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Animal behaviour

When the birds go unheard: highway noise disrupts information transfer between bird species

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Highway infrastructure and accompanying vehicle noise is associated with decreased wildlife populations in adjacent habitats. Noise masking of animal communication is an oft-cited potential mechanism underlying species loss in sound-polluted habitats. This study documents the disruption of between-species information transfer by anthropogenic noise. Titmice and chickadees broadcast specific calls to alert kin of predator threats, and sympatric vertebrates eavesdrop on these alarm calls to avoid predators. We tested if tufted titmouse alarm call eavesdropping by northern cardinals is disrupted by road noise. We broadcast recorded alarm calls to cardinals in natural areas near and far from highways. Cardinals reliably produced predator avoidance responses in quiet trials, but all birds in noisy areas failed to respond, demonstrating that highway noise is loud enough to disrupt this type of survival-related information via masking or cognitive distraction. Birds in family Paridae are abundant, highly social and vocal residents of woodlands across the Holarctic whose alarm calls are used by many species to mediate predation risks. Our work suggests that communication network disruption is likely to be widespread, and could help explain the pattern of reduced biodiversity near roadways.

1. Introduction

Road networks, a defining component of the built environment, have numerous negative effects on ecological systems. Vehicle noise is particularly pervasive, extending far into surrounding habitats [1]. Organisms' acoustic signals can be masked by loud noise [2], and a commonly observed wildlife response to highway noise is reduced population density near noise sources [3]. Animal communication is clearly degraded by masking of signals, but connections between signal masking and population densities remain speculative [2]. Here, we show that disruption of between-species transfer of survival-related information represents a promising link between road noise and its associated negative consequences for animal populations.

In acoustic information transfer, a signal can either be directed from signaller to receiver or it can be used by an inadvertent receiver (i.e. eavesdropper; [4]). Eavesdropping on social information is common among mammals, reptiles and birds [4]. When multiple prey species share similar predator assemblages, eavesdropping on heterospecific alarm calls can reduce risk of predation. More than 30% of North American woodland birds likely rely on alarm calls of Paridae (parids), a widespread family of birds including tit and chickadee species [5]. Alarm call signals propagated by parids encode precise and accurate assessments of predation threat by common predators [6], and this information is exploited by species that share predators with parids [7].

We assessed disruptive effects of highway noise on eavesdropping by northern cardinals (*Cardinalis cardinalis*; hereafter 'cardinals') on alarm calls of

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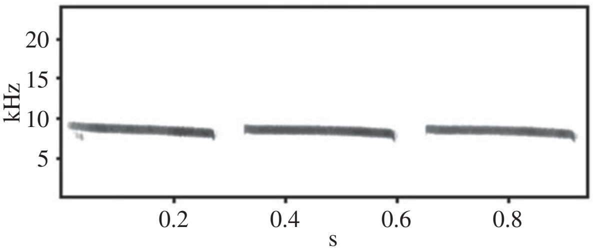

Figure 1. Spectrogram of titmouse 'Z note' alarm call.

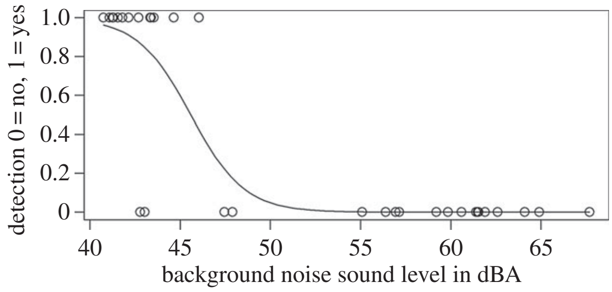

Figure 2. Mean background noise (sound level) in A-weighted decibels (dBA) versus response to alarm call playbacks (0, no response; 1, response) showing responses drop off at approximately 47 dBA.

tufted titmice (*Baeolophus bicolor*; hereafter 'titmice'). Cardinals are abundant resident birds with a range that largely coincides with that of titmice. Cardinals reliably respond to the 'high-seet' titmouse alarm call (indicating detection of a flying predator; figure 1) by freezing in place for extended periods, terminating vocalizations and scanning for predators [8]. We tested whether highway noise could disrupt this between-species information transfer by performing a playback experiment in which we exposed free-living cardinals to alarm call playbacks in suitable habitats by major roadways. We performed playbacks in more distant quiet locations (control), or closer locations exposed to interstate highway noise (treatment), and predicted that typical cardinal anti-predator responses would diminish with increased noise.

2. Material and methods

(a) Study areas

Study locations were in state-managed parks adjacent to either Interstate 75 or US Highway 441 (both high traffic, average vehicles per day 3200 and 3600, respectively; [9]) in northcentral Florida, USA. All playback locations were more than 200 m from paved road edges, to minimize non-acoustic road-edge effects [1] and located in the same habitat (closed canopy mixed hardwood–pine forest). *A priori*, we used SPreaD-GIS sound modelling [10,11] and site visits to choose treatment ('noisy'; greater than or equal to 50 dBA) and control ('quiet'; less than or equal to 49.9 dBA) locations (more than 150 m apart to ensure independent sampling of cardinal territories). Playbacks were conducted from 07.00 to 13.00 h, from 6 May to 8 July 2014, and in fair weather during cardinal breeding season.

(b) Set-up and survey

At playback locations, we measured sound level of background noise before and after the trials and averaged these measures for precise estimates of ambient noise. One playback speaker (for broadcasting the titmouse alarm call) was mounted on a painter's pole at 3.7 m height (titmouse foraging height), and a second Bluetooth speaker was placed less than 1 m high in vegetation (for initial broadcast of cardinal territorial call to attract the playback subject into the sample area). Observers stood still in cover 10 m or more from the alarm call playback speaker. To ensure the absence of cardinal natural predators and habituation to observer presence, we conducted a 5 min survey prior to the playback trial with a fixed radius of 20 m centred on the alarm call speaker. If avian predators were detected, then trials were discontinued.

(c) Playback

Immediately following the survey, we broadcast cardinal territorial calls from the low speaker until a cardinal responded and was within range for the alarm call playback (2–20 min, mean = 4.6). This stimulus attracted cardinals within the sample area and elicited conspicuous territorial display behaviours (e.g. chipping, rapid movement [8]). Behaviours were recorded and playback continued until the cardinal was within 20 m of the alarm call speaker, then the playback was switched to the 'Z note' alarm call broadcast from the high speaker (see electronic supplementary material for playback recording/calibration), and recording of exhibited behaviours continued. In all trials, alarm call playbacks were 30 s in duration at 52.2 dBA (1 m from speaker). Sound stimuli were played at realistic sound levels (K.E.S. and A.M.G. 2015, personal observation).

Using cardinal behaviours exhibited during aviary playbacks of titmouse alarm calls [8] and preliminary field trials, we developed a key (ethogram) for typical behaviours exhibited towards either conspecific territorial or titmouse alarm call playbacks. Using this key, we could readily detect the transition from agonistic to anti-predator behaviours when playback stimuli were switched (electronic supplementary material, table S1), and determine *in situ* if the cardinal responded or not to the alarm call. In a pilot study, we determined that cardinals exhibited no obvious response to control playbacks or observer presence alone ($n = 18$, see electronic supplementary material), thus control playback responses were omitted. Finally, we measured distance between responding cardinal and alarm speaker at time of playback (1–19.9 m, mean = 6.6) and conducted a detailed vegetation assessment following the trials (see the electronic supplementary material).

(d) Statistical analyses

Our primary hypothesis was that sound level could disrupt alarm call detection. But both the distance of cardinals from the playback speaker and vegetation structure at playback sites could also potentially influence signal detection by cardinals. We parametrized a generalized-linear model with a logit link function and a maximum alpha of 0.05 (R v. 3.2.3 statistical software). Using information theoretical model comparisons with Akaike information criterion for finite sample sizes AICc [12], we compared models that included possible interactions of sound level (dBA), distance from speaker and vegetation structure (represented by five significant principal components from a principal components analysis; see electronic supplementary material for statistical methods and table S3 for model comparisons). We used a KAPPA statistic to confirm that model results were in agreement with predicted values [13].

3. Results

We performed $n = 15$ 'noisy' and $n = 19$ 'quiet' playbacks. None of the birds in noisy areas responded to the playback, whereas 15 of 19 responded in quiet areas. The best fit model had high predictive power (KAPPA = 0.82) and included only background noise levels as a significant predictor (figure 2). Higher noise levels corresponded to reduced likelihood of cardinal behavioural response to alarm calls ($p = 0.036$).

4. Discussion

We provide clear evidence that highway noise disrupts information transfer from titmice to cardinals, two abundant species in the woodlands of eastern North America. We could not determine whether cardinals simply could not hear the alarm calls (i.e. masking) or if road noise caused cognitive distraction, thereby inhibiting response behaviours even if test subjects could 'hear' the alarm calls. Indeed, some non-responsive cardinals were well within probable hearing range (2 m) of the speaker. Cognitive distraction is the monopoly of an individual's attention by one stimulus over others [14], and has been implicated or experimentally demonstrated in the inhibition of communication [15,16]. Cardinals reliably use information regarding predation risk encoded in parid alarm calls to adjust their anti-predator decision-making [17], and rapid responses (e.g. freeze) to the 'Z note' call could increase cardinals' chances of avoiding lethal raptor attacks [8]. Based on our experiences with cardinal reactivity, it is unlikely that cardinals living near roads are simply ignoring alarm calls of titmice, but our design cannot distinguish this from disruption of normal responses. Nor do we know what raptor densities and rates of titmouse alarm calls were near roads; if both were low, this could encourage unwary cardinal behaviour. We did, however, find a reduction in cardinal densities and no difference in titmouse densities in noisy versus quiet study locations [11]. Therefore, given the available evidence, our analysis and logical parsimony, we conclude that the loud highway noise most likely disrupted communication and suppressed (via masking or distraction) normal anti-predator responses of cardinals.

Reduced wildlife densities in noisy habitats is a pattern that appears in both experimentally and naturally occurring noise-polluted study sites [3,18]. Our findings suggest that the loss of appropriate response to social information of high fitness value should be included in any enumeration of mechanisms to explain small bird declines near anthropogenic noise sources [3]. Appropriate and reliable anti-predator responses to parid alarm calls have been documented in more than 8 bird species across the Holarctic [5], suggesting widespread reliance on parid anti-predator information. As a result, raptors that prey on small birds could experience higher rates of successful attacks in noise-affected habitats. Additionally, non-lethal effects on prey behaviour could lower bird densities in noisy areas. That is, if prey perception of risk was elevated by noise [18] because of the lack of social (this study) or personally collected information concerning lethal risks, then prey might selectively avoid such areas [19]. In sum, either a loss of anti-predator information or disruption of appropriate responses to alarm calls could lead to decreased density of prey birds via increased predation success or prey avoidance. This aligns with evidence that loss of other types of acoustic cues (unrelated to predation) can dramatically alter other important behaviours, including foraging, provisioning of young and, ultimately, fitness [20]. Our study does not establish causal links between highway noise and population reductions. We provide compelling evidence, however, that highway noise disrupts a common form of heterospecific information transfer and, in turn, anti-predator behaviours important to the survival of numerous woodland birds that participate in the finely tuned anti-predator communication networks organized around parids [21]. Based on the widespread importance of alarm call eavesdropping for mitigating predation risk in animal communities, our work suggests a valid mechanism to explain reduced wildlife populations near roads.

Ethics. All animal use was conducted in accordance with institutional guidelines under IACUC Study no. 201308, University of Florida. Permission was obtained through the Florida Division of Recreation and Parks under permit no. 01311412-A to conduct this research.

Data accessibility. Data and statistical codes are available from the electronic supplementary material.

Authors' contributions. A.M.G. designed the study and collected data. Both authors participated in study design, analysed the data and drafted the manuscript. Both authors agree to be held accountable for the content therein and approved the final version of the manuscript.

Competing interests. We have declared no competing interests.

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