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# Heterospecific alarm call recognition in a non-vocal reptile

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**The ability to recognize and respond to the alarm calls of heterospecifics has previously been described only in species with vocal communication. Here we provide evidence that a non-vocal reptile, the Galápagos marine iguana (*Amblyrhynchus cristatus*), can eavesdrop on the alarm call of the Galápagos mockingbird (*Nesomimus parvulus*) and respond with anti-predator behaviour. Eavesdropping on complex heterospecific communications demonstrates a remarkable degree of auditory discrimination in a non-vocal species.**

**Keywords:** eavesdropping; heterospecific recognition; animal communication; marine iguanas

## 1. INTRODUCTION

Predation can represent a strong selective factor in prey populations, sometimes resulting in the development of complicated and unique behavioural defences (reviewed in Griffin 2004). The trade-off between maintaining anti-predator vigilance and devoting resources to other activities has been ameliorated in many group-living species by the development of alarm calls, specific vocalizations that signal the presence of predators to neighbouring conspecifics (Macedonia & Evans 1993; Hauser 1996). Some mammalian and avian species demonstrate an ability to respond to the alarm calls of heterospecifics, thereby gaining access to an additional source of information about the presence of shared predators. This ability has typically been found in closely related species pairs and among alarm-calling species living in close association with one another (Nuechterlein 1981; Seyfarth & Cheney 1990; Ramakrishnan & Coss 2000; Fichtel 2004). In some cases complex information, including predator size and type, can be gleaned from heterospecific calls (Rainey *et al.* 2004; Templeton & Greene 2007).

It is not clear how individuals recognize heterospecific alarms (Hurd 1996). Some evidence suggests that heterospecific response can result from a learned association between predator presence and alarm calls (Shriner 1999). Alternatively, this response could be innate and may be triggered by acoustical properties shared between alarm calls (Johnson *et al.* 2003; Russ *et al.* 2004). Heterospecific alarm call

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recognition has been documented only among species that communicate vocally, and we know of no evidence that non-alarm calling species associate complex auditory stimuli with the threat of predation.

We tested whether heterospecific alarm call recognition was present in the Galápagos marine iguana (*Amblyrhynchus cristatus*), a reptile that does not emit any kind of vocalizations or auditory alarm signals (though non-communicative sound accompanies salt expulsion), and would benefit greatly from eavesdropping. Marine iguanas on Santa Fe Island live in close proximity to alarm-calling Galápagos mockingbirds (*Nesomimus parvulus*), and both species are preyed upon by the Galápagos hawk (*Buteo galapagoensis*). An average of 2.1 hawk predation attempts per day on iguanas inhabiting the southeast coast of Santa Fe were observed annually between 2000 and 2005.

Although the majority of successful predation events involve juvenile marine iguanas, adult-sized females are occasionally preyed, and typically perform alert and escape behaviours in the presence of hawks (Boersma 1984). Hawk flyovers during the 2004 mating season elicited alert or escape behaviour 53.4% of the time ( $n=204$ ) in adult females (M. Vitousek 2004, unpublished data). Simulated flyover experiments at the nesting ground found that 73% of females scattered in response to a hawk model, whereas only 2% scattered in response to a frigate bird model (M. Wikelski 1989, unpublished data).

Iguanas are frequently unable to observe hawks until they are in close proximity due to the topography of the rocky shoreline. Marine iguanas appear to communicate with each other primarily through visual and olfactory means that are less reliable than auditory signals for the rapid transmission of information over long distances (Endler 1993; Lengagne *et al.* 1999). Eavesdropping on the auditory signals of heterospecifics to gain information about predator presence from a greater distance could enable a more effective escape response, particularly in environments where predator-safe locations are widely spaced.

## 2. MATERIAL AND METHODS

Data were collected in January of 2007 at three sites near Bahía Paraiso on the island of Santa Fe, Galápagos (figure 1). Sites are separated by approximately 300 m of coastline, and site boundaries delineated by distinct topographical features. Female marine iguanas are highly site faithful, and movement between sites is rare (Vitousek *et al.* 2007).

The song and alarm calls of a habituated Galápagos mockingbird were recorded from a distance of less than 1 m and edited to produce two soundtracks, each consisting of two to three exemplars of song or alarm calls. Vocalizations were recorded with a directional microphone (Sennheiser-K6, Saul Mineroff Electronics, Elmont, NY) and Panasonic RR-QR150 digital recorder. The peak level of the call as recorded is  $-0.78$  dBFS and of the song is  $-2.11$  dBFS (noise on this recording reached  $-0.12$  dBFS). The ratio of peak sound intensity of the call to song was 1.36 (figure S1 in the electronic supplementary material).

Sequences of song and call, preceded by 30 s of recorded ambient noise, were broadcast using a Sony MZ-R700 minidisc player and an amplified field speaker (SME-AFS, Saul Mineroff Electronics, Elmont, NY) at approximately 100 dB (10 cm from the source; Radio Shack sound level meter no. 33-2055) to clusters of iguanas. The behaviour of 10–15 juvenile and female-sized iguanas was recorded during the first 15 s of vocalization playback. When clusters contained more than 15 possible subjects, individuals were randomly selected for observation prior to the start of the trial. Juvenile and adult female iguanas were investigated because these size categories are most vulnerable to hawk predation. Owing

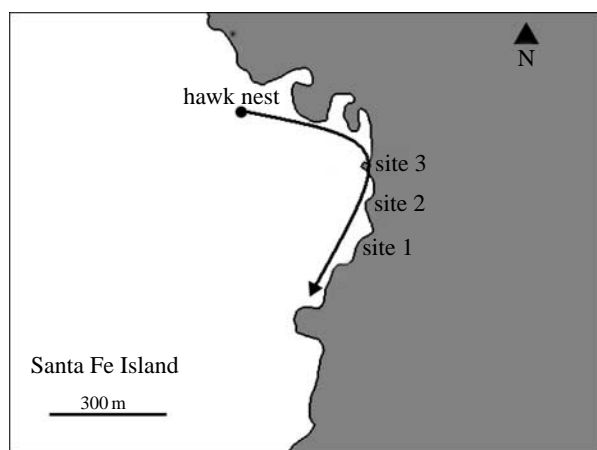


Figure 1. Study sites on Santa Fe, Galápagos. The typical hunting flight trajectory of the hawk pair inhabiting this region is marked with an arrow.

to overlapping size distributions, potential effects of age class were not addressed. The behaviour was coded as 'non-response', 'alert' (head raise) or 'escape' (walk/run). The order of playback (song or call) was randomized, and treatments were separated by at least 15 min. Sites did not differ in exposure to tracks or playback order. Each cluster of animals was sampled once in the morning and once in the afternoon. During playbacks, resident mockingbirds were present at all sites.

Data were analysed using SPSS v. 15.0. As all variables were normally distributed, no transformations were performed. Owing to the small number of escape responses recorded (16 of 438 individuals), the data for alert and escape were combined, and the proportion of animals responding to each playback was analysed using a univariate general linear model, with 'site' and 'playback type' as fixed factors, and 'time' and 'distance to speaker' as covariates. Analyses of interaction terms indicated that the assumption of homogeneity of slopes was met.

### 3. RESULTS

Across sites,  $45.0 \pm 5.9\%$  of iguanas ( $n=19$  playbacks; 226 iguanas) exhibited vigilance behaviour during playback of the alarm call of the Galápagos mockingbird, and  $28.1 \pm 5.3\%$  ( $n=19$  playbacks; 212 iguanas) showed vigilance behaviour during playback of mockingbird song. Playback type (song/call; figure 2;  $F_{1,30}=7.32$ ,  $p=0.011$ ), time of day ( $F_{1,30}=5.60$ ,  $p=0.025$ ) and site ( $F_{2,30}=2.29$ ,  $p<0.001$ ) were all significant factors in predicting the proportion of iguanas that exhibited anti-predator behaviour during playbacks ( $F_{7,30}=4.13$ , d.f.=7,  $p=0.003$ ,  $r^2=0.491$ ). The interaction between playback type and site was non-significant ( $F_{2,30}=0.70$ ,  $p=0.503$ ).

### 4. DISCUSSION

Our results indicate that marine iguanas are able to differentiate between the alarm call and song of Galápagos mockingbirds and increase anti-predator vigilance behaviours in response to alarm calls. This is the first demonstration that a species that lacks vocal communication can associate the auditory alarm signals of another species with the threat of predation.

The relative response of iguanas to alarm call versus song was consistent across sites, but sites differed in overall responsiveness to playbacks. This could result from variation in the ambient noise affecting receiver volume and/or sound quality. The distance from the playback speaker to the iguanas was not a significant

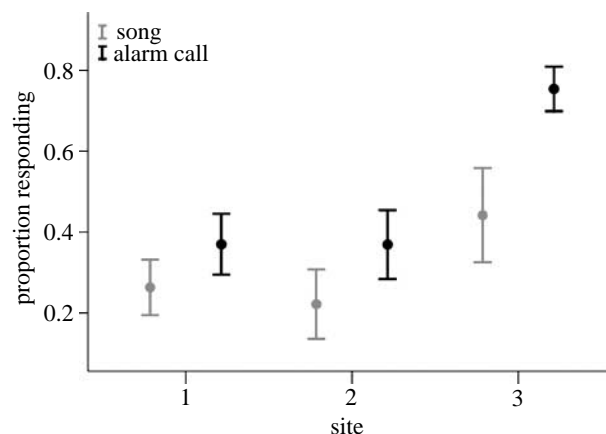


Figure 2. Marine iguanas differentiate between mockingbird alarm call and song. At each site, a higher proportion of marine iguanas exhibit anti-predator behaviour (alert or escape) during playback of mockingbird alarm call than during mockingbird song. Error bars represent one standard error of measurement.

factor in predicting response, but ambient noise might have varied between sites due to differences in wind speed and distance from the ocean. Alternatively, there may be a true difference in the responsiveness of animals between sites, which could be due to a variety of factors including variations in predation pressure, topography or the frequency of mockingbird vocalizations. The flight trajectory of hunting hawks is highly predictable on Santa Fe—hawks appear first at the northern end of each site and then proceed along the island's coastline in a clockwise direction until prey is captured (figure 1). It is possible that this consistent flight pattern results in higher predation rates at site 3, where individuals exhibited the highest level of responsiveness to both types of playbacks.

Iguanas displayed greater responsiveness to playbacks earlier in the day. It is conceivable, but was not tested here, that marine iguanas with lower body temperatures are more responsive to alarm calls because they are less agile and thus escape more slowly than individuals with high body temperatures during the midday or afternoon periods (Wikelski & Trillmich 1994).

The behaviour of iguanas during playbacks may have been influenced by conspecifics; however, the higher proportion of alert behaviour exhibited during alarm calls indicates that at least some individuals are capable of discriminating between these acoustic stimuli. Because we wanted to standardize our sound playback, both of the mockingbird recordings we used for playbacks came from the same individual. However, the downside of this experimental paradigm was that we were not able to correct for possible variations in individual vocalizations (Kroodsma 1989). Nevertheless, we suggest that our use of mockingbird song as a control may ameliorate potential bias introduced by using just one alarming individual.

The adoption of anti-predator defences can impose significant costs in prey species (Blumstein 2002). Marine iguanas adopt thermoregulatory postures that involve orienting either directly towards the Sun or at  $90^\circ$  angles to it. This behavioural thermoregulation is vital; individuals unable to adjust their body position

quickly overheat and succumb (Bartholomew 1969). Even though hunting hawks predictably approach the site from the north, marine iguanas are unable to maintain vigilance in this direction, as doing so would probably impair their thermoregulatory capabilities. The ability to capitalize on the auditory alarm system of another species, particularly an endotherm less constrained by thermoregulatory needs, could provide a significant benefit to marine iguanas. Auditory communication is rapid and can travel over long distances without a direct line of sight, making it an ideal way to transmit information about impending predation in locations with varied topography.

The energetic cost of escape behaviours can also be substantial (Ydenberg & Dill 1986; Cooper & Frederick 2007). Juvenile and female-sized marine iguanas often walk or run towards a position of safety during hawk hunting flights; these short bursts of locomotion greatly increase the heart rate and energetic expenditure of iguanas (Vitousek *et al.* in preparation). Female marine iguanas face high energetic constraints, particularly during the breeding season (Vitousek *et al.* 2007). The ability to gain additional information about the presence of a predator might enable a more effective and/or less costly anti-predator response. Energetics may also explain the low rate of escape behaviour in response to playbacks. Confirming predator location prior to flight provides the most energetically efficient means of capitalizing on heterospecific signals.

This is the first finding that a species lacking vocal communication eavesdrops on and discriminates between heterospecific vocalizations. Heterospecific call recognition in marine iguanas cannot result from generalizing conspecific alarm calls and may instead involve associative learning of complex auditory signals. It is unclear whether this ability is indeed learned or whether naive iguanas are able to recognize and respond appropriately to the alarm calls of mockingbirds. Further research will address this question and investigate whether this ability is localized to the Santa Fe population or is a more general phenomenon.

Our protocol adhered to the Animal Behavior Society Guidelines for the Use of Animals in Research, and was approved by the Princeton University IACUC Committee #1439.

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