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Lay Summary

Dwarf mongooses increase their vigilance and sentinel activity in response to traffic noise, but there are age-class and dominance-status differences. Playback experiments with wild mongooses were used to test how traffic noise impacts foraging–vigilance trade-offs. Pups were more affected than adults, whilst dominants responded more strongly than subordinates. Consideration of such intraspecific variation in responses is vital for a full understanding of how noise pollution affects animals.

Intrapopulation Variation in the Behavioural Responses of Dwarf Mongooses to Anthropogenic Noise

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Short title: Intraspecific variation in responses to noise

Anthropogenic noise is an increasingly widespread pollutant, with a rapidly burgeoning literature demonstrating impacts on humans and other animals. However, most studies have simply considered if there is an effect of noise, examining the overall cohort response. Whilst substantial evidence exists for intraspecific variation in responses to other anthropogenic disturbances, this possibility has received relatively little experimental attention with respect to noise. Here, we used field-based playbacks with dwarf mongooses (*Helogale parvula*) to test how traffic noise affects vigilance behaviour, and to examine potential variation between individuals of different age class, sex and dominance status. Foragers exhibited a stronger immediate reaction and increased their subsequent vigilance (both that on the ground and as a sentinel) in response to traffic-noise playback compared to ambient-sound playback. Traffic-noise playback also resulted in sentinels conducting longer bouts and being more likely to change post height or location than in ambient-sound playback. Moreover, there was evidence of variation in noise responses with respect to age class and dominance status, but not sex. In traffic noise, foraging pups were more likely to flee and were slower to resume foraging than adults; they also tended to increase their vigilance more than adults. Dominants were more likely than subordinates to move post during sentinel bouts conducted in traffic-noise trials. Our findings suggest that the vigilance–foraging trade-off is affected by traffic noise, but that individuals differ in how they respond. Future work should therefore consider intrapopulation response variation to understand fully the population-wide effects of this global pollutant.

Keywords: distraction; intraspecific variation; masking; playbacks; traffic noise; stress

INTRODUCTION

Rapid human population growth in the last century has driven an associated increase in noise-generating activities, such as urban development, resource extraction and transportation networks (Krausmann et al. 2009; Shannon, McKenna et al. 2016; United Nations 2017). Since anthropogenic noise can differ greatly in acoustic properties to naturally occurring sounds, and is often of greater amplitude, it can significantly alter acoustic conditions across habitat types (Katti and Warren 2004; Hildebrand 2009). Consequently, anthropogenic noise has been internationally recognised as a pollutant of growing concern. The negative impacts of additional noise on humans have been well-documented for many decades, with effects ranging from annoyance to impaired cognitive development to severe health problems (Finegold et al. 1994; Stansfeld et al. 2005; World Health Organisation 2011). Over the last 15 years, research has broadened to non-human animals and established numerous detrimental effects for aquatic and terrestrial invertebrates and vertebrates (Morley et al. 2014; Shannon, McKenna et al. 2016).

Anthropogenic noise can disrupt biological processes across a range of scales, from ecosystems, communities and populations (Bayne et al. 2008; Francis et al. 2012; Nedelec et al. 2017) to the behaviour, physiology, development and fitness of individuals (Slabbekoorn and Peet 2003; Nedelec et al. 2015; Simpson et al. 2015, 2016; Peng et al. 2016). At the individual level, this disruption can arise via four mechanisms, which are not mutually exclusive. First, masking occurs when anthropogenic noise overlaps in frequency with biologically relevant acoustic cues (e.g. prey movement) and signals (e.g. vocalisations); sounds are either completely masked and inaudible, or partially masked such that full or accurate information is not received (Brumm and Slabbekoorn 2005; Zhou et al. 2019). Second, noise can be viewed as threatening by animals, such that they respond in ways similar to, for instance, a predation threat (Frid and Dill 2002). Third, noise can distract attention and thus reduce performance in, for example, foraging and anti-predator behaviour (Chan et al. 2010; Purser and Radford 2011; Morris-Drake et al. 2016). Lastly, noise can act as a stressor, inducing a cascade of both physiological and behavioural changes (Wysocki et al. 2006; Simpson et al. 2015, 2016).

To date, most noise-impact studies simply consider if animals are affected, examining the overall cohort response. Differences in intrinsic characteristics (e.g. age, sex, body

condition) and extrinsic factors (e.g. experience, environmental context, presence of multiple stressors) can explain significant intraspecific diversity (Bolnick et al. 2011), including in responses to other environmental disturbances such as the general presence of humans (Stankowich et al. 2008) and heavy-metal and organic pollutants (Isaksson 2010). These varied responses can affect the likelihood of mortality or the ability to emigrate, and the possibility of plasticity within an individual's lifetime or adaptation across evolutionary time (Engås et al. 1996; Höglund et al. 2008; Cripps et al. 2014). Moreover, intraspecific response variation can have far-reaching consequences for population dynamics, community structure and ecosystem function (Post et al. 2008; Rudman et al. 2015; Des Roches et al. 2017). Considering how different members of the same species are impacted by anthropogenic noise is therefore crucial for a full understanding of this global pollutant.

Research exploring intrapopulation variation in response to anthropogenic noise is growing but is still limited in extent. A recent comprehensive review found that the majority of papers that had experimentally tested such differences in noise effects had focused on variation in extrinsic factors (Harding et al. 2019). For example, studies have shown that animals respond differently to additional noise as a result of current context (Lengarde 2008; Bruintjes and Radford 2013), repeated exposure (Anderson et al. 2011; Radford et al. 2016), experience (Harding et al. 2018; Senzaki et al. 2018) and the presence of other stressors (McMahon et al. 2017; McCormick et al. 2018). Experimental consideration of how intrinsic characteristics affect responses to noise is rarer (Harding et al. 2019). Purser et al. (2016) found that body condition can affect fish responses to noise playback, and a few studies have shown an influence of body size (Casper et al. 2013; Wale et al. 2013; Kastelein et al. 2017). Only occasionally have potential differences due to age (McClure et al. 2017; Dorado-Correa et al. 2018) or sex (Bruintjes and Radford 2013; Mancera et al. 2017) been described, and we know of no examples testing variation due to differences in dominance status; dominant individuals may be more experienced or have different trade-offs compared to subordinates.

Here, we examine how age class, sex and dominance status affect vigilance responses to traffic noise in dwarf mongooses (*Helogale parvula*). Widely distributed road networks expose large areas of land to traffic noise, and irregular noise from roads may make habituation challenging (Muzet 2007; Ware et al. 2015). Anthropogenic noise has been shown to disrupt key foraging–vigilance trade-offs, and can induce a shift towards vigilance, with potential energetic costs (Rabin et al. 2006; Shannon et al. 2014; Ware et al. 2015).

However, no studies have explored whether individuals within populations moderate foraging–vigilance trade-offs differently. Dwarf mongooses are an ideal study species to investigate intraspecific variation in behavioural responses to noise: they live in mixed-sex groups of 5–30 individuals comprising a dominant breeding pair and non-breeding subordinates; individuals are highly vulnerable to predation; and two types of vigilance behaviour occur – personal vigilance when foraging on the ground, and sentinel behaviour when an individual scans the surroundings from an elevated position (Rasa 1977; Kern and Radford 2013, 2016). Playback experiments have established that traffic noise can have a detrimental effect compared to ambient sound: dwarf mongooses respond less to sentinel surveillance calls by increasing personal vigilance (Kern and Radford 2016) and are less likely to flee in response to heterospecific alarm-call playbacks (Morris-Drake et al. 2017); individuals also respond less appropriately to olfactory predator cues (faeces), indicating a cross-modal effect of anthropogenic noise (Morris-Drake et al. 2016). The reduced response to acoustic information (Kern and Radford 2016; Morris-Drake et al. 2017) suggests that dwarf mongooses may need to compensate by gathering information in other ways (e.g. visually through increased vigilance). The study population is habituated to close observation on foot (<5 m), allowing detailed data collection and field-based experiments, and the study site has a tar road (R530) running alongside it, meaning that traffic is an ecologically relevant source of anthropogenic noise.

We used field-based playback experiments to examine intrapopulation variation in the vigilance responses of foraging and sentinel dwarf mongooses to traffic noise compared to ambient sound. We predicted that foragers would be more likely to flee in response to traffic noise and would increase the proportion of time spent vigilant, either due to an increase in perceived threat level or to compensate for potential masking of acoustic predator cues or conspecific and heterospecific vocalisations. Pups were expected to be more likely to flee and to have a proportionally greater vigilance increase in traffic noise than adults, since young animals are generally worse at predator avoidance (Hollén and Radford 2009), are less familiar with traffic, and are often more vigilant than adults generally (Hanson and Coss 2001a). We predicted that, in traffic noise, foragers would be more likely to become a sentinel and that sentinels would remain on duty for longer, for the same reasons underpinning the expected increase in vigilance on the ground (see above). We also predicted that sentinels would be more likely to adopt a lower post and move position to enhance vocal communication, especially with respect to low-amplitude surveillance calls, although there

could be some compromise with the likelihood of detecting predators (Radford et al. 2009). These responses were expected to be more prevalent in dominants and females than in subordinates and males since the former have, on average, a higher relatedness to other group members; dwarf mongoose groups are formed around a dominant breeding pair and their retained offspring, with the addition of unrelated immigrants (Rasa 1977; Rood 1990).

METHODS

Study site and population

Data were collected as part of the long-term Dwarf Mongoose Research Project on Sorabi Rock Lodge Reserve, a 4 km^2 private game reserve located in Limpopo Province, South Africa (24° 11'S, 30° 46'E). The lowveld climate is characterised by hot, wet summers (from September to April), and cold, dry winters (from May to August). Full study site details are provided in Kern and Radford (2013). The study population comprised six groups of wild dwarf mongooses (mean ± SE group size: 11.2 ± 2.4, range: 4–18) habituated to the close presence (<5 m) of observers; the population has been monitored since 2011, so the identity and age of most individuals is known (Kern and Radford 2013, 2014). Individuals older than 1 year were classified as adults, while individuals born that summer were classified as pups; adults were classified as either dominant (the breeding pair) or subordinate (Kern and Radford 2013, 2014). Sex was determined through observation of ano-genital grooming, and dominance was inferred from aggression, food-displacement and scent-marking behaviour (Rasa 1977).

Experimental overview

To investigate the effect of traffic noise on dwarf mongoose vigilance behaviour, and potential intraspecific variation in responses with respect to age class (adult vs pup), sex (male vs female) and dominance status (dominant vs subordinate), focal individuals were exposed to two playback treatments: ambient sound (as a control) and traffic noise. Two separate experiments were run to consider how noise affects foragers and sentinels. Playback methods followed those used in our previous work investigating how traffic noise affects behaviour in the study population (Kern and Radford 2016; Morris-Drake et al. 2016, 2017). Behavioural scoring also followed the methods we have used in previous work on forager vigilance and sentinel activity (Kern and Radford 2013, 2016, 2017, 2018; Morris-Drake et al. 2019). All work was conducted under permission from the Department of Environmental

Affairs and Tourism, Limpopo Province (permit number: 001-CPM403-00013) and the Ethical Review Group, University of Bristol (University Investigator Number: UIN/17/074).

Acoustic recordings and playback tracks

All original sound recordings were made using a Marantz PMD660 MKII professional solid-state recorder (Marantz America, Mahwah, NJ, USA), and a handheld ME 66 short gun directional microphone (UK, High Wycombe, Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). Recordings were made at a sampling rate of 48 kHz with a 24-bit resolution and saved onto a Transcend SD card (Transcend, Taipei, Taiwan). Ambient sound was recorded from the centre of each group's territory at similar times of day, in calm conditions when no dwarf mongooses were nearby, and naturally occurring anthropogenic noise (e.g. passing planes and cars) could not be heard. The microphone was oriented in the opposite direction to the main tar road (R530), which is adjacent to the south-eastern reserve boundary, and at a height of 10 cm to mimic the head height of a foraging mongoose. Natural ambient-sound peak amplitude (40 dB(A) at 1 m) was recorded for 1–2 min at a time with a MASTECH MS6700 sound-level meter (Yunxia, Yantai, Shandong, China). Recordings were made twice within the season (January and May) to ensure seasonal changes in the soundscape were reflected in the playback tracks; the recording from the closest date to a given experimental trial was used. Traffic-noise recordings from a previous study (Kern and Radford 2016) were used. These recordings were made 10 m from and perpendicular to the R530 at 10 cm height, and the peak amplitude of passing vehicles (65–70 dB(A) at 10 m) was measured for each vehicle pass with a HandyMAN TEK 1345 sound-level meter (Metrel UK Ltd., Normanton, West Yorkshire, UK).

Playback tracks were created and edited in Audacity 2.1.2. (http://audacity.sourceforge.net/), using original recordings with good sound-to-noise ratios, and with any loud extraneous noise (e.g. heterospecific alarm calls in any recordings, traffic noise in ambient-sound recordings) removed. Ten ambient-sound tracks of 10 min duration were generated for each group by looping 1-min recordings from the centre of the focal group territory. The traffic-noise tracks (N=8) from Kern and Radford (2016) were each looped to be of 10 min duration. Traffic-noise tracks contained the mean number and type of vehicles observed on the R530 during 10 1-h traffic counts (Kern and Radford 2016).

Playback experiments

All playback tracks were broadcast from an iPhone 5 (Apple Inc., Cupertino, California), via a Rokono B10 loudspeaker (frequency response: 90–20,000 Hz) held by the experimenter at 1 m height and 3–5 m from the focal individual. Tracks were randomly selected and played at an amplitude representative of natural occurrence (see Acoustic recordings and playback tracks). Playbacks were conducted when there had been no natural alarm calls for at least 10 min, no major encounters (e.g. snake mobbing or intergroup interactions) for at least 15 min, and no traffic-noise playback to any group member for at least 30 min (as per Kern and Radford 2016). If there was excessive naturally occurring anthropogenic noise (planes or road vehicles) or a natural predator appeared, trials were abandoned and repeated after 24 h where possible. To standardise the influence of environmental conditions, playbacks were only completed in calm conditions (no wind or light wind).

Playback to foragers

Fifty foraging individuals (dominant adults: N=5 females, 6 males; subordinate adults: N=8 females, 11 males; pups: N=13 females, 7 males) from five groups (those that survived the whole field season) were exposed to the two playback treatments in a matched design. Foragers were classified as individuals searching for prey in a head-down position. Treatment order was counterbalanced both within and between groups to control for order effects. There were no significant differences between individuals of different age class, sex or dominance status in the order that they received the two treatments (Mann-Whitney U tests: all U<93.5, all z<0.476, all p>0.176). Habitat type (open: <33% ground cover; medium: low-lying shrubs and 33–66% ground cover; dense: >66% ground cover), group size and composition, and time of day were matched for pairs of trials to the same individual. All trials were filmed with a handheld Nikon D3300 SLR camera equipped with a Nikon 18–55 mm f/3.5–5.6 zoom lens (Nikon, Kingston upon Thames, UK).

Trials were conducted opportunistically during morning foraging sessions (0730–1200 h) between January and July 2017, with a minimum of 1 h and maximum of 1 day between trials in a pair. There were no significant differences between individuals of different age class, sex or dominance status in the time of season when they received playback trials (Mann-Whitney U tests: all U<72, all z<1.399, all p>0.162). A 1-min pre-playback observation period was conducted, when the start and end of all vigilance scans was dictated to the video camera. Vigilance scans were classified as pauses in foraging behaviour

where an individual lifted its head and actively scanned its surroundings. Following this, either an ambient-sound or a traffic-noise playback was conducted for a minimum of 1 min; playback ended when an individual stopped foraging to interact with another group member (e.g. grooming, playing), commenced sentinel duty or was lost from sight. During playbacks, the following were dictated: immediate response (none, look up, flee); time to resume foraging (if applicable); start and end of all vigilance scans and sentinel bouts. Sentinel bouts were defined as periods when individuals actively scanned their surroundings for predators from an elevated position (with their feet at least 10 cm above ground level; Kern and Radford 2013), while groupmates were engaged in other activities (e.g. foraging, grooming). Trials were abandoned if the following occurred during the pre-playback observation period or the first minute of the playback period: the focal individual stopped foraging; the focal individual was lost from sight; or any group member gave an alarm call. Videos of trials were subsequently analysed blind to the sound treatment, and the following response variables extracted: immediate response; time to resume foraging (if applicable); proportion of time spent vigilant; vigilance scan-rate; and sentinel behaviour (yes or no).

Playback to sentinels

Sixty-nine trials were conducted opportunistically on 27 adult sentinels (dominants: N=5 females, 4 males; subordinates: N=7 females, 11 males) in six groups; some individuals received only one playback treatment, whilst some received more than one repeat of one or both treatments. A random number generator determined whether the first treatment to an individual was a traffic-noise or ambient-sound playback. Subsequent trials to that individual alternated between treatment types and were separated by a minimum of 1 h; no more than two trials were conducted on the same individual on a given day. There were no significant differences between individuals of different sex or dominance status in the order in which treatments occurred (Mann-Whitney U tests: all U<61, all z<0.186, all p>0.350). Trials were abandoned if an individual in the group gave an alarm call or if the sentinel bout was less than 10 s. Trials were conducted throughout the day (0730–1700 h), when groups were foraging, from January to July 2017. There were no significant differences between individuals of different sex or dominance status in the time of season when they received playback trials (Mann-Whitney U tests: all U<69, all z<0.618, all p>0.112).

On detection, sentinels were approached and the relevant sound treatment immediately commenced. Playback trials continued until the focal individual terminated the

sentinel bout (i.e. came down from its post or engaged in another behaviour). The following were recorded during each trial: change in post height (yes vs no; if yes: up vs down); change in post location (yes vs no); and bout duration (using a stopwatch). After bout termination, the following were recorded where possible: whether the sentinel had been accompanied; whether the full bout was observed; group size; approximate horizontal distance to nearest neighbour (<2 m, 2–5 m, >5 m, present inside refuge); habitat type (as above); wind level (still, light breeze); and sentinel post type (rock, termite mound, tree). None of these environmental and social factors differed significantly between ambient-sound and traffic-noise trials (paired-sample t-tests: all $t_4<0.135$, all $p>0.899$; McNemar tests: all $\chi^2<1.500$, all $p>0.219$).

Data analysis

All statistical analyses were performed using R (version 3.2.2; R Core Team 2017). Initial analyses were conducted with intercepts-only mixed models comprising both fixed and random effects to account for the repeated-measures element of the experimental design; trials to the same individual within the same group. Data and residual plots were examined visually, and when these (or their transformation; specified where relevant) conformed to the assumptions of homoscedasticity and normality, linear mixed models (LMMs) with an identity link function were generated (package: 'nlme', Pinheiro et al. 2012). For binary response variables, binomial generalised linear mixed models (GLMMs) with a logit link function were used (package: lme4; Bates et al. 2014).

Maximal models incorporated all potential explanatory terms and two-way interactions of interest. Model simplification was achieved using stepwise backwards regression to eliminate non-significant terms (Crawley 2007). The minimal model was determined using Likelihood Ratio Tests (LRT) upon removal of terms to compare the change in deviance (ANOVA model comparison, Chi-square test) and Akaike Information Criterion values (AIC; Akaike 1974). The least significant fixed effect was sequentially removed until the elimination of any further terms reduced the explanatory power of the model. Significance values for non-significant removed terms was obtained by individually adding them to the minimal model. Presented p and X^2 values for significant terms or interactions were obtained from comparisons to null models or minimal models with the term of interest removed. Effect size $\pm$ SE for significant terms and variance of the random terms

(± SD) were obtained from the minimal model; non-significant terms were returned to the minimal model to obtain correct significance levels. All tests were two-tailed and considered significant at p<0.05.

Playback to foragers

To determine if sound treatment affected the immediate response to playback, two binomial GLMMs were conducted: one considered whether individuals stopped foraging (look up/flee) in the first 10 s (yes vs no); and the other considered whether individuals fled in the first 10 s (yes vs no). For both models, sound treatment (traffic noise or ambient sound) was incorporated as a fixed effect, and individual identity nested within group identity was included as a random effect. Models with additional fixed effects (age class, sex, dominance and their interactions with sound treatment) failed to converge due to lack of variation. So, to ascertain if there was intrapopulation variation in the immediate response to traffic-noise playback, separate Fisher's exact tests compared responses across population classes: adults vs pups; adult males vs adult females; male pups vs female pups; and dominant adults vs subordinate adults. First, tests were run on traffic-noise trials to assess the likelihood that an individual fled in the first 10 s of playback. Second, tests were run on traffic-noise trials lasting longer than 30 s where individuals stopped foraging, to consider the likelihood that an individual resumed foraging within 30 s of playback.

To investigate if traffic-noise playback changed the vigilance behaviour of foragers, and if there was intrapopulation variation in this response to playbacks, two LMMs were run: one on the vigilance scan rate (number per minute); and the other on the proportion of time spent vigilant (following arcsine square-root transformation). Models incorporated fixed effects of sound treatment and of age class, sex, dominance status (using only the adult data) and their interactions with sound treatment, and random effects of individual identity nested within group identity. Models investigated the change in the response variable from the 1-min pre-playback observation period to the playback period. There were no significant differences between adults and pups, dominants and subordinates or males and females, in either pre-playback vigilance scan rate or pre-playback proportion of time spent vigilant (Mann Whitney U tests: all U<301, all z<1.322, all p>0.189), but the change-based analyses controlled for baseline behaviour at the time of a trial.

To assess whether sound treatment affected the likelihood that an individual became a sentinel (yes vs no), a binomial GLMM was run. Sound treatment (traffic noise or ambient sound) was incorporated as a fixed effect, and individual identity nested within group identity as a random effect. To explore intrapopulation variation in sentinel behaviour, four Fisher's exact tests were run on traffic-noise trials: adults vs pups; adult males vs adult females; male pups vs female pups; and dominant adults vs subordinate adults.

Playback to sentinels

To explore the effect of traffic-noise playback on sentinel bout duration, and any intrapopulation variation in this response, analyses were only conducted on adult individuals who received both sound treatments (N=22). Repeated trials were averaged to generate one ambient-sound and one traffic-noise value per individual. A LMM was subsequently run on log-transformed data, incorporating fixed effects of sound treatment and of sex, dominance status and their interactions with sound treatment, and random effects of individual identity nested within group identity.

To determine the effect of traffic-noise playback on the likelihood that an adult individual changed sentinel post height (yes vs no) or moved to another sentinel post (yes vs no), two binomial GLMMs were run on all trials to individuals. Sound treatment was incorporated as a fixed effect, and random effects of trial pair and individual identity were nested within group identity. Considering all traffic-noise trials where the focal individual changed post height, directionality (up vs down) was assessed using a two-tailed binomial test. Intrapopulation variation in height-change and post-change behaviour were explored using Fisher's exact tests considering dominants vs subordinates and males vs females, and using the first traffic-noise trial to each individual.

RESULTS

Initial response of foragers

Sound treatment had a significant overall effect on the likelihood that an individual stopped foraging (looked up or fled vs continued foraging; Table 1a) or fled (fled vs looked up or continued foraging; Table 1b) within the first 10 s of playback. These behaviours occurred more frequently during playback of traffic noise compared to ambient-sound playback (Figure 1a, b).

Since most individuals stopped foraging in traffic-noise trials (45/50), there was no inherent intrapopulation variation to investigate. However, there was some evidence of intrapopulation variation in the likelihood of fleeing to traffic-noise playback. Pups were significantly more likely than adults to flee in response to traffic noise (Fisher's exact test: $N_{adults}=30$; $N_{pups}=20$, p=0.017; Figure 1c). There was no significant difference in the proportion of individuals who fled based on sex (adults only: $N_{females}=13$, $N_{males}=17$, p=1.000; pups only: $N_{females}=13$, $N_{males}=7$, p=0.158) or dominance status ($N_{dominants}=11$, $N_{subordinates}=19$, p=0.279).

Considering only traffic-noise trials longer than 30 s where individuals stopped foraging (N=39), adults were significantly more likely to resume foraging than pups (Fisher's exact test: $N_{adults}=24$, $N_{pups}=15$, p=0.015; Figure 1d). There was no significant difference based on sex (adults only: $N_{females}=9$, $N_{males}=15$, p=0.511; pups only: $N_{females}=9$, $N_{males}=6$, p=0.698) or dominance status ($N_{dominants}=10$, $N_{subordinates}=14$, p=0.493).

Vigilance behaviour of foragers

In general, sound treatment had a significant effect on forager vigilance (Table 2). Individuals exhibited a greater increase in both vigilance scan rate (Figure 2a) and the proportion of time spent vigilant (Figure 2b) in traffic-noise playback compared to ambient-sound playback. The increase in vigilance scan rate associated with traffic-noise playback was not significantly affected by the interaction between sound treatment and any of age class, sex or dominance status (Table 2a). For the proportion of time spent vigilant, there was also no significant interaction between sound treatment and either sex or dominance status (Table 2b). However, there was a non-significant trend for an interaction between sound treatment and age class (Table 2b): while pups spent a greater proportion of time vigilant in both sound treatments compared to adults, the former showed a greater vigilance increase in traffic-noise playback (Figure 2b).

The likelihood that an individual became a sentinel was significantly affected by sound treatment (Table 3). Traffic-noise playback elicited more sentinel behaviour than ambient-sound playback (Figure 3). Since the majority (11/13) of sentinel occurrences were in traffic-noise trials, these were used to consider intrapopulation variation. The likelihood that an individual became a sentinel was not significantly affected by age class (Fisher's

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exact test: $N_{adults}=27$, $N_{pups}=12$, $p=0.709$), dominance status ($N_{dominants}=10$, $N_{subordinates}=17$, $p=0.709$) or sex (adults only: $N_{females}=12$, $N_{males}=15$, $p=1.000$; pups only: $N_{females}=7$, $N_{males}=5$, $p=0.222$).

Behaviour of sentinels

Sound treatment had a significant effect on sentinel bout duration, with individuals remaining on duty for longer in traffic-noise playback than in ambient-sound playback (Table 4; Figure 4a). Dominant individuals exhibited longer sentinel bouts than subordinates in general (Table 4; Figure 4b), but there was no evidence of a proportionally larger increase in bout duration in traffic-noise playback compared to that by subordinates (no significant interaction term between sound treatment and dominance status; Table 4). Similarly, there was no significant effect on sentinel bout duration of sex or its interaction with sound treatment (Table 4).

Sound treatment had a significant effect on the likelihood that a sentinel changed its post height (Table 5a) and the likelihood that it moved to another post (Table 5b). Both behaviours occurred more frequently in traffic-noise playback than ambient-sound playback (Figure 5a, b). When individuals changed post height in traffic-noise playback ($N=10$), they were not significantly more likely to move up ($N=8$) or down ($N=2$; two-tailed binomial test: $p=0.109$).

Since the majority (10/11) of cases where individuals changed post height occurred in traffic-noise playback, the first traffic trial to each individual was used to investigate intrapopulation variation. There was no significant effect of dominance status (Fisher's exact test: $N_{dominants}=8$, $N_{subordinates}=16$ $p=0.363$) or sex ($N_{females}=12$, $N_{males}=12$ $p=0.667$) on the likelihood of a post-height change. As individuals only moved to another post in traffic-noise playback ($N=5$), again these trials were used to investigate intrapopulation variation. There was no significant effect of sex ($N_{females}=12$, $N_{males}=12$, $p=1.000$) on the likelihood of post movement. However, dominants were significantly more likely to move to another post compared to subordinates ($N_{dominants}=8$, $N_{subordinates}=16$, $p=0.028$; Figure 5c).

DISCUSSION

Foraging dwarf mongooses exhibited a stronger immediate reaction and increased their subsequent vigilance (both that conducted from the ground and acting as a sentinel) in

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response to traffic-noise playback compared to ambient-sound playback. Traffic-noise playback also resulted in sentinels remaining on duty for longer and being more likely to change post height or move to another post than in ambient-sound playback. Moreover, there was evidence of intraspecific variation in responses to noise with respect to both age class and dominance status, although no difference between the sexes. Foraging pups were more likely to flee and were slower to resume foraging than were adults; they also tended to increase their vigilance more than adults in traffic noise. Dominants conducted longer sentinel bouts than did subordinates in both sound treatments, but there was no evidence for a greater increase in bout duration in traffic noise. However, dominant individuals were more likely than subordinates to move to another post during sentinel bouts conducted in traffic-noise trials.

General noise effects

The finding that traffic-noise playback can induce flee behaviour in dwarf mongooses is consistent with observations of noise-induced flight responses in birds, fishes and marine mammals (Brown 1990; Delaney et al. 1999; Handegard et al. 2003; Ng and Leung 2003; Shannon, Crooks et al. 2016). Similarly, the documented increase in dwarf mongoose vigilance during traffic-noise playback aligns with previous studies on birds and mammals (Delaney et al. 1999; Rabin et al. 2006; Shannon et al. 2014), including the same species (Kern and Radford 2016; Morris-Drake et al. 2017). To the best of our knowledge, this is the first evidence that sentinel behaviour, which has evolved in a range of birds and mammals (Bednekoff 2015), is affected by additional noise. Unnecessary escape behaviour, vigilance and sentinel activity is likely energetically expensive due to reduced time for foraging and, in the case of fleeing, additional movement. If such responses to noise were sustained across time, and there was no compensation during quieter times, then there could be implications for survival; field studies testing fitness consequences directly are logistically challenging but are vital moving forward (Halfwerk et al. 2011; Simpson et al. 2016; Nedelec et al. 2017).

All the behavioural differences seen between sound treatments could potentially result from noise being perceived as threatening by the dwarf mongooses. Noise can induce the same responses as a predation threat ('risk-disturbance hypothesis'; Frid and Dill 2002). Fleeing and vigilance are common behavioural responses to threatening stimuli (Lima and Bednekoff 1999; Hollén and Radford 2009). Sentinel activity has also been shown to increase in response to heightened risk (Ridley et al. 2010; Hollén et al. 2011; Kern and Radford

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2014). That could be either for selfish reasons, because sentinels are safer than foragers, or for cooperative reasons, because the benefits to others are most valuable when the risk is highest (Clutton-Brock et al. 1999; Ridley et al. 2010; Bednekoff 2015). Changes in post position (height or location) during noise might then reflect attempts by a sentinel to improve their own safety (e.g. by moving to a lower or more-protected post) or to improve their likelihood of spotting danger (e.g. by moving higher) for the benefit of others (Radford et al. 2009; Ridley et al. 2010).

At least some of the documented behavioural responses to traffic-noise playback could also arise if dwarf mongooses are compensating for potential masking of acoustic cues and signals. Anthropogenic noise is known to mask acoustic information (Brumm & Slabbekoorn 2005; Zhou et al. 2019); previous work on dwarf mongooses has shown this to be the case with respect to sentinel surveillance calls and heterospecific alarm calls (Kern and Radford 2016; Morris-Drake et al. 2017). In such circumstances, animals may then choose to increase their vigilance to compensate; an attempt to maintain the same level of information but from different sensory modalities (Barber et al. 2010). Greater sentinel activity may reflect a heightened risk when acoustic information is compromised; individuals may decide to become a sentinel if that is the safer option or because there is a greater cooperative need (see above). Movement of sentinels to different positions could either be a consequence of this greater perceived risk or represent an attempt to improve communication with groupmates. A previous study has shown that dwarf mongooses are less likely to respond to low-amplitude surveillance calls during traffic-noise playback compared to ambient-sound playback, possibly because receiver detection is compromised (Kern and Radford 2016). If sentinels were trying to minimise masking of these calls, they might be expected to move lower (to be closer to foragers). Whilst there was some indication that this might be the case (8 out of 10 occurrences), there was no strong evidence from our (small) sample that this was more likely than movement to a higher post.

A final possible explanation for the behavioural differences is stress. Noise may act as a stressor, with fleeing comprising an acute stress response following elevation of glucocorticoid levels (Wright et al. 2007). Stressed individuals may make maladaptive decisions, including relating to foraging–vigilance trade-offs. Distinguishing between underlying mechanisms for noise effects remains one of the major challenges in this research field (Francis and Barber 2013; Shannon, McKenna et al. 2016). Understanding mechanisms

is important because it can help predict effects of noise and suggest methods to ameliorate these effects (Francis and Barber 2013). We suggest that sentinel behaviour offers a tractable system for field-based experiments in this regard.

Intraspecific variation in noise responses

The stronger response to traffic-noise playback of pups compared to adults is consistent with the notion that younger individuals may be more sensitive to anthropogenic disturbance. For instance, a meta-analysis found young ungulates appeared to flee to human disturbances at greater distances than adults (Stankowich 2008), and younger individuals within migrating bird communities avoided areas with traffic-noise playbacks (a "phantom road") more strongly than did older individuals (McClure et al. 2017). This greater apparent susceptibility of pups to traffic noise may relate to different levels of experience: our study population is regularly exposed to traffic noise from a neighbouring road, to which pups will have had less exposure than adults. Support for a lessened response to noise following repeated exposure (Anderson et al. 2011; Wale et al. 2013; Radford et al. 2016) or because of experience (Harding et al. 2018; Senzaki et al. 2018) is building. Thus, the age-class-related differences in dwarf mongoose responses could be because traffic noise is a more novel and stressful stimulus for pups than for adults. In the future, it would also be valuable to consider age-related differences among adults; i.e. within the same life-history stage, where changes across time might result from differences in individual experience.

An alternative explanation for the age-class-related differences in noise responses is that pups have different foraging–vigilance trade-offs to adults. If flight behaviour was moderated predominantly by energetic costs, better-condition individuals might be expected to flee more readily than those in poorer condition, since the cost of lost foraging time would be lower (Beale and Monaghan 2004). However, dwarf mongoose pups weigh less and likely have greater energetic requirements for growth than adults, so flee behaviour may instead relate to elevated predation risk. Younger individuals of many species are worse at predator detection and avoidance, and thus more vulnerable than adults to predation (Whiting et al. 2003; Lingle et al. 2008; Putman et al. 2015). Furthermore, young may need to learn about how to respond appropriately to vocalisations such as alarm calls and surveillance calls (Hollén and Radford 2009), and might therefore initially rely more on visual cues (Hollén and Manser 2006; Hanson and Coss 2001b). Consistent with this suggestion, previous mammalian studies have established that younger individuals have greater levels of overall

vigilance than adults (Mateo 1996; Hanson and Coss 2001a). If noise is analogous to a predator threat, pups might then be expected to respond with greater vigilance increases than adults due to higher vulnerability to predation (Frid and Dill 2002; Lea and Blumstein 2011). Further work would be needed to disentangle the exact reason for the age-class difference, but our findings add to the small number of experimental studies showing that adults and young may be affected differently by anthropogenic noise (McClure et al. 2017; Dorado-Correa et al. 2018).

Dominant individuals were more likely than subordinates to move to another post when acting as a sentinel in traffic noise. Since dominants contribute more to sentinel duty (Kern et al. 2016; this study), they have more experience in this role than subordinates, and may be able to make more appropriate decisions. For instance, dominant sentinels select higher sentinel posts than subordinates (Kern et al. 2016), likely enhancing predator detection (Radford et al. 2009). Moving to a new sentinel post further from a noise source may reduce the detrimental effects of masking or stress, whilst moving closer to foraging groupmates would enhance vocal transmission in noise. Future work, with larger sample sizes, would need to explore the exact details of the post-movement behaviour of sentinels and how variation in bout duration (on average, dominants conduct longer bouts than subordinates) affects the likelihood of movement. We know of no previous studies demonstrating differences in noise responses in relation to dominance status, but this fits with the more general intraspecific variation arising from intrinsic characteristics (Harding et al. 2019).

Conclusions

It is now well-established that a variety of anthropogenic noise sources, including vehicle traffic, can have negative effects on species in all taxa studied (Morley et al. 2014; Kunc et al. 2016; Shannon, McKenna et al. 2016), including in dwarf mongooses (Kern and Radford 2016; Morris-Drake et al. 2016, 2017). Our work adds to the small, but growing, body of literature experimentally demonstrating that such noise effects can differ between members of the same species (Harding et al. 2019). We have focused on differences in intrinsic characteristics, finding variation in responses dependent on both age class and dominance status, but extrinsic factors (such as experience and environmental context) are also likely to play a role (Harding et al. 2019). Expanding our knowledge of intraspecific variation in noise responses, ideally through field-based experiments on wild populations (as we have done here) and with real noise sources (for example, see: Francis et al. 2009; Simpson et al. 2016),

is important both for a full understanding of the impacts of this global pollutant and for designing effective management and mitigation strategies.

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Data accessibility

The data used for analysis in this paper will be made available through Dryad if the paper is accepted for publication.

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Figure Legends

Figure 1. The effect of sound treatment (playback of ambient sound or traffic noise) on the proportion of individuals that (a) stopped foraging (dark grey) or continued foraging (light grey), and (b) fled (dark grey) or did not flee (light grey) in the first 10 s (N=50 individuals). For traffic-noise playbacks, the effect of age class on the proportion of individuals that (c) fled (dark grey) or did not flee (light grey) (N=30 adults, 20 pups), and (d) resumed foraging (dark grey) or did not resume foraging (light grey) within 30 s of a playback to which they had looked up or fled (N=24 adults, 15 pups).

Figure 2. The effect of sound treatment (playback of ambient sound or traffic noise) on the change (from pre-playback to playback period) in (a) vigilance scan rate for all individuals, and (b) the proportion of time spent vigilant by different age classes in ambient-sound (light grey) and traffic-noise treatments (dark grey) (N=27 adults, 12 pups). Means ± SEs are shown as calculated from the raw data. N=78 trials, 39 individuals, five groups.

Figure 3. The effect of sound treatment (playback of either ambient sound or traffic noise) on the proportion of trials where an individual became a sentinel (dark grey) or did not become a sentinel (light grey). N=78 trials, 39 individuals, five groups.

Figure 4. The effect on sentinel bout duration of (a) sound treatment (playback of either ambient sound or traffic noise) and (b) dominance status (N=8 dominants, 14 subordinates). Means ± SEs are shown as calculated from the raw data. N=44 bouts, 22 individuals, six groups.

Figure 5. The effect of sound treatment (playback of either ambient sound or traffic noise) on the proportion of trials where a sentinel (a) changed post height (dark grey) or did not (light grey), and (b) moved to another post (dark grey) or did not (light grey), N=69 bouts, 27 individuals, six groups. For the first traffic-noise playback to each individual, the effect of dominance status on (c) the proportion of sentinels that moved to another post (dark grey) or did not (light grey), N=24 bouts, 24 individuals, six groups.

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Table 1. Generalised linear mixed models investigating how sound treatment (playback of either ambient sound or traffic noise) influenced the likelihood that a focal individual (a) stopped foraging or (b) fled in the first 10 s. Variance (± SE) for the random terms (in italics) are reported, and significant fixed terms noted in bold. N=100 trials, 50 individuals, five groups.

Fixed effect	χ^2	df	P	Effect ± SE
(a) Stopped foraging in first 10 s				
Treatment	**83.26**	**1**	**<0.001**	**4.949 ± 0.760**
Intercept				-2.752 ± 0.596
Group ID				<0.001 ± <0.001
Individual ID in group				<0.001 ± <0.001
(b) Fled in first 10 s				
Treatment	**37.13**	**1**	**<0.001**	**109.9 ± 330.1**
Intercept				-121.8 ± 330.1
Group ID				<0.001 ± <0.001
Individual ID in group				0.171 ± 0.413

Table 2. Linear mixed models investigating the effect of sound treatment (playback of either ambient sound or traffic noise), and individual age class, sex and dominance, on the change in (a) vigilance scan rate, and (b) the proportion of time spent vigilant, from the pre-playback period to the playback period. Variance ($\pm$ SE) for the random terms (in italics) are reported, and significant fixed terms noted in bold. N=78 trials, 39 individuals, five groups.

Fixed effect	$\chi2$	df	P	Effect $\pm$ SE
(a) Change in vigilance scan rate				
Treatment	**6.00**	**1**	**0.014**	**1.200 $\pm$ 0.484**
Age class	0.02	1	0.898	-0.073 $\pm$ 0.532
Sex	0.25	1	0.615	-0.233 $\pm$ 0.490
Adults only – Dominance	0.26	1	0.611	-0.324 $\pm$ 0.655
Treatment:Age class	0.15	2	0.927	-0.383 $\pm$ 1.061
Treatment: Sex	0.49	2	0.783	0.466 $\pm$ 0.979
Adults only – Treatment:Dominance	1.45	2	0.483	1.387 $\pm$ 1.301
Intercept				0.533 $\pm$ 0.422
Group ID				0.267 $\pm$ 0.517
Individual ID in group				<0.001 $\pm$ <0.001
(b) Change in the proportion of time spent vigilant				
Treatment	**32.98**	**1**	**<0.001**	**0.348 $\pm$ 0.055**
Age class	**6.94**	**1**	**0.008**	**0.159 $\pm$ 0.060**
Sex	0.51	1	0.477	0.039 $\pm$ 0.056
Adults only – Dominance	0.00	1	0.973	-0.001 $\pm$ 0.065
Treatment:Age class	3.72	1	0.054	0.224 $\pm$ 0.118
Adults only – Treatment:Dom	2.01	2	0.367	0.177 $\pm$ 0.128
Adults only – Treatment:Sex	3.02	2	0.221	0.153 $\pm$ 0.124
Pups only – Treatment:Sex	1.22	2	0.543	-0.132 $\pm$ 0.178
Intercept				0.049 $\pm$ 0.043
Group ID				<0.001 $\pm$ <0.001
Individual ID in group				<0.001 $\pm$ <0.001

Table 3. General linear mixed model investigating the effect of sound treatment (playback of either ambient sound or traffic noise) on the likelihood that the focal individual became a sentinel. Variance (± SE) for the random terms (in italics) are reported, and significant fixed terms noted in bold. N=78 trials, 39 individuals, five groups.

Fixed effect	χ^2	df	P	Effect ± SE
Treatment	**8.47**	**1**	**0.004**	**2.151 ± 0.903**
Intercept				-3.328 ± 1.082
Group ID				0.300 ± 0.548
Individual ID in group				0.482 ± 0.695

Table 4. Linear mixed model investigating the effect of sound treatment (playback of either ambient sound or traffic noise), and individual sex and dominance status, on sentinel bout duration. Variance (± SE) for the random terms (in italics) are reported, and significant fixed terms noted in bold. N=44 bouts, 22 individuals, six groups.

Fixed effect	χ2	df	P	Effect ± SE
Treatment	**46.69**	**1**	**<0.001**	**1.734 ± 0.190**
Dominance	**13.04**	**1**	**<0.001**	**-0.855 ± 0.213**
Sex	0.08	1	0.783	0.055 ± 0.213
Treatment:Dominance	0.14	1	0.706	-0.145 ± 0.403
Treatment:Sex	0.27	2	0.872	0.165 ± 0.387
Intercept				3.830 ± 0.194
Group ID				<0.001 ± <0.001
Individual ID in group				0.032 ± 0.178

Table 5. Generalised linear mixed models investigating the effect of sound treatment (playback of either ambient sound or traffic noise) on the likelihood that a sentinel (a) changed post height, and (b) moved to another post. Variance (± SE) for the random terms (in italics) are reported, and significant fixed terms noted in bold. N=69 bouts, 27 individuals, six groups.

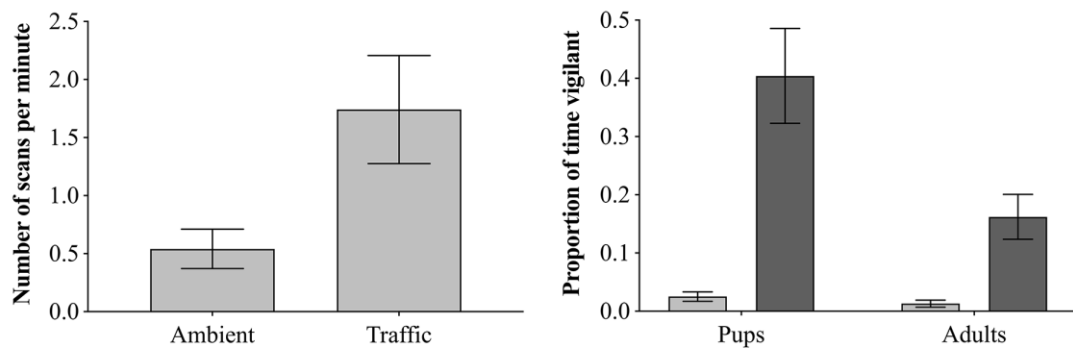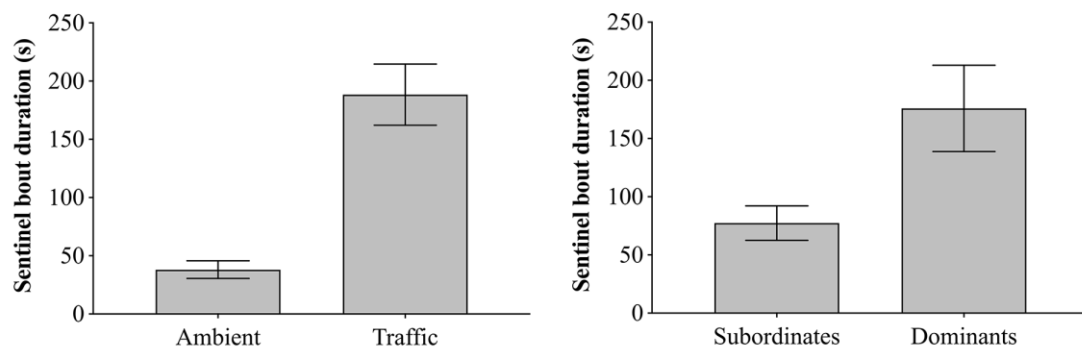| Fixed effect	χ2	df	P	Effect ± SE
(a) Changed sentinel post height				
Treatment	**12.61**	**1**	**<0.001**	**2.862 ± 1.079**
Intercept				-3.555 ± 1.014
Group ID				<0.001 ± <0.001
Individual ID in group				<0.001 ± <0.001
Trial pair in individual ID in group				<0.001 ± <0.001
(b) Moved to another sentinel post				
Treatment	**22.30**	**1**	**<0.001**	**128.4 ± 227.2**
Intercept				-140.2 ± 227.2
Group ID				<0.001 ± <0.001
Individual ID in group				<0.001 ± <0.001
Trial pair in individual ID in group				<0.001 ± <0.001

Figure 1
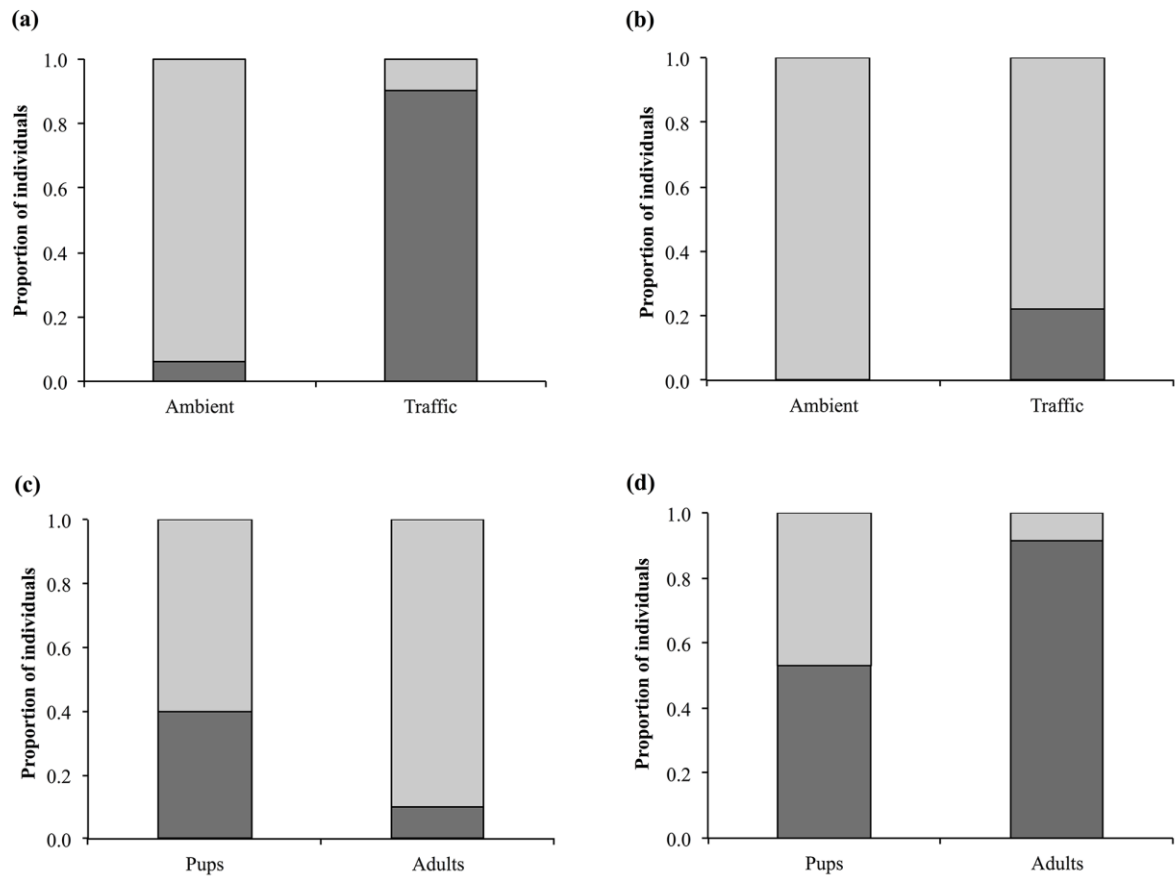
Figure 2

Figure 3

Figure 4

Figure 5