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Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls*



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ABSTRACT

Anthropogenic noise is an evolutionarily novel and widespread pollutant in both terrestrial and aquatic habitats. Despite increasing evidence that the additional noise generated by human activities can affect vocal communication, the majority of research has focused on the use of conspecific acoustic information, especially sexual signals. Many animals are known to eavesdrop on the alarm calls produced by other species, enhancing their likelihood of avoiding predation, but how this use of heterospecific information is affected by anthropogenic noise has received little empirical attention. Here, we use two field-based playback experiments on a habituated wild population of dwarf mongooses (Helogale parvula) to determine how anthropogenic noise influences the response of foragers to heterospecific alarm calls. We begin by demonstrating that dwarf mongooses respond appropriately to the alarm calls of sympatric chacma baboons (*Papio ursinus*) and tree squirrels (*Paraxerus cepapi*); fleeing only to the latter. We then show that mongoose foragers are less likely to exhibit this flee response to tree squirrel alarm calls during road-noise playback compared to ambient-sound playback. One explanation for the change in response is that noise-induced distraction or stress result in maladaptive behaviour. However, further analysis revealed that road-noise playback results in increased vigilance and that mongooses showing the greatest vigilance increase are those that do not subsequently exhibit a flee response to the alarm call. These individuals may therefore be acting appropriately: if the greater gathering of personal information indicates the absence of an actual predator despite an alarm call, the need to undertake costly fleeing behaviour can be avoided. Either way, our study indicates the potential for anthropogenic noise to interfere with the use of acoustic information from other species, and suggests the importance of considering how heterospecific networks are affected by this global pollutant.

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1. Introduction

Over the last century, noise pollution has increased globally as a result of human activities such as urban development, resource extraction and transportation networks (Barber et al., 2010; Slabbekoorn et al., 2010). The acoustic characteristics of manmade sounds are often very different to those emitted from biotic and abiotic sources (Hildebrand, 2009), and there is a growing body of research documenting noise-induced effects in a variety of taxa, across a range of scales; from individual behaviour to ecosystem and community ecology (reviewed in: Barber et al., 2010;

Slabbekoorn et al., 2010; Radford et al., 2014; Shannon et al., 2015). Perhaps the greatest focus to date has been on acoustic communication, but there has been a bias towards avian species and sexual signals in this regard (Morley et al., 2014; Read et al., 2014; Shannon et al., 2015).

Anthropogenic noise can interfere with acoustic communication in four main ways which are not mutually exclusive: by masking information either completely or partially (Brumm and Slabbekoorn, 2005); by diverting an individual's finite attention away from detecting or responding to a signal (Chan and Blumstein, 2011); by inducing physiological stress that results in inappropriate responses (Kight and Swaddle, 2011); or by increasing perceived threat levels and thus indirectly affecting behaviour (Frid and Dill, 2002). The consequences of masking for signallers has received considerable research attention, with numerous studies showing that anthropogenic noise can lead to adjustments in the acoustic parameters of vocalisations via behavioural plasticity, ontogenetic

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changes or adaptation (Slabbekoorn and Ripmeester, 2008; Gross et al., 2010; Luther and Baptista, 2010; Roca et al., 2016). Equally important, but relatively understudied, is the potential disruption to receiver responses (Halfwerk et al., 2012; McMullen et al., 2014; Kern and Radford, 2016).

Alarm calling, the production of particular vocalisations to warn others of danger, is a key anti-predator strategy in many species (Klump and Shalter, 1984; Hollén and Radford, 2009), The few studies exploring the impact of anthropogenic noise on alarm-call behaviour have mostly considered conspecific communication, particularly how the acoustic parameters of the alarm calls themselves differ depending on noise conditions (Lowry et al., 2012; Potvin et al., 2014; Templeton et al., 2016), but also how responses may be disrupted (Rabin et al., 2006; McIntyre et al., 2014; Templeton et al., 2016). However, many animals are known to eavesdrop on heterospecific alarm calls, responding appropriately to warnings of danger and even the additional information often contained within such vocalisations (Magrath et al., 2015). To our knowledge, only one study has examined the impact of anthropogenic noise on heterospecific alarm-call use: Grade and Sieving (2016) showed that eavesdropping on tufted titmouse (Baeolophus bicolor) alarm calls by northern cardinals (Cardinalis cardinalis), which is apparent in areas far from roads, did not occur in noisier sites closer to roads.

Here, we use experimental playbacks to examine the effect of road noise on the anti-predator responses of dwarf mongooses (Helogale parvula) to heterospecific alarm calls. Dwarf mongooses are vocal, cooperatively breeding, diurnal carnivores that live in large (5–30 individuals) mixed-sex groups (Rasa, 1977). Since they frequently forage in a head-down position, dwarf mongooses rely on the auditory transfer of information about predator presence, and have evolved a complex alarm-call system which conveys information on the type of predator and urgency of the threat (Beynon and Rasa, 1989; Collier et al., in review). Additionally, they join mixed-species foraging parties, eavesdropping on heterospecific alarm calls produced from a range of animals (Rasa, 1983, 1985; Sharpe et al., 2010). Previous experimental work has demonstrated that anthropogenic noise can disrupt dwarf mongoose use of information about predation risk, including that provided by the surveillance calls of conspecific sentinels (Kern and Radford, 2016; Morris-Drake et al., 2016).

In this study, we first demonstrate that dwarf mongooses respond similarly to tree squirrel (*Paraxerus cepapi*) alarm calls as to conspecific alarm calls; tree squirrels are a sympatric species which, due to their small size and terrestrial foraging, are vulnerable to the same suite of predators as dwarf mongooses (Rasa, 1985). We then investigate whether dwarf mongooses continue to respond to these heterospecific calls during road noise and whether the nature of the response is affected. Finally, we consider a possible vigilance-related explanation for the difference in response found to heterospecific alarm calls during road-noise playback.

2. Materials and methods

2.1. Study site and population

This study was conducted on Sorabi Rock Lodge Reserve, South Africa, a 4 km² private game reserve in north-eastern South Africa (24°11′S, 30°46′E); full details are available in Kern and Radford (2013). The reserve borders a tar road (R530), thus anthropogenic noise from this source is ecologically relevant (Kern and Radford, 2016), and is home to a wide range of terrestrial and aerial predators (Sharpe et al., 2010; Kern, 2012). Data were collected in February–May 2014 and April–June 2015 from seven wild dwarf

mongoose groups (mean group size \pm SE: 10.9 \pm 0.9, range: 5–13) habituated to close observation (<5 m) on foot (Kern and Radford, 2013, 2014; Kern et al., 2016). Monitoring of the population has occurred since 2011, therefore the age of most individuals is known. All individuals are uniquely identifiable through small blonde dye marks on their fur (Wella UK Ltd, Surrey, UK; applied using an elongated paintbrush) or distinctive physical markings (e.g. a scar or missing body part). Individuals are sexed through observing anogenital grooming sessions.

2.2. Playback experiment 1

To investigate the anti-predator responses of dwarf mongooses to heterospecific alarm calls, seven adults (one from each study group) each received four playback treatments: alarm calls from two heterospecifics — a tree squirrel and a chacma baboon ($Papio\ ursinus$) — a conspecific alarm call given to aerial predators (Collier et al., in review), and a conspecific close call as a non-alarm control (N=28 trials in total). Both heterospecifics occupy the same habitat as dwarf mongooses, but while tree squirrels share the same suite of predators, chacma baboons (hereafter baboons) are generally vulnerable to different predators.

Original sound recordings were made at a sampling rate of 44.1 kHz with a 16-bit resolution, using a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ, USA) and a handheld ME 66 shotgun directional microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). The frequency response of the recording system was flat within 3 dB from 500 to 10,000 Hz. Recordings were stored on a Transcend SD card (Transcend, Taipei, Taiwan). Dwarf mongoose aerial alarm calls were recorded from dominant males when heard during observation sessions or elicited by throwing a Frisbee over those individuals when they were slightly apart from the rest of the group and were being vigilant (Rogerson, 2014). Close calls, given throughout foraging bouts (Kern and Radford, 2013), were recorded ad libitum from the same individuals. Baboon and tree squirrel alarm calls were also recorded ad libitum on the reserve. Spectrograms of example calls are provided in Fig. 1. To standardise playbacks across groups, the peak sound-pressure amplitude of different calls (in dB) was measured using a HandyMAN TEK 1345 sound meter (Metrel UK Ltd., Normanton, UK).

Each trial consisted of a 20-s playback of ambient sound (recorded in the territory of the focal mongoose) with the relevant call played from the same loudspeaker 10 s after the start of the trial. Playback tracks were constructed from recordings of good signal-to-noise ratio using Raven Lite 1.0 (Cornell Lab of Ornithology, Ithaca, NY). Different ambient-sound and call exemplars were used for every trial and all sounds were played back at natural amplitudes (ambient sound: peak amplitude = 40 dB soundpressure level A (SPLA) at 10 m; all alarm-calls: peak amplitude = 55 dB SPLA at 1.5 m; control close calls: peak amplitude = 45 dB SPLA at 1.5 m). Playbacks were from an Excel Audio loudspeaker (Guangzhou, China) placed on the ground and connected to a Kubic Evo EV8B mp3 player (ARC UK). Two trials were conducted to each focal individual in the morning (0800–1200) on each of two days (separated by 1–3 days); trials on the same day were separated by at least 1 h, and treatment order was counterbalanced between individuals. Trials were conducted in calm conditions when the focal individual had been foraging in a relatively open area for at least 5 min prior to playback, and at least 10 min after any natural disturbance, such as a natural alarm call, encounter with a predator, or inter-group interaction (Kern and Radford, 2013; Kern et al., 2016). The immediate response of the focal individual to each vocalisation (no response, look up or flee)

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