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Exposure to traffic noise weakens territory defence in the Southern Emu-wren (*Stipiturus malachurus*)

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Anthropogenic noise has the potential to negatively impact wildlife by disrupting communication and reducing overall fitness. Understanding the effects of traffic noise on signalling behaviour can be important for managing threatened populations. The Southern Emu-wren *Stipiturus malachurus* is a threatened, sedentary and territorial songbird, with a broad distribution in areas with and without main traffic roads. In this study, we ask if four subspecies of Southern Emu-wren show a similar territory defence response when tested with a traffic noise stimulus, and if either defence behaviour, song characteristics or both change when experimentally tested in relation to distance from the nearest road (proxy for noise exposure). We exposed territory holders to a simulated intruder using playback consisting of two treatments: song only and song with an added traffic noise stimulus. We then measured changes in territory defence behaviour and song characteristics between the two treatments. When exposed to the traffic noise stimulus, Southern Emu-wrens had a weaker behavioural response to a simulated intruder. Irrespective of the playback treatment and distance from the nearest road (noise exposure), Southern Emu-wrens did not change their song characteristics. Response to traffic noise stimulus differed across subspecies as the Mount Lofty Ranges subspecies *S. m. intermedius* had a weaker behavioural response. The Coorong subspecies *S. m. polionotum* sang truncated songs compared to all other subspecies. Our results add to a large body of evidence that the territorial defence behaviour of songbirds can be altered by short-term traffic noise exposure. Our study highlights threatened subspecies differences in response patterns to traffic noise that may be important to consider as part of conservation management approaches. Future studies could aim to better understand component traits that show plasticity and individual variability across systems in response to noise from traffic.

Keywords: anthropogenic noise, behaviour, birdsong, disturbance, roads, territory.

As urbanization expands, anthropogenic noise increasingly reaches areas beyond its sources, raising concern about impacts on wildlife (Barber *et al.* 2010). Most animals use sound for communication, navigation, or detection of predators and prey (Abrams 2000, Brumm 2013). Intensifying traffic noise can disrupt these behaviours through *signal masking*, where noise overlaps and interferes with acoustic signals (Patricelli & Blickley 2006, Barber *et al.* 2010, Francis & Barber 2013, Shannon *et al.* 2016). For instance, Great Tits *Parus major* experience complete masking of alarm calls by traffic, increasing predation risk (Templeton *et al.* 2016). Traffic noise may also reduce attention to key stimuli, delaying detection of predators or a territory takeover attempt by a conspecific intruder (Chan & Blumstein 2011, Zhou *et al.* 2019). Physiologically, traffic noise has been linked to reduced cognitive performance and sexual trait expression in Zebra Finches *Taeniopygia guttata* (Osbrink *et al.* 2021, Daria *et al.* 2022),

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with broader implications for selection on behaviour and morphology (Slabbekoorn & Ripmeester 2008, Wilson *et al.* 2020). This last example highlights the need to better understand selection pathways on individuals and populations in an increasingly noisy world, as there is growing evidence that noisy environments can alter traits under selection (Slabbekoorn & Ripmeester 2008, McGregor *et al.* 2013, Wilson *et al.* 2020). Furthermore, improving our knowledge of the impacts of traffic noise on species can help guide mitigation efforts to prevent biodiversity loss (Sutherland *et al.* 2004).

To mitigate negative traffic noise effects, birds may modify movement patterns or vocal behaviour. Songbirds, which rely on song for mating and territory defence, may benefit from moving and occupying quieter areas (Habib *et al.* 2007, Zwart *et al.* 2016). However, as human populations increase and there are fewer noise-free refuges, birds often adapt by altering vocal traits, such as amplitude, frequency, timing and duration (Patricelli & Blickley 2006, To *et al.* 2021). For example, birds may sing at higher frequencies or louder volumes to overcome the generally low-frequency traffic noise (Hu & Cardoso 2010, Walters *et al.* 2019), lengthen songs to increase detectability during quiet intervals (Francis *et al.* 2011, Grabarczyk *et al.* 2019) or sing earlier in the day to avoid peak noise periods (Fuller *et al.* 2007, Arroyo-Solís *et al.* 2013). Species exposed to aircraft have been shown to adjust the timing of their songs to avoid masking during takeoff or when noise is above certain amplitude thresholds (Dominoni *et al.* 2016, Gallardo Cruz *et al.* 2021). However, not all birds adjust similarly; some reduce song frequency or duration, while others show no change (Dowling *et al.* 2012, Brumm & Zollinger 2013). Understanding variation in singing behaviour and the ability of species to adjust their singing behaviour to traffic noise can help predict species vulnerability to noise.

Traffic noise not only affects birds' ability to communicate for mating, but also influences how they defend their territories, as changes in detection and response behaviour can directly affect territorial outcomes. For songbirds, the use of song communication is critical for identifying and repelling potential territorial intruders (Searcy & Andersson 1986). During territory defence, songbirds may be affected in several ways by signal masking or distraction effects during noisy conditions. First, any intruder into a territory would be more difficult to hear. Often noise has been correlated with response times, with territory holders taking longer to detect the intruder (Kleist *et al.* 2016, Lenis & Guillermo-Ferreira 2020, Waldinger 2020, Reed *et al.* 2021). Second, the vocal response of the territory owner may not be detectable by the intruder, who may miss the 'keep out' message encoded in the signal. To compensate for being inaudible in noisy conditions, territory owners may change their behaviour once an intruder is detected. For example, birds may spend more time searching for the intruder and more time displaying body plumage and body posture displays (Uy *et al.* 2009, Partan 2017, Onsal *et al.* 2022). In the presence of noise, resident birds may also approach the intruder more closely, spending more time inspecting the source, flying past more frequently and physically attacking the source more often (Phillips & Derryberry 2018, Akçay *et al.* 2020, Diniz & Duca 2021, Hohl *et al.* 2025). Birds may also increase call or song production by extending the length or rate of vocalization (Barrero *et al.* 2020, Diniz & Duca 2021, Chavez-Mendoza *et al.* 2023, de Kort *et al.* 2024, Hohl *et al.* 2025) to increase the probability of detection by an intruder in noisy environments. However, these changes in signalling depend on the bird's ability to change flexibly to overcome the traffic noise (Hu & Cardoso 2010, Aplin 2019, Onsal *et al.* 2022). Where birds fail to make such changes, it could lead to an increase in territory disputes and territory turnover, and overall energy expenditure for both birds resulting in a decrease of reproductive output (Patricelli & Blickley 2006, Halfwerk *et al.* 2011, Zwart *et al.* 2016).

Much urban noise research focuses on species common in urban areas, comparing behaviour along an urban–rural gradient (Dowling *et al.* 2012, Diniz & Duca 2021, Onsal *et al.* 2022). However, there is a lack of research on how cryptic, non-urbanized species that typically avoid human development respond behaviourally to increased urban noise whilst also facing increasing habitat fragmentation and human encroachment. In this study, we test a vulnerable non-urbanized species, the Southern Emu-wren *Stipiturus malachurus*, whose range is largely surrounded by urbanization (Pickett 2016, Rudder 2023) and which is listed as threatened by human encroachment (Skroblin & Murphy 2013, Garnett & Baker 2022), making it an ideal candidate for measuring how cryptic non-urban birds respond to traffic noise. As a sedentary bird with limited dispersal ability that subsists largely in small, fragmented habitats (Abrams 2000, Pickett 2002, 2016), territoriality may be a critical component in the persistence of individual Southern Emu-wrens. This view is supported by the species' strong territorial responses to playback (Pickett 2002) which also make it a good species to study the effects of traffic noise on territorial behaviour. With multiple threatened subspecies in South Australia (Garnett & Baker 2022), this also provides an opportunity to investigate potential divergence between subspecies in behavioural response to traffic noise, and adaptive potential. Behavioural divergence may occur quickly, making subspecies useful indicators of rapid divergence in recently separated populations (Lamichhaney *et al.* 2018, Yandell *et al.* 2018). If subspecies differ in their behavioural traits in response to traffic noise, this may indicate behavioural divergence through isolation and provide further justification for response such as subspecies classification and conservation management intervention. Finally, this species is important because the Southern Emu-wren is under-studied and we lack information on its use of song or territory behaviour, which is relevant to gain insight into the tolerance thresholds and the persistence of this species. From a conservation management perspective, it is important to understand if cryptic species, such as the Southern Emu-wren, can adapt to rapid environmental change and increased anthropogenic (traffic) noise.

We conducted playback experiments to assess the impact of traffic noise on the territorial behaviour of the Southern Emu-wren, as well as to identify any potential behavioural differences between subspecies. Specifically, we (1) tested whether birds altered their responses to playback of conspecific song with and without traffic noise and (2) examined whether these responses differed based on proximity to roads as a proxy for noise exposure. We predicted that playback with traffic noise would elicit delayed response times, reduced proximity to the speaker, fewer vocalizations and altered song traits (e.g. higher frequencies, longer duration; Hu & Cardoso 2010, Roca *et al.* 2016, Blackburn *et al.* 2024). We further predicted that individuals closer to roads would show compensatory behaviours (approaching faster and vocalizing more) reflecting adaptation to chronic masking effects (Zwart *et al.* 2016, Weaver *et al.* 2019, Reed *et al.* 2021).

METHODS

Subspecies and study sites

We included all four South Australian subspecies of the Southern Emu-wren in this study. These include (1) *S. m. polionotum* in the South-east/Coorong area, (2) *S. m. intermedius* in the Mount Lofty Ranges/Fleurieu Peninsula, (3) *S. m. halmaturinus* on Kangaroo Island and (4) *S. m. parimeda* in the Eyre Peninsula (Fig. 1). The Southern Emu-wren is listed as Endangered within South Australia under the National Parks and Wildlife Act 1972 (Garnett & Baker 2022). Individually, three subspecies are listed as Endangered: *S. m. intermedius*, *S. m. halmaturinus* and *S. m. parimeda* (Garnett & Baker 2022), with the fourth *S. m. polionotum* having a 'data deficient' status. The species is known to be shy and cryptic in its behaviour, preferring to remain quietly hidden within dense vegetation, particularly in the presence of humans (Pickett 2016). Its known preferred habitat consists predominantly of coastal or swampy areas dominated by dense shrub and/or sedge vegetation and dry mallee with dense undergrowth (Wilson & Paton 2004, Pickett 2006). As a consequence of its small, rounded wings, the species is a poor flyer, tends to hop through low undergrowth, and is therefore thought to be largely sedentary with limited dispersal ability (Pickett 2016). As a result, the species is highly susceptible to extreme weather events, such as fire or flooding, introduced predators and habitat modifications (Skroblin & Murphy 2013, Pickett 2016, Garnett & Baker 2022). To date, very little systematic research has been carried out on this species; most knowledge is derived from personal observations and, in general, available data are limited.

Field surveys

During spring (September–November) 2022, researchers undertook systematic surveys of the four South Australian subspecies of Southern Emu-wren. These were carried out in both historical sighting locations and areas of interest based on habitat structure to identify where Southern Emu-wren were present. The surveys consisted of

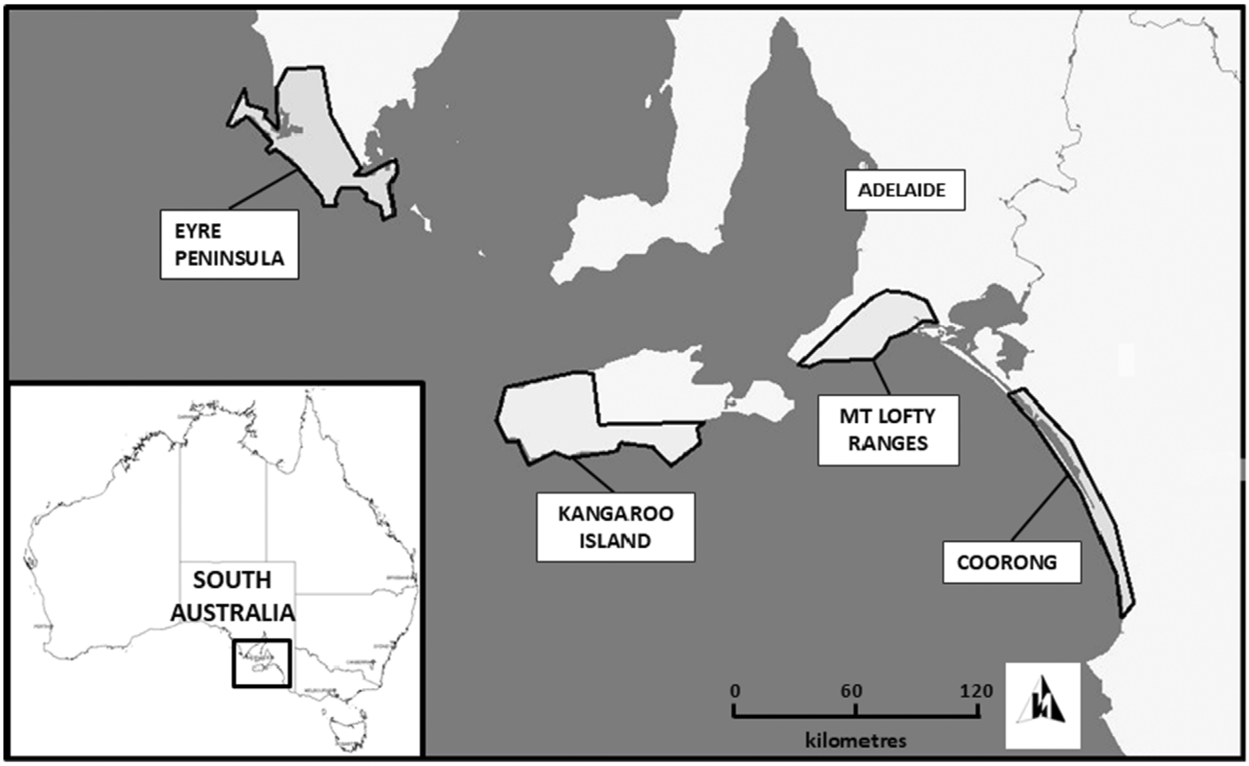

Figure 1. Map illustrating the distribution of the four Southern Emu-wren *Stipiturus malachurus* subspecies in South Australia. Left to right: Eyre Peninsula *S. m. parimeda*, Kangaroo Island *S. m. halmaturinus*, Mount Lofty Ranges *S. m. intermedius*, and Coorong/ Southeast *S. m. polionotum*.

standardized 20-min 2-ha area searches and with the addition of Southern Emu-wren song playback periodically throughout the search (approx. four bursts of 1 min duration), as per recommended methods in the 'Survey guidelines for Australia's threatened birds' (Magrath *et al.* 2010). GPS points were recorded where a 'family group/group' of birds, usually a pair, were found (referred to as Playback location; Table S1), and later used for the playback experiments subsequently performed in 2023. GPS points were recorded using the KoBoCollect application (KoboToolbox, https://www.kobotoolbox.org/) on a GPS-enabled smartphone with a GPS location accuracy in the range 3.8–5.0 m with an average of 4.5 m across all sites.

Distance from the nearest road

The 'distance from the nearest road' measure was created using the 'Ruler' function on Google Earth Pro (Google Earth Pro v.10.59.0.2; Google LLC). Measurement (m) was made in a straight line from the GPS point of playback location (see definition in Table S1) to the closest point of the nearest road.

Playback experiments

Playback tracks

Separate playback tracks for each of the four subspecies in South Australia were created in Audacity software v.3.6.1 (Muse Group). Playbacks for this study were made using songs that we recorded opportunistically during the 2022 surveys (see Fig. S1). All Southern Emu-wren songs were recorded as wave files at 48-kHz sampling rate, 24-bit depth, using an ME67 directional microphone (Sennheiser electronic GmbH & Co.) connected to an H6 recorder (Zoom). Six unique 'control' playback tracks were created for each of the four subspecies (total 24 tracks; see Fig. S2). For each control playback track, a unique 'song stimulus' was made using two unique bursts of song from one individual (from their respective subspecies). These two songs from an individual were alternated and each repeated three times with even spacing (every 10 s) during the 1 min of 'song stimulus' (e.g. Song 1, Song 2, Song 1, Song 2, Song 1, Song 2). This created a set of six unique playbacks per subspecies each with two songs from a single individual. Each playback track consisted of 3 min: 1 min song stimulus, 1 min silence and one repeat of the 1 min song stimulus. Until this study, Southern Emu-wrens have not been systematically recorded or tested with playback. We therefore based our song rate and inter-song duration for playback stimuli on a closely related species, the Superb Fairywren *Malurus cyaneus*, which is in the same family (Maluridae). Based on the recordings made for this study (authors 2025, unpublished data) the typical frequency range of the Southern Emu-wren song is 5.6–12.5 kHz (Table S2 and Fig. S3). Background noise <3 kHz was removed, the tracks were normalized at −15 dB and were saved as 16-bit wave files (.wav).

Another six playback tracks per subspecies (24 tracks) were created for the 'noise' playback study by using the 'control' playback tracks and adding a 'traffic stimulus' (see Fig. S2). Thirty minutes of traffic noise were recorded using the Sennheiser ME67 directional microphone and Zoom H6 recorder between 3 PM and 4 PM, at a busy intersection of a major road (Main South Road: 35°06′55.2″S, 138°31′22.2″E) in South Australia. Three 60-s segments of traffic noise ('Traffic noise' stimulus = 'TNS') were manually selected from random points within the original traffic recordings and were superimposed on the song playback tracks during the designated minute of song stimulus, using copies of the previously created 'control' playback tracks. The TNS consisted mostly of cars and vans with an average power density of −36.76 (bD Fs/Hz) and an average frequency range of 0–3.3 kHz (Fig. S3). The three TNS recordings were used on four occasions, with different order patterns employed across the six playback tracks for each subspecies (see Fig. S2). The result was a total number of 48 playback tracks: 24 'control' ('song stimulus' only) tracks and 24 'noise' ('song stimulus' and 'traffic noise' stimulus) tracks. The amplitude of the control tracks was ~77–81 dB (at 1 m distance, measured with the 'Sound Meter – Decibel Meter' application), which is equivalent to the upper limit of naturally singing Southern Emu-wrens (43–78 dB; 'Sound Meter – Decibel Meter'). The amplitude of the 'noise' tracks was ~81–84 dB (at 1 m distance), which is consistent with the noise threshold of high-density/heavy traffic (70–90 dB; NSW Government 2022).

Playback treatments

We conducted all playback experiments at the start of the active breeding season from late August to late November. During this time, birds are likely to be paired and become active with more frequent calling/singing (Pickett 2000, Higgins 2001) and would therefore have a higher detection rate. Southern Emu-wrens also have been found to be more responsive to song playback during the early phases of the breeding season, becoming less responsive to playback once they have chicks in the nest or fledglings (Pickett 2002, Magrath *et al.* 2010). The playback locations were based on the GPS records from the researchers' own surveys of the species in 2022 in addition to GPS records obtained from previous survey efforts conducted by the South Australian Department of Environment and Water Biological Database of SA (record no. DEWNRBDBSA220225-1). At each playback location, we conducted our experiments closest to suitable habitat and vegetation structure in which the species commonly occurs (freshwater swamp and dry heath with dense vegetation up to 1 m high; Garnett & Baker 2022).

Playback methods

Once at a selected GPS playback location, a loudspeaker (XB12 Extra Bass Portable Bluetooth Speaker (Sony Australia Ltd); frequency response 20 Hz–20 kHz) was placed on the branches of a shrub or tree (at a height of ~1–1.5 m). Territory occupancy was tested across 3 days using visual inspection and/or 1 min playback to test for response. If birds were present or responded within the 3 days, the territory was considered active and occupied. After detecting presence on Day 3, we observed a cool-down period of a minimum of 10–15 min allowing the birds to return to 'normal activity' (as determined by pilot trials). 'Normal activity' was visually observed by seeing the birds return to the location or in the direction from which they arrived (i.e. moving away from and no longer investigating the speaker) and when birds had ceased all vocalizations, which usually occurred within 5 min, as per personal observation during the pilot trials. Following this, we conducted either the 'noise' or 'control' trial, using one of the six corresponding local playback tracks (from the same subspecies). The six playback stimuli for each treatment (control & noise) were rotated through evenly, across all trials. Before each trial, the playback track was checked to ensure that it did not contain songs from the same location (potentially the same individuals) or from close neighbours, to avoid possible response biases. However, this never occurred so there was no overlap between song in playbacks and potential test subjects. The order in which the two trials (control or noise) were conducted changed with every subsequent playback location to evenly use both trial treatments first and second. Once set up, the researcher positioned themselves 10–15 m from the loudspeaker in a position of best visibility and played the chosen playback track to start the trial from a smartphone (OppoA53s; Oppo Ltd) or iPod (Touch 7; Apple Inc.; at ~80 dB at 1 m; Sound Meter – Decibel Meter) connected to the loudspeaker via Bluetooth. During the trial, all observed behaviours were recorded verbally into a Sennheiser ME67 directional microphone connected to a Zoom H6 recorder following published methods (Colombelli-Négrel *et al.* 2023, Hohl *et al.* 2025). Verbal recording of information allowed for quick in-time observations without missing potential behaviour, and to gain accurate latencies within the recording by observing the timestamps (see Table S3 for detailed definitions and instructions of behaviour observations). As there was no way to separate responses from birds sharing the territory, we tested all birds at that location simultaneously as a 'group'. At the end of the first playback trial, we observed another cool-down period during which we performed trials on other groups in the area. Depending on travel time between groups and birds still returning to 'normal behaviour', we then performed the second trial, on average 15 min later. Keeping this time short ensured that the same group of birds were observed in the following trial and minimized the chance of large movements away from the area where birds would no longer respond. All playbacks were performed systematically for separate groups/family groups with unique GPS points within a short time frame (usually 1–2 days after determination of territory occupancy) and with a minimum buffer of 200 m between other GPS locations. This was to minimize the likelihood of birds moving between territories and sampling an individual more than once. This buffer distance was established as twice the average estimated territory size (0.9 ha) based on the only published study that identifies territory size for this species (Maguire 2006).

Playback analyses

Audio recordings were assessed visually in Raven Pro v.2.0.5 (The Cornell Lab of Ornithology) using the Hann algorithm (DFT = 512 samples; frequency resolution = 124 Hz; time resolution = 11.6 ms; frame overlap = 50%). Behavioural variables scored upon listening and observing visually to the recordings were: (1) latency (s) to first response (approach or vocalization), (2) latency to 1 m of speaker (s), (3) time within 1 m of speaker (s) and (4) total number of vocalizations (this included all vocalizations produced such as songs, trills and contact calls). The chosen behavioural variables are good indicators of territory response in songbirds and reflect the strength of aggression (Reed *et al.* 2021, Colombelli-Négrel *et al.* 2023, Akçay *et al.* 2024). In cases where birds did not respond at all during a trial, they received the 'maximum time to respond' of 360 s for all latency measures. Songs detected in the sonograms that were fully visible (without any overlap from background noise or other songs) also were measured for (i) length (s), (ii) minimum frequency (Hz), (ii) maximum frequency (Hz) and (iv) bandwidth (frequency range; Hz). We selected our song variables based on published studies showing that these variables were commonly adjusted in response to noise (Brumm & Zollinger 2013, Roca *et al.* 2016, Diniz & Duca 2021). To standardize our analysis, we used a pre-set −24 dB threshold below the peak amplitude following the threshold method (Podos 1997, Zollinger *et al.* 2012, Brumm *et al.* 2017). All song measures were obtained using the 'Selection Mode' function in Raven Pro whereby the song edges were manually defined by a single researcher.

Statistical analyses

We used SPSS v.29.0.1.0 for Windows (IBM SPSS Inc.) for all statistical analysis. We analysed the four behavioural responses and the four song characteristics separately. As some variables were correlated and to reduce the number of variables/tests, we used two principal components analyses

(PCAs) to create new derived variables. For the behavioural responses, we obtained one principal component, PC_Behaviour, with an eigenvalue of 1.93 that explained 48% of the variance. Higher values correspond to a stronger behavioural response: shorter latency to respond, more time within 1 m of the speaker and higher number of vocalizations produced (Table 1). For the song characteristics, we extracted one principal component, PC_Song, with an eigenvalue of 2.44 that explained 61% of the variance. Higher values correspond to higher minimum and maximum frequencies, larger bandwidths and longer songs (Table 1). Bartlett's test of sphericity confirmed the suitability of our response variables for PCAs: behavioural response variables (Bartlett's test: $\chi^2 = 309.35$; $P < 0.001$) and song characteristic variables (Bartlett's test: $\chi^2 = 226.45$; $P < 0.001$). We also confirmed adequate sampling with the Kaiser–Meyer–Olkin measure: behavioural response variables (KMO: 0.577) and song characteristic variables (KMO: 0.499).

We analysed playback variables (PC_Behaviour & PC_Song) using two separate generalized linear mixed models (GLMMs), with Gaussian distribution and link function identity. Both models included 'subspecies', 'playback trial type' (noise, control), 'playback order' (first, second), 'sex' (male, female), 'Julian Date' and 'distance from the nearest road' as fixed factors. We checked our fixed factors for collinearity using variance inflation factors, and all factors were close to 1, confirming no issue with multicollinearity. To account for potential response variation between playback stimuli or location, 'playback track ID' and 'playback location' were included as random factors in our model. The name given to the location of a playback experiment was used for 'playback location'. Pearson's residuals from the GLMMs were checked for normal distribution using Q–Q plots and homogeneity of the residuals were checked in a scatterplot of residuals and predicted values. All assumptions were met upon visual inspection of the graphs.

Table 1. Factor loadings from principal component analysis (PCA) of the Southern Emu-wren responses to playback ($n = 209$ individuals).

Response variables	Factor loadings
(1) PC_Behaviour	
First response latency	−0.57
Latency to 1 m	−0.88
Time within 1 m	0.82
Number of vocalizations	0.37
(2) PC_Song	
Minimum frequency	0.82
Maximum frequency	−0.84
Range of frequency	−0.96
Length of song	−0.36

PC_Behaviour had an eigenvalue of 1.93 and explained 48% of the variance. High values for PC_Behaviour indicated a stronger behavioural response: shorter latencies, longer times spent within 1 m of speaker and many vocalizations produced. PC_Song had an eigenvalue of 2.44 and explains 61% of the variance. High values for PC_Song indicated that individuals produced longer songs at higher frequencies and with broad bandwidths.

RESULTS

We conducted trials at 123 playback locations ($n = 121$ trials with 'Noise' and 122 'Control' trials, 243 trials). At each playback location, we tested all members of the 'family group' (pairs and sometimes trios) simultaneously and we recorded a total of 411 individual responses ($n = 202$ trial with 'Noise' and 209 'Control' trials; $n = 249$ males, 159 females). See Table S4 for detailed sample size per subspecies.

Birds showed a weaker behavioural response when presented with the noise playback compared to the control playback (Tables 2 and S5; Fig. 2), which was more pronounced for the Mount Lofty subspecies as demonstrated by the pairwise comparison of the estimated means (Table 3; Fig. S4). We found an effect of 'sex' with males showing a stronger behavioural response ($m = 0.04$) compared to females ($m = -0.59$) in the pairwise comparison ($F_{1,387} = 72.88$, $P < 0.001$). We also found an effect of 'Julian date' with the behavioural response becoming stronger later in the study period, going further into spring (R^2 linear = 0.028). We found no difference in behavioural response based on 'playback order' or 'distance from the nearest road' and there was no interaction effect of 'distance from the nearest road by trial type' (Table 2). The random effect 'playback track ID' did not account for variation in PC_Behaviour (Wald $Z = 0.670$; $P = 0.50$), but the random effect 'playback location' did account for variance within PC_Behaviour (Wald $Z = 5.124$; $P < 0.001$), which indicates a difference in response from birds at different sites.

Table 2. Outputs from the generalized linear mixed model of Southern Emu-wren behaviour and song characteristics.

Response variable	Coefficients	Estimate	se	*t*	*P*
PC_Behaviour	Intercept	−17.02	4.347	−3.91	**<0.001**
	Playback trial type [Control vs noise]	0.23	0.104	2.27	**0.02**
	Subspecies [Coorong vs Mt Lofty]	1.10	0.241	4.57	**<0.001**
	Subspecies [Eyre Peninsula vs Mt Lofty]	1.08	0.252	4.31	**<0.001**
	Subspecies [Kangaroo Island vs Mt Lofty]	1.02	0.253	4.01	**<0.001**
	Playback order [first vs second]	0.13	0.072	1.81	0.07
	Sex [male vs female]	0.63	0.074	8.53	**<0.001**
	Julian Date	0.001	0.0002	3.53	**<0.001**
	Distance to road	0.00	0.0004	0.78	0.43
	Distance to road * Playback trial type	0.00	0.0003	0.53	0.59
PC_Song	Intercept	−5.79	5.951	−0.97	0.33
	Playback trial type [Control vs noise]	0.13	0.233	0.57	0.56
	Subspecies [Coorong vs Mt Lofty]	−1.05	0.336	−3.12	**0.002**
	Subspecies [Eyre Peninsula vs Mt Lofty]	0.35	0.343	1.02	0.30
	Subspecies [Kangaroo Island vs Mt Lofty]	0.10	0.354	0.30	0.76
	Playback order [first vs second]	−0.20	0.147	−1.37	0.17
	Sex [male vs female]	0.05	0.148	0.34	0.73
	Julian Date	0.00	0.0003	1.06	0.29
	Distance to road	−0.001	0.0006	−1.71	0.09
	Distance to road * Playback trial type	−0.001	0.0009	−0.76	0.44

Both models included ‘playback trial type’ (control, noise), ‘subspecies’ comparison (Mount Lofty, Coorong, Kangaroo Island, Eyre Peninsula), ‘playback order’ (first, second), ‘sex’ (male, female), ‘Julian Date’ and ‘distance nearest to road’ as fixed factors. Random factors of ‘playback track ID’ and ‘playback location’ were included. Significant *P*-values are presented in bold.

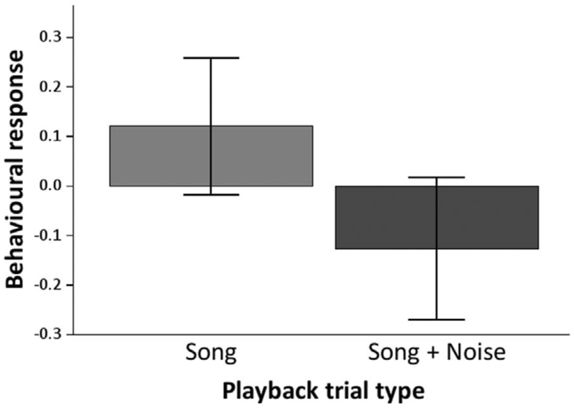

Figure 2. Behavioural response (PC_Behaviour values shown as mean ± 2 se) of Southern Emu-wrens to playback of ‘song’ (n = 122) vs ‘song + traffic noise’ (n = 121). High values for PC_Behaviour indicate a fast response (s), long time within 1 m of speaker (s) and many vocalizations.

However, because the model accounted for the variance between individuals’ responses using ‘playback location’, we conclude that there was still a significant effect of ‘playback type’ and ‘subspecies’ on behavioural response, but no effect of ‘distance from the nearest road’.

We found a significant effect of ‘subspecies’ on song characteristics (Table 2) with individuals from the Coorong subspecies showing a weaker vocal response compared to all other subspecies (Table 4; Fig. S5). Although not significant, there was a weak trend for individuals living closer to a road to have stronger vocal response during our playback (irrespective of playback type) compared to those that lived far from a road (R^2 linear = 0.125; Table 2; Fig. S6). We found no difference in song characteristics in response to ‘playback trial type’, ‘playback order’, ‘sex’, ‘Julian date’ or ‘distance from the nearest road’ and there was no interaction effect of ‘distance from the nearest road by trial type’ (Table 2). The random effects ‘playback track ID’ (Wald Z = 1.162; P = 0.24) and ‘playback location’ (Wald Z = 0.569; P = 0.56) did not account for variation in PC_Song.

DISCUSSION

Anthropogenic noise can disrupt communication systems in wildlife and reduce overall fitness (Patricelli & Blickley 2006, Barber *et al.* 2010, Ortega 2012, Schroeder 2012). This study aimed to

Table 3. Outputs from the *post hoc* pairwise contrast analyses for the fixed factor subspecies in relation to PC_Behaviour.

Subspecies	Estimate	Standard error	*t*	df	*P*	95% CI lower	95% CI upper
Coorong – Eyre Penisula	0.01	0.17	0.09	387	0.92	−0.320	0.352
Coorong – Kangaroo Island	0.08	0.18	0.46	387	0.64	−0.271	0.440
Coorong – Mt Lofty Ranges	1.10	0.24	4.57	387	**<0.001**	0.630	1.580
Eyre Penisula – Coorong	−0.01	0.17	−0.09	387	0.92	−0.352	0.320
Eyre Penisula – Kangaroo Island	0.06	0.18	0.37	387	0.70	−0.293	0.431
Eyre Penisula – Mt Lofty Ranges	1.08	0.25	4.31	387	**<0.001**	0.593	1.585
Kangaroo Island – Coorong	−0.08	0.18	−0.46	387	0.64	−0.440	0.271
Kangaroo Island – Eyre Penisula	−0.06	0.18	−0.37	387	0.70	−0.431	0.293
Kangaroo Island – Mt Lofty Ranges	1.02	0.25	4.01	387	**<0.001**	0.521	1.520
Mt Lofty Ranges – Coorong	−1.10	0.24	−4.57	387	**<0.001**	−1.580	−0.630
Mt Lofty Ranges – Eyre Penisula	−1.08	0.25	−4.31	387	**<0.001**	−1.585	−0.593
Mt Lofty Ranges – Kangaroo Island	−1.02	0.25	−4.01	387	**<0.001**	−1.520	−0.521

Significant *P* values are presented in bold. CI, confidence interval.

Table 4. Outputs from the *post hoc* pairwise contrast analyses for the fixed factor subspecies in relation to PC_Song.

Subspecies	Estimate	Standard error	*t*	df	*P*	95% CI lower	95% CI upper
Coorong – Eyre Penisula	−1.40	0.23	−5.87	82	**<0.001**	−1.881	−0.930
Coorong – Kangaroo Island	−1.16	0.24	−4.77	82	**<0.001**	−1.642	−0.677
Coorong – Mt Lofty Ranges	−1.05	0.33	−3.12	82	**0.002**	−1.722	−0.382
Eyre Penisula – Coorong	1.40	0.23	5.87	82	**<0.001**	0.930	1.881
Eyre Penisula – Kangaroo Island	0.24	0.26	0.94	82	0.34	−0.271	0.763
Eyre Penisula – Mt Lofty Ranges	0.35	0.34	1.02	82	0.30	−0.330	1.036
Kangaroo Island – Coorong	1.16	0.24	4.77	82	**<0.001**	0.677	1.642
Kangaroo Island – Eyre Penisula	−0.24	0.26	−0.94	82	0.34	−0.763	0.271
Kangaroo Island – Mt Lofty Ranges	0.10	0.35	0.30	82	0.76	−0.598	0.813
Mt Lofty Ranges – Coorong	1.05	0.33	3.12	82	**0.002**	0.382	1.722
Mt Lofty Ranges – Eyre Penisula	−0.35	0.34	−1.02	82	0.30	−1.036	0.330
Mt Lofty Ranges – Kangaroo Island	−0.10	0.35	−0.30	82	0.76	−0.813	0.598

Significant *P* values are presented in bold. CI, confidence interval.

assess the impact on the behavioural and vocal response of Southern Emu-wrens to a simulated intruder with and without a traffic noise stimulus based on exposure (distance from the nearest road). Furthermore, we aimed to assess whether the Southern Emu-wren subspecies vary in behavioural and vocal response patterns in response to anthropogenic noise (traffic stimulus). We have two main findings. First, birds had a less aggressive response toward the simulated territorial intruder song with traffic noise stimulus regardless of the distance of the playback location from the nearest road. Second, there were differences between the subspecies for both behaviour and song characteristics in response to a simulated intruder with and without noise. Our results support the growing number of studies showing that traffic noise can affect avian communication (Dowling *et al.* 2012, Templeton *et al.* 2016, Lenis & Guillermo-Ferreira 2020, Chavez-Mendoza *et al.* 2023), which could have long-term fitness consequences for individuals as they may need to engage in energy trade-offs between vigilance and defence (Brumm 2004, Slabbekoorn & Ripmeester 2008, Francis & Barber 2013).

Studies across taxa find various effects of traffic noise on territorial birds' response pattern to territory threats (Kleist *et al.* 2016, Lenis & Guillermo-Ferreira 2020). In Galapagos Yellow Warblers *Setophaga petechia aureola*, birds were more aggressive to an intruder in a noisy environment and when closer to a road (Hohl *et al.* 2025). It is possible that strong selection is shaping this behaviour because the Galapagos Yellow Warbler experiences the greatest relative mortality cost of vehicle traffic on Santa Cruz Island, making up >70% of the roadkill (García-Carrasco *et al.* 2020). In this study, Southern Emu-wrens had a less aggressive response when exposed to an intruder in a noisy environment, and there was no effect of distance from the nearest road on the behavioural response of the birds. In terms of the behavioural response differences to a stimulus with and without traffic noise, traffic noise has the potential to mask other sounds, in this case the intruder, making it harder for the responders, or territory owners, to detect and determine the location of the intruder (Patricelli & Blickley 2006, Francis & Barber 2013). However, emu-wren song was not adjusted as expected if they were compensating for traffic noise, as birds sang similarly regardless of distance from the nearest road in all four subspecies. A probable explanation is our finding that Southern Emu-wrens typically sing at higher frequencies (5.6–12.5 kHz, see Table S2), above the thresholds of common traffic noise (1–3 kHz; Wood *et al.* 2006, Rochat & Reiter 2016), from which we would expect that they should be able to detect an intruder song even with traffic noise. Conversely, traffic noise masking is expected to be stronger in birds that produce low-frequency songs (Rheindt 2003, Hu & Cardoso 2010, Cardoso *et al.* 2020). In addition, as the Southern Emu-wren is a highly territorial species (owing to lack of habitat and dispersal ability), they may seek to uphold their signalling of aggressive intent to intruders by maintaining their song characteristics. There is evidence from other studies that birds which alter their song (frequency) characteristics also have a weaker behavioural response (Luther & Magnotti 2014), potentially increasing the likelihood of territory contests.

The weaker behavioural response to a conspecific intruder with traffic noise that we found in this study may be caused by other factors associated with traffic that we did not measure. Perhaps local traffic noise masks the sounds of predators or other competitors in the area, making a defensive response more costly. If noise is masking predator presence and increases perceived predation threat by concealing the sounds of predators and conspecific predator alert calls, this could change predator–prey dynamics, often with an advantage to the predator (Chan & Blumstein 2011, Kern & Radford 2016, Templeton *et al.* 2016, Zhou *et al.* 2019, Chou *et al.* 2023). Predation may therefore be a greater concern when traffic noise is present ('increased threat' hypothesis) resulting in increased time spent in predator vigilance behaviour, distracting and taking away time to respond quickly to territory intruders (Frid & Dill 2002, Meillère *et al.* 2015, Matyjasiak *et al.* 2024). Sound masking of predators and mates may cause an increase in time spent checking on each other, including more visual inspection behaviour (Swaddle & Page 2007, Halfwerk *et al.* 2012, Gill *et al.* 2015, Chavez-Mendoza *et al.* 2023, Matyjasiak *et al.* 2024). Future research may benefit from investigating whether birds are performing increased predator vigilance or surveillance behaviours of mates when responding to intruders in the presence of traffic noise. In addition to masking, traffic noise may be associated with distraction effects associated with lower attention in noisy environments as well as reduced detectability of territory intruders (Chan & Blumstein 2011, Dooling *et al.* 2019, Zhou *et al.* 2019). Traffic noise also has been linked to increased physiological stress in some bird species (Campo *et al.* 2005, Shannon *et al.* 2016, Injaian *et al.* 2018) and higher stress hormone levels are often associated with inhibited behaviour (Cockrem 2007). For this reason, it is possible that Southern Emu-wrens may be reducing and/or slowing their territorial behaviour responses when stressed.

Song characteristics were stable with and without experimental traffic noise regardless of the distance the birds lived from the nearest road. In Galapagos Yellow Warblers, birds showed short-term behavioural and acoustic plastic responses when exposed to traffic noise (Hohl *et al.* 2025), whereby the response changed when close to the road, but the song response changed irrespective of distance to the road, with decreased minimum frequency when exposed to traffic noise. Perhaps selection favoured behavioural plasticity in these birds to respond to rapidly changing environments, which are hallmarks of the Galapagos Islands. Possibly colonist or long-distance migratory species are selected for plasticity (Price *et al.* 2003, Morganti 2015, Fontanari *et al.* 2023). In contrast to Galapagos Yellow Warblers, Southern Emu-wrens did not alter their song characteristics in response to traffic noise or distance to road. It could be that Australia's mainland status and relatively stable predator community promotes consistent behaviour in the Southern Emu-wren, compounded by the species' poor ability to disperse and coastally restricted habitat (Maguire &

Mulder 2004). This raises the idea that some species may have been previously selected for song traits to overcome masking, instead of engaging in habitat–phenotype matching for song characteristics (Francis 2015, Job *et al.* 2016, Shirani & Miller 2024), and therefore do not show plasticity to respond to short-term changes in the noise treatment. Southern Emu-wrens frequently occur along noisy shorelines, where they are subjected to prolonged and frequent low-frequency sounds from sea turbulence or wind (Copeland 1993, Barrett 2003). Southern Emu-wrens may therefore have previously adapted their song with higher frequencies to overcome environmental noise, a hypothesis which remains to be tested (Gomes *et al.* 2021). Future work could aim to disentangle the effect of coastal ambient noise and anthropogenic noise, especially from traffic, as birds are known to change their vocalizations given environmental background noise, from sources including water, wind and insects (Lengagne *et al.* 1999, Pytte *et al.* 2003, Brumm & Slater 2006, Davidson *et al.* 2017, To *et al.* 2021, Reed *et al.* 2022). Lastly, it is important to note that our study focused solely on song responses and did not include other common bird vocalizations. Calls that may be relevant to include in future studies are contact calls and alarm calls as they are often produced at a lower frequency, and thus may be more susceptible to noise masking (Morton 1977). Contact calls are critical for social recognition, such as mate cohesion (courtship and movement/location tracking) and male–male aggression during territory disputes (Kondo & Watanabe 2009). Alarm calls are used to warn kin of nearby predators (Hollen & Radford 2009, McLachlan & Magrath 2020). Future studies could investigate whether vocalizations other than songs, which are also important to fitness, may be disrupted/masked by anthropogenic noise.

The Mount Lofty Ranges subspecies had the weakest behavioural response to traffic noise compared to the other three subspecies, which is likely to be a result of the greater distance of their home-range from human disturbance, as suggested in other studies in birds (Mockford & Marshall 2009, Francis *et al.* 2011, Dowling *et al.* 2012, Oden 2013, To *et al.* 2021, Onsal *et al.* 2022). Our finding that the Mount Lofty subspecies was, on average, located farther from roads than the other subspecies supports the hypothesis that varying levels of disturbance exposure may contribute to behavioural differences between populations, or in this case subspecies. However, this idea requires formal empirical testing to be confirmed.

It should be noted that our measure of traffic noise disturbance may not accurately reflect the degree of impact of traffic noise on different subspecies and the extent to which communication is actually masked. We did not measure environmental noise in the field but used distance from the nearest road as a proxy for probable exposure and experience. The addition of information such as number of vehicles and ambient sound levels (dB) in future studies may help to better determine the effect of exposure and noise levels to which specific populations or subspecies are subjected (Gill *et al.* 2015). The use of sound meters/recorders, which can be placed at different intervals and over different areas of a site, could be used to record noise over time and analysed to provide further information on noise exposure at the site. It also should be noted that this secretive species is difficult to detect or track when not responding to a playback, as birds otherwise remain concealed and silent in dense vegetation (JB, pers obs.). Thus, in the scope of this study, we were unable to determine territory boundaries or the centre of the territory to standardize playback location within a territory. As a result, our findings could be subjected to biases if playbacks consistently occurred in different positions between the subspecies; however, this seems unlikely. Rather, it is more likely that variance in playback placement relative to territory centre was random across trials and subspecies. We suggest that future studies focus on territory mapping using banding and surveying (Maguire 2006), or bioacoustics array tracking techniques to better determine territory boundaries (Blumstein *et al.* 2011). Playback studies could then benefit from this knowledge on boundaries by factoring in territory edge effects.

In summary, we found that traffic noise can affect territory response in songbirds, as Southern Emu-wrens had a weaker territorial response toward a simulated territorial intruder when exposed to traffic noise. Furthermore, birds did not adjust their behaviour or song based to an intruder, regardless of their natural exposure to traffic. Lastly, there were some differences in behavioural and song characteristic in response to traffic noise treatments across subspecies. These results provide evidence that: (1) territorial birds can suffer from behavioural disruption when responding to territory threat owing to traffic noise, even with species that sing longer and higher frequency songs, which may be less prone to masking effects of noise; (2) birds may be selected for song traits to overcome masking but are not necessarily selected for plasticity in song behaviour to respond to changes in noise levels; and (3) behavioural responses to anthropogenic disturbances can vary at the subspecies level, which should be considered for future conservation efforts. In particular, these results raise questions about which biological mechanisms, such as selection for plasticity versus habitat–phenotype matching, may be selecting survival traits in human-modified landscapes. Vulnerable species that are unable to avoid or adapt behaviourally to noise disturbance may suffer fitness losses and reduced population stability. With growing evidence that noisy environments can alter traits under selection (Ortega 2012, Shannon *et al.* 2016, Wilson *et al.* 2020), it is increasingly important to understand the different selection pathways that may be shaping wild populations and how they may be adapting or failing to adapt to a world of increasing urbanization and human impact.

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AUTHOR CONTRIBUTIONS

Julian Behrens: Conceptualization; methodology; data curation; formal analysis; investigation; visualization; writing – original draft; writing – review and editing. **Diane Colombelli-Négrel:** Conceptualization; formal analysis; funding acquisition; methodology; project administration; resources; supervision; writing – review and editing. **Sonia Kleindorfer:** Conceptualization; formal analysis; funding acquisition; methodology; supervision; writing – review and editing.

CONFLICT OF INTEREST

The authors report there are no competing interests to declare.

ETHICAL NOTE

Our research protocols have been approved by the Flinders Animal Ethics Committee (AEC), project reference no. E480, BIOL5563. Fieldwork was conducted under permit from the South Australian Department for Environment and Water (Z24699).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Supporting glossary of terminology with their descriptive definitions used in this study.

Table S2. Frequency parameters of Southern Emu-wren songs recorded in this study.

Table S3. Behaviour definitions and instructions researchers used to verbally record behaviour during playback trials.

Table S4. Sample sizes of the total number of playback trials for each treatment type ('Control' and 'Noise') and individual Southern Emu-wren that responded by subspecies across all trials.

Table S5. Southern Emu-wren behavioural response (mean ± se) to playback trials of conspecific local song (control) and conspecific local song with noise (noise).

Figure S1. Examples of Southern Emu-wren songs.

Figure S2. Schematic of playback track (PB) design.

Figure S3. Spectrograms of playback treatments.

Figure S4. Behavioural response (PC_Behaviour values shown as mean ± 2se) to playback of song with noise between the Southern Emu-wren subspecies (Coorong, Eyre Peninsula, Kangaroo Island, Mount Lofty Ranges) in South Australia. Low values for PC_Behaviour indicate slow response (s), less time within 1 m of speaker (s) and fewer vocalizations.

Figure S5. Song characteristics (PC_Song values shown as mean ± 2se) to playback song with noise between the Southern Emu-wren subspecies (Coorong, Eyre Peninsula, Kangaroo Island, Mount Lofty Ranges) in South Australia. Higher values for PC_Song indicate higher minimum frequency, higher maximum frequency, broader frequency bandwidth and longer song.

Figure S6. Scatterplot indicating the negative relationship between song characteristics (PC_Song) and the distance to the closest road (m) of each territory in Southern Emu-wren. Line of best fit (R^2 linear = 0.125), with confidence intervals of mean (solid) and individual (dash). Higher values for PC_Song indicate higher minimum frequency, higher maximum frequency, broader frequency bandwidth and longer song.

Data S1.