Animal Behaviour 108 (2015) 33–41

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Does signal deterioration compromise eavesdropping on other species' alarm calls?

Trevor G. Murray*, Robert D. Magrath

Division of Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra, ACT, Australia

ARTICLE INFO

Article history:
Received 5 February 2015
Initial acceptance 18 March 2015
Final acceptance 22 June 2015
Published online
MS. number: 15-00093R

Keywords:
alarm call
communication
eavesdropping
signal attenuation
signal degradation
superb fairy-wren
white-browed scrubwren

Individuals gain valuable information by eavesdropping on others species' signals, but there are potentially greater constraints on eavesdropping than reception of signals from conspecifics. Eavesdroppers rely on signals addressed to others, which may come from unpredictable directions and distances. Furthermore, eavesdroppers might lack familiarity with other species' calls or perceptual adaptations to detect and recognize them, and these difficulties may be exacerbated by signal changes during transmission. We tested whether signal changes differentially affected the response to heterospecific compared with conspecific aerial ('hawk') alarm calls in two sympatric species that respond to each other's alarms, superb fairy-wrens, *Malurus cyaneus*, and white-browed scrubwrens, *Sericornis frontalis*. We assessed the effects of signal attenuation (reduced amplitude) and degradation (including reverberation). Attenuation caused a reduction in probability of fleeing to cover, and birds were less likely to flee to heterospecific than conspecific alarms. Signal changes did affect the response to heterospecific compared to conspecific calls, but not in the simple way expected. For conspecifics, degradation had no effect, and attenuation caused a similar reduction in fleeing for degraded and undegraded calls. By contrast, for heterospecifics, attenuation caused a reduction in fleeing for undegraded but not degraded calls, which prompted constant, low fleeing rates. Additional measures of response suggest that a lower probability of fleeing was partly a consequence of poorer detection or recognition of calls, and not merely assessment of reduced danger. Overall, the results are consistent with greater constraints on heterospecific eavesdropping than conspecific communication, perhaps because of lower familiarity or perceptual specialization.

Individuals often gain valuable information by eavesdropping on the signals of other species. Signals evolve because, on average, they benefit senders by affecting the behaviour of intended receivers during the process of communication (Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). Receivers, in turn, are selected to respond only if they benefit from the signal, which means that communication requires the evolution of both signalling by senders and their reception and use by receivers (Maynard Smith & Harper, 2003). In contrast to communication, eavesdropping entails individuals gaining information from signals intended for others, including other species, and the sender often does not benefit and can even pay a cost from such eavesdropping (reviews: McGregor & Dabelsteen, 1996; Peake, 2005; Wiley, 1983). For example, individuals can locate suitable habitat by eavesdropping on the signals of individuals already resident (e.g. Pupin, Sacchi, Gentilli, Galeotti, & Fasola, 2007), many predators or parasites locate prey by eavesdropping on their mating signals (review: Zuk & Kolluru, 1998), and prey may avoid predators by eavesdropping on their signals (e.g. Li, Wang, Tan, Qu, & Nieh, 2014). The information gained by eavesdroppers is not necessarily similar to the information gained by intended receivers; a mating signal, for example, reveals the location of food to an eavesdropping predator but helps find a mate for the intended receiver. Overall, eavesdropping provides valuable information to individuals and is probably common in all complex communities (reviews: Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Schmidt, Dall, & Van Gils, 2010; Seppänen, Forsman, Monkkonen, & Thomson, 2007; Zuk & Kolluru, 1998).

A special case of eavesdropping entails ecologically similar species at the same trophic level, which require similar resources and are vulnerable to the same threats. Information acquired from

---

* Correspondence: T. G. Murray, Division of Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia.

E-mail address: Trevor.Murray@anu.edu.au (T. G. Murray).

http://dx.doi.org/10.1016/j.anbehav.2015.07.015

these species, either through eavesdropping on signals or detecting other cues, is therefore likely to be particularly relevant in revealing valuable resources or relevant threats (Seppänen et al., 2007). Here, we focused specifically on eavesdropping on alarm calls among species with shared predators as a model for eavesdropping more broadly. Such eavesdropping is particularly revealing because eavesdroppers are likely to benefit by decoding the same information from signals as does the intended receiver. This means we can directly compare communication with the process of eavesdropping.

Eavesdropping on other species' alarm calls is widespread and important, because most species are vulnerable to predators, and alarm calls potentially convey detailed information about danger. Many species of birds and mammals give alarm calls, designed primarily to warn conspecifics and deter predators (reviews: Caro, 2005; Klump & Shalter, 1984; Zuberbuhler, 2009). Furthermore, alarm calls can communicate to conspecifics detailed information about the type of predator (e.g. Evans, Evans, & Marler, 1993; Seyfarth, Cheney, & Marler, 1980; Suzuki, 2012), its behaviour (e.g. Griesser, 2008) and the degree of danger (e.g. Leavesley & Magrath, 2005; Templeton, Greene, & Davis, 2005). Some species can even communicate simultaneously about both the type and degree of danger (Manser, 2001; Manser, Bell, & Fletcher, 2001). Given the value of the information, it is not surprising that many species eavesdrop on heterospecific alarm calls: playback experiments have demonstrated eavesdropping on about 70 species, which include closely and distantly related species (review: Magrath, Haff, Fallow, & Radford, 2015). For example, many birds eavesdrop on other species of birds, and mammals on mammals, but some mammals also eavesdrop on birds, birds on mammals, and a few lizards eavesdrop on birds (Fuong, Keeley, & Blumstein, 2014; review: Magrath et al., 2015). Such eavesdropping is beneficial in avoiding immediate danger, and also by enhancing foraging, affecting habitat use and facilitating learning about predators (review: Magrath et al., 2015).

Despite the extent and benefits of eavesdropping on other species' alarm calls, there are likely to be more constraints on the interception of signals during heterospecific eavesdropping than on signal reception during conspecific communication. (1) Eavesdroppers may lack species-specific perceptual specializations that can allow better detection of conspecific than heterospecific calls, or better discrimination among conspecific calls (review: Dooling, 2004). (2) Heterospecific calls come from more unpredictable directions and distances than conspecific calls from known group members, and there can be further uncertainty about which heterospecific calls will occur. Such uncertainty about signal properties reduces their detectability (review: Wiley, 2006). (3) Eavesdroppers by definition must intercept calls intended for others, and so do not benefit from adaptations such as variation in amplitude, orientation and timing of calls designed to target intended receivers and which may minimize the potential for eavesdropping (reviews: Brumm & Slabbekoorn, 2005; Dabelsteen, 2005; Yorzinski & Patricelli, 2010). (4) Individuals are likely to be more familiar with conspecific calls, which in itself can lead to better discrimination (Dooling, 2005; reviews: Wiley, 2006). Furthermore, the lack of species-specific perceptual abilities, reduced familiarity and greater uncertainty about signal properties are likely to mean that eavesdropping will become particularly difficult when signal quality or signalling conditions are poor, such as when calls are of low amplitude, degraded during transmission, or when there is a low signal to noise ratio. Despite the widespread importance of eavesdropping on alarm calls, there has been little study of constraints on eavesdropping, and we are aware of no study of constraints on eavesdropping imposed by signal attenuation or degradation. On the contrary, most experimental tests of communication and eavesdropping have assessed responses to playbacks presented under ideal conditions for reception, using high-quality calls broadcast at a clearly audible amplitude.

In this study, we compared the responses of two species of birds to their own and the other species' alarm calls, including testing whether call attenuation or degradation exacerbated any constraints on eavesdropping. White-browed scrubwrens, *Sericornis frontalis*, and superb fairy-wrens, *Malurus cyaneus*, have similar predators, both produce multi-element aerial alarm calls given to predators in flight, and each responds by fleeing to cover to playback of both their own and the other species' alarm calls when presented under ideal conditions (Magrath, Pitcher, & Gardner, 2007). Furthermore, both species respond to urgency information encoded in each other's calls by being more likely to flee to cover to calls indicating more immediate danger (Fallow & Magrath, 2010; Leavesley & Magrath, 2005). The alarm calls of the two species share several acoustic characteristics (Methods), but are known to be perceptually distinct because individuals ignore playback of the other species' alarm calls when unfamiliar (Haff & Magrath, 2013; Magrath, Pitcher, & Gardner, 2009b). Finally, there is some evidence that fairy-wrens find eavesdropping on scrubwren alarms more difficult when playbacks are at lower amplitude (Magrath et al., 2007), although there has been no study of the effects of either attenuation or degradation on the response to heterospecific compared to conspecific calls.

Our study used systematic variation in signal attenuation (reduction in amplitude) and signal degradation (such as the accumulation of reverberations), since they are the two primary ways that signals change during transmission, to compare the response of focal birds to conspecific and heterospecific alarm calls. We hypothesized that attenuated or degraded signals would prompt lower rates of fleeing to cover in response to heterospecific than conspecific calls, with the greatest difference occurring when calls were both of low amplitude and degraded. Consistent with previous work, the probability of fleeing to conspecific and heterospecific calls should be similar when they are both high amplitude and undegraded.

METHODS

Study Site and Species

We studied superb fairy-wrens and white-browed scrubwrens in the Australian National Botanic Gardens and parks around Lake Burley Griffin in Canberra, Australia. The study sites were within a 4.5 km diameter, and all contained a combination of open areas, often used for foraging, and dense cover, used for breeding and foraging. Most individuals of each species were colour-banded in the Botanic Gardens, where they are the subject of long-term studies (Cockburn, Osmond, Mulder, Double, & Green, 2008; Magrath, 2001).

Fairy-wrens and scrubwrens are ecologically similar. They are predominantly ground-foraging passerines that lay their eggs between August and January (Higgins & Peter, 2002; Higgins, Peter, & Steele, 2001; Magrath et al., 2000). Each species holds breeding territories, occupied by simple pairs or cooperatively breeding groups including one or more male helpers (Higgins & Peter, 2002; Higgins et al., 2001). The mean group sizes at the study site are about 2.9 for fairy-wrens and 2.7 for scrubwrens (Higgins et al., 2001; Magrath & Whittingham, 1997). Territories overlap between the species, and fairy-wren territoriality partly breaks down in the nonbreeding season, when birds can form transient mixed-species flocks (Higgins & Peter, 2002). The two species are vulnerable to the same predators, which at the study sites include pied currawongs, *Strepera graculina*, laughing kookaburras, *Dacelo*