nature ecology & evolution

Article

https://doi.org/10.1038/s41559-025-02855-9

Learned use of an innate sound-meaning association in birds

Received: 9 October 2024

Accepted: 19 August 2025

Published online: 03 October 2025

Check for updates

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Signals in vocal communication systems range from innate to learned. Although innate and learned signals are often assumed to be independent, Darwin speculated that they could be evolutionarily related, with the former being the foundation of the latter even in our own communication system, language. Here we test this hypothesis by studying the vocal communication systems of avian hosts of brood parasites. First, we show that 21 bird species separated by approximately 53 million years of evolution produce structurally similar 'whining' vocalizations towards their respective brood parasites. Exploring the social correlates of whining vocalization production, we find that species that produce this vocalization often exist in areas with dense parasite–host networks, suggesting that its production facilitates interactions among host species. Experiments across three continents show that this vocalization is referential towards brood parasites in multiple host species, that hearing them elicits an innate rapid recruiting response, and that host species from different continents respond equally to the whining vocalizations of each other, indicating that convergent use facilitates cooperative defences across species. Our results provide an example of a referential animal vocalization for which sound production in the correct context is learned but for which hearing it elicits an innate response, representing an intermediate between innate and learned signals.

In *The Descent of Man*[1], Darwin speculated that the origins of spoken language could be traced to the imitation and modification of instinctive sounds that humans and other animals produce, such as a scream made in response to pain. This view remains a subject of ongoing debate owing to the lack of evidence for evolutionary continuity between these vocalizations and the conventional linguistic units that humans use in their communication system, such as words and phrases[2,3]. For instance, screams in humans and functionally similar distress vocalizations in other species are innate vocal reactions that contain acoustic features tuned to elicit immediate responses in receivers[4–6]. By contrast, linguistic units in spoken languages contain learned sounds that exhibit arbitrary and therefore symbolic associations with their meanings[7–10].

In humans, the use of learned-symbolic sounds is regarded as the cornerstone of linguistic communication[7], yet mounting evidence suggests that the process of assigning a sound to a meaning is at least partially rooted in innate predispositions. For instance, recent studies of linguistic diversity have revealed that independent spoken languages converge on similar solutions when it comes to pairing sounds and

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https://doi.org/10.1038/s41559-025-02855-9

meanings[8–12], such as the concept of 'round' often including an 'r' sound[8]. This aligns with the finding that novel non-linguistic sounds have similar semantic associations across languages[12]. At least some innate associations between sounds and meanings can also extend beyond humans to include other species, such as humans and chimpanzees (*Pan troglodytes*) both tending to pair high pitch with high luminance[13]. These studies suggest that some aspects of behavioural responses in an otherwise learned vocal production system harness phylogenetically generalizable innate associations between sounds and their meanings[2,14,15], which is contrary to the suggestion that learned-symbolic and innate-reactionary vocalizations are evolutionarily unrelated[3]. However, if innate vocal reactions are evolutionary precursors of learned-symbolic vocalizations, we should be able to identify vocalizations that are learned for their production while eliciting innate responses in relevant receivers that deliver benefits to both the receiver and signaller[2]. In addition to reflecting an evolutionary intermediary between innate-reactionary and learned-symbolic vocalizations, such a hybrid vocalization would also fulfil many of the criteria for a language precursor[16].

The interactions between avian brood parasites and their hosts offer a potentially informative model system to explore the relationship between innate-reactionary and learned-symbolic vocalizations. Brood parasites, such as the parasitic cuckoos (Cuculidae), lay their eggs in the nests of other birds and rely on manipulating the host to raise their offspring[17]. Unlike most enemies, brood parasites threaten the reproductive output of the host but not the adult host[18], which selects highly specific reciprocal adaptations and counter-adaptations that shape the biology and ecology of the species involved[19–21]. Hosts of the world's approximately 100 obligate brood parasite species include an ecologically, geographically and phylogenetically diverse array of over 1,500 species, most of which (about 85%) are vocal-learning songbirds (Passeri)[22]. Although vocalizations towards brood parasites are rarely described[23], two host species have been experimentally shown to possess functionally referential vocalizations (signals that are associated with a specific referent and elicit an appropriate response[24]) that denote brood parasites[25,26], which contain both learned and innate components[27–29]. In particular, the 'whining' vocalization of the superb fairy-wren (*Malurus cyaneus*) sits between the two extremes of innate and learned signals. For instance, despite eliciting an innate rapid recruiting response that facilitates extremely aggressive cooperative mobbing that can lower parasitism likelihood[26,30], cuckoo-experienced individuals only respond towards cuckoos when they present a threat, and cuckoo-naive individuals do not produce whining vocalizations until they learn to by watching the response of more experienced individuals[26–28]. Closely related splendid fairy-wrens (*Malurus splendens*) also produce whining vocalizations towards parasitic cuckoos, and only do so when they present a threat, such as when nests contain eggs or chicks[31]. Outside of the fairy-wrens, strikingly similar vocalizations have been reported towards cuckoos in the large-billed gerygone (*Gerygone magnirostris*) in Australia[32], as well as in multiple species of leaf warblers (Phylloscopidae) throughout Eurasia[33], which also elicit similar brood parasite-specific behaviours to those seen in the fairy-wrens[26,33]. Fairy-wrens (Maluridae) and leaf warblers (Phylloscopidae) are separated by approximately 53 million years of evolution[34], have allopatric distributions, and are parasitized by different species of brood-parasitic cuckoos that also exist in allopatry. Given this, the use of similar vocalizations by these species in the same context raises the possibility that an array of host species may have converged on producing a similar learned vocalization to denote the specific threat presented by brood parasites that elicits an ecologically appropriate innate response in relevant receivers.

Results

Acoustic features of brood parasite-associated whining vocalizations

Two species of leaf warbler, Hume's leaf warbler (*Phylloscopus humei*) and the greenish warbler (*Phylloscopus trochiloides*)[33] have been experimentally shown to produce vocalizations towards common cuckoos (*Cuculus canorus*) that resemble the cuckoo-referential whining vocalizations of the superb fairy-wren[26]. To confirm that these three species produce structurally similar whining-type vocalizations, we extracted 43 acoustic measurements from the vocalizations they produce either in response to their brood parasites (hereafter 'brood parasite-associated' vocalizations) or towards terrestrial predators (hereafter 'alarm' vocalizations, per ref. 35). We summarized these features in ten principal components (in a single analysis, with the vocalizations from additional species described below) and used the resultant principal component scores to conduct a permuted linear discriminant analysis. This classified 98% (N = 59 out of 60) of brood parasite-associated and 100% (N = 57) of alarm vocalizations to the correct context. The linear discriminant function, a linear transformation of principal component scores, had the largest coefficient on principal component 3 (PC3), which in turn was positively associated with spectral flatness and negatively associated with frequency bandwidth (Extended Data Fig. 1). For each of the three species, their brood parasite-associated vocalizations had low spectral flatness (sound energy concentrated into frequency bands) and high frequency bandwidth (sound energy distributed over a large frequency range) (Fig. 1a). Vocalizations with similar characteristics, such as distress vocalizations, have been shown to elicit strong behavioural responses across species[5,36]. Thus, following the terminology used for fairy-wrens, as they are the group in which whining vocalizations were first described[31], we conclude that these three species all produce brood parasite-associated whining vocalizations.

Evolutionary history of a sound-meaning association

Given the use of strikingly similar vocalizations towards brood parasites that elicit similar behavioural responses[26,33], despite geographical isolation and ancient divergence between fairy-wrens and leaf warblers[34], we explored whether other host species also harness this sound-meaning association. We obtained brood parasite-associated vocalizations and alarm vocalizations from 23 additional host species from 9 avian families that are parasitized by 3 obligate brood parasite lineages: cuckoos (Cuculidae), cowbirds (Icteridae) and viduid finches (Viduidae)[37]. We used the linear discriminant function described above to classify the brood parasite-associated and alarm vocalizations of the 23 species. For 22 of these species, more than 86% of their brood parasite-associated vocalizations (between N = 9 and 20 vocalizations per species) were classified as whining vocalizations, including hosts of various cuckoos and the cuckoo finch (*Anomalospiza imberbis*), which suggested that there is convergent use of a specific sound-meaning association in these species. For a single species, the yellow warbler (*Setophaga petechia*), none (N = 20) of their parasite-associated vocalizations were classified as whining vocalizations. This result is interesting, as it is the only other species (outside the superb fairy-wren) to have an experimentally verified referential vocalization towards its brood parasite, the brown-headed cowbird (*Molothrus ater*)[25]. Most hosts of brood parasites deter brood parasitism with aggressive physical mobbing[23,26,38] and subsequent defences that are centred around detecting deception and calibrated according to their perceived parasitism risk, such as rejection of a parasitic egg or chick[39,40]. By contrast, the yellow warbler's referential 'seet' vocalization prompts a rapid return to the nest and an attempt to block direct access by the parasite to the nest[25]. Although parasitism by most brood parasites results in the elimination of all host chicks, including all species towards which we found evidence of whining vocalizations, the offspring of brown-headed cowbirds are raised alongside some of the offspring of the host[17]. Correspondingly, although most brood parasites rely heavily on deception, brown-headed cowbirds can monitor and retaliate against hosts that reject their eggs by destroying their entire egg clutch to force the host to renest and accept raising its offspring alongside their own[41]. Under these circumstances, a vocalization that facilitates rapid detection, recognition and an aggressive response may not be adaptive.

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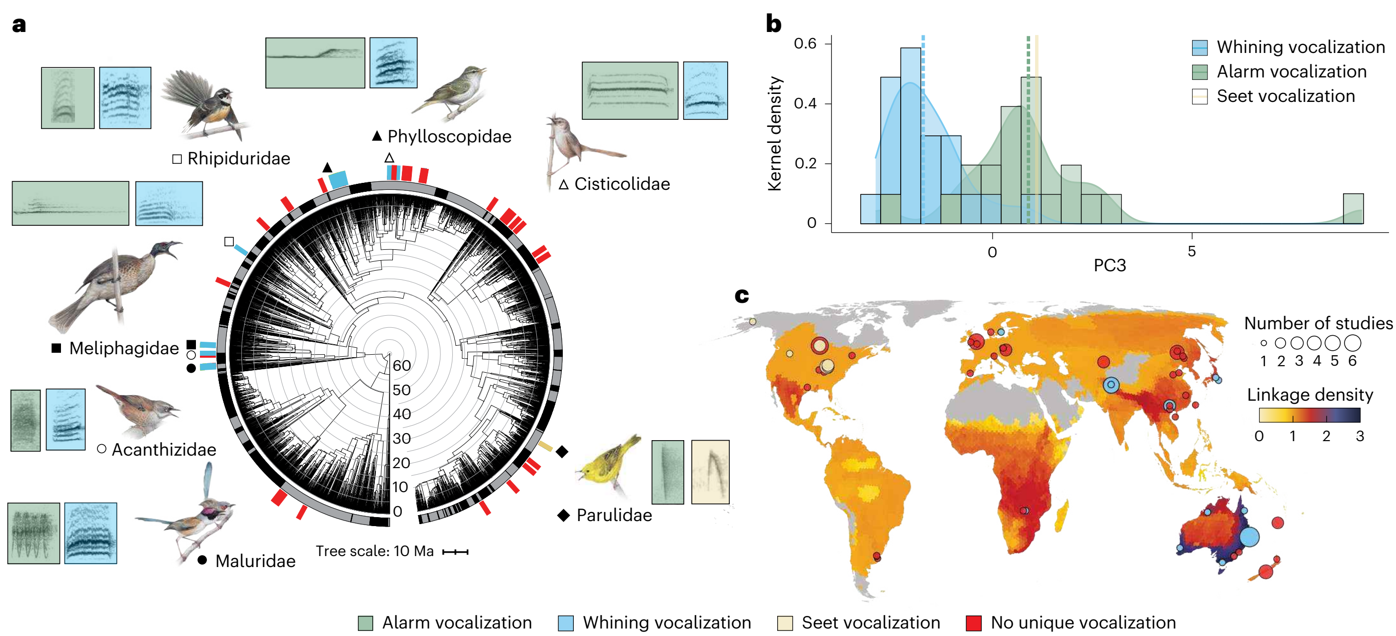

Fig. 1 | Evolutionary history of vocalizations by hosts of brood parasites and macroecological correlates of whining vocalization production. **a**, Phylogenetic distribution of passerine species that have been documented to produce distinct vocalizations towards brood parasites (whining (blue, $N = 23$ species) or seet (yellow, $N = 1$ species)) and those for which there is no evidence that they produce a distinct vocalization towards a brood parasite compared to predators (no unique vocalization (red, $N = 29$ species)) according to information available from studies included in our literature analysis. Images are of a candidate species from each family from which at least one species produces a unique vocalization towards a brood parasite, as well as spectrograms of their brood parasite-associated (whining (blue) or seet (yellow)) and alarm (green) vocalizations. Blocks of black and grey around the circumference of the phylogram indicates family, and each concentric circle indicates 5 million years (Ma) of evolutionary history. **b**, Histogram of PC3 scores for whining and alarm vocalizations produced by the 21 species determined to have whining vocalizations. PC3 scores were derived from a principal components analysis based on 43 acoustic measurements of vocalizations from all 26 species that met our inclusion criteria. Vertical dashed lines provide ancestral character state estimates for whining and alarm vocalizations, whereas the solid yellow line represents the mean value for the yellow warbler's seet ($N = 1$) vocalization. Ancestral character states were estimated using the within-species average of PC3 scores and a consensus phylogeny using all 21 species determined to produce whining vocalizations in response to brood parasites. Negative PC3 scores, characteristic of the whining vocalizations, are associated with high frequency bandwidth with defined frequency bands. This was determined on the basis of principal component loadings with acoustic measurements. **c**, The global distribution of species that have been documented to produce brood parasite-associated whining (blue) or seet (yellow) vocalizations or the species for which there is no evidence of a unique brood parasite-associated vocalization (red) overlaid on a map of brood parasite–host interaction networks, whereby a higher linkage density indicates more complex networks of interacting brood parasites and hosts. Note that a single species can be represented on this map several times if a particular vocalization has been documented on more than one occasion (for example, all seet vocalization records in North America are from the yellow warbler). The map depicting linkage densities for brood parasite–host networks provides a visual aid for interpreting the results of the Bayesian threshold models used to estimate the correlation between the presence of whining vocalization behaviour in a species and their coooperative breeding status and the median linkage density across the range of the species. The heat map was produced using a previously published method and datasets[22]. See Methods for more details on the statistical procedures. Bird illustrations in **a**, Pedro Fernandes.

Even if a given species produces whining-like vocalizations in response to a brood parasite, they would be unable to communicate specific information about the threat to relevant receivers if their whining vocalizations are indistinguishable from vocalizations produced by the same species in response to other threats. Thus, we examined the distinctiveness of the brood parasite-associated and alarm vocalizations produced by each of the remaining 22 species, as well as the superb fairy-wren, Hume's leaf warbler and the greenish warbler (25 species in total after removing the yellow warbler). We generated linear discriminant scores for each vocalization, which represent acoustic variation along the axis separating brood parasite-associated and alarm vocalizations. There was significant variation in the distinctiveness of brood parasite-associated and alarm vocalizations across species (likelihood ratio test (LRT) comparing models with and without an interaction between species and vocalization type: $\chi^2_{24} = 966.9$, $P < 0.0001$). Specifically, 21 species produced distinct brood parasite-associated and alarm vocalizations (post hoc differences, all $P < 0.001$), whereas 4 species, including the great reed warbler (*Acrocephalus arundinaceus*), oriental reed warbler (*Acrocephalus orientalis*), chalk-browed mockingbird (*Mimus saturninus*) and the fan-tailed gerygone (*Gerygone flavolateralis*), did not ($P = 0.69$, 0.13, 0.17 and 0.98, respectively). Overall, our analysis classified 21 species as producing distinctive whining vocalizations when confronting their respective brood parasites.

Finally, to investigate the evolutionary history of sound-meaning associations in whining vocalizations, we analysed whether low spectral flatness and high bandwidth (that is, low PC3 scores) distinguished whining and alarm vocalizations across the 21 species that produce distinctive whining vocalizations towards brood parasites. We found that whining vocalizations had lower PC3 values than alarm vocalizations (95% confidence interval for ancestral character estimate of the difference between whining and alarm PC3 = −4.27 to −0.97; Fig. 1b). Moreover, we found clear evidence that PC3 scores of whining and alarm vocalizations have distinct evolutionary rates (LRT comparing models with and without vocalization-specific evolutionary rates: $\chi^2_1 = 13.1$, $P < 0.001$). A model with distinct rates showed that PC3 scores have evolved >5 times more slowly in whining than in alarm vocalizations. This result suggests that alarm vocalizations evolve relatively quickly across species, which is consistent with previous studies[33] and potentially reflects their use across a variety of contexts[42]. It also suggests that at least 21 host species, which last shared a common ancestor about 53 million years ago, use a consistent pairing of sound with meaning in their whining vocalization responses to brood parasites, which

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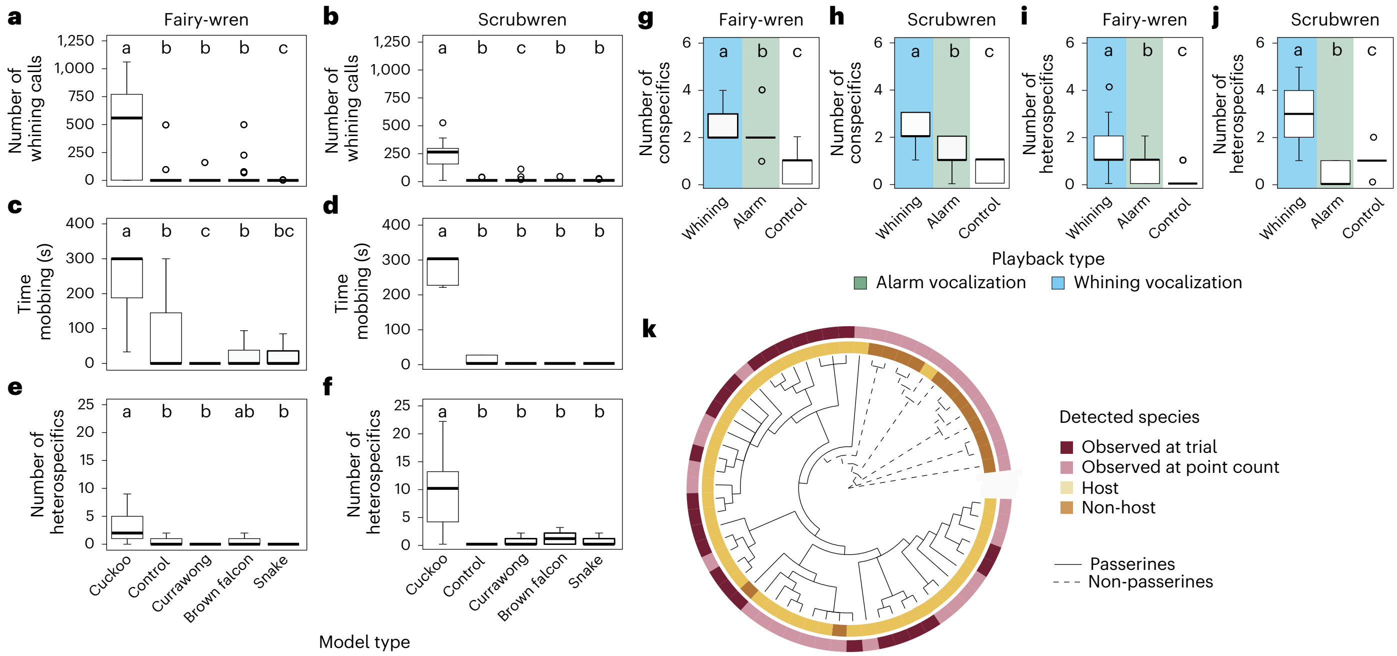

Fig. 2 | Whining vocalizations are functionally referential in superb fairy-wrens and white-browed scrubwrens and attract the attention of nearby passerines. a–**f**, Responses of superb fairy-wrens (**a**,**c**,**e**) and white-browed scrubwrens (**b**,**d**,**f**) towards 5-min presentations of a prepared model brood parasite (shining bronze-cuckoo and fan-tailed cuckoo), nest predator (eastern brown snake), predator of adult birds (brown falcon), predator of both nests and adult birds (pied currawong) and non-threatening control (yellow-faced honeyeater) ($N = 17$ for each treatment). **g**–**j**, Responses of superb fairy-wrens (**g**,**i**) and white-browed scrubwrens (**h**,**j**) towards 30 s of audio playbacks ($N = 17$ for each treatment). **k**, Distribution of species that attended cuckoo model presentation experiments or were detected in the vicinity of nests during point counts but did not attend the trial, as well as whether these species are hosts or non-hosts and passerines or non-passerines (see Extended Data Fig. 3 for a phylogram that includes species names). Blue shading indicates behavioural responses towards whining playbacks and green shading indicates behavioural responses towards terrestrial alarm vocalization playbacks (**g**–**j**). Values from the model presentation (**e**,**f**) and playback (**i**,**j**) experiments were not designed, or intended, for a direct comparison. Boxes represent the median and the upper and lower quartiles. Whiskers are 1.5 times the interquartile range, and circles represent data that lie outside this range. Letters denote results of post hoc analyses. See Supplementary Tables 1 and 2 for summary data and Methods for more detail on statistical procedures.

contain conserved acoustic features known to elicit innate responses across taxa[4,5,35]

Macroecological correlates of whining vocalization evolution

Vocalizations act to provide information to receivers, and information about brood parasitism risk has been shown to facilitate cooperative defences against parasites[26,39,40,43,44]. Although most research has focused on interactions between one parasite and one host, most parasites (>80%) target multiple host species[22], yet whether selection can favour phenotypes that facilitate cooperation among host species remains largely unknown[31,33,45]. If within-species cooperation is a primary benefit of whining vocalization production, owing to larger groups being better able to defend their nests against brood parasitism[26,46–49], species that produce them should be more socially cooperative[26]. Alternatively, if between-species cooperation is a primary benefit of whining vocalization production, species that produce whining vocalizations should reside in areas with more interacting brood parasite species and host species[22], as these areas offer more opportunity for cooperation among host species against shared parasites.

We conducted phylogenetic comparative analyses to examine whether the distribution of host species that produce whining vocalizations could be explained by the opportunity for within-species cooperation (cooperative breeding versus pair breeding) or between-species cooperation (the complexity of underlying brood parasite–host networks). To complement our existing dataset, we compiled studies that presented hosts with models of brood parasites, predators and controls to measure host behaviour and extracted information about the vocalizations produced by hosts towards brood parasites ($N = 32$ species from 38 studies, including an additional 2 species that produce whining-type vocalizations towards brood parasites[31,32]). We found that the production of whining vocalizations is phylogenetically conserved (Pagel's $\lambda = 0.91$). Moreover, when correcting for phylogeny, the opportunity for within-species cooperation did not predict which species produce whining vocalizations (95% highest posterior density (HPD) interval was significant for 0.1% resolutions of the Ericson backbone and 0% resolutions of the Hackett backbone, for which 1 and 0 out of 1,000 trees, respectively, had posterior distributions excluding zero, but see Supplementary Information). By contrast, the opportunity for between-species cooperation, as measured by the linkage density of the underlying brood parasite–host network, did predict which species produce whining vocalizations (95% HPD interval significant for 97.0% resolutions of the Ericson (mean = 0.45) backbone and 98.5% resolutions of the Hackett backbone (mean = 0.45), where 970 and 985 out of 1,000 trees, respectively, had posterior distributions excluding 0; Extended Data Fig. 2). For example, species with a median linkage density below the global median (1.02 interactions per species) rarely produce whining vocalizations (2 versus 22 species), whereas 3 times as many species with a median linkage density above the global median produce whining vocalizations (20 versus 6 species) (Fig. 1c). These results suggest that between-species interactions are more associated with the emergence and/or maintenance of whining vocalizations than within-species interactions globally. Moreover, given the geographical bias of brood parasitism research towards Europe and North America (70% of field-based brood parasitism research has been conducted in these areas)[22], our finding that most species that produce whining vocalizations are in areas that have historically received less research attention (for example, Africa, Asia and Oceania) suggests that this relationship may become stronger as research across these areas increases.

https://doi.org/10.1038/s41559-025-02855-9

Whining vocalizations are functionally referential towards brood parasites

So far, whining vocalizations have only been confirmed as functionally referential in superb fairy-wrens[26], a primary host of the Horsfield's bronze-cuckoo (*Chalcites basalis*). To experimentally investigate whether it is also functionally referential in a host of another brood parasite, we compared responses towards vocalization playbacks and prepared models of brood parasites and predators by the superb fairy-wren and the white-browed scrubwren (*Sericornis frontalis*), which is the primary host of the fan-tailed cuckoo (*Cacomantis flabelliformis*) in Australia[50]. First, when presented with models ($N = 17$ per species), we found that model treatment significantly affected the number of whining vocalizations produced by breeding groups (generalized linear mixed model: superb fairy-wren, $\chi^2_4 = 3352.9$, $P < 0.0001$, mean ± s.e.m. (towards cuckoo) = 459.2 ± 92.9 versus (other treatments) ≤ 51.2 ± 31.3; and white-browed scrubwren, $\chi^2_4 = 1666.5$, $P < 0.0001$, mean (towards cuckoo) = 213.8 ± 34.6 versus (other treatments) ≤ 8.4 ± 6.1). How aggressive groups were was also significant (time that at least one bird was within 0.5 m of the presented model: superb fairy-wren, $\chi^2_4 = 1062.7$, $P < 0.0001$, mean (towards cuckoo) = 237.9 ± 23.9 versus (other treatments) ≤ 59.2 ± 22.6; and white-browed scrubwren, $\chi^2_4 = 1580$, $P < 0.0001$, mean (towards cuckoo) = 248.4 ± 20.6 versus (other treatments) ≤ 25.2 ± 11.9). The treatment also significantly affected how many individuals from other species approached the models (came within 5 m of the model: superb fairy-wren, $\chi^2_4 = 49.2$, $P < 0.0001$, mean (towards cuckoo) = 3.7 ± 1.0 versus (other treatments) ≤ 0.8 ± 0.4; and white-browed scrubwren, $\chi^2_4 = 176.4$, $P < 0.0001$, mean (towards cuckoo) = 9.7 ± 1.7 versus (other treatments) ≤ 1.2 ± 0.4) (Fig. 2a–f and see Supplementary Table 1 for summary data). These data show that both superb fairy-wrens and white-browed scrubwrens produce whining vocalizations primarily towards their cuckoo parasite, which is accompanied by aggressive physical mobbing of the cuckoo model and more birds from other species attending the experimental trial.

Next, when superb fairy-wren and white-browed scrubwren breeding groups were presented with 30 s playbacks of their own whining and alarm vocalizations, as well as control vocalizations[26], we found that playback type significantly affected the number of individuals from their own species that approached the speaker (superb fairy-wren, $\chi^2_2 = 23.9$, $P < 0.0001$, mean (whining) = 2.6 ± 0.2 and (alarm) = 1.9 ± 0.2; and white-browed scrubwren, $\chi^2_2 = 25.5$, $P < 0.0001$, mean (whining) = 2.3 ± 0.1 and (alarm) = 1.24 ± 0.16). Playback type also significantly affected the number of individuals from other species (superb fairy-wren, $\chi^2_2 = 21.6$, $P < 0.0001$, mean (whining) = 1.5 ± 0.2 and (alarm) = 0.7 ± 0.2; and white-browed scrubwren, $\chi^2_2 = 25.4$, $P < 0.0001$, mean (whining) = 2.9 ± 0.3 and (alarm) = 1.00 ± 0.15) (see Supplementary Table 2 for summary data). Approaches by more individuals were recorded when the whining vocalization was played compared with the alarm and control vocalizations in both species (Fig. 2g–j).

Finally, to explore whether hearing whining vocalizations elicit a qualitatively different response to that elicited by hearing alarm vocalizations, we examined whether birds rapidly (that is, within 30 s) approached the sound source to within a distance that could present danger from a predator (<2 m) or only to a distance that offered an opportunity to safely gain information (2–5 m). We found that significantly more superb fairy-wrens (Wilcoxon signed-rank test with continuity correction: $V = 28$, $P = 0.011$; mean (0–2 m) = 2.2 ± 0.2 versus mean (2–5 m) = 0.4 ± 0.1) and white-browed scrubwrens ($V = 1.5$, $P = 0.0008$; mean (0–2 m) = 2.1 ± 0.2 versus mean (2–5 m) = 0.2 ± 0.1) approached closer to the sound source during the whining vocalization playbacks, thereby suggesting more aggressive responses. By contrast, there was no significant difference between the number of superb fairy-wrens ($V = 7.5$, $P = 0.2981$; mean (0–2 m) = 1.12 ± 0.17 versus mean (2–5 m) = 0.8 ± 0.1) and white-browed scrubwrens ($V = 38$, $P = 0.61$; mean (0–2 m) = 0.7 ± 0.2 versus mean (2–5 m) = 0.5 ± 0.2) that approached close compared with farther from the sound source during the alarm vocalization playbacks, thereby suggesting more cautious responses. Overall, these results suggest that whining vocalizations are functionally referential towards their respective brood parasite in both superb fairy-wrens and white-browed scrubwrens. Moreover, compared with alarm vocalizations, hearing whining vocalizations rapidly rallies both conspecific and heterospecific birds directly towards a sound source to facilitate aggressive cooperative mobbing.

Innate recruiting responses towards whining vocalizations within and across host species globally

The diversity of species that produce and respond to whining vocalizations may be a product of an innate response in relevant species, such as potential hosts of brood parasites. Alternatively, whining may represent a directional and detectable vocalization that elicits a response in all nearby species. If the former, we expected that whining vocalizations would primarily attract the attention of species that are potentially vulnerable to brood parasitism (that is, passerines, as they constitute 93% of the world's hosts[22]). If the latter, we expected that it would attract the attention of all nearby birds, regardless of whether they are threatened by brood parasites. To test these alternative hypotheses, we examined the composition of species that attended after presentation of the cuckoo model and compared this to the wider species community in the vicinity of superb fairy-wren and white-browed scrubwren nests. We found that more host than non-host species (Pearson's chi-square test: $\chi^2 = 6.6$, Monte-Carlo-simulated P value, $P_{MC} = 0.0143$) (Supplementary Table 3a) and more passerine than non-passerine species ($\chi^2 = 11.9$, $P_{MC} = 0.0012$) (Supplementary Table 3b) attended cuckoo model presentations, despite no difference in the proportion of passerine hosts and passerine non-hosts attending the cuckoo trials compared with the surrounding environment ($\chi^2 = 0.2$, $P_{MC} = 1$) (Supplementary Table 3c). This result was in contrast to when the control model was presented, in which the composition of hosts relative to non-host species ($\chi^2 = 2.2$, $P_{MC} = 0.32$) (Supplementary Table 3d) and passerines relative to non-passerine species ($\chi^2 = 1.8$, $P_{MC} = 0.32$) were not different (Supplementary Table 3e). This result suggests that whining vocalizations attract the attention of passerines, regardless of their host status (Fig. 2k and Extended Data Fig. 3).

To further test whether these vocalizations elicit a general response in passerines, we conducted a playback experiment in territories of yellow warblers in North America ($N = 14$), where they are hosts of brown-headed cowbirds. When presented with playbacks of superb fairy-wren whining vocalizations (brood parasite-associated vocalization that does not exist in the Americas; Fig. 1c), yellow warbler 'chip' vocalizations (alarm vocalization), yellow warbler seet vocalizations (their brood parasite-associated vocalization[25]) and a control vocalization (wood thrush, *Hylocichla mustelina*, song), we did not find a difference in the number of yellow warblers that responded towards the different vocalization types ($\chi^2_3 = 2.7$, $P = 0.44$). While we found no difference in behavioural response towards the various alarm vocalizations, the absence of a difference between these and the control vocalization precludes our ability to draw meaning from them. By contrast, we did find a difference in the number of other species that responded towards the different vocalization types ($\chi^2_3 = 11.4$, $P = 0.0099$). As we did not find a difference in response by other species towards chip (mean = 0.6 ± 0.2) and whining vocalizations (mean = 0.5 ± 0.2) ($P = 0.65$) (Extended Data Fig. 4), this result suggests that despite being socially learned for their production[27,51], whining vocalizations seem to elicit an innate exaggerated recruiting response in passerines globally.

Finally, if whining vocalizations function equivalently across species to indiscriminately attract the attention of passerines because of deeply conserved biases towards their specific acoustic properties, we expected that all species would respond similarly to them,

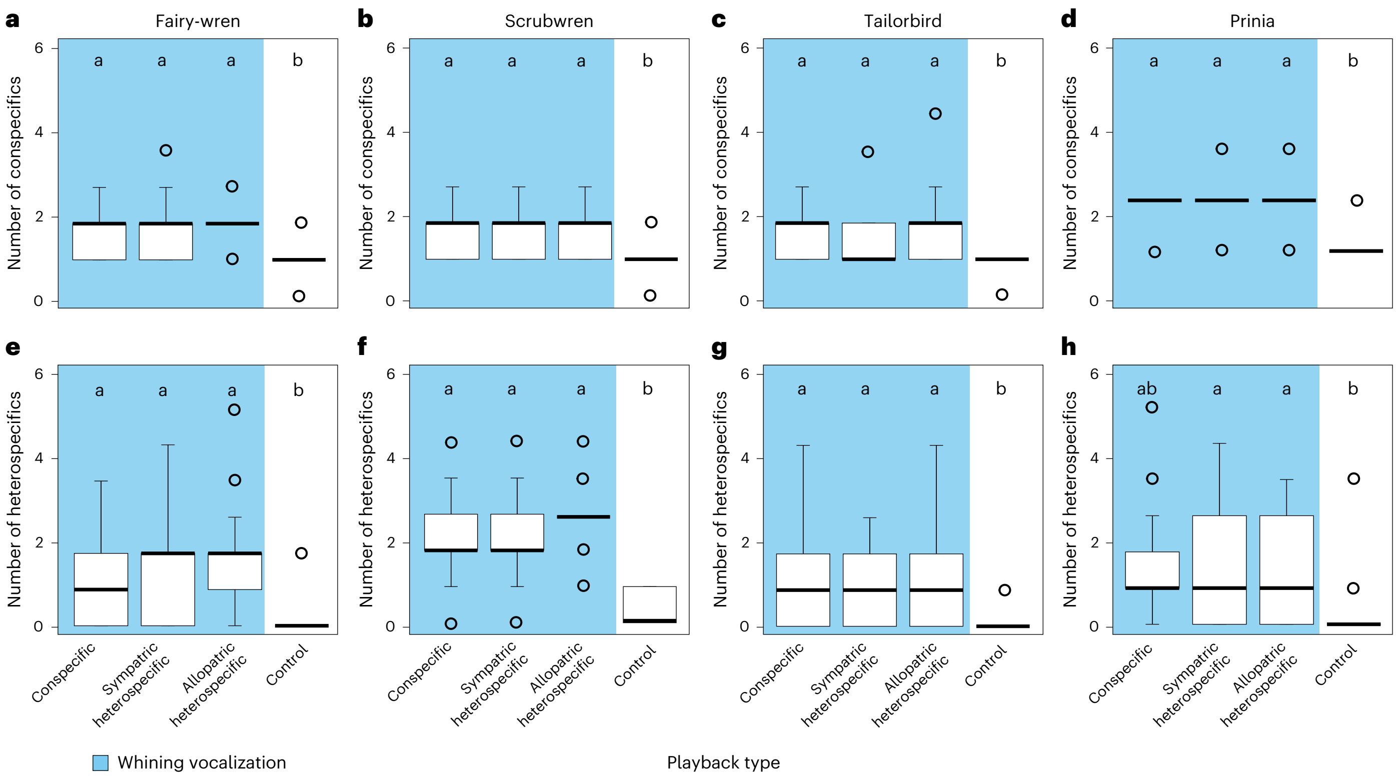

Fig. 3 | Whining vocalizations elicit an equivalent behavioural response at sympatric and allopatric host nests. a–h, Similar recruiting responses were elicited in conspecifics (**a**–**d**) and heterospecifics (**e**–**h**) in Australia (superb fairy-wren (**a**,**e**) and white-browed scrubwren (**b**,**f**)) and China (common tailorbird (**c**,**g**) and rufescent prinia (**d**,**h**)) towards 30 s playbacks of conspecific, sympatric heterospecific and allopatric heterospecific (Australia–China or China–Australia) whining vocalizations compared with a control vocalization (*N* = 17 for each treatment across all species). Blue backgrounds indicate behavioural responses towards whining vocalization playbacks compared with control (white). Boxes represent the median and the upper and lower quartiles. Whiskers are 1.5 times the interquartile range, and circles represent data that lie outside this range. Generalized linear mixed models were used, or Friedman tests if model assumptions were not met (Supplementary Table 4). Letters denote results of post hoc analyses. See Methods for more detail on statistical procedures.

regardless of whether they are conspecific or not, as well as whether they are sympatric with the signaller or not. To test this hypothesis, we conducted a playback experiment that used whining vocalizations from three species (conspecific, sympatric heterospecific or allopatric heterospecific) as well as a sympatric control at host nests in Australia (superb fairy-wrens and white-browed scrubwrens) and in China (common tailorbirds, *Orthotomus sutorius*, and rufescent prinias, *Prinia rufescens*), which are hosts of the plaintive cuckoo (*Cacomantis merulinus*). Playback type had a significant effect on the number of individuals from their own species (superb fairy-wren, $\chi^2_3 = 26.3$, $P < 0.0001$, mean = 1.7 ± 0.2; white-browed scrubwren, $\chi^2_3 = 17.4$, $P = 0.0006$, mean = 1.8 ± 0.2; common tailorbird, $\chi^2_3 = 21.9$, $P < 0.0001$, mean = 1.7 ± 0.2; and rufescent prinia, $\chi^2_3 = 19.6$, $P = 0.0002$, mean = 1.8 ± 0.1, versus controls ≤ 1.24 ± 0.11) and individuals from other species (superb fairy-wren, $\chi^2_3 = 34.7$, $P < 0.0001$, mean = 1.2 ± 0.3; white-browed scrubwren, $\chi^2_3 = 50.8$, $P < 0.0001$, mean = 2.6 ± 0.3; common tailorbird, $\chi^2_3 = 31.2$, $P < 0.0001$, mean = 1.8 ± 0.5; and rufescent prinia, $\chi^2_3 = 23.5$, $P < 0.0001$, mean = 1.8 ± 0.1 versus controls ≤ 0.35 ± 0.24) that approached the speaker (Supplementary Table 4). More birds responded to whining vocalization playbacks compared with controls in all experiments (Fig. 3a–h). This finding indicates that each of the hosts and the surrounding bird communities responded equally to whining vocalizations, regardless of whether they were produced by their own species or another species, including those they have never interacted with.

Discussion

Our results suggest that the pressure imposed on hosts by brood parasites has selected the convergent use of a functionally referential vocalization that contains both innate and learned components. Previous research on superb fairy-wrens has shown that although distinct, the structure of whining vocalizations resembles that of distress vocalizations[26]. The acoustic characteristics that are shared between distress and whining vocalizations have been shown to elicit an innate response when the threat to the signaller is high and imminent[5,35]. However, unlike distress and other innate-reactionary vocalizations that have been observed to be similar across species[52,53] or learned referential vocalizations that contain no apparent innate component[54,55], the production of whining vocalizations in response to the sight of an adult brood parasite is socially learned[27,28], despite it eliciting an innate response in receivers. Given the structural and behavioural response similarity between distress and whining vocalizations, as well as the diversity of species that produce both, we speculate that the origin of whining vocalizations may be found in distress vocalizations that have been modified and repurposed for use in a novel context (high danger to offspring but low danger to the signaller). Overall, our results are consistent with Darwin's early thoughts on the origin of language by providing evidence for an intermediate step between innate-reactionary and learned-symbolic linguistic units[1].

Building on a wave of recent research challenging the long-standing tenet that language is defined by symbolic sound-meaning associations[8–12], our results suggest that this phenomenon can be phylogenetically generalizable and that innate-reactionary linguistic units may be the evolutionary precursors of learned-symbolic units[1]. They also highlight the potential opportunities offered by studying the innate components of communication systems. For instance, in the study of language, linguistic descriptions capture the conventional aspects of words and grammar while overlooking other innate

https://doi.org/10.1038/s41559-025-02855-9

communicative behaviours, such as crying, screaming and other affective vocalizations[56,57]. Researchers investigating animal communication systems also tend to isolate referential, specific and learned signals as the core components of communication, to the extent that they often overlook innate signals like alarm vocalizations[58]. By highlighting a deep evolutionary link between learned and innate communicatory items, our results suggest that innate vocalizations may be central for understanding the origin and evolution of complex learned communication systems, including language.

Methods

Vocalization dataset

Recordings of vocalizations in response to brood parasites (median number of vocalizations per species = 20, range = 9–20) and in response to terrestrial predators (median number of vocalizations per species = 19, range = 10–40) were obtained using two methods: (1) presenting a model of a brood parasite or a terrestrial predator (often near an active nest as described for the model presentation experiments below) with the vocal response recorded on a digital audio recorder (most often a Marantz PMD561 or PMD660); or (2) from ad hoc observations of individuals producing vocalizations designated as alarm vocalizations that were archived in xeno-canto (https://xeno-canto.org). Note that we do not include discussion of alarm vocalizations towards aerial predators in this study. For archival recordings (15 out of 90 total recordings used in the analyses), we cannot be completely certain of the context in which the vocalizations were being produced. However, for 4 out of 8 of the species for which we acquired archival recordings (chalk-browed mockingbird, *M. saturninus*, willow warbler, *P. trochilus*, Japanese leaf warbler, *Phylloscopus xanthodryas*, and yellow warbler), the obtained vocalizations were identical to those verified to be used in response to terrestrial predators. In total, vocalizations were obtained for 27 species from 9 passerine families (Acanthizidae, 3 species; Acrocephalidae, 2 species; Cisticolidae, 3 species; Dicruridae, 1 species; Maluridae, 3 species; Meliphagidae, 3 species; Mimidae, 1 species; Parulidae, 1 species; Phylloscopidae, 9 species; Rhipiduridae, 1 species). A single species, the fork-tailed drongo (*Dicrurus adsimilis*), was excluded from subsequent analyses for two reasons: (1) the vocalizations recorded in each context were highly diverse and the recordings contained vocalizations from multiple individuals, which made it difficult to identify which vocalizations were associated with the model presentation; and (2) drongos are known acoustic mimics[59], which made it challenging to make inferences about the species specificity of the vocalizations they produce. In our resultant dataset (N = 26 species), we had 17 species with 2 recordings per context and 9 species with 1 recording for one or both contexts. For one species, rufescent prinia, available recordings of alarm vocalizations visibly varied, so we included four individual recordings of alarm vocalizations, selected to capture this variation. Most recordings (76 out of 90) contained 10 unique individual vocalizations. The minimum number of individual vocalizations per recording was three, whereas the minimum number for a given species and context was nine. Representative spectrograms of both vocalization types from each species included in our analyses are presented in Extended Data Fig. 1.

Ethics

Research was conducted with approval from the University of Queensland's Animal Ethics Committee (SBS200/15/UQPF), Griffith University's Animal Ethics Committee (ENV/08/19/AEC), Monash University's Animal Ethics Committee (BSCI/2011/28; BSCI/2015/11), Hainan Provincial Educational Centre for Ecology and Environment's Animal Research Ethics Committee (HNECEE-2012-002, HNECEE-2012-003 and HNECEE-2017-001), the University of Illinois at Urbana-Champaign's Animal Ethics Committee (IACUC 21125) and Cornell University's Animal Ethics Committee (IACUC 2009-0105), as well as the Queensland Government (WISP16200615), the State of Illinois (NH19.6220) and the Zambia Wildlife Authority (receipt number: 521049).

Acoustic analysis

Acoustic analyses of all vocalizations were performed using Luscinia (v.2.16.10.29.01; https://github.com/rflachlan/Luscinia). Acoustic measurements were extracted for each vocalization in 1 ms time bins. Over each vocalization, the mean, maximum, minimum, variance, start and end values for mean frequency (Hz), peak frequency (Hz), frequency bandwidth (Hz), spectral flatness (Hz), change in mean frequency between successive time bins (Hz) and absolute value of change in mean frequency between successive time bins (Hz) were extracted. Additional measurements (peak frequency, maximum frequency, minimum frequency, frequency quartiles, 5% and 95% quantiles and vocalization length in ms) were extracted over entire vocalizations. In total, 43 acoustic measurements per vocalization were extracted. All subsequent analyses were conducted in R[60], and the code underlying the following methods is available in the Supplementary Information. To summarize acoustic variation, we conducted a principal components analysis using princomp in base R[60] on all species and vocalizations. Scores for the first ten principal components were extracted and, together, they explained 90% of the variation in the acoustic measurements.

Distinctive vocalizations in response to brood parasites and predators

The superb fairy-wren's whining vocalization has been experimentally shown to be functionally referential to cuckoos[26]. However, two additional species (Hume's leaf warbler and the greenish warbler) have been shown to produce a similar vocalization when they see their cuckoo species, which elicits a similar behavioural response[33] and differs to those made towards predators. Moreover, these brood parasite-associated vocalizations (previously labelled as 'rasp' vocalizations[35]), like the superb fairy-wren's whining vocalization, evoke responses in other host species. Following the observation that whining and rasp vocalizations are acoustically similar[35], we examined whether they have shared acoustic features. To do this, we performed 1,000 discriminant function analyses based on all ten principal components. For each analysis, we randomly sampled an equal number of vocalizations (13) from each context and from each genus and trained a discriminant function (a linear transformation of the principal component scores) using lda in the package MASS[61] to classify vocalizations to contexts (that is, brood parasite-associated or alarm). Then, using the resultant discriminant function, we classified the remaining vocalizations from each species and recorded whether each vocalization was classified as a whining or alarm vocalization. This procedure was performed 1,000 times, which led to between 215 and 715 classifications for each vocalization depending on the number of times the vocalization was part of the testing set. We considered a vocalization to be classified as a whining vocalization if it was classified as a whining vocalization more than 50% of the times it was classified, assessed using binomial tests, binom.test in base R[60], on each vocalization. We then summed classifications within species.

For the remaining 23 species, we classified their vocalizations using the same set of 1,000 discriminant functions, trained on the above listed 3 species, and performed an identical procedure to classify brood parasite-associated vocalizations as whining or alarm vocalizations. We performed a Pearson's chi-square test on the resultant contingency table using chisq.test in base R[60] to determine whether classifications of brood parasite-associated vocalizations varied across species. For each species, we calculated the classification residuals for both whining and alarm vocalization categories of their brood parasite-associated vocalizations ((observed − expected counts)/square root(expected counts)). For the whining vocalization category, any species with residuals less than −2 was considered to produce brood parasite vocalizations that classified significantly less often than expected as whining vocalizations.

Next, to determine whether whining vocalizations of a given species are distinct from their alarm vocalizations, we averaged the principal component coefficients across all 1,000 linear discriminant functions to generate consensus linear discriminant scores for each vocalization. These scores captured the acoustic features of vocalizations along the axis separating whining (negative consensus linear discriminant scores) and alarm (positive scores) vocalizations. We applied linear mixed-effects models using glmmTMB in the package glmmTMB[62] to explain variation in linear discriminant scores. The dataset that we analysed included 816 calls from 25 species, including the superb fairy-wren, Hume's leaf warbler and the greenish warbler, with between 9 and 40 calls per species and vocalization context (that is, brood parasite-associated versus alarm). Species and vocalization context, as well as an interaction between these terms, were included as fixed effects, and individual was included as a random effect. We performed post hoc tests using emmeans in the package emmeans[63]. We considered a species to produce distinct whining vocalizations when two conditions were satisfied in post hoc tests: (1) their brood parasite-associated vocalizations were estimated to have negative linear discriminant scores, similar to those of the superb fairy-wren, Hume's leaf warbler and the greenish warbler; and (2) the difference between their linear discriminant scores of their brood parasite-associated and alarm vocalizations was significantly different from 0 and negative. The resultant 21 species were determined to produce distinct, whining-type vocalizations in response to brood parasites.

Evolutionary history and ancestral-state reconstruction

To examine the evolutionary rates of whining and alarm vocalization types and to conduct an ancestral-state reconstruction, we generated a consensus phylogenetic tree for all 21 species using the ls.consensus function in the package phytools[64] using 1,000 randomly sampled trees based on the Hackett backbone[34]. For two species (Japanese leaf warbler and grey fantail, *Rhipidura albiscapa*), we used sister species (arctic warbler, *Phylloscopus borealis*, and New Zealand fantail, *Rhipidura fuliginosa*, respectively)[34]. The summarized linear discriminant function had the largest coefficient on PC3. We averaged PC3 scores within species and contexts, beginning within individuals. Using the consensus phylogeny, the Adams' [65] likelihood method was used to compare the evolutionary rates of species' mean principal component scores for brood parasite and predator vocalizations on the same phylogeny. The Adams' [65] method uses a LRT to compare the likelihood of a model in which both traits have a common evolutionary rate to that of a model in which the traits have distinct rates. On the basis of a model with distinct rates, the method estimates the evolutionary rates of each vocalization type. Ancestral-state reconstruction was performed for each vocalization type separately, as well as the difference between the measurements for each vocalization type within each species using ace in the package ape[66]. This provided a comparison of acoustic differences between brood parasite and predator vocalizations that is unbiased by phylogeny.

Ecological correlates of whining vocalization production

To investigate the ecological correlates of whining vocalization production, we included data on 25 out of the 27 species for which recordings were obtained. The fork-tailed drongo was excluded for the reasons listed above, as was the mountain chiffchaff (*Phylloscopus sindianus*), which is not confirmed as a host species. We also included 33 species identified through a literature review, of which 28 species were in addition to the 25 already included from recordings. This produced a dataset of 53 species, of which 23 species were identified as producing whining vocalizations and 30 species that did not when presented with the same conditions. Information obtained from the literature was conducted following a previously described method[67]. Peer-reviewed studies were only included if they met the following five criteria:

1. studies experimentally tested for host responses with model, playback and/or live stimulus presentation of an obligate brood parasite and predator near a host nest or on a host territory;
2. experiments compared host responses to an obligate brood parasite, predator and control model in one nest stage or across multiple nest stages;
3. host aggression towards an obligate brood parasite and predator were numerically or categorically quantified (for example, alarm vocalization rate, number of strikes or swoops, closest approach and aggression score) and compared between the types of models and nesting stages tested. Studies that only examined responses that were not directly related to aggression and nest defence, such as time spent foraging, were excluded;
4. researchers provided host aggression data for one or more known stages: laying and incubating, or nestling, and data were provided separately for each stage tested;
5. studies were required to use a control model or playback to generate effect sizes.

For each study ($N = 38$ studies), the species tested was noted along with whether it produced a specific vocalization in response to the presentation of a brood parasite or the same vocalization was produced to the predator and brood parasite and how this compared to the response to a control.

To investigate whether the production of whining vocalizations is associated with within-species interactions, we recorded whether each species was a cooperative breeding or pair breeding species according to a previous study[68]. To investigate whether between-species interactions are associated with the production of whining vocalizations, we calculated the opportunity for between-species communication based on the underlying complexity of brood parasite–host networks for each recording location, as more interacting species provide more opportunity for between-species information transmission. We produced a 'hexgrid' by following a previously described method[22] and overlaid a grid of equal-area hexagons (ISEA3H resolution 7; hexagon area about 23,323 km^2 per a previous study[69]) onto a global map of coastline boundaries to obtain 7,483 hexagons covering terrestrial regions of the world (hereafter 'land hexagons'). For each of the 53 focal species we identified as either producing or not producing whining vocalizations, we intersected the BirdLife International and Handbook of the Birds of the World species' native breeding range shapefile[70] with the hexgrid to generate focal areas of interest. For each focal area, we constructed brood parasite–host interactions networks for each land hexagon by intersecting breeding range shapefiles[70] for all brood parasite and host species to obtain presence–absence data for each species in each hexagon. Next, we used a brood parasite–host interaction dataset[22] to compile a list of pairwise interactions between brood parasites and their respective hosts for each land hexagon. Using these data, we constructed a brood parasite–host interaction network for each land hexagon that describes documented relationships between each brood parasite and host somewhere within each species' range but not necessarily within the region bounded by a particular land hexagon. Continuing with the previously described method[22], we used the function networklevel in the package bipartite (v.2.18)[71] to calculate the linkage density (that is, the number of interactions divided by the total number of species) of each brood parasite–host network. Next, for each species, we calculated the median linkage density across their range, which we used as a measure of complexity and a proxy for the opportunity for interspecific cooperation about the threat of brood parasitism. When the linkage density of the reported location was greater than the global median (1.02 links per species), the region was classified as having a high linkage density, whereas those lower than the global median were classified as having a low linkage density.

We used a Bayesian threshold model to estimate the evolutionary correlation between the presence of the whining vocalization behaviour in a species and cooperative breeding status[68] and the median linkage density across the species' range. Specifically, the threshBayes function in the package phytools[64] was used with the default flat priors.

https://doi.org/10.1038/s41559-025-02855-9

Markov chain Monte Carlo (MCMC) sampling was conducted over 5,000,000 iterations with a thinning rate of 1,000. The first 20% of iterations (1,000,000 iterations) was discarded as burn-in, leaving 4,000 posterior samples for analysis. Using our combined dataset, analyses were then repeated across 1,000 randomly sampled trees based on the Hackett backbone and 1,000 randomly sampled trees based on the Ericson backbone, which were downloaded from BirdTree.org[34]. This provided an indication of whether the distribution of species that produce whining vocalizations could be explained by intraspecific interactions, interspecific interactions or shared ancestry.

Study sites for field experiments

Field experiments were conducted across multiple sites in three countries. In Australia, nests of the superb fairy-wren and white-browed scrubwren, two species frequently parasitized by multiple cuckoo species[50], were located at Lake Samsonvale (27° 16′ S, 152° 51′ E) (hereafter Samsonvale) between July and December from 2015 to 2018. The populations of study species were colour banded to enable identification of individuals, and nests were monitored for egg laying, hatching and fledging. In China, research was conducted in the vicinity of Wang Na village (hereafter Wang Na) in south-west Guangxi (22° 29′ N, 106° 58′ E) between May and June 2017. Nests of two host species, the common tailorbirds and rufescent prinias were located. In North America, research was conducted at multiple sites during 2019 in Champaign (40° 12′ N, 88° 14′ W) ($N = 3$), Iroquois (40° 46′ N, 87° 41′ W) ($N = 1$) and Vermillion (40° 07′ N, 87° 41′ W) counties ($N = 3$) in central Illinois. Here, nests of yellow warblers, a frequent host of the brown-headed cowbird[45,72], were located.

Model presentation experiments to examine whether hosts produce unique vocalizations towards brood parasites

At Samsonvale, superb fairy-wren ($N = 17$) and white-browed scrubwren ($N = 17$) breeding groups were presented with freeze-dried specimens of a brood parasite (shining bronze-cuckoo, *Chalcites lucidus*, for superb fairy-wrens, and brush cuckoo, *Cacomantis variolosus*, for white-browed scrubwrens). Other predators were also presented: eastern brown snake (*Pseudonaja textilis*), a nest predator; brown falcon (*Falco berigora*), a predator of adult passerines; and pied currawong (*Strepera graculina*), a predator of both adults and nestlings. A yellow-faced honeyeater (*Caligavis chrysops*) was used as a non-threatening control. Shining bronze-cuckoo and brush cuckoo models were used as both species are known to parasitize the superb fairy-wren and white-browed scrubwren[50]. Additionally, shining and Horsfield's bronze-cuckoos are congeneric, as are brush and fan-tailed cuckoos, and several studies have found that superb fairy-wrens respond strongly to both Horsfield's and shining bronze-cuckoos[26–28,30]. The eastern brown snake was used as a model nest predator, as this species is a known predator of superb fairy-wrens nests[73] and has been video-recorded preying on nests at this location (W.E.F., personal observations).

Model presentation experiments were conducted during laying or early incubation, as this is when nests are at risk of both predation and brood parasitism. All trials took place between approximately 5:30 and 13:00 during calm, dry weather. A camouflaged hide was erected 10–30 m from a target nest, providing a clear view of the nest and its surrounding area, and a protective cage (0.5 m tall × 0.5 m diameter wire cage, with 1.5 cm diameter mesh) was placed at nest height, 1–2 m from the nest at least 30 min before experimentation to allow for habituation. Following this, and once the target birds had left the area, a model bird was placed on a perch in the cage. During trials involving the eastern brown snake model, the model was placed on the ground by the nest entrance, as this more closely resembles how reptiles approach nests.

The trial commenced when a member of the target breeding group either came within 2 m of the model or started conspicuously vocalizing in response to the model. At Samsonvale, each presentation lasted 5 min and was recorded with a Sennheiser (MKH416-P48U3) shotgun microphone and a Marantz (PMD561) audio recorder. The behavioural responses of the focal birds, as well as the number of heterospecific individuals and species that came within 5 m of the model, were dictated into the recorder during the trial. At the end of the trial, the model was removed, and the next model was presented after an interval of approximately 60 min to allow for carry-over aggression to diminish.

To test whether the model type affected the number of whining vocalizations produced by nest owners, generalized linear mixed models were constructed using the glmmTMB function in the package glmmTMB[62]. The trial number (order) was set as a random effect. Scaled residuals from the fitted model were generated using the function simulateResiduals in the package DHARMa[74] and we checked whether the scaled residuals fitted model assumptions. If assumptions were met, an analysis of variance was performed comparing the fitted model to the null model using the anova function in base R[60]. When assumptions of the generalized linear mixed models were not met, a Friedman rank sum test was performed with the trial number set as a blocking variable using the friedman.test function in base R[60]. To test whether the total time spent within 0.5 m of a model by at least one bird differed by treatment and whether the total number of heterospecific individuals that approached within 5 m of a model differed by treatment, the same methods for constructing a generalized linear mixed model (as described above) were used, but the dependent variable was changed as appropriate. To test which treatments produced significantly different results, post hoc tests were run using emmeans in the package emmeans[63] if generalized linear mixed model assumptions were met or with Conover's all-pairs test with a Holm correction using the function frdAllPairsConoverTest in the package PMCMRplus[75] if they were not.

Playback experiments to test whether host vocal responses towards brood parasites elicit a unique behavioural response

Playbacks were conducted at Samsonvale to investigate whether superb fairy-wrens and white-browed scrubwrens perform a predictable (and unique) behavioural response to whining vocalizations. Playbacks of superb fairy-wren whining vocalizations, superb fairy-wren predator-context vocalizations and the 'bell' vocalization of crimson rosellas (*Platycercus elegans*), a non-threatening control, were collated from multiple locations to avoid biases. Recordings of 30 s in duration were constructed from recorded sequences that were at least 3 s in duration using Raven Pro (v.1.6.4)[76]. Vocalizations were standardized to their natural amplitude as tested in the field using a D-1411E Dawe Instruments England acoustical calibrator (alarm vocalizations 72 dB, whining vocalizations at 75 dB and crimson rosella bell vocalizations at 78 dB at about 10 m). At least five recordings of treatment were assembled and a unique playback series created for each trial to avoid pseudo replication. Trials were conducted at superb fairy-wren and white-browed scrubwren nests during laying or early incubation, as this is when nests are at risk of both predation and brood parasitism. Trials commenced when a nest owner came within 2 m of the speaker and continued for the duration of the playback. The number of conspecifics and heterospecifics that came within 2 m and within 5 m of the speaker was recorded. At the end of the trial, an interval of at least 30 min was allowed before commencing the next trial to allow for carry-over aggression to diminish (similar to a previous study[26]). The same methodology used to analyse the data from the model presentation experiment was applied to examine whether vocalization type had an impact on the number of conspecific and heterospecific individuals that responded. Additionally, to assess whether there was a qualitative difference in the behavioural response towards whining and alarm vocalizations, we used Wilcoxon signed-rank tests with continuity corrections, using the wilcox.test function in base R[60], to analyse how birds approached these threats: whether to a distance where mobbing could occur but also pose a potential risk if the threat is misidentified or miscalculated (0–2 m), or to a distance that offers the opportunity to gain information about a threat without direct engagement (2–5 m).

Point counts

To sample the avian community when no model treatment was present to enable a comparison with the community attracted to model presentation experiments, a series of point counts were completed at Samsonvale between July and December in 2017 and 2019. Point counts were conducted at randomly selected nest sites of superb fairy-wrens ($N = 24$) and white-browed scrubwrens ($N = 21$) after nests were no longer in use. Point counts took place between sunrise and 2 h after sunrise, when most birds are typically the most vocal. After a 2-min rest period to account for human disturbance on arrival at the location, point counts ran for 10 min, during which time an experienced observer recorded all individual birds within 50 m to the species level. A repeat count was conducted at least 1 week later and during the 1 h period that had not been counted during the previous count to account for temporal bias.

To examine whether the composition of species that attended model cuckoo presentation trials differed from the wider species community based on point counts, we compiled a list of species recorded during all superb fairy-wren and white-browed scrubwren model presentation trials involving cuckoo and control models, and associated point counts. Here point count data were used as a representation of the whole species community in the vicinity of nests. Some superb fairy-wren nests were located close to water, such that the point count area overlapped with wetland areas. These habitats are not ecologically relevant to this study as cuckoo hosts at Samsonvale are all terrestrial species; therefore, species classified as being associated with 'wetland', 'coastal', 'marine' and 'riverine' habitats as previously described[77] were excluded from subsequent analyses. Furthermore, domestic chicken (*Gallus gallus domesticus*) and helmeted guineafowl (*Numida meleagris*) were excluded from analyses, as individuals of these species are present owing to being deliberately released. Pearson's chi-squared tests with a Monte-Carlo-simulated P value (based on 10,000 replicates) were performed, using the chisq.test function in base R[60], to determine the following aspects: (1) whether more host species attended model cuckoo presentation trials compared with the wider environment; (2) whether more passerines (93% of host species are passerines) attended model cuckoo presentation trials than non-passerines; and 3) whether more passerine hosts attended model cuckoo presentation trials than passerine non-hosts. Chi-square tests were then repeated using data on species that attended control model presentation trials.

Playback experiment to investigate whether whining vocalizations elicit an innate response

Playback experiments were conducted in Illinois, United States, to investigate whether whining vocalizations elicit an innate response in a region where no species produce whining vocalizations. Identical methods were followed as the experiments conducted at Samsonvale, which tested whether host vocal responses towards brood parasites elicit a unique behavioural response, except the following treatments were used: superb fairy-wren whining vocalizations, yellow warbler seet vocalizations, yellow warbler alarm vocalizations (chip vocalization) and wood thrush (*Hylocichla mustelina*) songs, a non-threatening control. Trials were conducted at active yellow warbler nests or in active yellow warbler territories ($N = 14$) where behavioural cues indicated breeding was occurring[78]. The same methodology used to analyse the data from the model presentation experiment was applied to examine whether vocalization type had an impact on the number of conspecific and heterospecific individuals that responded.

Playback experiment to examine sympatric and allopatric, conspecific and heterospecific responses to whining vocalizations

Playbacks were conducted at Samsonvale, Australia, and at Wang Na, China, to examine how sympatric and allopatric, conspecific and heterospecific birds responded to whining vocalizations. Identical methods were followed as the experiments conducted at Samsonvale that tested whether host vocal responses towards brood parasites elicit a unique behavioural response, except trials were conducted at superb fairy-wren and white-browed scrubwren nests at Samsonvale and at common tailorbird and rufescent prinia nests at Wang Na. The following treatments were used: superb fairy-wren, white-browed scrubwren, common tailorbird and rufescent prinia whining vocalizations, and the vocalizations of crimson rosella, in Australia, and oriental turtle dove (*Streptopelia orientalis*), in China, as non-threatening controls. Each of the four experimental species received conspecific whining vocalization, sympatric heterospecific whining vocalization, allopatric heterospecific whining vocalization and a control vocalization playback treatment ($N = 17$ for each treatment). The same methodology used to analyse the data from the model presentation experiment was applied to examine whether vocalization type had an impact on the number of conspecific and heterospecific individuals that responded.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Datasets used in this study are available in the Supplementary Data.

Code availability

An R script containing all the codes used for statistical analyses is available in the Supplementary Code.

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Acknowledgements

This work was supported by the Alexander von Humboldt Foundation (to W.E.F. and M.E.H.), Birds Queensland (to W.E.F. and M.S.W.), the British Trust for Ornithology (to W.E.F.), the Hermon-Slade Foundation (no. HS15/1 to W.E.F.), Griffith University and the University of Queensland (to W.E.F.), a Whitten PhD Studentship in the Department of Zoology, University of Cambridge (to J.A.K.), a Clare Hall Research Award, University of Cambridge (to J.A.K.), an Edward W. Rose Postdoctoral Fellowship in the Cornell Lab of Ornithology for part of this work (to J.A.K.), the US National Science Foundation (no. 1353681 to M.S.W., no. 1953226 to M.E.H. and no. 1952726 to S.A.G.), the National Key R & D Program of China (2023YFF1304600 to W.L.), the National Natural Science Foundation of China (32270526 and 32470513 to W.L.), the National Geographic Society (NGS-60453R-19 to M.E.H.), the Australian Research Council (FT110100505 and DP150103595 to A.P.), the Australian Wildlife Conservancy (to N.T. and A.P.), a Royal Society Dorothy Hodgkin Fellowship (to C.N.S.), a Biotechnology and Biological Sciences Research Council David Phillips Research Fellowship (BB/J014109/1) (to C.N.S.), the National Agency for the Promotion of Science and Technology (ANPCyT), National Science Centre, Poland (grants 2012/05/E/NZ8/02694, 2016/23/B/NZ8/03082 and 2022/45/B/NZ8/03740 to A.A., R. Gula and J.T.), and the National Scientific and Technical Research Council (CONICET) (to V.D.F.). We also thank E. Miller for sharing pipelines, which helped with constructing phylogenetically corrected linear models, as well as B. Kempenaers, C. Riehl and J. Fischer for comments on the manuscript. Finally, we thank all our field assistants (E. Aarsvold, A. Branney, R. Bracken, C. Brock, J. D. Brooks, M. Chan, L. Clarke, J. Cosentino, Z. Davis, W. Deptula, B. Donnelly, V. Drolet-Gratton, S. Dougill, R. Green, D. Erickson, M. Freeby, D. Ferraro, L. Fried, J. Grayum, K. Gielow, M. Grundler, J. Grudens, C. Hawey, N. Hunt, L. Huntsmith, O. Kashembe, S. LeQuier, L. Lichtenauer, M. Marsh, A. Miller, C. Moya, S. Mwanza, J. Platzer, R. Neil, A. Sargent, M. Scheuering, D. Thrasher, D. Tolman, R. Weisbeck, J. Welklin, A. Werrell, J. Upton and E. Zarri) for their time and expertise, without which this research would not have been possible.

Author contributions

W.E.F. conceived the study with input from J.A.K., D.W., D.E.B., A.M., W.L. and M.S.W. W.E.F., J.A.K., B.Z., S.L.L., J.K.E., N.M.R., N.T., M.A., S.A.G., V.D.F., J.B., M.Z., A.A., R. Gula, J.T. and M.E.H. collected the data. W.E.F., J.A.K., A.M. and D.W. implemented the analyses. W.E.F., J.A.K., D.W. and D.E.B. wrote the manuscript with input from all authors.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-025-02855-9.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-025-02855-9.

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Peer review information *Nature Ecology & Evolution* thanks Sonia Kleindorfer, Jingyi Yang and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

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https://doi.org/10.1038/s41559-025-02855-9

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