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Anthropogenic noise limits resource distribution without changing social hierarchies

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Highlights

- Experimental evidence shows that anthropogenic noise limits resource distribution
- Fewer individuals in the population benefitted from the arrival of new resources
- Size-based hierarchies were resilient to anthropogenic noise
- Anthropogenic noise can disrupt resource distribution in populations

Abstract

Increasing evidence demonstrates that anthropogenic noise is a global pollutant that threatens marine ecosystems. Mounting numbers of studies show its diverse effects on individuals and their behaviour. However, little is known about how individual changes in response to anthropogenic noise could cascade through groups and populations affecting resource distribution vital for survival and fitness. Here we test the hypotheses that anthropogenic noise could alter resource distribution, associated hierarchies and consequently individual benefits. We used groups of hermit crabs, a globally distributed model system for assessing impacts of environmental change on wildlife and measured in controlled laboratory conditions the resource distribution of their reusable shelters (gastropod shells) under ship noise and ambient control playbacks. We applied vacancy chain theory to test three predictions about how new resource units create benefits for a population. A new resource unit leads to (i) a cascade of resource abandonments and acquisitions (= chain of vacancy moves) based on an internal (ii) hierarchy (here size-based) which allows (iii) more than one individual to benefit. All three predictions were supported under control sound. Under anthropogenic noise however, fewer individuals benefitted from the arrival of a new, empty shell, while the size-based hierarchy was maintained. The latter was apparent in chain structures, which were concordant between sound treatments. This experiment shows that anthropogenic noise can affect individual behaviours that cascade through groups. This has the potential to disrupt wider resource distribution in populations.

Keywords: cross-modal pollution, global change, group behavior, noise pollution, sensory ecology

1. Introduction

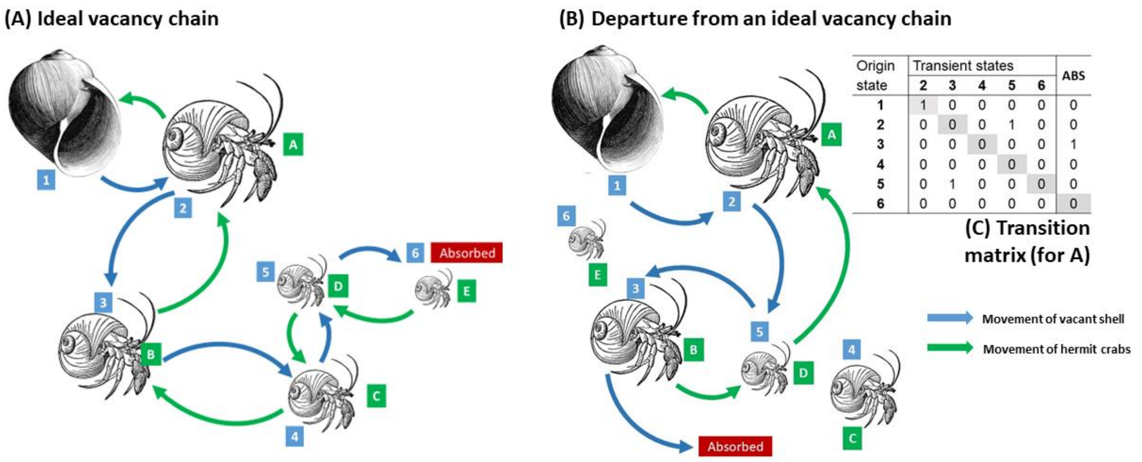
Anthropogenic noise is an increasingly well-studied global pollutant affecting various biological responses, taxa, and ecosystems. An ever-larger number of taxa with primary sensory systems other than sound are nevertheless shown to be affected by anthropogenic noise (Sole et al. 2023a, 2023b; Sordello et al., 2020; Tidau and Briffa, 2019a; Wale et al., 2019). Increasing evidence corroborates that anthropogenic changes to animals' sensory environment affect stimuli detection, processing, and responses across modalities (Halfwerk and Slabbekoorn, 2015) such as noise interfering with visual, chemical, or tactile information (Chan et al., 2010; Herbert-Read et al., 2017; Leiva et al., 2021; Sara et al., 2007; Sole et al. 2023b; Tidau and Briffa, 2019a, 2019b; Wale et al., 2013, 2019). Yet, acoustic communication and behaviour remain the most studied responses to noise (Jerem and Mathews, 2021; Sordello et al., 2020). Behaviour is the most plastic phenotypic component, and hence often the initial response to human induced environmental change (Briffa et al., 2024; Sih et al., 2011). A central question on the impacts of anthropogenic noise is how cross-sensory disruption not only affects foraging, antipredator responses, and habitat choice (Chan et al., 2010; Leiva et al., 2021; Wale et al., 2013) but how these changes may scale-up by altering intra-specific interactions, and thus resource distribution. Experiments show that noise changes grouping preferences (Herbert-Read et al., 2017; Sara et al., 2007; Tidau and Briffa, 2019a), social hierarchies and agonistic interactions (Bruintjes and Radford, 2013; Butler and Maruska, 2020; Kareklas et al., 2021). While these are all expected to influence the distribution of resources among members of a population, little is known about the extent to which group level processes that drive resource distribution are affected by noise. Given that patterns of resource distribution will affect individual fitness, survival and potentially population health, our current knowledge gap on how anthropogenic noise affects these undermines our understanding the scope of this threat to marine ecosystems.

The distribution of resources partly results from competitive and aggressive interactions between conspecifics, where the winner "takes it all" (Briffa and Hardy, 2013). Such processes take place when resources are limited and indivisible. However, when resource units are also reusable (e.g., territory, shelter, and sometimes mates), alternative processes can emerge in which the benefits of a single new (or newly available) resource unit spread beyond the individual that acquires it. This is especially likely when each individual can only possess one resource unit at a time. Upgrading to a newly available unit of increased value requires abandoning the previously held unit of lesser value, which then becomes available to other individuals, typically of lower status. Vacancy chains describe this process, where discrete and limited but reusable resources cascade through populations. The theory predicts that the arrival of a new resource, which is of higher quality than those resource units currently available to a population, initiates a process of resource redistribution of current ownerships within that group (Chase, 1991; Weissburg et al., 1991).

Vacancy chains occur across human and non-human populations, within vertebrate and invertebrate taxa. Examples range from redistribution of jobs (Rosenfeld, 1992), homes (Persky and Felsenstein, 2008) and second hand cars (Chase, 1991) in humans to mates in fish (Forsgren, 1997), territory in bobcats (Benson et al., 2004), birds (Eikenaar et al., 2009) in fiddler crabs (Fayed et al., 2008), and shelter in hermit crabs (Briffa, 2013; Laidre, 2012; Rotjan et al., 2010). Hermit crabs for instance rely on portable gastropod shells to protect their weakly calcified exoskeleton against predators and environmental extremes (Shumway, 1978; Vance, 1972). Most commonly these crustaceans obtain shells not by preying upon gastropods but by finding empty shells or through agonistic interactions (Briffa and Elwood, 2004). Importantly, populations and groups of hermit crabs are structured by size hierarchies which determines access to shells. Hermit crabs rely on diverse sensory modalities to assess resource quality of their shells (size and species), i.e. visual, tactile and chemical cues (Elwood and Neil, 1992). Anthropogenic noise has been shown to disrupt this information assessment across non-acoustic sensory modalities in hermit crabs such as *Pagurus bernhardus* (Tidau and Briffa, 2019a, 2019b; Walsh et al., 2017). *P. bernhardus* is widespread in intertidal and shallow subtidal marine ecosystems across Europe's Atlantic coasts and belongs to the superfamily Paguroidea with over 1,100 known species (McLaughlin et al., 2010). Hermit crabs are an established model species for investigating the behavioural responses to global change and anthropogenic pollution (Briffa et al., 2024). Vacancy chains in hermit crabs provide a unique opportunity to determine whether behavioural changes due to anthropogenic noise at the individual level cascade upwards to localised groups (e.g., within the bounds of tide pools) and ultimately populations.

Vacancy chain theory predicts the optimal resource distribution in groups through three experimentally testable characteristics (Weissburg et al., 1991): (i) the multiplier effect, which quantifies the aggregated number of individuals benefitting from the arrival of a single new resource unit; (ii) the linearity of chains, which quantifies the hierarchical structure of the population as the correlation between ranked resource value and the ranks of individuals within a group; and (iii) the overall structure of the chain, which describes the expected sequence of resource acquisitions and abandonments given the hierarchical relations between participants. Vacancy chain processes are initiated when a new, unoccupied resource unit of higher value than currently existing resources (gastropod shell) arrives to a population of hermit crabs (due to death of a conspecific or the gastropod itself). In an 'ideal' vacancy chain that follows the population's hierarchy (Figure 1A), the largest (i.e., heaviest), top-ranked hermit crab (crab rank A) will occupy the highest quality resource unit (= shell rank 1). As the highest ranked crab abandons its previously occupied resource (= shell rank 2), it creates a vacancy (= empty shell). The vacancy may now cascade through the population. Theory predicts that the second ranked individual (crab ranked B) will occupy the newly available resource (= shell rank 2) and consequently the vacancy will now move from the second to the third level of the chain (= shell rank 3). Through this sequence of individual decision-making, the vacant shell resource continuous to propagate through the population allowing the three key characteristics of vacancy chains to be quantified: the multiplier effect, linearity, and chain structure.

In nature, vacancy chains frequently depart from the ideal (Figure 1B). Some individuals may obtain greater benefits than predicted by their rank while others may experience reduced resource quality due to ‘backwards moves’ and ‘skipping’ (Edquist and Rotjan, 2012; Rotjan et al., 2010) caused by for instance imperfect information gathering, internal and external factors like predation risk (Briffa and Austin, 2009) and habitat type (Edquist and Rotjan, 2012) as well as for stochastic reasons. Given that anthropogenic noise pollution is known to disrupt individual resource assessment behaviour in hermit crabs (Tidau and Briffa, 2019b; Walsh et al., 2017), and grouping preferences (Tidau and Briffa, 2019a), we test four hypotheses: Under anthropogenic noise (i) chain structures will depart further from the ideal than under ambient sound, which will (ii) lower the multiplier effect (i.e., the number of individuals benefitting) and (iii) disrupt linearity (i.e., the group hierarchy). As hermit crabs have a preferred, optimal shell weight to body weight ratio (quantified as the percentage of an individual’s preferred shell weight based on well-established linear regression between mass and shell (Briffa, 2013; Briffa and Austin, 2009)), (iv) the exposure to noise lowers the average individual gain in shell quality. In other words, we predict that if noise disrupts the individual decisions that underpin the structure of vacancy chain processes, then the aggregate benefits from these will also be lower.



Origin state	Transient states					ABS
	2	3	4	5	6	
1	1	0	0	0	0	0
2	0	0	0	1	0	0
3	0	0	0	0	0	1
4	0	0	0	0	0	0
5	0	1	0	0	0	0
6	0	0	0	0	0	0

Figure 1 Illustration of (A) an ideal vacancy chain, and (B) a chain departing from ideal exemplified for gastropod shells and hermit crabs. Five freely moving crabs, initially occupying shells of suboptimal size, form a size-based group hierarchy (A-E in descending size). Shell 1 represents the arrival of a new resource unit, which is of higher value than currently occupied resources (Shells 2-6). Green arrows indicate the movement of hermit crabs, moving up the chain. Blue arrows show the movement of the shell vacancy through the group and down the chain. (C) Transition matrix that summarises the movement of the vacant resource (here shell). Illustrations of *P. bernhardus* and the gastropod shell are re-used from Foote Arnold (1901).

Figure 1A) Ideal vacancy chain: Crabs *move up* the chain and vacancies move *down in* chains. Shell 1 is closest to the optimal shell size of crab A. Upon encounter, crab A decides to move and abandons its original shell 2. Shell 2 is now unoccupied and the next crab in the size hierarchy, crab B, will move into shell 2, which represents an incremental improvement in resource quality. When all moves have been completed, the smallest shell 6 is vacant and has transited to an 'absorption state'.

Figure 1B) Departure from an ideal vacancy chain: After crab A abandons its original shell 2, crab D is the first individual to move into the newly vacated shell resource. Crab D 'skipped' shell 3 and 4, which represents a significant improvement in resource quality. Crabs can also make less beneficial decisions by moving backwards like crab B moving into the smaller shell 5.

Figure 1C) Transition matrix: Summary of all shell movements through groups (read by row from left to right). Shells move from the 'Original state' (old) to the 'Transient states' (new). The observed vacancy moves are summarised in the inset transition matrix. In an ideal vacancy chain, all moves would occur on the central diagonal (grey shaded). Skips appear above the central diagonal and backward moves below it.

2. Methods

2.1. Animals collection, husbandry and group composition

We collected hermit crabs from the rocky intertidal of Hannafore Point, Cornwall, UK (50° 20' 42'' N, 4° 28' 0'' W) in January and February 2018 and transported the animals directly to the laboratory at the University of Plymouth, UK. Crabs were kept in a temperature controlled room at 15 °C with a 12:12 h light:dark cycle in a single holding tank containing 125 l of continuously filtered and aerated seawater. Crabs were fed once a week with white shellfish. Following Briffa and Austin (2009), the morning before initiating vacancy chains, crabs were carefully removed from their shells with a bench vice, sexed and weighed. Since breeding is likely to affect the shell preferences and behaviour of egg-carrying females, we used only male crabs without damaged appendages, visible parasites, or recent moult. Each vacancy chain contained five crabs of the following five weight classes and corresponding rank: (1) 0.99-0.90 g, (2) 0.89-0.80 g, (3) 0.79-0.70 g, (4) 0.69-0.60 g, and (5) 0.59-0.50 g. Hereafter, crabs are referred to as rank 1 (heaviest crab) to 5 (lightest crab). We set the experiment up so that all crabs would be able to gain in shell quality by moving up one rank in the chain (moving into a shell that is bigger than the current shell but not exceeding their optimal shell size). To identify each individual crab within its group of five, the major cheliped of each crab was marked with a different colour of non-toxic nail polish. Each crab was assigned a labelled shell, of the common periwinkle *Littorina littorea*, at 50 % of its preferred shell weight (%PSW), calculated from a regression line relating body weight to the preferred shell weight obtained from previous shell selection experiments (Briffa, 2013; Briffa and Austin, 2009). Afterwards, each crab was housed individually in a white plastic dish of 15 cm diameter containing continuously aerated seawater, fed with white fish, and kept in at 15 °C until the vacancy chain was initiated the following day. After the experiment, all crabs were supplied with shells of their preferred weight and returned to the collection point.

2.2. Tank set up and sound treatments

The tank setup and sound treatments followed previously established protocols (see Supplement for details; Tidau and Briffa, 2019a, 2019b). Briefly, we used a 80 x 50 x 50 cm sized glass tank (with 1 cm thick aquarium glass) similar as in Akamatsu et al. (2002).The tank was filled with aerated seawater to a depth of 40 cm (~ 130 l) placed on a free-standing trolley cushioned with 1 cm Styrofoam plates between tank and trolley as well as the trolley and floor. An underwater speaker (DNH Aqua-30 underwater speaker, effective frequency range 80 – 20 000 Hz, DNH A/S, Kragerø, Norway) was suspended from a cushioned bamboo stick at 20 cm distance to one end of the tank, facing towards two observation arenas that were submerged within the large tank (see Supplement Figure S1). Soundtracks were playback from a Toshiba Portégé R830-13C laptop (Tokyo, Japan) connected to the speaker via an amplifier (Lvpin LP-200 amplifier Lvpin Technology Suzhou Co., Taiping Town, China). Sound measurements were taken at the position of the animals within their observation arenas. We used two acoustically transparent plastic dishes (15 cm diameter) glued to bottom of the tank at 30 cm distance from the speaker as observation arenas.

The sound treatments consisted of three ship noise playbacks recorded at three major UK harbours and three ambient control playbacks from the same sites (same recordings as in Wale et al., 2013, 2019). We used Audacity 2.1.2 (Audacity Team, 2016) to create six audio tracks. A group of hermit crabs was exposed to one out of the three ship playbacks (A, B, C) and the corresponding ambient control sound (ambient A, B, C). For the noise treatment, we alternated 2 minutes ship noise with 2 minutes ambient control sound from the same site including 15 seconds fading in and out to simulate the passing by of a ship.

As in previous experiments, the power spectrum analysis of the acoustic pressure (see Supplement for details) confirmed that hermit crabs were exposed to two distinct sound treatments (Figure 2; Tidau and Briffa, 2019a, 2019b). We are aware that hermit crabs like other marine crustaceans and indeed invertebrates more generally, perceive the particle motion component of sound (Simpson et al. 2015; Sole et al. 2023b; Tidau and Briffa, 2019a, 2019b; Wale et al. 2019, 2021). As noted in previous studies (e.g., Simpson et al. 2015; Sole et al. 2023b; Tidau and Briffa, 2019a, 2019b), we do not aim to establish absolute sound sensitivity levels. Instead, the aim is to provide a mechanistic insight into the effects of anthropogenic noise on resource distribution, which could not be quantified in the field. Our sound analysis shows that crabs were exposed to two distinct sound treatments, over timeframes that the animals could experience in nature, and at intensities comparable to previous studies (e.g. Wale et al. 2019).

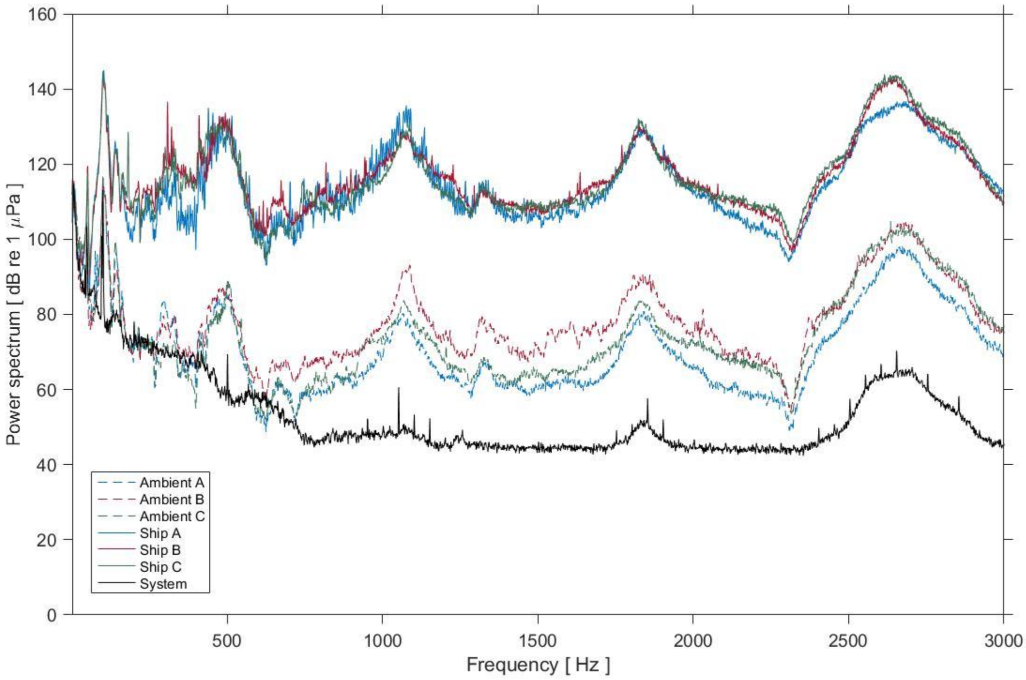


Figure 2 Power spectrum of the acoustic pressure for three ship noise playbacks and three corresponding ambient sound playbacks recorded at 30 cm distance to the speaker. The system self-noise characterises the sound output by the equipment without playbacks. Filtered for 100 – 3 000 Hz frequency bandwidth.

2.3. Experimental design and data collection

We designed a fully orthogonal experiment with the factors sound (ambient control/ ship noise) and time at which shell occupation was recorded (1 h/ 24 h). Vacancy chains were initiated in the mornings (between 10:00 am and 11:00 am). The individually housed crabs were allocated to groups of five in one of the two arenas within the observation tank and given 5 minutes without any sound treatment to acclimate. We then started the sound playback and placed a vacant shell of a 100% PSW of the largest crab (crab rank 1) in the centre of the arena marking the initiation of the vacancy chain. After 1 h from initiating the vacancy chain, we recorded the resource distribution i.e., the size of the vacant shell and shell size occupied by each crab. Afterwards crabs were left undisturbed for a further 23 h. After a total of 24 h from initiation of the vacancy chain, we recorded the same information again. We randomly assigned each vacancy chain to one of the two sound treatments and one of the three alternative soundtracks. Sound treatments were alternated between the subsequent observations. We initiated 42 vacancy chains (crabs: *n* = 210) but had to exclude some chains due to technical problems including sound treatment equipment failure prior to sampling points, crabs not occupying a shell or moulting either overnight prior to initiating a chain or during the chain process (see Supplement Table S2 for sample sizes of each treatment level sound*time). Moulting prior to the sound exposure i.e., overnight meant that we were able to initiate 23 chains for the ambient sound treatment and 19 chains for the noise treatment. Quantifying vacancy chains

Vacancy chains are quantified via the three key characteristics mentioned above (Chase, 1991; Weissburg et al., 1991): (i) the multiplier effect; (ii) the linearity of chains, and (iii) structure of the chain (ideal chains, random chains and differences between chains). The multiplier effect measures aggregated number of individuals benefitting from vacancy chains. A length ≥ 1 shows that vacancy chains have occurred. In our experiment, the multiplier effect has a maximum of 5 possible moves; 1 per hermit crab and time point (Briffa, 2013; Briffa and Austin, 2009). In optimal chains, the resource distribution process ends either when a new recruit arrives (e.g., a naked crab enters the group filling the vacancy) or when all chain participants own a resource unit which is of higher value than the lowest value unit available (here shell rank 6). The latter is the absorbance (ABS) state in which no individual would benefit by occupying the lowest available resource unit (Chase, 1991). Linearity measures the individual resource occupation in relation to the group's hierarchical structure expressed as the correlation between crab rank (rank 1 – 5) and the rank of the occupied shell (6 shells = 1 * 5 crabs + 1 new vacancy) (Briffa, 2013). To analyse the structure of chains, vacancy moves across all chains within one of the four treatment combinations (sound * time) were summarised in four grand transition matrices (see Figure 1C; Chase, 1991). Transition matrices were then individually tested for (i) the randomness of moves assuming that there is no underlying pattern in the vacancy moves and (ii) the proximity of vacancy chains to an ideal chain assuming that all moves occur according to the rank hierarchy of the chain participants and thus along the main diagonal of transition matrices (Figure 1C). The comparison of matrices against each other quantifies (iii) structural differences between treatment groups (sound * time). Together, these measurements allow us to quantify whether sound treatment and time point affect the resource distribution in a group. In addition to the group benefits, we quantified the individual gain expressed as %PSW (Briffa, 2013; Briffa and Austin, 2009).

2.4. Statistical analysis

To test the effects of sound (ambient control/ ship noise), time (1 h/ 24 h) and their interaction (sound * time) on the multiplier effect and linearity we used generalised linear mixed effect models (CRAN: lme4; Bates et al., 2015) implemented in R (version 3.4.3). We included three random effects to account for the experimental design: chain-ID as each chain was observed twice (1 h/ 24 h), day as two vacancy chains were observed simultaneously (accounting for potential non-independence of paired observations within the same session) and playback-ID (1-6) as each of the six soundtracks was re-used multiple times. The significance of the GLMM parameters was quantified using the Type III ANOVA approach of stepwise model selection (Harrison et al., 2018). Multiplier effect was bound by the maximum of 1 move per crab, so we converted the number of moves into the proportion of 5 possible moves (one for each animal per time point) and applied a binomial error structure. Linearity was calculated as Pearson's correlation coefficient between crab and shell rank for each chain at each of the two time points (CRAN: dplyr; Wickham et al., 2023). As linearity can contain negative values, the response variable was converted to positive values by adding a constant of 1 and treated as continuous response analysed using a Gamma distribution. % PSW ranged from 35% - 139.3% and thus was best described by a Gamma error distribution. In addition to the factors above, we fitted rank as a fixed effect and the interaction term (sound*time*rank) and crab ID to account for repeated measurements per individual (1 h/ 24 h).

The structure of the vacancy chains was quantified by analysing the four grand transition matrices (one for each factor combination sound * time). We conducted three separate tests. First, to test whether the moves differed from random (i.e. an equal number of moves in each cell of the matrix), we conducted a Fisher's exact test (base R) for each of the four matrices (Briffa, 2013). Since Fisher's tests does not work well for matrices with tables larger than 2 x 2, we chose to calculate a simulated *P*-value with 8000 simulations. This is sufficient to determine whether the chains are non-random. Second, to determine how closely the chains conformed to ideal, we conducted Bartlett's test of sphericity (CRAN: psych; Revelle, 2022) for each of the four grand transition matrices (Bartlett, 1951). This test compares the observed moves to the predicted moves based on an ideal vacancy chain (Chase, 1991). Since the test cannot be performed with a determinant = 0, we transformed the frequency counts to proportions and added 1 to every cell on the main diagonal of each matrix (Wothke, 1993). Third, to determine whether matrix structures in the four groups differed from each other, we conducted pairwise comparisons of matrices using a procrustean randomization test of concordance (CRAN: ade4; Dray and Dufour, 2007) with 9999 replicates (Dray et al., 2003; Jackson, 1995). A significant test result of $P < 0.05$ means that chains are significantly similar to each other.

Ethical note: The experiment complied with the ARRIVE guidelines, ASAB Ethical Committee/ABS Animal Care Committee and did not require licensing. No animals were harmed during the experiment. After the experiment, each crab was supplied with an optimal shell, fed, and returned to the collection point. No licences or permits were required at the time this study was conducted.

3. Results

The multiplier effect, the group-level aggregated number of shell moves, was not affected by the interaction between time and sound ($\chi^2_1 < 0.01$, $P = 0.96$) but it was lower under ship noise than under ambient control (Figure 3A; $\chi^2_1 = 6.45$, $P = 0.01$). This indicates that fewer moves occurred under noise (mean per chain = 1.97 moves; Table 1) compared to ambient control (mean per chain = 2.48 moves). The multiplier effect was higher after 24 h compared to 1 h (Figure 3B; Table 1; $\chi^2_1 = 5.55$, $P = 0.02$) meaning that, regardless of the sound treatment, more moves had occurred after 24 h (2.46 moves) compared to 1 h (2.05 moves). The aggregated benefits from the arrival of a new resource unit percolated through the experimental groups with time (higher multiplier effect after 24h vs 1h) but to a lesser extent under anthropogenic noise (17% had 3 moves; 7% had 4 moves) compared to ambient sound (35% had 3 moves; 10% had 4 moves). Compared to noise, resource distribution was more dynamic under ambient sound. No vacancy chain showed the possible maximum number of 5 moves.

Table 1 Multiplier effect (group-level aggregated number of shell moves) as a proportion of all observed chains in the sound treatment across the two time points (1 h and 24 h).

Sound treatment & number of moves	Multiplier effect as a proportion of all observed chains					
	Mean	One	Two	Three	Four	Five
Ambient control: 140	2.48	0.08	0.48	0.35	0.10	0.00
Ship noise: 116	1.97	0.25	0.56	0.17	0.03	0.00

While the multiplier effects shows that hermit crabs changed shells in all treatment, none of the treatment combinations altered the size-based group hierarchy measured as chain linearity. The linearity of the chains (correlation between rank of the crab and its occupied shell) was not affected by the interaction between time and sound (Figure 3C; $F_1 = 0.59$, $P = 0.44$), or by the main effects of sound ($F_1 = 0.58$, $P = 0.45$) or time ($F_1 = 0.04$, $P = 0.85$). None of the treatment groups showed perfect linearity of 1 (Ambient – 1 h: 0.59; Noise – 1 h: 0.61; Ambient – 24 h: 0.57; Noise – 24 h: 0.64). The individual gain in shell quality, measured as the percentage of preferred shell weight (%PSW), was neither affected by the three-way interaction of sound, time, and rank ($\chi^2_8 = 5.04$, $P = 0.75$), by the two-way interactions sound * rank ($\chi^2_4 = 0.29$, $P = 0.99$) and sound * time ($\chi^2_2 = 0.70$, $P = 0.71$), or sound as the main factor ($\chi^2_1 = 0.12$, $P = 0.73$). However, %PSW was influenced by the interaction between time and rank (Figure 3D; $\chi^2_8 = 49.37$, $P < 0.0001$). Compared to the start of the experiment, all crabs improved their resource quality after 1h. Only the largest crabs had a higher %PSW after 24 h compared to 1 h.

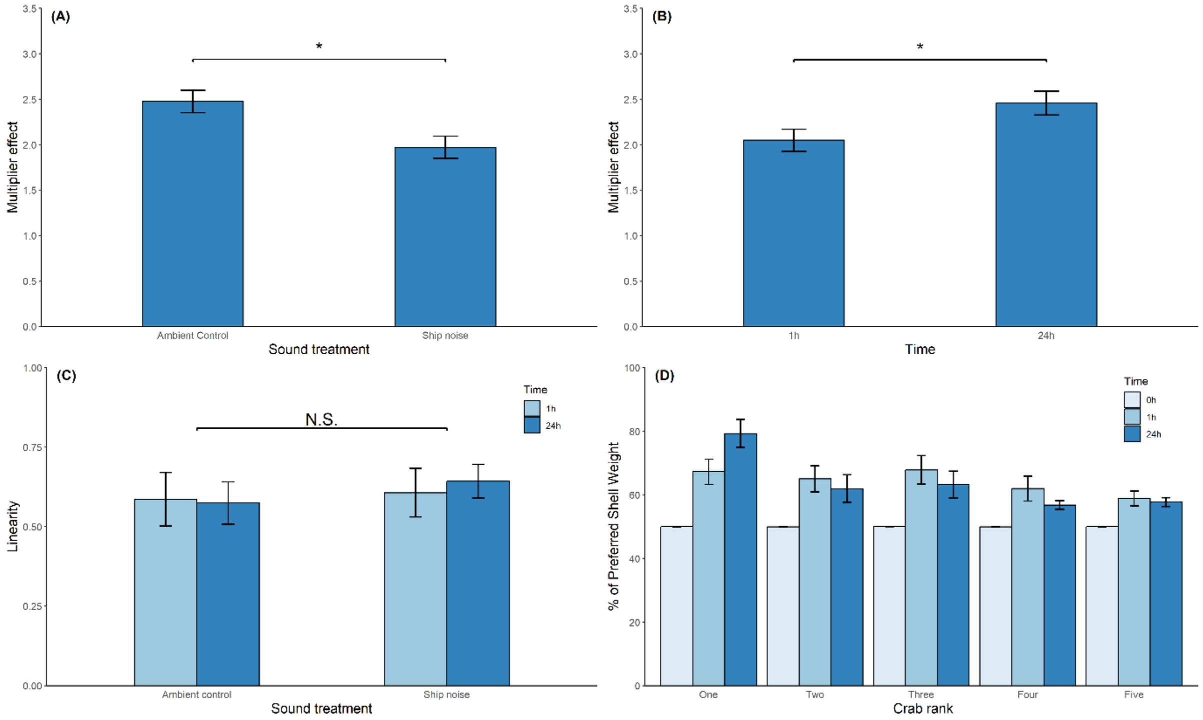


Figure 3 A) Effect of sound treatment on the multiplier effect (aggregated number of shell moves) across both time points. B) Effect of time on the multiplier effect across sound treatments. C) Effect of sound * time on group hierarchy measured as the linearity (N.S.). D) Effect of time * rank on the percentage of the preferred shell weight. The bars indicate means and the error bars the standard errors.

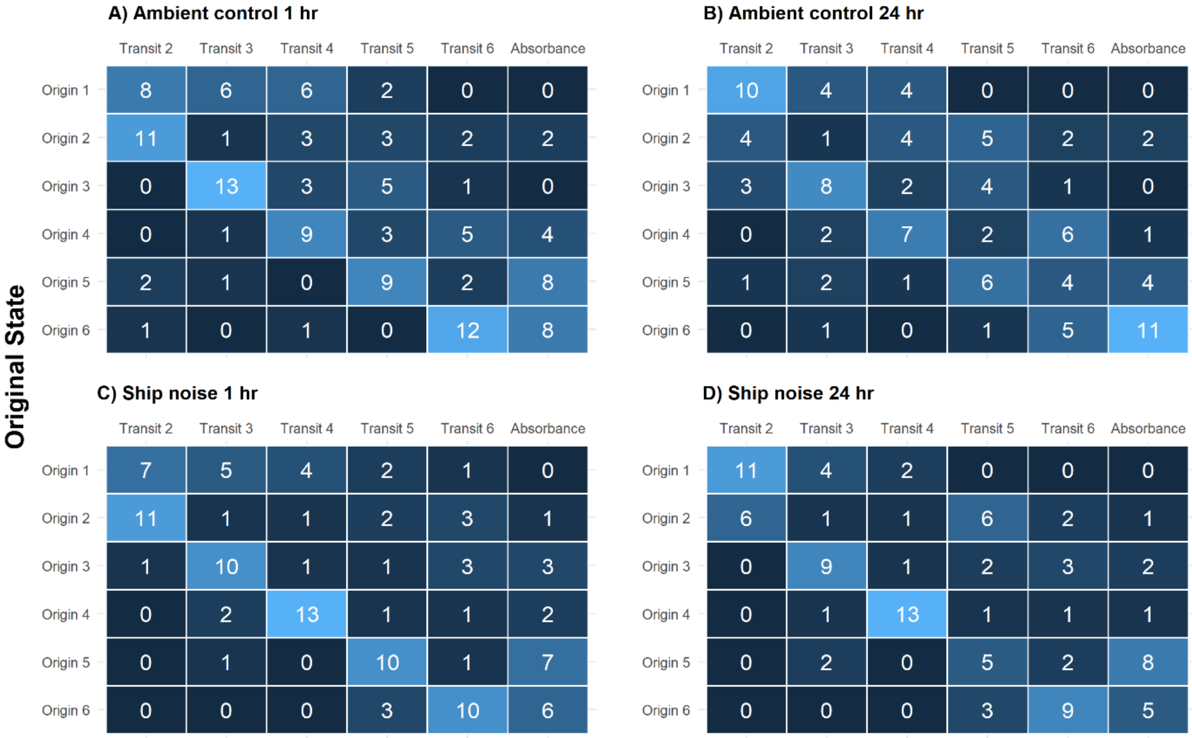
Four grand transition matrices sum up all shell movements and hence the structures of the vacancy chains*;* one for each treatment combination sound * time (Figure 4). Vacancy moves under all four treatment combinations were significantly different from random (Fisher's exact test; all four matrices: P = <0.0001) indicating that the patterns of shell exchange were structured according to crab ranks. However, these patterns deviated from the prediction of ideal vacancy chains (Bartlett's test of sphericity; ambient 1 h: $\chi^2_{15} = 48.9$, $P < 0.0001$; ambient after 24 h: $\chi^2_{15} = 41.4$, $P < 0.001$; noise 1 h: $\chi^2_{15} = 34.6$, $P < 0.01$; noise 24 h: $\chi^2_{15} = 34.0$, $P < 0.01$) because a significant number of moves occurred off their main diagonals (Figure 4; Table 2).

Finally, pairwise comparisons of the structure of the vacancy chains between the two time points and between the two sound treatments showed that the overall chain structures did not differ from one another. The pattern of moves was concordant across 1 h and 24 h in both ambient sound (P =

0.01; Figure 4A, B, E) and ship noise (*P* = 0.007, Figure 3C, D, E). Similarly, the pattern of moves was concordant across ambient control and ship noise at both 1 hour (*P* = 0.01; Figure 4A, C; Table 2) and 24 hours (*P* = 0.003; Figure 4B, D; Table 2). In summary, ship noise reduced the number of individuals that benefitted from vacancy chains (multiplier effect) but did not affect the group hierarchies (linearity) and therefore chain structures.

Table 2 The table summarises the vacancy moves as percentage of all observed moves under the four treatment combinations (A = ambient; N = noise).

Time	Sum of moves		Off main diagonal		% Off main diagonal		On main diagonal		% On main diagonal	
	A	N	A	N	A	N	A	N	A	N
1 h	132	114	107	97	81.1	85.1	25	17	18.9	14.9
24 h	108	102	78	81	72.2	79.4	30	21	27.8	20.6



A) Ambient control 1 hr

	Transit 2	Transit 3	Transit 4	Transit 5	Transit 6	Absorbance
Origin 1	8	6	6	2	0	0
Origin 2	11	1	3	3	2	2
Origin 3	0	13	3	5	1	0
Origin 4	0	1	9	3	5	4
Origin 5	2	1	0	9	2	8
Origin 6	1	0	1	0	12	8

B) Ambient control 24 hr

	Transit 2	Transit 3	Transit 4	Transit 5	Transit 6	Absorbance
Origin 1	10	4	4	0	0	0
Origin 2	4	1	4	5	2	2
Origin 3	3	8	2	4	1	0
Origin 4	0	2	7	2	6	1
Origin 5	1	2	1	6	4	4
Origin 6	0	1	0	1	5	11

C) Ship noise 1 hr

	Transit 2	Transit 3	Transit 4	Transit 5	Transit 6	Absorbance
Origin 1	7	5	4	2	1	0
Origin 2	11	1	1	2	3	1
Origin 3	1	10	1	1	3	3
Origin 4	0	2	13	1	1	2
Origin 5	0	1	0	10	1	7
Origin 6	0	0	0	3	10	6

D) Ship noise 24 hr

	Transit 2	Transit 3	Transit 4	Transit 5	Transit 6	Absorbance
Origin 1	11	4	2	0	0	0
Origin 2	6	1	1	6	2	1
Origin 3	0	9	1	2	3	2
Origin 4	0	1	13	1	1	1
Origin 5	0	2	0	5	2	8
Origin 6	0	0	0	3	9	5

Figure 4 Summary of all observed vacancy moves under the four treatment combinations sound and time (total counts of shell moves). Transition matrices summarise the number of vacant shell moves from original ('old') state to transient ('new') state under A) ambient control after 1 h, B) Ambient control after 24 h, C) ship noise after 1 hr and D) ship noise after 24 h. A vacancy has moved into absorption when all chain participants own a resource unit higher than the lowest. The main diagonal represents an ideal vacancy chain.

4. Discussion

While anthropogenic noise has been shown to affect various group processes (Bruintjes and Radford, 2013; Sara et al., 2007; Tidau and Briffa, 2019a), how noise influences resource distribution through animal groups and populations, a key process in groups that shapes the survival and fitness of individuals, has received very little attention. To address this research gap, we quantified the effects of ship noise playbacks on resource distribution processes and outcomes in hermit crabs using a critical resource (empty gastropod shells) on which their survival depends. Our results show that anthropogenic noise reduced the aggregated number of hermit crabs benefitting from newly vacant resource units (i.e., empty snail shells) without altering the size-based group hierarchy through which resources flow.

Resource distribution within populations is often envisaged as (a series of) dyadic interactions, whereby the winner of an agonistic event archives exclusive ownership of a discrete and usually limited resource unit (Briffa and Hardy, 2013). However, when resource units are reusable (e.g., territory, shelter, mates), additional processes can influence how resources spread through a population. Vacancy chain theory predicts that the arrival of a new resource unit, that is of higher value than the existing resources, will initiate a cascade of redistribution according to the hierarchical order of the population (Chase and DeWitt, 1988; Weissburg et al., 1991). In nature, a new resource units will often ‘arrive’, or become available, though demographic processes such as the death or emigration of the individual occupying them. Resources have to be discrete and limited but reusable for vacancy chains to occur. Changes in resource ownership such as mates, shelter, and territory are taxonomically widespread making them prime examples for the cascading effect of redistribution processes that vacancy chains characterise (Benson et al., 2004; Briffa 2013; Eikenaar et al., 2009; Fayed et al., 2007). In marine environments for instance mantis shrimp and fiddler crabs inhabit naturally occurring refugia like crevices and burrows. Fiddler crab burrows are long-lasting, and individuals frequently occupy burrows they did not construct (Wolfrath, 1992).

Using groups of hermit crabs, shell exchange behaviour and gastropod shells as a resource, we investigated the effects of anthropogenic noise on both resource distribution processes, outcomes and their underpinning social structure in a laboratory setting. We tested three hypotheses associated with resource distribution via vacancy chains. We found that first, the multiplier effect, which measures how many group members benefit from the arrival of a new resource unit, was lower under noise compared to ambient control meaning that fewer group members befitted from the new resource. Although the multiplier effect increased the longer the experiment went on (higher after 24 h compared to 1 h), the difference between ambient control and ship noise was maintained. Second, the size-based hierarchy of groups, measured as the linearity of chains, was maintained under both ambient sound and ship noise playbacks. This was supported by the third characteristic, the structure of the vacancy chains. As in previous studies (Briffa, 2013; Edquist and Rotjan, 2012; Rotjan et al., 2010), the movement patterns of the vacant shells neither conformed to ideal vacancy chains nor to random ones. This is illustrated in all four transition matrices (Figure 3) that showed a strong diagonal element below the ideal main diagonal indicating that vacancy chains occurred in all treatments. In addition, we quantified the population average gain in shell quality, the percentage preferred shell weight (% PSW) and found that it was unaffected by noise. In summary, our results demonstrate that anthropogenic noise had no effect on group hierarchies (linearity and chain structure) and population mean gains in resource value expressed as %PSW but the value of a new resource was shared between fewer individuals (lower multiplier effect).

Not surprisingly, the multiplier effect increased over time. This can occur as quickly as within 30 minutes (Laidre, 2012). Naturally occurring intrinsic and extrinsic factors (personality type, social context, predation risk) have been shown to alter vacancy chains in both humans (Persky and Felsenstein, 2008) and non-human animals (Briffa and Austin, 2009; Edquist and Rotjan, 2012). Our results demonstrate that anthropogenic noise can have the same effect. Hermit crabs rely on well-fitting shells as a defence against predators and environmental extremes such as desiccation during low tide (Taylor, 1981; Young, 1978), optimal reproduction (females carry their eggs inside the shells) and growth (Bertness, 1981). The biological consequence of a lower multiplier effect is that fewer individuals obtain the resources that allow optimal survival and ultimately fitness benefits associated with better shell fit.

Previous studies on vacancy chains indicate similarly that that hierarchies are stable and remain unaffected (i.e. there is no effect on linearity or matrix structure) by group intrinsic factors, i.e. personality type (Briffa, 2013) and social context (Rotjan et al., 2010). To the best of our knowledge, there are only few experiments on the impacts of anthropogenic noise or other extrinsic stressors on social hierarchies and those studies indicate opposing results. For instance, dominant cichlid fish *Neolamprologus pulcher* showed more aggression towards subordinate conspecifics under noise (Bruintjes and Radford, 2013) but red swamp crayfish *Procambarus clarkii* encountered each other less frequently and engaged less often in agonistic interactions (Celi et al., 2013). Other environmental stressors show similarly contrasting effects on social hierarchies. Under drought, the initial social structure which benefitted dominant conspecifics of brown trout *Salmo trutta* with higher growth rates broke down (Sloman et al., 2001). On the contrary, droughts induced more conflict but did not change the overall social organization or rank stability in Eastern mosquitofish *Gambusia holbrooki* (Flood and Wong, 2017). Altered decision-making under anthropogenic noise has been explained by distraction attention and interfering with the integration of information across sensory modalities (Chan et al., 2010; Halfwerk and Slabbekoorn, 2015). Hierarchies, however, are linked to intrinsic factors such as body size. In contrast to extrinsic information such as shell quality, it appears that the effect of variation in body size on intraspecific interactions is unaffected by noise. The fact that the size-based hierarchy was unaffected by anthropogenic noise implies that the capacity to assess body-size disparity is robust to sensory pollutants like noise (Chan et al., 2010). This is perhaps unsurprising given the importance of intra-specific size-based assessments in hermit crabs such as in agonistic interactions. The lower multiplier effect following the arrival of a new resource unit stems from reduced the frequency of shell exchanges within these robust size-based hierarchies. Explanations for reduced interactions among individuals could be a general decrease in activity and locomotion (Fewtrell and McCauley, 2012; Filiciotto et al., 2016) and less effective assessment of information across sensory modalities, here resource quality (Tidau and Briffa, 2019b). Further studies are warranted to determine the causation of reduced resource exchange and thus lower resource redistribution under noise including potential physiological mechanisms that underlie behavioural responses to anthropogenic noise (Cheng et al., 2011; Filiciotto et al., 2016; Filiciotto et al., 2014).

5. Conclusion

A growing body of research shows that anthropogenic noise alters intraspecific interactions and group processes (Fewtrell and McCauley, 2012; Filiciotto et al., 2014; Herbert-Read et al., 2017; Sara et al., 2007; Tidau and Briffa, 2019a). We demonstrate that noise also disrupts resource distribution processes whereby fewer animals benefit from available resources without affecting the size-based hierarchy of resource distribution. Vacancy chains, which have been shown across terrestrial and marine taxa such as bobcats (Benson et al., 2004), birds (Eikenaar et al., 2009) fiddler crabs (Fayed et al., 2008), and various species of hermit crabs (Briffa, 2013; Laidre, 2012; Rotjan et al., 2010), not only provide insight into behavioural mechanisms of how noise affects groups, but also broaden our understanding of the natural diversity of resource distribution systems. For hermit crabs, losing out on better quality shelter can have detrimental effects as they rely on optimal size of shelter for protection against predators, the environment and for successful reproduction (Elwood and Neil, 1992; Shumway, 1978; Vance, 1972). Our study contributes to a better understanding of cross-sensory noise impacts beyond predominantly studied individual behaviour and acoustically-guided interactions (Jerem and Mathews, 2021). Social hierarchies in animals can be robust to noise but that effects on individuals can impact wider population processes of resource distribution, which provides further evidence for the adverse impacts of sensory pollutants like noise.

CRediT author statement

Svenja Tidau: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Software; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing

Mark Briffa: Conceptualization; Data curation; Formal analysis; Funding acquisition; Methodology; Project administration; Resources; Software; Supervision; Validation; Visualization; Writing - review & editing

Data accessibility

Detailed methods and READme tables for the data are available as electronic supplementary material. Data in form of csv files and R code (Tidau and Briffa, 2023) are available under DOI: 10.6084/m9.figshare.24711306.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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