Animals often mimic dangerous or toxic species to deter predators; however, mimicry of such species may not always be possible and mimicry of benign species seems unlikely to confer anti-predator benefits. We reveal a system in which a bird mimics the alarm calls of harmless species to fool a predator 40 times its size and protect its offspring against attack. Our experiments revealed that brown thornbills (*Acanthiza pusilla*) mimic a chorus of other species’ aerial alarm calls, a cue of an *Accipiter* hawk in flight, when predators attack their nest. The absence of any flying predators in this context implies that these alarms convey deceptive information about the type of danger present. Experiments on the primary nest predators of thornbills, pied currawongs (*Strepera graculina*), revealed that the predators treat these alarms as if they themselves are threatened by flying hawks, either by scanning the sky for danger or fleeing, confirming a deceptive function. In turn, these distractions delay attack and provide thornbill nestlings with an opportunity to escape. This sophisticated defence strategy exploits the complex web of interactions among multiple species across several trophic levels, and in particular exploits a predator’s ability to eavesdrop on and respond appropriately to heterospecific alarm calls. Our findings demonstrate that prey can fool predators by deceptively mimicking alarm calls of harmless species, suggesting that defensive mimicry could be more widespread because of indirect effects on predators within a web of eavesdropping.

1. Introduction

Prey animals often use dishonest signals to fool predators and escape predation. For example, prey species can make themselves appear larger or displeasing, and thus deter predators from attacking [1,2]. Mimicry is another classic example of a dishonest signal and is often used by otherwise undefended organisms to deceive predators into misidentifying them as toxic or dangerous species (defensive mimicry [3]). This is generally accomplished by mimicking attributes of dangerous models, including predators themselves, or the aposematic coloration or warning sounds of noxious prey (Batesian mimicry [1,4–6]). However, mimicking dangerous species is not always possible, and it is unknown whether mimicking harmless species can provide protection against predators.

Although the protective benefits of traditional examples of mimicry are well known, such as for Batesian and Müllerian mimicry [7,8], it is still unclear if avian vocal mimicry has an anti-predator function [9,10]. Mimicry of other species’ vocalizations or sounds is widespread among songbirds, but the function of these mimetic vocalizations is known for only a handful of species (reviews: [9,10]). In response to predators, birds often mimic sounds that are associated with danger, such as calls of predators or alarm and aggression calls of heterospecifics, suggesting that vocal mimicry confers anti-predator protection by similar mechanisms as Batesian mimicry [11–14]. Indeed, mimicry of rattlesnake (*Crotalus viridis*) rattling sounds by burrowing owls (*Athene cunicularia*) has been shown to deter heterospecific competitors from entering owl burrows and thereby potentially evicting owls [4]. Yet surprisingly, how predators respond to mimetic
is present, the production of aerial alarm calls by thornbills when humans disturb their nests [14]. As no flying predator (e.g. *Dicrurus adsimilis* of danger to distract competitors and steal their food [14], or use deceptive alarms as a mate-guarding strategy (e.g. *Hirundo rustica* [19]). This deception is possible between species because individuals often eavesdrop on and respond to alarm calls of other species [20]. There are two main types of avian alarm calls: (i) aerial alarm calls are produced to predators in flight and provoke listeners to scan the sky or fly into cover, and (ii) mobbing alarm calls are produced to terrestrial predators or stationary avian predators, and provoke listeners to inspect and harass the predator [21]. Aerial alarm calls are particularly effective signals for startling others because predators in flight are extremely dangerous and require listeners to respond immediately [21]. However, just like the story of the boy who cried wolf, the effectiveness of deception can decline when deceptive alarms are used too frequently [17,22,23]. Callers can potentially avoid resistance to deception by mimicking the alarm calls of other species, thereby reducing the frequency of any one type of deceptive call [17]. Although the use of non-mimetic and mimetic alarms to deceive competitors is well documented, it is unclear whether alarms of any type are used to deceive predators.

For most bird species studied, human disturbance or predator attacks on a nest provoke parents to produce mobbing alarm calls, which is appropriate when predators are not in flight [21]. However, brown thornbills (*Acanthiza pusilla*; figure 1a) mimic a chorus of other species’ aerial alarm calls when humans disturb their nests [14]. As no flying predator is present, the production of aerial alarm calls by thornbills during nest defence conveys inaccurate information about danger and may serve to deceive predators into responding as if they themselves are in immediate danger from above [14,24]. Mimicking a chorus of aerial alarm calls may also stimulate multiple callers, a reliable indication of immediate danger [20,25–27], which may increase the effectiveness of deception.

Here, we experimentally tested the anti-predator function of mimetic aerial alarm calls used by brown thornbills during nest defence. We examined the interactions between thornbills and their primary nest predators, pied currawongs (*Strepera graculina*; figure 1a), and tested the hypotheses that (i) thornbills use aerial alarm calls to deceive currawongs that attack their nest, and that (ii) mimicking a chorus of alarm calls is better at deceiving currawongs than using a single, non-mimetic type of alarm call. Currawongs are susceptible to being deceived by aerial alarm calls because they themselves are prey to Accipiter hawks, such as *A. fasciatus* (figure 1a; [28]), which are dangerous top predators that provoke aerial alarm calls from thornbills and other sympatric species.

### 2. Material and methods

#### (a) Study site, species and experimental overview

We studied free-living colour-banded thornbills and unbanded pied currawongs in and around the Australian National Botanic Gardens, Canberra, Australia (35°16’ S, 149°6’ E). Both species are highly territorial, pair-breeding passerine birds common throughout southeastern Australia [29,30]. Brown thornbills are 7 g and build dome-shaped nests typically 0.5–1 m above the ground and in dense vegetation [29]. Currawongs are 280 g specialized nest predators that can capture up to 2 kg of young birds to raise a single brood to maturity [31]. An estimated 52% of brown thornbill nests with nestlings suffer mortality at our study site, with 61–83% of these losses attributed to nest predators. (For discussions, see [10,15]). Vocal mimicry is often placed outside the evolutionary framework of traditional mimicry systems (e.g. *Dicrurus adsimilis* [18]), or use deceptive alarms as a mate-guarding strategy (e.g. *Hirundo rustica* [19]). This deception is possible between species because individuals often eavesdrop on and respond to alarm calls of other species [20]. There are two main types of avian alarm calls: (i) aerial alarm calls are produced to predators in flight and provoke listeners to scan the sky or fly into cover, and (ii) mobbing alarm calls are produced to terrestrial predators or stationary avian predators, and provoke listeners to inspect and harass the predator [21]. Aerial alarm calls are particularly effective signals for startling others because predators in flight are extremely dangerous and require listeners to respond immediately [21]. However, just like the story of the boy who cried wolf, the effectiveness of deception can decline when deceptive alarms are used too frequently [17,22,23]. Callers can potentially avoid resistance to deception by mimicking the alarm calls of other species, thereby reducing the frequency of any one type of deceptive call [17]. Although the use of non-mimetic and mimetic alarms to deceive competitors is well documented, it is unclear whether alarms of any type are used to deceive predators.

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predation by avian predators, primarily pied currawongs [32]. There
are no data on the rate of predation by hawks for either species; how-
ever, the annual rate of survival for brown thornbills and pied
currawongs is, respectively, 63% and 82% [32,33].

To test our hypotheses, we first tested experimentally whether
thornbills mimic aerial alarm calls in response to currawongs on
the ground during nest defence, and if so whether these are likely
to function in preventing attack or helping young escape when
attacked. We then tested whether currawongs are deceived by thorn-
bill alarm calls and mimicry at simulated thornbill nests. Finally, we
examined the response by currawongs to thornbill, heterospecific,
and mimetic alarms to test their salience when broadcast alone.

(b) Thornbill response to nest threat
To test when thornbills use mimetic aerial alarms, we simulated
three levels of threat to 8- to 10-day-old nestlings of breeding thorn-
bill pairs in 2011, approximately 6 days before normal fledging
age. We presented 10 thornbill pairs with taxidermic mounts
1 m in front of their nests in combination with broadcasting
sounds to simulate three levels of threat: (i) no threat control—a
crimson rosella (Platycercus elegans), a harmless sympatric parrot
near the nest in combination with rosella contact calls, (ii) potential
threat from a searching nest predator—a pied currawong near the
nest in combination with rosella contact calls, and (iii) immediate
threat from a predator attacking the nest—a pied currawong near the
nest in combination with nestling distress calls, which are produced by
nestlings only when disturbed (electronic supplementary material, figure S1). All three treatments
were presented to a pair in random order during a single day. Additional
details of experimental protocol are provided in the electronic sup-
plementary material. To test the specificity of responses in relation
to nestling distress calls, each sound was broadcast only once for 4 s
at the start of a 5 min period when the model was presented.

Sons were broadcast at the average amplitude of nestling distress
calls (mean = 49.2 dBA from 4 m; s.e.m. = 0.63; n = 10). We
recorded vocalizations produced by parents following protocols
described in Igic & Magrath [14]. For ethical reasons, we conducted
experiments before nestlings were old enough to prematurely
fledge as that may reduce their survival.

We examined production of non-mimetic and mimetic alarm
calls by parents: (i) over the full 5 min threat treatment, and
(ii) specifically during the 4 s period that nestling distress calls
were present during our experiments and we considered their
combinations of non-mimetic and mimetic aerial alarms, and
(iii) thornbill song as a control. We used a mixture of non-mimetic
and mimetic alarms, rather than mimetic alarms alone, because
thornbills generally use mimetic alarms in combination with non-
mimetic alarms [14]. For mimetic alarms, we used mimicry of
New Holland honeyeater (Phylidonyris novaehollandiae) aerial
alarm calls, the call most frequently mimicked during nest defence
[14]. We predicted that the aerial alarms would distract currawongs
and that mimicry would prolong this distraction. Under natural cir-
cumstances, a delay would allow older thornbill nestlings to
scramble out of the nest and hide in surrounding vegetation [29].

We trained currawongs to feed from custom-made feeders that
simulated a thornbill nest environment (electronic supplementary
material, figure S2), where we broadcast the recordings of thornbill
vocalizations. Full details of training protocol and creation of
playbacks are provided in the electronic supplementary material.
Once currawongs were habituated to feeders and our experimental
equipment, we broadcast each recording on a separate date, in
random order, and in the absence of species aggressive towards
currawongs or any aerial alarm calls nearby in the previous
10 min. Upon setting up the feeder and equipment, we allowed
currawongs to make two visits to the feeder before broadcasting
a recording the moment a currawong was about to pick up food
on its next visit. All recordings were broadcast from a Response
Dome Tweeter speaker mounted on a tripod 0.7 m from the
ground and 5 m from the feeder. We played sounds from an
Edirrol R-09HR solid-state digital player and custom-built amplifier
at an amplitude of 60 dBA at 5 m (average amplitude of thornbill
aerial alarms recorded during nesting banding [14]), and we video
recorded currawong behaviour.

We examined how currawongs responded to playbacks by ana-
lysing video recordings using Microsoft Windows Movie Maker
v. 2.6 (Microsoft Corporation). We classified the immediate behaviour
of currawongs following sounds into three categories that reflected
the intensity of their alarm response: flight from the feeder’s
location, aerial scanning (defined as looking up for more than
1 s), or other response. Currawong behaviour was classified into
these categories by a scorer blind to the playback treatment: the
video recordings were in random order, the sound was muted
and the timing of playbacks was marked visually. The intensity
of an individual’s alarm response can also be measured as the
delay until their behaviour returns to normal (e.g. [35,36]), so we
also measured how long currawongs delayed collecting food
after playbacks, again using blind scoring (to the nearest 0.1 s).

(d) Currawong response to thornbill and real
honeyeater alarms
We conducted a follow-up experiment in 2013 to examine how cur-
rawongs respond to New Holland honeyeater aerial alarms and test
whether these alarms are more salient to them than thornbill alarms.
Currawongs might respond more strongly to a mixture of non-
mimetic and mimetic alarms than non-mimetic alarms alone
because (i) the mimetic alarm itself is more salient or (ii) the mixture
of different species’ alarms is more salient than alarms of a single
species. We therefore broadcast four types of calls alone over 0.8 s
to currawongs feeding in the open: (i) thornbill song as a control,
(ii) thornbill non-mimetic aerial alarms, (iii) thornbill mimetic honey-
eater aerial alarms, and (iv) the honeyeater’s own aerial alarms
(figure 1b). We used the same currawong population as in the previ-
ous experiment, but only 10 pairs produced nests during 2013
and could be used for this experiment.

We used a modified protocol compared with the previous
experiment. We placed food on the ground, rather than in a
feeder, to examine the salience of alarms as opposed to their effec-
tiveness in nest defence. Recordings were broadcast using the
same equipment and methods, but the equipment was mounted
around the waist of an observer standing 10 m away from the
focal bird. We again video recorded currawong responses and
used blind scoring to classify the initial response of currawongs to playbacks and the amount of time they spent aerial scanning following alarm calls (to the 0.1 s).

**3. Results**

In support of a function in helping young escape when attacked, thornbills mimicked heterospecific aerial alarm calls specifically during simulated nest attack, and not when a predator model was merely nearby. Mimetic aerial alarms were used despite the absence of a flying predator and were the most common type of call used by parents during the playback of nestling distress calls (ZINB effect: $\chi^2 = 20.85, p < 0.01$; all post hoc comparisons, $p < 0.05$; figure 2a; electronic supplementary material, table S3). Mimicry of aerial alarms coincided specifically with the 4 s that nestling distress calls were broadcast (figure 2b), beginning on average 1.9 s (± 1.1 s.e.m.) after the onset of nestling distress calls and continuing for an average 5.9 s (± 3.2 s.e.m.). During this time, parents mimicked between one and four different species’ aerial alarms (average 1.9 ± 0.4 s.e.m.). After the simulated attack had finished or when a currawong was merely present nearby, parents produced non-mimetic and mimetic mobbing alarms, such that over the full 5 min mimetic aerial alarm calls were used less often than non-mimetic (potential threat: $t_{20} = 10.28, p < 0.001$; immediate threat: $t_{27} = 4.44, p < 0.001$) and mimetic (potential threat: $t_{20} = 7.43, p < 0.001$; immediate threat: $t_{27} = 2.82, p = 0.04$) mobbing alarms (figure 2b,c; electronic supplementary material, tables S1 and S2).
In support of a deceptive anti-predator function, currawongs treated all aerial alarms as if they were themselves threatened by a predator in flight, and the specific benefit of incorporating mimicry was prolonging this distraction (figure 3a; electronic supplementary material, video S1). Currawongs were more likely to scan the sky or flee following either alarm playback than following song, suggesting that they were deceived by thornbill alarms (McNemar’s test versus song: non-mimetic alone: $\chi^2 = 15.1$, $p < 0.001$; mixture: $\chi^2 = 12.5$, $p < 0.001$; figure 3a). As a result of distraction, currawongs delayed feeding 8.3 s ($\pm 0.4$ s.e.m.) longer following non-mimetic aerial alarms alone than following song ($t_{22} = 5.11$, $p < 0.0001$), and prolonged this delay a further 8 s ($\pm 0.9$ s.e.m.) if non-mimetic and mimetic aerial alarm calls were broadcast together ($t_{22} = 2.47$, $p = 0.02$; figure 3a; electronic supplementary material, table S4).

We found no evidence that thornbill aerial alarms were less salient to currawongs than aerial alarms of the most frequently mimicked heterospecific. When foraging in the open, currawongs scanned the sky for danger following honeyeater alarms, thornbill non-mimetic alarms and mimetic honeyeater alarms (figure 3b). There was no difference in the duration of scanning across the alarm types (linear mixed model effect: $F_{2,13} = 1.91$, all $p = 0.2$; figure 3b; electronic supplementary material, table S5). Two out of 10 currawongs fled to mimetic alarms, but this was not statistically different compared with real honeyeater alarms (McNemar’s test: $\chi^2 = 0.5$, $p = 0.5$; figure 3b).

4. Discussion

Taken together, our findings demonstrate that brown thornbills deceive a major nest predator by mimicking alarm calls of other harmless species. This sophisticated behavioural strategy exploits the interactions among multiple species across several trophic levels (figure 1a): thornbills exploit currawong eavesdropping on the salient alarm calls of heterospecifics, signalling about top predators that are dangerous to all three species, in order to deceive currawongs into delaying attack on their nestlings. Given the 40-fold size difference between thornbills and currawongs, physical attacks by thornbills are likely to be both ineffective and risky, and deception is perhaps the only effective defence once a nest is attacked [42].

Although used in the presence of an avian predator, the aerial alarm calls used by thornbills during nest defence were deceptive. The alarms were not simply communicating about danger to mates (e.g. [43]) because they were produced in the absence of a flying threat—the currawongs were always stationary on the ground. Indeed, in other circumstances, thornbills produce aerial alarm calls to avian predators in flight and mobbing alarm calls to stationary avian predators, including to currawongs [14]. They were also not merely communicating the presence of danger to offspring [44] because the alarms were only used once nestlings were already under attack. Lastly, these aerial alarms are not used in aggressive contexts by thornbills or the mimicked heterospecifics, and thereby do not signal aggression [13,45]. Deception is a likely explanation whenever an alarm signal conveys inaccurate information about the type, or presence, of danger and in doing so provokes a response by the predator that benefits the caller but is costly to the predator [2]. Currawongs indeed treated the alarms as if they were themselves in danger from above (e.g. [18]). Although predators can pay attention to prey alarms [46,47] and use them to locate feeding opportunities [48], the use of alarm calls by prey to fool predators has not been shown previously. This is therefore a novel diversionary display employed by birds during nest defence, similar to injury feigning and false brooding [49].

A surprising feature of thornbill mimicry is that they mimicked harmless species rather than dangerous or toxic ones [4,13]. Unlike many taxa that mimic related or similarly sized noxious prey, such as the abundant examples of Batesian and Müllerian mimicry among invertebrates, reptiles and fishes [1,50], the opportunity for such mimicry is rare for birds. We know of only three cases. The New Guinean *Pitoehus* and *Irita* genera are toxic, resulting in one case of Müllerian, and potentially also Batesian, mimicry within *Pitoehus* [31,52]. The nestlings of *Lanioura hypopyra* are also considered to be Batesian mimics of a toxic caterpillar [53]. Finally, burrowing owls mimic rattlesnake sounds to deter competitors [4]. The absence of noxious models, or difficulties in accurately mimicking vocalizations of much larger predators, might constrain thornbills into mimicking the alarm calls of harmless species, which are cues of dangerous flying predators. Aerial alarms might also signal a more urgent threat than predator calls because predators are usually...
silent when hunting prey. Demonstrating that dangerous model species are not required for protective function shows that mimicry can confer protection through unexpected mechanisms and expand upon the circumstances in which defensive mimicry could evolve. Indeed, it is the information conveyed by the mimetic signal that is important for its function, rather than any danger posed by the model itself. As mimicry of heterospecific alarm calls is common among songbirds [9,10], similar protective mechanisms for mimicry may also be common and requires further investigation.

Aerial alarms caused temporary distraction such that deception would specifically be advantageous when nestlings are capable of fleeing the nest. Older nestling birds, including those of thornbills, commonly scramble or ‘explode’ from the nest prematurely when disturbed [29,54], and on an evolutionary timescale there is selection for young to fledge earlier and be more mobile when predation risk is higher [55]. Thornbill nests are surrounded by thick vegetation into which young can flee, so even short distraction of predators should increase nestlings’ chances of survival. Protecting older broods is more profitable because the fitness value of broods increases, and re-nesting opportunity decreases, with brood age [42]. Older nestlings can also be more vulnerable to predation because of louder begging that can attract predators [56,57]. A potential anomaly is that thornbills used aerial alarms in circumstances when nestlings are too young to flee, such as during our experiments. However, producing aerial alarm calls probably carries little risk to parents when a predator is attacking their nest, and in the absence of selection to restrict usage to circumstances when nestlings are capable of fleeing, mimicking aerial alarm calls could have evolved as a general response to nestling distress calls. Responses of thornbill parents to nestling distress calls appear similar throughout the nestling period, and older thornbill nestlings do explode from their nests when disturbed by humans while parents simultaneously mimic aerial alarm calls (B. Igic 2010–2011, personal observation). The effectiveness of this defensive strategy during natural nest predation situations requires further investigation.

There are three potential mechanisms by which including mimicry prolonged distraction. First, mimicry may help evade identification, and thereby reduce the risk that targets identify alarms as deceptive [17]; however, non-mimetic aerial alarms still caused some distraction, suggesting this is not the complete explanation. Second, mimicry may enable thornbills to use alarms that are more salient to currawongs, such as alarms of larger heterospecifics that are more likely to share predators with currawongs [58]. Contrary to this hypothesis, currawongs foraging in the open responded similarly to honeyleater and thornbill alarms broadcast alone, although a larger sample might detect small effects. A third explanation is that including mimicry simulates a chorus of alarm calling species, thereby increasing the perceived urgency or reliability of alarm information. Not only may alarm calls from multiple callers be a more reliable indication of danger than alarm calls from a lone caller [25,26], but more dangerous predators, such as hawks, generally provoke aerial alarms from multiple species [27]. Regardless of the exact mechanism, we show that mimicry confers an anti-predator advantage. Further work is required to disentangle the mechanisms by which the inclusion of mimicry increased the effectiveness of deception.

In summary, we revealed the use of deceptive alarms to manipulate predator behaviour and an unexpected protective mechanism of mimicry. Similar anti-predator mechanisms for alarm signals and mimicry may be widespread in nature. For example, wild potato plants (Solanum berthaultii) deter herbivory by aphids (Myzus persicae) by mimicking aphid alarm pheromones [59], and myrmecophilous beetles mimic alarm pheromones of their ant hosts to evade aggressive interactions [60]. Eavesdropping on heterospecific alarm calls is widespread among vertebrates [20], so the use of either non-mimetic or mimetic alarm calls to deceive predators may also be common but overlooked. This is because researchers may assume incorrectly that alarm calls function only to warn others, or signal honestly to predators, rather than being used as deceptive signals directed at the predator.

References
