and the morphology of their own young (Langmore and Kilner 2007; see also Grim 2002). In other words, Horsfield's Bronze-Cuckoos may target naïve individuals for parasitism, so as to increase the likelihood that the Cuckoo chick is accepted and reared to independence.

General discussion

We have reviewed the evidence for defences against parasitism in Superb Fairy-wrens, and counter-adaptations in Horsfield's Bronze-Cuckoos. The portfolio of Superb Fairy-wren defences ranges from those that carry minimal costs, through to those that bear high costs even when they are successful. Prevention of parasitism carries the lowest parasitism cost, because the host's own reproductive attempt can continue undisturbed. However, even prevention of parasitism may carry costs, because mobbing might attract predators and other brood parasites, or may even prove fatal if recognition errors lead to mobbing of avian predators rather than cuckoos (Welbergen and Davies 2009). Rejection of cuckoo eggs is a highly effective defence against parasitism, because the host's own nesting attempt can continue to the nestling stage. However, this defence is less beneficial than
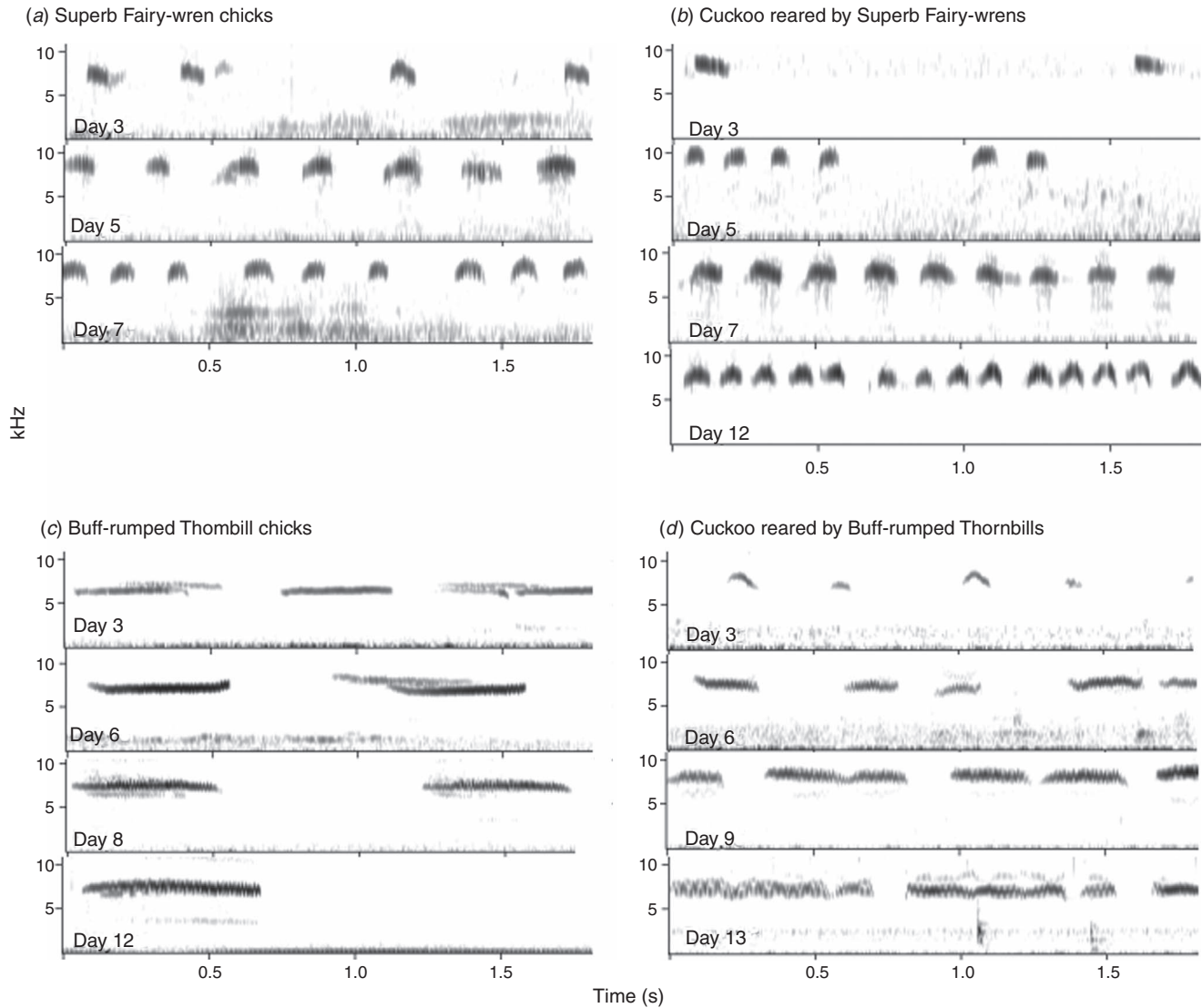
Fig. 2. Sonagrams of nestling begging calls at different stages of the nestling period, for: (*a*) Superb Fairy-wren chicks; (*b*) Horsfield's Bronze-Cuckoos reared by Superb Fairy-wrens; (*c*) Buff-rumped Thornbill chicks; and (*d*) Horsfield's Bronze-Cuckoo chicks from eggs laid in Superb Fairy-wren nests, but cross-fostered to Buff-rumped Thornbills before hatching. Cross-fostered Cuckoo chicks initially produced a 'fairy-wren type' begging call, but rapidly modified their calls to resemble those of Thornbills. Reproduced from Langmore *et al.* (2008).

prevention of parasitism in the first place, because the cuckoo removes one host egg before laying her own egg. Rejection of eggs may also carry additional costs, such as the accidental breakage or eviction of one of the host's own eggs (Davies *et al.* 1996). Rejection of cuckoo chicks saves time and energy that otherwise would be invested in rearing the cuckoo, and is thus possibly of greatest benefit to hosts that have a sufficiently protracted breeding season to allow re-nesting after rejection of the cuckoo chick (Langmore *et al.* 2003). However, rejection of chicks is much the least efficient defence against brood parasitism because the host's own brood is lost and the host invests substantial time and energy incubating the egg before rejecting the chick. This defence may also entail recognition costs, because hosts may inadvertently mistake a lone chick of their own for a

cuckoo chick, leading to a rejection error (Langmore *et al.* 2003, 2009).

As each successive line of defence is breached by the cuckoo, parasitism therefore becomes increasingly costly for the host. Consequently, we suggest that the temporal sequence in which they are presented also reflects the sequence in which the defences evolved, that is (1) recognition and mobbing of adult cuckoos, (2) recognition and rejection of cuckoo eggs, (3) recognition and rejection of cuckoo chicks, and (4) discrimination of cuckoo chicks based on indirect cues (Table 1). Nevertheless, although some cuckoo hosts possess multiple defences against cuckoo parasitism (e.g. Eurasian Reed-Warblers (*Acrocephalus scirpaceus*); Davies 2000; Grim 2007; Welbergen and Davies 2009), it is rare for a host species to exhibit a complete portfolio of

Table 1.   Some traits of Superb Fairy-wrens and Horsfield's Bronze-Cuckoos that are likely to have evolved as reciprocal coevolutionary adaptations
Sources (in parentheses): 1, Payne *et al*.(1985); 2, N. E. Langmore and R. M. Kilner, pers. obs.; 3, Brooker *et al*. (1988); 4, Langmore and Kilner (2007); 5, Langmore *et al*. (2003); 6, Brooker and Brooker (1989*b*); 7, Krüger and Davies (2004); 8, Payne and Payne (1998); 9, Langmore *et al*. (2008); 10, Langmore *et al*. (2009); 11, Langmore *et al*. (2007)

Host defence	Cuckoo counter-adaptation
Mobbing of adult cuckoos (1, 2)	Rapid laying when host is absent from nest (3)
	Preferential parasitism of novice female fairy-wrens? (4)
Rejection of large eggs (5)	Evolution of small eggs for body size (6, 7)
Rejection of eggs laid before or after laying period of host (5)	Eggs usually laid during laying period of host (5)
Rejection of cuckoo chicks (5)	Vocal mimicry of host chicks by cuckoos (5, 8, 9)
Improved cuckoo recognition through breeding experience (10)	Preferential parasitism of novice female fairy-wrens? (4)
Improved chick-rejection decisions through use of indirect cues such as the presence of adult cuckoos (10)	Transitory breeding pattern to evade detection by hosts? (11)

all the defences possible. Perhaps this reflects diminishing returns from a later line of defence if an earlier strategy is successful ('strategy blocking'; Britton *et al*. 2007; see also Grim 2006). A successful first line of defence, for example, means that hosts will rarely be parasitised. Mounting subsequent defences then becomes a potentially costly gamble that could lead to the mistaken rejection of host young (an instance of the 'rare enemy effect'; Dawkins 1982). If nest-defence is almost always successful then the evolution of egg discrimination and rejection may prove maladaptive owing to the relatively low benefits (because cuckoo eggs are rare) and potentially high costs (errors in recognition of eggs). Following the same argument, chick discrimination might only evolve when it is not 'blocked' by egg discrimination, and this could account for the evolution of rejection of cuckoo chicks in Superb Fairy-wrens (Langmore *et al*. 2003; Britton *et al*. 2007).

In short, the defences evolved by hosts are not only dependent on attributes of the cuckoo, such as rate of parasitism (Davies *et al*. 1996; Langmore *et al*. 2009) and their degree of specialisation on a particular host species (Takasu 1998*b*; Table 1), but are also dependent on the success of other behaviours in host-defence portfolios. Superb Fairy-wrens rely heavily on rejection of Cuckoo chicks even though it is the costliest possible line of defence, because Horsfield's Bronze-Cuckoos can usually breach the cheaper defences against parasitism mounted earlier in the breeding attempt.

Acknowledgements

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