



## Batten down the thatches: front-line defences in an apparently defenceless cuckoo host



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Avian brood parasites lay their eggs in the nests of other species, imposing high costs on their hosts. In theory, this should select for the evolution of defences against parasitism in hosts, yet eviction of parasite eggs or chicks is absent in many host species. One such host is the yellow-rumped thornbill, *Acanthiza chrysorrhoa*, the primary host of the shining bronze-cuckoo, *Chalcites lucidus*, in Australia. Here we tested whether the lack of egg and chick rejection in yellow-rumped thornbills has led to the evolution of alternative defences against brood parasitism. We provide evidence that this host has evolved two types of frontline defences. First, yellow-rumped thornbills responded to the presence of a cuckoo mount near the nest with mobbing behaviour and by occupying their dome-shaped nests, potentially as a means of blocking the small entrance hole. Second, we show that brood parasitism imposes directional selection for early breeding on the yellow-rumped thornbill and that yellow-rumped thornbills show a concomitant shift in their breeding phenology, breeding earlier than both congeneric and sympatric species. Our results highlight the importance of studying apparently defenceless hosts in order to identify alternative defence strategies.

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Brood parasites lay their eggs in nests of other species, thus avoiding the costs of raising their own offspring (Davies, 2000). Cuckoos are particularly virulent brood parasites (Kilner, 2005), and when their chick hatches it usually evicts all the other eggs of its foster parents, resulting in extremely high costs to hosts. This strongly antagonistic interaction between hosts and cuckoos has led to the evolution of host strategies to prevent cuckoo parasitism, which have, in turn, selected for counter-adaptations in cuckoos to circumvent host defences (Davies, 2011).

As a defence against parasitism, many hosts evict brood parasite eggs from the nest, or they might even abandon the nest and build a new one (Davies, 2000). Although rejection of a foreign egg allows the host's own breeding attempt to continue, the host still typically loses one egg because the cuckoo female usually removes one host egg when she lays her own (Davies, 2000). Egg rejection is possibly the best-studied type of host defence strategy, and it has led to the evolution of egg mimicry by parasites (Aviles et al., 2012; Landstrom, Langmore, & Heinsohn, 2010; Spottiswoode, Stryjewski, Quader, Colebrook-Robjent, & Sorenson, 2011). Similarly, hosts may also reject the parasite chick (Langmore, Hunt, &

Kilner, 2003; Sato, Tokue, Noske, Mikami, & Ueda, 2010; Tokue & Ueda, 2010), and this in turn has selected for the evolution of brood parasite chicks that mimic the appearance of host chicks (Langmore et al., 2011). Nevertheless, almost 40% of the main hosts of brood parasites are unable to recognize and reject parasitic eggs (Medina & Langmore, 2015) and cuckoo chick rejection is rare (Davies, 2011). Possible explanations for the lack of defences in some species are that the evolution of such defences may be too costly to evolve in some species, or there has been insufficient time for these defences to evolve (e.g. 'evolutionary lag hypothesis', Takasu, 1998). Another possibility is that the host has evolved effective defences, but at other stages of the breeding cycle.

Several 'frontline' defence strategies are used by hosts in response to parasitism. These are defences deployed before parasitism occurs, and they are potentially the most beneficial defences to hosts, because the host's entire clutch is preserved if frontline defences are successful. Host species may attempt to prevent parasitism physically, by mobbing the female brood parasite (Davies & Welbergen, 2008; Feeney, Welbergen, & Langmore, 2012; Glog, Fiorini, Reboreda, & Kacelnik, 2013; Krüger, Davies, & Sorenson, 2007; Langmore et al., 2012; Tong, Horrocks, & Spottiswoode, 2015; Welbergen & Davies, 2011). Physical attacks can successfully prevent parasitism (Krüger, 2011; Neudorf & Sealy, 1994; Webster, 1994) and may even result in the death of the

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parasite (Gloag et al., 2013; Molnár, 1944; Moyer, 1980). Although such behaviours may represent some energetic cost to the host, the overall outcome should be beneficial if cuckoo egg laying is prevented. Mobbing behaviour has been well studied in some cooperative breeders, such as superb fairy-wrens, *Malurus cyaneus*, where it has been found that large groups mob cuckoos more aggressively and experience lower rates of parasitism than small groups (Feeney et al., 2013). However, the degree of mobbing success for hosts that breed in pairs or small groups requires further investigation (but see Welbergen & Davies, 2009).

Another 'frontline' defence strategy may involve hosts avoiding brood parasitism by adjusting their breeding phenology to breed when cuckoos are not present (Boves, Sperry, Comolli, & Weatherhead, 2014; Brooker & Brooker, 1989a, 1989b). This idea has been poorly explored (Feeney et al., 2012) but has been suggested in some hosts, such as the red wattlebird, *Anthochaera carunculata*, which is exploited by the pallid cuckoo, *Cuculus pallidus* (Brooker & Brooker, 1989a, 1989b). Red wattlebirds breed at the same time as pallid cuckoos in southeastern Australia, where they are not a major host of the cuckoo, but commence breeding 3 months earlier than the cuckoo in southwestern Australia, where they are a primary host (Brooker & Brooker, 1989a, 1989b). A rationale for being an early breeder is that it may offer an alternative defence to hosts when the evolution of other types of defences is constrained.

Here, we tested for two types of frontline defences in the yellow-rumped thornbill, *Acanthiza chrysorrhoa* (Family: Acanthizidae), the primary host of the shining bronze-cuckoo, *Chalcites lucidus*, in Australia (Brooker & Brooker, 1989a, 1989b). Shining bronze-cuckoos are a highly virulent parasite: the cuckoo nestling evicts the host's eggs and then becomes the sole beneficiary of the host's care for over a month. Yellow-rumped thornbills build dome-shaped nests with very dark interiors (Langmore & Kilner 2009), which may constrain the evolution of egg rejection in this species (Langmore et al., 2005) and favour the evolution of alternative defences. Two previous studies showed that yellow-rumped thornbills are indeed poor egg rejecters, with rejection of nonmimetic model eggs recorded at 0% (Brooker & Brooker, 1989a, 1989b) and 10% (Langmore et al., 2005) of experimental nests. Moreover, there is no evidence of cuckoo chick rejection in this species ( $N = 15$  shining bronze-cuckoo chicks reared to fledging, none rejected, N.E. Langmore, n.d.). Thus, contrary to theoretical expectations that cuckoo parasitism should select for host defences, previous studies suggest that yellow-rumped thornbills are defenceless cuckoo hosts (Langmore & Kilner, 2009; Langmore et al., 2005). However, there is no information on frontline defence strategies in this species. Yellow-rumped thornbills are well known as early breeders, and can be observed 'carrying nesting material through the freezing fog, just one day after the winter solstice' (McComas (1992), p. 140). Here we explored whether yellow-rumped thornbills have evolved frontline defences and whether this can explain the anomaly of an apparently defenceless, yet heavily exploited host. Specifically, we tested whether yellow-rumped thornbills (1) mob shining bronze-cuckoos, (2) breed earlier than other insectivorous passerine species breeding at similar latitudes, (3) breed earlier than other congeneric species and (4) experience lower parasitism rates if they breed earlier, which would suggest that there is directional selection for early breeding.

## METHODS

### *Study Species and Study Site*

Yellow-rumped thornbills are small (9 g), insectivorous, nonmigratory passerines endemic to Australia (del Hoyo, Elliott,

Sargata, Christie, & de Juana, 2014). They may breed cooperatively, with the breeding pair receiving assistance in caring for young from one or two nonbreeding helpers, although most published observations of breeding are of pairs (Higgins & Peter, 2002). They breed multiple times during the season, and both sexes participate in building and lining the nest, but only females incubate. They are the primary host of the shining bronze-cuckoo in Australia (Brooker & Brooker, 1989a, 1989b). Shining bronze-cuckoos are breeding migrants, overwintering in Queensland or Papua New Guinea and arriving at our study site in August. The nests of yellow-rumped thornbills are relatively conspicuous, dome-shaped structures with a very small entrance, and may be built in dense clusters of foliage in trees, particularly in mistletoe (Family Loranthaceae) growing on *Eucalyptus* species, or in thorny bushes, such as boxthorn, *Lycium ferocissimum*. We studied yellow-rumped thornbills in Campbell Park, an open eucalypt woodland in Canberra, southeastern Australia (149°9' E, 35°16' S), from 1999 to 2015. During our study, nests were located by following adults during nest building or incubation. Nest success was scored as the total number of chicks fledged (with zero for abandoned or depredated nests).

### *Cuckoo Model Presentation*

To test whether yellow-rumped thornbills mob cuckoos, we presented groups of thornbills with freeze-dried specimens of a shining bronze-cuckoo and a nonthreatening control species of similar size that occurs commonly at the study site (white-plumed honeyeater, *Lichenostomus penicillatus*), during two breeding seasons, from August to December in 2012 and 2013. Most of the presentations in both years were done in September, when many of pairs had their second clutch. We used two different specimens each of the shining bronze-cuckoo and the honeyeater and tested for individual specimen effects. The two treatments were presented on the same day, separated by at least 60 min to avoid carryover effects, and the order of presentation was alternated. Trials were conducted during egg laying or early incubation, since this is the period when thornbills are most vulnerable to parasitism. Models were placed inside a fine 1.5 cm wire-mesh cage (50 × 50 cm) to protect them from damage and the cage was placed 2 m from the thornbill nest, at roughly the same height as the nest. The trial commenced when a yellow-rumped thornbill came within 2 m of the model, and continued for 5 min. A video camera (Canon EOS 40D) was positioned at least 10 m from the cage and thornbill responses to the models were filmed. From the video recordings we extracted movements, number of vocalizations in 5 min, and quantified the proportion of time spent within 1 m of the cage. Birds were habituated to the presence of the camera by setting up the camera and tripod from 10 to 15 min before placing the models. This species is very used to anthropogenic intervention, and in several instances birds would continue to mob the model even when the researcher was removing it.

### *Shifts in Breeding Phenology*

To explore whether yellow-rumped thornbills have shifted their breeding phenology in response to brood parasitism, we investigated whether they commence egg laying earlier than other comparable passerine species that breed at similar latitudes in southeastern Australia. Species used for comparison are shown in Appendix Table A1. Like the yellow-rumped thornbill, these are all small insectivorous species and are therefore likely to experience similar constraints on breeding based on food availability. For this analysis, we gathered data on the first month when at least 5% of the eggs were found. We also gathered data on average minimum

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