Animal communication: Lyrebirds ‘cry wolf’ during mating

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PTI signaling, then simultaneous transformation of recognition proteins for multiple effectors into crops may not only make the evolution of pathogen resistance more difficult, but also quantitatively increase plant defense responses when more than one effector is recognized.

Together, these two papers elegantly redefine the nature of two intertwined pathways in plant immunity, with implications and opportunities, from the study of signaling mechanisms to crop protection.

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Animal communication: Lyrebirds 'cry wolf' during mating

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During courtship, male lyrebirds create acoustic illusions of a flock of birds fending off a predator. These realistic illusions fool the imitated species to engage in mobbing, but intriguingly lyrebirds produce them only preceding or during copulation.

Mimicry comes in many guises[1]. Bright, gaudy colours in frogs and insects can make them resemble conspicuously coloured poisonous species. Foul smells of carrion flowers or stinkhorn fungi attract flies and beetles as unwilling pollinators. The first examples illustrate classic Batesian visual mimicry, where non-poisonous species reduce risk of predator attacks by mimicking the warning colours of poisonous species. The second example is a case of olfactory mimicry: the carrion smell attracts pollinators that remain unrewarded because they were duped into expecting carrion. These examples illustrate the 'trinity of mimicry'[1,2]: a mimic, a model and a selecting agent (the intended receiver). A mimic needs to resemble a heterospecific model closely enough to be mistaken by potential receivers as the model. These relations are often difficult to completely ascertain. Bird vocal mimicry is a case in point. Many examples of heterospecific sound copying are documented[3–6], including such intriguing examples as the imitation of human speech or artefacts like car alarms, ringtones or chainsaws[3,4,6]. However, there has been little consensus on the function of such vocal mimicry, likely because of an overly strong conditional focus on vocal learning[2–7]. Consequently, the investigative framework of bird vocal mimicry differed from other fields and thus perhaps caused some oversight of its adaptive function(s)[2,5]. In a recent study in *Current Biology*, Anastasia Dalziell and colleagues[8] present a previously undescribed form of functional mimicry that adds a new, strikingly different dimension to avian vocal mimicry and a bold functional explanation to go with it[8]. Male lyrebirds (Figure 1) can create acoustic illusions of mixed-species flocks mobbing a predator, and intriguingly so just before or during copulations. These findings stimulate exciting questions regarding the function, evolution and development of this extraordinary form of mimicry.

Figure 1. A male lyrebird, *Menura novaehollandiae*.
Photo: Alex Maisey.

Lyrebirds, one of Australia's iconic birds and mimics, are ground dwelling forest birds with a polygynous mating system with uniparental female care. Males clear a display area in the forest undergrowth to perform spectacular song and dance to attract and mate with females. Dalziell and colleagues[8] now present impressive data from years of field observations, careful analyses of audio and video recordings from camera traps, and playback experiments that together uncover a spectacular new form of vocal mimicry. During their courtship, male lyrebirds recreate the cacophony of a mixed-species flock in the process of mobbing a predator including such fine details as wing flapping of the agitated birds. These illusions of a whole ecological community event are woven into their already dazzling multimodal song and dance courtship display as the 'D-song'[9] at a crucial sequential position (just before and during copulations). The mimetic mobbing showed striking associations with crucial determinants of fertilisation. Males would start the mimetic mobbing event prior to and during all copulations but also when visiting females started leaving prior to copulation but never in any other context. The mimicry shows extraordinary similarity with real mobbing as validated by detailed bioacoustic analyses and playback experiments. Broadcasts of mimetic and real mobbing events were equally recruiting and engaging the various passerine species normally forming the mobbing flocks, demonstrating the behavioural salience of the mimicry to the bird flocks modelled by the lyrebird. This makes it likely that other potential receivers would also perceive the two as one. But is this mimicry an antipredator strategy or meant to deceive conspecifics? The exclusive usage of the mimicry as an integral part of males' complex multimodal courtship and during ensuing copulations suggests females as intended receivers.

But why would males produce such an elaborate acoustic illusion of a mobbing flock just before and during copulations? Is this a sensory trap as the authors hypothesize? A 'sensory trap' requires a mating signal that is similar to an already existing signal or cue. Outside the mating context, it should trigger an adaptive response in the receiver (e.g. approach or freezing as an anti-predator strategy) but during courtship now 'traps' receivers to show the same response non-adaptively in the wrong context and to the advantage of the sender[10]. Applied to the lyrebird example, females would initially react to the males' courtship, but upon hearing the mimetic mobbing they would react with antipredator behaviour (e.g., freezing or moving to join the mobbing). Either response would keep her longer near the male, which may benefit mating success. However, a *sine qua non* of sensory traps is the (demonstration of) deception of the receiver. For this, future work would have to compare females' reactions to mimetic versus real predator mobbing sounds. As discussed by the authors, playing back the original and mimetic events to females away from a courtship arena could provide such a test, but will be logistically challenging. Alternative scenarios might be worth considering too. Interpreting the D-song as a sensory trap seems a possible evolutionary scenario from a unimodal signalling perspective. However, lyrebird courtship shows important hallmarks of a multimodal mating display, raising the possibility of cross-modal integration of the visual and acoustic components into a multimodal percept[11–13]. This differs by definition qualitatively from a unimodal percept, which makes it unlikely that the female is deceived into mistaking this part of the courtship as a mobbing event. Even if the male stops dancing with the onset of copulation, the preceding (audio-)visual display could still affect the trailing acoustic part of the mimetic event[12]. While this is an argument from a mechanistic perspective, it is also worth considering alternative functional scenarios to explain the evolution and maintenance of this intriguing behaviour. Mobbing can decrease the risk of predator attacks. If the mimicked mobbing deters potential lyrebird predators, then the safest moment to copulate might be when the male is producing the illusion. Under this scenario, both males and females would benefit from the acoustic illusion deterring predators from approaching them when most vulnerable.

Lyrebirds are known vocal learners and apt mimics which — as the authors suggest — make it likely that the acoustic illusion is learned too. The females' experience with the acoustic displays and predator events might affect their responsiveness, as social learning process can influence model selection, usage and perception of alarm and mimetic signals[14,15]. The observation that lyrebirds in the two studied populations with different surrounding avifauna had incorporated their local species is in line with learning at least parts of the signal. This raises the interesting question of model choice. Young males could learn from the mobbing flocks directly or from the courtship displays of other males. Notably, all studied males produced the illusions of mobbing flocks during the 'D-song' part of courtship and combined it with specific parts of the dance routine[9]. This raises the possibility that the mimicry originally evolved as an antipredator strategy but has undergone ritualisation since[16], and is now decoupled from its original function. Lyrebirds copying from lyrebirds could learn the D-song together with the associated dance elements and its sequence in the courtship display[9], something they could not learn from the ecological model. The mimetic mobbing vocalisations do not occur in female lyrebirds' repertoires, although females, like males, are versatile singers and mimics of other bird species in their environment[17]. Such sex differences in learned vocalisations arising from sex-specific model choice are an important window into potential functions of sex-specific behaviour[18] because unravelling sex-specific cultural transmission routes can reveal social relations and important receivers. Males cannot learn D-song from their mothers, and because females raise their young alone, these are unlikely to later relocate their father as a song model. This raises the question of which males in the population are chosen as song models but also how this specific mimicry became sex-limited to males. The noticeable absence of these mobbing but not other mimetic vocalisations in female repertoires remains suggestive of a male-specific function. The occurrence of this signal during mating only is in line with a sensory trap. The same signal could, however, also be positively selected as an anti-predator adaptation, protecting males and females during a prolonged copulation on the ground, which is a most vulnerable situation for the birds. There must be costs to using this signal in other contexts as females do not use it at all and males only at clearly defined moments within their mating display, suggesting that — as in the Aesop fable — it might not be advantageous to cry wolf too often.

The study by Dalziell and colleagues[8] presents an exciting novel finding — the mimicry of an ecological community event embedded in a mating signal points to multi-layered interspecies communication across modalities and contexts digressing into a complex mating signal with potential dual or multiple functions. These findings should inspire us to expand our views on vocal mimicry and increase awareness of multimodal components of warning and mating signals (and their surprising marriage in this example). They are fascinating as they provide a new perspective on how signalling and information transfer in one species in its most intimate moments is interwoven with the communication systems of friend and foe in the forest.

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