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Animal behaviour

Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*)?

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Animals living around humans may habituate to us, but little is known about the consequences of this habituation. Some wildlife managers assume that habituation to humans makes individuals less likely to respond to natural predators, which is something to be avoided in captive breeding programmes where animals are destined for release. We conducted a playback experiment where we broadcast the sounds of a terrestrial predator and the song from a non-threatening bird to Gunther's dik-diks (*Madoqua guentheri*), a small ungulate that is vulnerable to many predators, in areas where dik-diks were and were not habituated to humans. Contrary to our expectation, habituated dik-diks discriminated the predator sounds from the birdsong, while unhabituated dik-diks failed to make this discrimination. Our results demonstrate that humans may influence predation hazard assessment, but we should not generally assume that human-habituated animals will be especially vulnerable to predators.

Keywords: habituation; conservation behaviour; reintroduction; acoustic predator discrimination

1. INTRODUCTION

Animals are expected to adaptively habituate to non-threatening stimuli (Shettleworth 1998). Wildlife managers commonly assume that such habituation to humans, or tameness, may have detrimental effects on the survival of animals that will later be translocated or reintroduced to the wild if it reduces general fearfulness, including fearfulness to natural predators (e.g. Jones & Waddington 1992; van Heezik *et al.* 1999). This assumption presumes that habituation to one stimulus may transfer to other stimuli. Such habituation transfer is not generally expected for very different stimuli, but ultimately whether or not animals transfer habituation depends on how the animals classify humans and natural predators (Shettleworth 1998). If humans are classified similarly to non-human predators, then we would expect that habituation to humans should influence the ability of animals to respond appropriately to non-human predators.

We tested this hypothesis by studying acoustic predator discrimination abilities in Gunther's dik-diks (*Madoqua guentheri*), a species that falls prey to numerous predators (Estes 1991), and which at our study site, either lived in or around human settlements or in areas more isolated from humans. If dik-diks transferred habitation from humans to non-human predators, we expected that dik-diks living closer to human settlements would be more habituated and therefore less able to distinguish between threatening and non-threatening animal sounds.

2. MATERIAL AND METHODS

We conducted this playback experiment over 48 km^2 of suitable dik-dik habitat in and around the Mpala Research Center (0°17′ N, 36°54′ E), Laikipia, Kenya. We performed playbacks along 71 km of road through areas that varied greatly in their frequency of use and proximity to human settlements (the research station, villages, schools and human-occupied bomas).

We collected five exemplars of side-striped jackal (*Canis adustus*) calls from the British Library Sound Archive for our experimental stimulus and five exemplars of rattling cisticola (*Cisticola chiniana*) song, recorded from three different individuals at our study site, for our control stimulus. We chose to use rattling cisticolas (*C. chiniana*) as our control for three reasons: they were a common sympatric resident with dik-diks; they sang during the hours of peak dik-dik activity; and dik-diks did not obviously respond to natural cisticola song. We edited the calls and song into 5 s files (44 kHz, 16 bit) and normalized them to 95% maximum amplitude using SoundEdit 16 (Macromedia 1995).

Playbacks were conducted in the morning (06.00–10.00 hours) and afternoon (15.00–18.00 hours) when dik-diks were most active (Estes 1991). We drove slowly, 5–10 km h^{-1}, along dirt roads in a Land Rover, which served as our experimental platform and hide. When we spotted a dik-dik, we immediately turned off the engine and placed our speaker at the open window directed at the focal individual. We recorded the first 30 s of activity by dictating behavioural transitions onto a microcassette recorder to obtain the baseline behaviour of the focal dik-dik. These focal observations were later scored, and the proportion of time allocated to behaviour was calculated using JWatcher v. 1.0 (Blumstein *et al.* 2006). This baseline period also quantified the response of the dik-dik to us and could be used to test for differences in habituation as a function of human exposure. After the 30 s baseline, we broadcast a 5 s exemplar from an iPod through a Tivoli PAL speaker at a mean (±s.d.) of 89 (±1) dB sound pressure level (SPL) for birdsong, or 93 (±4) dB SPL for jackal calls (amplitudes were measured 1 m from the speaker). Both these amplitudes were selected because they were natural amplitudes for these vocalizations and because, to our ears, they were loud but undistorted. We then recorded 30 s of post-playback behaviour. We selected 30 s baseline and post-playback periods because, while short the behaviours we aimed to evaluate were transient responses, and the low visibility in the habitat limited our ability to follow moving dik-diks: longer periods inevitably led to truncated observations. We alternated playing control and experimental stimuli in consecutive experiments and systematically rotated through exemplars. Between consecutive playbacks we drove more than 50 m away (a distance greater than the diameter of most dik-dik territories, Estes 1991).

Following each playback, we recorded the coordinates of our location using a global positioning system, so that distance to human settlement could later be calculated using a geographic information system. Observed dik-diks were categorized as near (less than 0.5 km) or farther (more than or equal to 0.5 km) from human settlement based on the recorded location.

We used t-tests to compare the baseline time allocation near or farther from human settlements and report Cohen's d as a measure of effect size. We fitted a two-way ANOVA with main effects—stimulus type and distance to human settlement—and the interaction between the two to explain variation in our dependent variables: difference in vigilance; foraging; and nose twitching (behaviours selected for their importance in anti-predator response, Estes 1991), using SPSS v. 14 (SPSS, Inc. 2007). We then tested to see whether distance to speaker, sex of focal individual and time of day had any significant main effects on the dependent variables or significant interactions with the main independent variables of interest—they did not, and we do not discuss these results here. For these ANOVA models, we used partial η^2 values as a measure of effect size. We also calculated 95% CIs to see whether the difference in time allocation included 0 and inferred that the dik-diks discriminated the stimuli if the responses were different from each other and if the response to at least one stimulus did not include 0.

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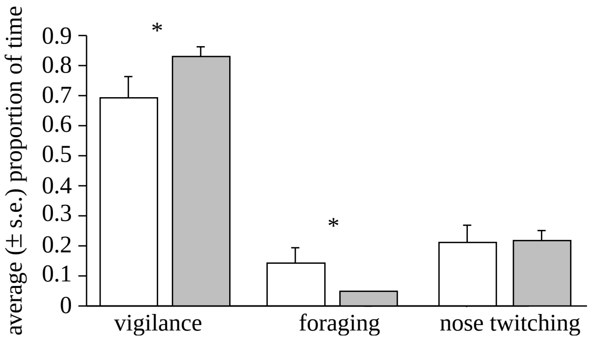

Figure 1. Average (±s.e.) proportion of time allocated to vigilance, foraging and nose twitching during the baseline period as a function of distance from human habitation (white bars, less than 0.5 km; grey bars, more than or equal to 0.5 km). Asterisks illustrate a significant ($p<0.05$) difference between less than 0.5 km and more than or equal to 0.5 km (Cohen's *d*-scores: vigilance = 0.445, foraging = 0.456, nose twitching = 0.016).

3. RESULTS

We conducted playbacks to 104 non-juvenile dik-diks (41 females and 63 males). Exemplars were broadcast an average (±s.d.) distance of 23 m (±13 m) from the focal subject.

Distance to human settlement influenced the time dik-diks allocated to some pre-playback behaviours (figure 1): they foraged more ($t_{100}=-2.23$, $p=0.028$, Cohen's $d=0.456$) and looked less ($t_{100}=2.10$, $p=0.0387$, $d=0.445$) when within 0.5 km of human settlements before hearing the playback. There was no effect of distance to humans on nose twitching, an investigative behaviour associated with the terrestrial mammalian predators (Kingdon 1982; Estes 1991).

Distance to human settlement influenced the ability of dik-diks to discriminate between the sound of the jackal and the non-threatening birdsong (figure 2). Habituated dik-diks near humans responded more aversively to the jackal call than to the birdsong, while unhabituated dik-diks failed to make this discrimination. Specifically, dik-diks close to the human settlement decreased stand-looking behaviour in response to birdsong ($X\pm\text{s.e.}=-0.257\pm0.112$) and increased stand-looking behaviour in response to jackal calls ($X\pm\text{s.e.}=-0.206\pm0.119$), while dik-diks farther than 0.5 km from human settlement decreased stand-looking behaviour in response to both birdsong ($X\pm\text{s.e.}=-0.115\pm0.046$) and jackal calls ($X\pm\text{s.e.}=-0.074\pm0.035$) with a greater reduction in vigilance in response to birdsong. Dik-diks within 0.5 km of human settlement responded to birdsong by foraging more ($X\pm\text{s.e.}=0.010\pm0.053$) than those farther than 0.5 km from human settlement ($X\pm\text{s.e.}=-0.006\pm0.029$); and in response to jackal calls, dik-diks near human settlement foraged less ($X\pm\text{s.e.}=-0.217\pm0.082$) than dik-diks farther from human settlement ($X\pm\text{s.e.}=-0.027\pm0.022$). Dik-diks nose twitched more in response to jackal calls ($X\pm\text{s.e.}=0.097\pm0.027$) than birdsong ($X\pm\text{s.e.}=-0.034\pm0.025$), but there was no effect of distance on this behaviour (ANOVA: $F_{1,98}=0.359$, $p=0.550$, $\eta_p^2=0.004$).

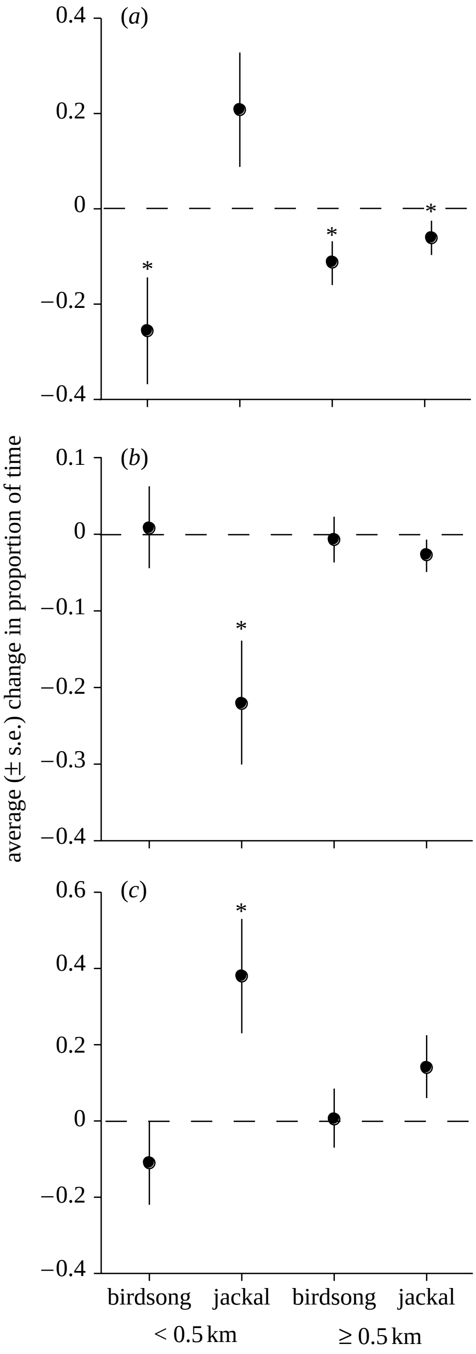

Figure 2. Changes from baseline in the average (±s.e.) proportion to time allocated to (*a*) vigilance, (*b*) foraging and (*c*) nose twitching as a function of playback stimulus to dik-diks less than 0.5 km or more than or equal to 0.5 km from human habitation. Asterisks illustrate responses significantly different from 0 (i.e. the 95% CIs did not include 0).

4. DISCUSSION

We assumed that dik-diks were relatively more habituated to people within 0.5 km of human settlements because they foraged more and looked less during the baseline part of our experiment, a time when they were exposed to us, but no other stimuli. We found that dik-diks' predator discrimination was influenced by the presence of humans, but not in the way we expected. Close to human settlements, dik-diks had distinctly different reactions to jackal calls and birdsong. In response to birdsong, we saw a decrease in vigilance and no change in foraging behaviour or nose twitching, suggesting no increase in wariness. In response to jackal calls, we saw no reduction in vigilance, but a decrease in foraging behaviour and an increase in nose twitching, suggesting an increase in wariness. These responses represent appropriate and predictable reactions to the vocalization of a non-threatening heterospecific and to the call of a threatening, terrestrial, coursing, mammalian predator (Kingdon 1982; Estes 1991). Our results suggest that habituated dik-diks did not transfer habituation from humans to jackals.

Farther from human settlements, dik-diks did not discriminate among stimuli. In response to both jackal calls and birdsong, they reduced vigilance and exhibited a small difference in foraging and nose twitching. These results suggest that far from human settlement dik-diks have a reduced ability to discriminate the predatory threats from the non-threatening stimuli. This finding contradicts our expectation of greater discriminatory abilities in non-habituated dik-diks.

We suspect the failure to discriminate the predatory from non-predator sounds was because distant dik-diks were not habituated to humans and our mere presence increased their overall wariness. Comparison between the baseline behaviours showed that dik-diks farther than 0.5 km from human settlement were more wary: they decreased foraging and increased vigilance compared with those within 0.5 km of human settlement. It is possible that our presence created a ceiling effect, whereby the dik-diks' ability to appropriately respond to threatening and non-threatening auditory stimuli was lost. However, we could not experimentally control for our presence and still directly observe their behaviour; therefore, we cannot conclude that the higher level of baseline wariness was a direct result of our immediate presence rather than a natural difference in wariness.

Regardless, our results clearly demonstrate that the interaction with humans significantly effected risk assessment in dik-diks. Moreover, we found that habituation to humans does not prevent jackal discrimination. This is consistent with the observation that many species habituate only after animals have had specific and direct interactions with a specific type of stimulus (McCullough 1982; Shalter 1984).

Our results suggest that the concern regarding reduced survival due to decreased general fearfulness of translocated or reintroduced animals that are habituated to humans may be unfounded. The high levels of mortality due to predation following release may result from captive reared animals having no experience with predators prior to release (e.g. Biggins *et al.* 1990; Griffin *et al.* 2000).

Our unexpected finding also has a speculative, but potentially important implication for ecotourism: it suggests that the presence of humans in areas where animals are not habituated to them may result in a failure to properly discriminate the predators from the non-predators. Thus, individuals in these areas may waste more time and energy responding to both the predatory and non-predatory stimuli. We expect that such overreacting to all potentially threatening stimuli may have fitness consequences. Future research should aim to identify the fitness consequences of failing to discriminate among the predators and the non-predators.

Research was consistent with the ABS/ASAB guidelines for the treatment of animals in behavioural research and teaching and complied with the laws of Kenya.

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