

Context-dependent impacts of anthropogenic noise on individual and social behaviour in a cooperatively breeding fish



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Anthropogenic (man-made) noise is a global problem and present in virtually all terrestrial and aquatic environments. To date, most studies investigating the potential impact of this pollutant have focused on individual behavioural responses and simply considered whether noise has an effect. However, most animals engage in social interactions, which may be vulnerable to the adverse effects of noise, and work in other fields suggests that individuals might react differentially to comparable noise stimuli depending on their own characteristics and the current situation. We used controlled experiments and standardized tests to investigate the impacts of playback of the noise of a passing boat, a dominant acoustic stressor in the aquatic environment, on nest-digging behaviour, antipredator defence and social interactions in small groups of *Neolamprologus pulcher*, a territorial and cooperatively breeding cichlid fish. Our results show that, in comparison to ambient noise, playback of boat noise: (1) reduced digging behaviour, which is vital to maintain hiding and breeding shelters; (2) decreased defence against predators of eggs and fry, with direct consequences for fitness; and (3) increased the amount of aggression received and submission shown by subordinates. Moreover, the context (presence or absence of eggs) affected individual and social behaviours in response to the same noise source. Our results demonstrate the need to consider whole behavioural repertoires for a full understanding of the impact of anthropogenic noise, and indicate that the effects of this global pollutant are likely to be context dependent.

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Anthropogenic (man-made) noise penetrates through all media and can potentially affect any animal capable of hearing (Slabbekoorn et al. 2010). In terrestrial environments, the prevalence of noise from transport networks, resource extraction and urban development is much greater today than in the past (Barber et al. 2010). Likewise, in aquatic environments, there have been considerable increases in commercial shipping, recreational boating, pile driving, seismic exploration and energy production (e.g. hydrocarbon extractions and offshore wind farms), making underwater noise a dominant stressor in such ecosystems (Richardson et al. 1995; Popper 2003). Consequently, anthropogenic noise is now recognized as a major global pollutant in the 21st Century and is included in both national and international legislation (European Union 2008).

There is increasing evidence that anthropogenic noise can have an impact on not just humans (Smith 1991; Stansfeld & Matheson 2003; Harrison 2008) but many other animals in a variety of taxa (Barber et al. 2010; Slabbekoorn et al. 2010). In general, studies have

focused on how noise affects the physiology or behaviour of individual organisms (but see Francis et al. 2009 and Herrera-Montes & Aide 2011 for community-level effects). For example, noise has been shown to increase stress levels (Stansfeld & Matheson 2003; Wysocki et al. 2006), damage hearing (Clark 1991; Smith et al. 2004), increase metabolic rate (Wale et al. 2013), mask/alter communication (Slabbekoorn & Peet 2003; Vasconcelos et al. 2007), cause avoidance (Engas et al. 1996; Schaub et al. 2008) and impair foraging (Quinn et al. 2006; Purser & Radford 2011). However, in most species, especially those that live in groups, individuals interact frequently with their conspecifics. Whether and how anthropogenic noise affects such social interactions has received little empirical consideration. This is an important issue because noise might influence the payoffs relating to group living differently for certain group members; other anthropogenic stressors have been shown to have particularly severe consequences for individuals of lower social standing, such as young and subordinates (see Wedermeyer 1997).

Previous work on the potential impacts of anthropogenic noise has also tended to consider the overall effects of noise in isolation from other factors. However, the response to a stimulus can be dependent on the current situation of an animal. For example, predator pressure can influence foraging behaviour (Kohler &

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McPeck 1989) and satiation levels can change the vigilance patterns exhibited by individuals (Clutton-Brock et al. 1999; Wright et al. 2001; Bell et al. 2010). More specifically, it is becoming apparent that the harmful effects of many human activities on animal welfare are condition dependent, and also depend on the species and the life history stage concerned (see Huntingford et al. 2006 and references therein). To our knowledge, no study has investigated whether anthropogenic noise stimuli might influence animal behaviour differently depending on the context.

In this study we investigated the potential for anthropogenic noise to affect various key behaviours and social interactions in the cooperatively breeding cichlid *Neolamprologus pulcher*, and whether the observed responses are context dependent. To explore these possibilities, we used playback of noise generated by a passing boat, the most common source of anthropogenic noise in the aquatic environment (Vasconcelos et al. 2007). *Neolamprologus pulcher* live at depths of 3–45 m (Taborsky 1984) around all the shores of Lake Tanganyika (Duftner et al. 2007), including harbours and other areas with intensive boat traffic. They are found in groups consisting of a dominant pair with up to 14 subordinates of different sizes and sex (Balshine et al. 2001; Heg et al. 2005). Subordinate individuals show submissive behaviours towards the dominant individuals (Hamilton et al. 2005; Brintjes & Taborsky 2008), and dominants exhibit aggressive displays towards subordinates (Taborsky 1985; Bergmüller & Taborsky 2005). Groups defend patches of half-buried stones that are used as breeding substrate and as shelters to hide from predators for all group members (Balshine et al. 2001; Brintjes et al. 2010; Heg & Taborsky 2010). Shelters are maintained by digging away sand from underneath the stones (Taborsky 1984), and eggs and immature individuals are guarded from potential predators by all group members (Desjardins et al. 2008; Brintjes & Taborsky 2011). We asked whether shelter maintenance and antipredator defence are negatively affected by playback of the noise of a passing boat and whether social interactions between dominants and subordinates are also affected. Moreover, we considered whether breeding context (presence or absence of eggs) influences the response of group members to playback of boat noise and, specifically, whether there is a weakened response when the immediate pressure to maximize reproductive success is stronger.

METHODS

Study Animals and Husbandry

Neolamprologus pulcher individuals used for the study were descendants of fish caught at the southern end of Lake Tanganyika, near Mpulungu, Zambia in 2006 and reared at the University of Bern, Switzerland. The study fish were transported to the University of Bristol, U.K. by car in June 2011 following standard procedures: no food was given 36 h prior to transport; a maximum of three fish were in each plastic bag (8 litres); and bags were filled with one-third aquarium water, two-thirds air and one Supa Oxygenating Tablet. All bags were put into a large Styrofoam box with thick walls (5 cm) that ensured minimal heat loss; water temperature was 27 °C and checked every 3 h. Transport followed approval of the Cantonal Veterinary Office of Bern, export/import licence reference: CH.2011.0002429–V1, 02025. After transport, all fish were kept in an 800-litre aggregation tank (size: 500 × 58 cm and 33 cm high, equipped with a Vecton 600 ultraviolet water sterilizer and a biological filter) for 3 months. During transport, the fish might have been exposed to louder noise than common aquarium noises (such as those generated by filters, water changes and the surrounding building). To minimize sound intensities during transport, we used thick-walled Styrofoam boxes that were

placed on several layers of cardboard (± 15 mm). Before and after the transport, the fish were only exposed to common aquarium noises, until the start of the experimental playbacks (see below).

After the settling period, 19 groups of three fish, comprising a dominant pair plus one subordinate, were established in individual aquaria (71 × 38 cm and 30 cm high; 70 litres) following standard procedures (Brintjes & Taborsky 2008). We first introduced the subordinate individual into the aquarium and then, after an acclimatization period of 1–3 days, the dominant individuals were introduced (see *Ethical Note*). Dominant males measured 45.9 ± 1.8 mm standard length (SL; mean \pm SE), dominant females 39.9 ± 1.6 mm SL and subordinates 30.0 ± 1.0 mm SL. Fourteen groups had a male subordinate and five groups had a female subordinate. One male subordinate died before the start of the experiments (see *Ethical Note*), making a total of 13 groups with a male subordinate. Each aquarium was placed on three layers of 3 mm thick insulation material (Acoustalay 250) and, to minimize internal ambient noise further, equipped with an external water filter with the water outflow placed below the water surface. Each aquarium had 3 cm of sand at the bottom, two 10 cm diameter flowerpot halves (used for hiding and breeding), two opaque tubes at either side of the aquarium near the surface (to provide escape possibilities from aggression), and an opaque partition behind which a water heater was placed (Rena smart heater 100 W). Small gaps between the partition and the tank walls allowed water flow, and thus transfer of heat to the rest of the tank, but no movement of fish between sections. This partition also provided space to introduce the underwater speaker without visual cues.

We chose to conduct our experiments in aquaria to control carefully the conditions and contexts of the study animals. Care must of course be taken when extrapolating results from tank-based experiments to meaningful implications for free-swimming fish in open water. From a biological perspective, captive animals are usually more constrained than in the wild. *Neolamprologus pulcher*, however, are highly territorial fish (Taborsky 1984; Desjardins et al. 2008) and stay close to their shelters (Brintjes et al. 2010), mainly because of a high predator pressure (Heg et al. 2004; Heg & Taborsky 2010). Therefore, they are unlikely to escape anthropogenic noise just by moving to more silent areas. From an acoustics perspective, the sound field in a tank is complex and therefore we took utmost care to refine noise distortion by following recommendations to minimize sound propagation in tanks (Akamatsu et al. 2002).

As potential egg predators (see below), we used *Julidochromis dickfeldi*, cichlid fish that are endemic to Lake Tanganyika and share their natural habitat with *N. pulcher*. We used eight *J. dickfeldi*, which measured 39.5 ± 1.0 mm SL (mean \pm SE) and were purchased from a reputable fish stockist (Maidenhead Aquatics, Thornbury, U.K.). The *J. dickfeldi* were housed in a 70-litre aquarium identical to those used for the behavioural experiments, except that it contained 10 round opaque pipes (4 × 8 cm) on the bottom, instead of two flowerpot halves, and no opaque partition. Water temperature of all aquaria was kept constant at 27.0 ± 0.5 °C with a 13:11 h light:dark regime. All fish (*N. pulcher* and *J. dickfeldi*) were fed five times per week with TetraMin flake food, once per week with frozen bloodworms and once with ZM-300 food (zmsystems.co.uk). All aquaria were checked every morning for newly produced clutches.

Sound Recordings

All sound recordings were made with an omnidirectional hydrophone (HiTech HTI 96-MIN with inbuilt preamplifier; manufacturer calibrated sensitivity -164.3 dB re 1 V/ μ Pa; frequency range 2–30 000 Hz) and a solid-state recorder (Roland Edirol

R09HR; 24-bit; sampling rate 44.1 kHz; calibrated using a pure reference tone of known amplitude). Acoustical analyses were performed with Avisoft-SASLab Pro software version 5.1.17 (Avisoft Bioacoustics, Berlin, Germany). Boat noise playbacks used in experimental trials were recorded at Bristol harbour from boats of similar size and with similar-sized engines as found in the harbour of Mpulungu, Zambia, Lake Tanganyika (see Table A1 in the Appendix for details). We created 10 files, each using three randomly chosen boat passes from a pool of 17 recordings, which had been highpass filtered at 100 Hz to play within the frequency range of the underwater speaker (see below) and lowpass filtered at 2 kHz to minimize resonant frequencies (Akamatsu et al. 2002). Each playback file consisted of two boat passes/min with a mean \pm SE of 18 ± 3 s per passing boat and had a total duration of 15 min. The files were played in the experimental aquaria using an MP3 player (Logik L2GMP309; frequency response range ca. 40–20 000 Hz), an amplifier (Kemo Electronics GmbH; 18 W; frequency response range ca. 40–20 000 Hz), a potentiometer (set to minimal resistance; Omeg Ltd; 10k logarithmic) and an underwater speaker (Aqua30; DNH; effective frequency range 80–20 000 Hz; www.dnh.no). Playback tracks were re-recorded in the centre of the aquarium and adjusted to play at 127 dB root mean square (RMS) re 1 μ Pa (mean \pm SE RMS: 127.2 ± 0.5 dB calculated over the loudest 2 s per playback). Ambient noise levels in the aquaria were of slightly higher sound pressure levels (SPL) below 500 Hz and lower SPL above 500 Hz compared to ambient noise levels in Lake Tanganyika (Appendix Fig. A1). The boat noise playbacks in the aquarium matched boat noises in the natural environment, although in the aquarium the SPL of boat noise was somewhat higher below 450 Hz than in the Lake (Fig. A1).

Behavioural Trials

For each of the three experiments (sand digging, antipredator defence in the absence of eggs, antipredator defence in the presence of eggs), groups were subjected to two standardized trials. One trial involved playback of the noise of a passing boat and the other was an ambient noise control during which the speaker was turned on but played a silent track. Trial order in a given experiment was counterbalanced between groups and no group received more than one trial per day. Five minutes before the start of a trial, the underwater speaker was placed into the aquarium behind the opaque partition and was turned on. In all trials, the MP3 player was switched to the relevant track as soon as any group member first performed the relevant behaviour (either digging or antipredator defence behaviour; see below); data were collected for the following 10 min period. All observations were conducted by R.B. between 0830 and 1215 hours using the Observer software (version XT 10; Noldus, Wageningen, The Netherlands).

To examine how the playback of boat noise affects nest-digging behaviour, we carefully covered both flowerpot halves with sand (Bergmüller et al. 2005; Brintjes et al. 2011; Brintjes & Taborsky 2011), which simulates conditions in the lake created by water movements (Taborsky & Limberger 1981). One day before the start of the acoustic trials, all groups were given a test trial involving no speaker to acquaint them with the sand manipulation procedure. Data were only collected from stable groups, those in which all individuals were free to swim throughout the aquarium without harassment from another group member ($N = 11$ groups). Digging involved either carrying sand away with the mouth or performing a stationary swimming movement while moving sand from the shelter with the tail (Heg & Taborsky 2010). After playback initiation, we recorded latency to the first digging event by any group member and digging frequency (number of separate digging events) of all group members.

To investigate how playback of boat noise affects antipredator defence, two *J. dickfeldi* (opportunistic egg predators) were presented for 10 min in a glass tube (height 9 cm, diameter 8 cm) 5 cm from both shelters (as in Brintjes et al. 2011). Predators were presented twice, once with playback of the noise of a passing boat and once without playback (the ambient control), to 11 groups when they had eggs in the breeding shelter and to 15 groups in the absence of eggs. Again, data were only collected from stable groups (see above). Half of the groups were first tested in the absence of eggs and the other half was first tested with eggs present; four groups were observed only in the absence of eggs because no clutch was laid within 6 weeks. Directly after testing in the presence of eggs, the clutch was removed for a study investigating the effects of boat noise on development (R. Brintjes & A.N. Radford, unpublished data). Antipredator defence behaviour involved ramming or biting of the tube, fast frontal approach and head-down display (Brintjes & Taborsky 2011). After playback initiation, we recorded latency to the first defence behaviour by any group member and defence frequency (number of separate events from time since first event in trial) for all group members. Furthermore, we recorded the activity levels of the egg predators on a scale of 0–5 (0 = no movement, 5 = very active; Brintjes et al. 2010, 2011).

In all experiments, we recorded the height in the aquarium and the distance from the breeding shelter of all group members every minute. Since these two parameters were significantly correlated (Spearman rank correlation: $r_s = -0.976$, $N = 15$, $P < 0.001$), only results relating to distance from the shelters are shown throughout the rest of the paper. For subordinate individuals, we also recorded the frequency with which they received aggression (fin spreading, fast frontal approach, head-down display, head jerking, opercula spreading and S-shaped bending) from the dominants and the frequency with which they showed submissive behaviour (escaping, hook displays and tail quivering) towards the dominants (see Taborsky 1984 for a detailed description of the behaviours).

Ethical Note

During group establishment, there was only a minimal amount of overt aggression between *N. pulcher* individuals. No injuries were detected during group formation or during the experiments, apart from one individual that was found dead because it had managed to jump out of the aquarium despite the lid. All *N. pulcher* individuals exhibited normal behavioural repertoires before, during and after the test procedures. Even during playbacks of boat noise, the fish showed high levels of defence and digging (see Results), and no behavioural indications (e.g. continuous head-up displays) of high stress.

The *N. pulcher* group members showed defensive behaviours against the egg predators (*J. dickfeldi*) at relatively high intensities, but no fish sustained any injuries by ‘ramming’ the tube containing the predator. Egg predators were carefully monitored in the aftermath, to check for stress-associated behaviour, but all *J. dickfeldi* resumed normal pre-experimental behaviour (i.e. foraging and social interactions) within minutes after removal from the experimental tank. Presentations did not last longer than 20 min/day per fish. All fish used in this study were kept for future research. All procedures were approved by the University of Bristol Ethical Committee (University Investigator Number: UB/10/034); the predator presentations were conducted under Home Office licensing (PPL 30/2860).

Statistics

All data were checked for normality with Shapiro–Wilk tests and checked for homogeneity of variance with Levene’s tests (based

on the mean). If necessary, data were normalized by logarithmic transformations. Normally distributed data sets were analysed with paired *t* tests; Wilcoxon signed-ranks tests were used in other cases. All statistical analyses were conducted with PASW statistics version 18.0.0. Too few subordinates showed digging or antipredator defence in any of the experiments to enable statistical analysis (sand digging: three out of 10; defence without eggs: four out of 14; defence with eggs: three out of 10; one subordinate died during experiments).

RESULTS

Sand Addition Trials

After the start of the trial, there was a significantly longer latency until the next digging event during playback of boat noise compared to the ambient-noise treatment (paired *t* test: $t_{10} = 3.46$, $P = 0.006$; Fig. 1a). Groups also exhibited significantly lower nest-digging frequencies during playback of boat noise than during ambient noise ($t_{10} = -2.60$, $P = 0.026$; Fig. 1b). Dominant males dug less frequently during playback of boat noise than during ambient noise ($t_{10} = 2.90$, $P = 0.016$), whereas dominant females did not show a significant difference between treatments in the frequency of digging (Wilcoxon test: $Z = -1.25$, $N = 11$, $P = 0.212$).

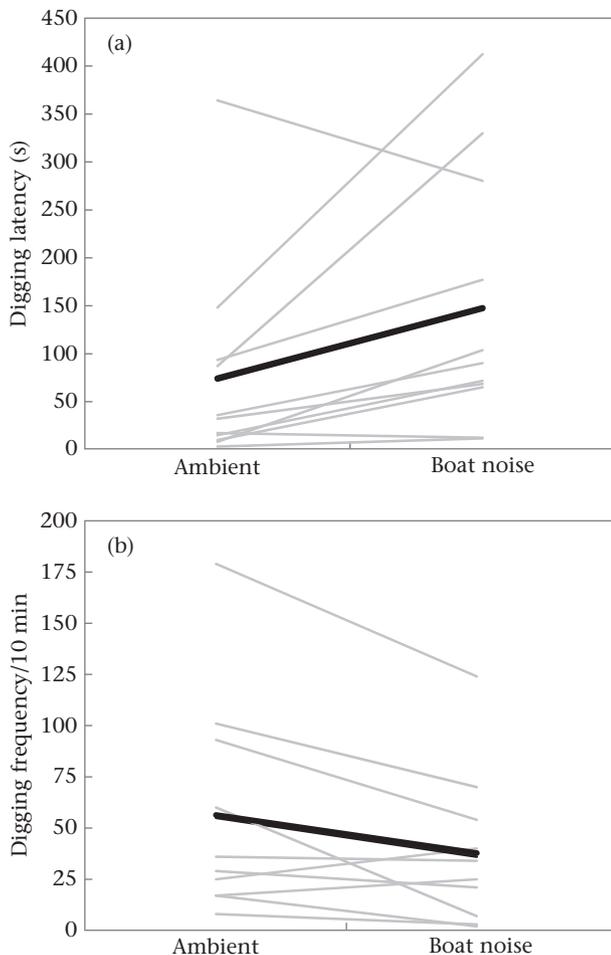


Figure 1. (a) Nest-digging latency and (b) total nest-digging frequencies per group during ambient controls and playback of boat noise. The thick black line represents the overall effect, whereas the grey lines connect values from the two treatments for each group.

No significant differences between the sound treatments in distance from the shelter were detected for dominant males (paired *t* test: $t_{10} = -0.53$, $P = 0.608$), dominant females ($t_{10} = 0.77$, $P = 0.459$) or subordinates ($t_9 = 0.35$, $P = 0.732$).

Subordinates received significantly more aggression from the dominant pair during playback of boat noise than during ambient noise (paired *t* test: $t_9 = 2.73$, $P = 0.021$). Subordinates did not, however, show a significant difference in the frequency of submissive behaviour towards the dominant pair between sound treatments ($t_9 = -0.73$, $P = 0.485$).

Predator Presentations without Eggs in Nest

Latency to first defence against the predators after the start of the trial did not differ significantly between the sound treatments (paired *t* test: $t_{14} = -0.08$, $P = 0.460$). However, group members defended significantly less often against the predators during playback of boat noise than during ambient noise ($t_{14} = -2.21$, $P = 0.044$; Fig. 2a). Dominant females were less likely to defend against the predators during playback of boat noise than during ambient noise (Wilcoxon test: $Z = -1.95$, $N = 15$, $P = 0.052$), whereas dominant males did not exhibit a significant difference in defence against the predators in the two treatments (paired *t* test: $t_{14} = 1.33$, $P = 0.206$). There were no significant differences between treatments in the distance from the shelter for dominant males ($t_{14} = -0.15$, $P = 0.885$), dominant females ($t_{14} = -0.38$, $P = 0.709$) or subordinates ($t_{13} = 0.34$, $P = 0.336$). Activity levels of the egg predators did not differ significantly between the treatments (Wilcoxon test: $Z = -0.36$, $N = 15$, $P = 0.718$).

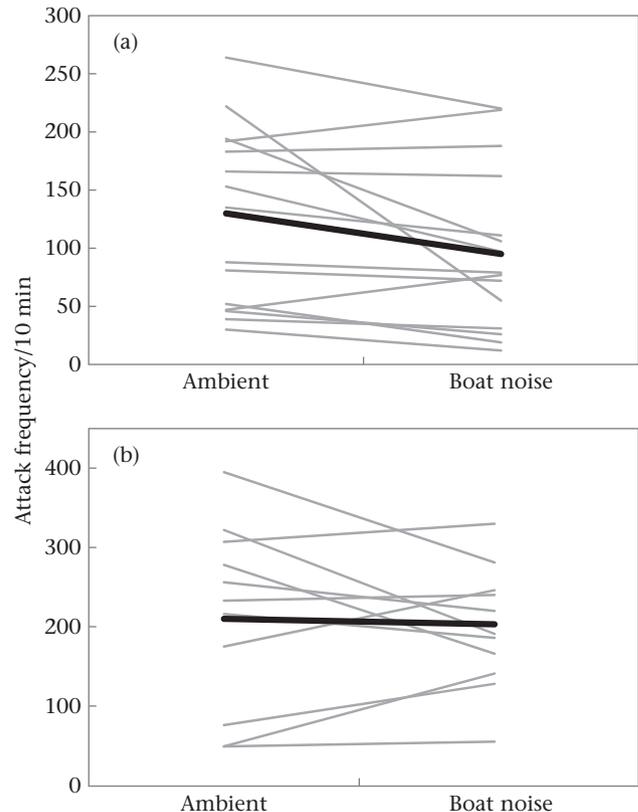


Figure 2. Total attack frequencies per group against the egg predators during ambient noise and playback of boat noise (a) without eggs present and (b) with eggs present. The thick black line represents the overall effect, whereas the grey lines connect values from the two treatments for each group.

Subordinates tended to receive more aggression from the dominants during playback of boat noise than during ambient noise (paired t test: $t_{13} = 1.98$, $P = 0.068$). Subordinates were also significantly more submissive towards the dominant pair during playback of boat noise than during ambient noise (Wilcoxon test: $Z = 2.37$, $N = 14$, $P = 0.018$).

Predator Presentations with Eggs in Nest

As in the absence of eggs, there was no significant difference between sound treatments in the latency to first defence against the predators (paired t test: $t_{10} = -0.05$, $P = 0.964$). However, in contrast to the context without eggs, there was no significant difference in antipredator defence depending on the sound treatment with eggs present in the nest ($t_{10} = 0.70$, $P = 0.503$; Fig. 2b). Neither dominant males ($t_{10} = -0.43$, $P = 0.134$) nor dominant females ($t_{10} = 1.63$, $P = 0.680$) showed a significant difference in the defence frequency between the boat noise and ambient-noise treatments. No significant treatment differences were found for distance from the shelter for dominant males ($t_{10} = -1.20$, $P = 0.259$), dominant females ($t_{10} = -0.74$, $P = 0.478$) or subordinates ($t_{10} = -0.52$, $P = 0.616$). Activity levels of the egg predators did not differ significantly between the treatments (Wilcoxon test: $Z = -1.16$, $N = 11$, $P = 0.248$).

We detected no significant treatment differences in the amount of aggression received by subordinates from the dominants (Wilcoxon test: $Z = 1.56$, $N = 10$, $P = 0.119$) nor in the amount of submissive behaviour directed by subordinates towards the dominant pair (paired t test: $t_9 = 1.49$, $P = 0.171$) when eggs were present.

DISCUSSION

Our findings suggest that playback of the noise of a passing boat negatively affects two key behaviours in *N. pulcher*: nest digging and defence against predators. Moreover, our results provide three indications that the same noise may not always have the same impact: (1) playback of boat noise resulted in a reduction in antipredator defence if no eggs were present in the nest, but not if eggs were present; (2) social interactions between dominants and subordinates were affected differently in the three experiments; and (3) dominant males and females responded differently to the same noise playbacks. Note that the fish are likely to respond similarly to a variety of noises with similar intensities (loudness) that lie within the hearing range of *N. pulcher*; the documented behavioural changes are not necessarily specific to boat noise.

While it is well established that context may change the response to a given stimulus (e.g. (Clutton-Brock et al. 1999; Pereyra et al. 2000; Wright et al. 2001; Gazit et al. 2005), our results suggest for the first time that this might also be true in relation to anthropogenic noise. For example, while previous work has shown that behavioural responses to the same vocal cues can differ depending on the context (Bell et al. 2009), we found that the antipredator defence of *N. pulcher* was only affected by playback of boat noise when there were no eggs in the nest. Similarly, aggressive and submissive behaviour between dominant and subordinate *N. pulcher* group members was not affected in the same way in the three experiments, even though the same pool of boat noise playbacks was used. For example, subordinates received more aggression in the sand addition experiments, but not during the predator presentations. In addition to a context-dependent effect, male and female *N. pulcher* appeared to respond differently to the same playbacks of anthropogenic noise: males dug less, whereas females tended to defend less. A sex-specific response to noise mirrors the sex differences often found in relation to vocalizations (Nelson &

Soha 2004) and highlights the complexity of responses to anthropogenic noise.

Studies of anthropogenic noise have often considered behaviours, such as vocalizations and movement patterns, that are difficult to translate into potential impacts on fitness (see Radford et al. 2012). Antipredator defence behaviour is different in this regard as it is of key importance for the survival of young in *N. pulcher* (Taborsky 1984) and other cooperative species (e.g. Rabenold 1984), and thus to lifetime reproductive success. For a full understanding of the impact of noise in this context, however, it would be necessary to consider how the predators themselves are affected. For example, Purser & Radford (2011) showed that during exposure to noise, food-handling errors increased in three-spined sticklebacks, *Gasterosteus aculeatus*. The outcome of predator–prey interactions is dependent on the relative impact on each party, but there is currently a general lack of knowledge concerning the effects of anthropogenic noise on dyadic interactions.

Defence frequency towards predators has previously been shown to be positively correlated with the activity of the presented predators in *N. pulcher* (Bruintjes et al. 2011). However, there was no difference in predator activity between the sound treatments in our experiments, and thus the decreased defence seen during playback of boat noise cannot be explained by a change in predator behaviour. Moreover, the reductions in digging and antipredator defence in response to playback of boat noise were not a consequence of the fish simply being further from the shelters. Hence, the behavioural changes we have documented appear most likely to be the result of a direct effect of noise.

Most studies investigating the impact of anthropogenic noise have focused on the response of single individuals (e.g. Wysocki et al. 2006; Picciulin et al. 2010; Purser & Radford 2011; Wale et al. 2013), but many species live in groups in which social interactions are common. Our experiments demonstrate that playback of boat noise can increase aggressive and submissive behaviour between dominant pairs and their subordinates. Both aggression and submission are costly, increasing routine metabolic rate more than threefold in the study species (Grantner & Taborsky 1998). Especially for subordinates, this greater cost and consequent need for increased energy consumption could detrimentally affect the payoffs relating to group membership and dispersal decisions (Bergmüller et al. 2005). Since subordinates showed very little digging or defence behaviour even in the ambient treatment, the increases in aggression received from dominants during playback of boat noise were not driven by any discernible decrease in helping behaviour; again, the behavioural changes appear to be a direct consequence of the introduced noise. Anthropogenic noise may not only increase costly intragroup activities, but could also affect social dynamics: in the digging experiment, aggression from dominants increased, but there was no related increase in submission by subordinates. Taken together, these results underline the importance of studying social interactions to obtain a more complete understanding of the impact of anthropogenic noise.

Animals have been shown to habituate to loud noises if they are presented continuously for a long period (Smith et al. 2004) and it is theoretically possible that fish might habituate, or become tolerant, to the associated sounds. However, variable or unpredictable exposure or the occurrence of novel noise might prevent this, and could even lead to a sensitized response to such disturbances. For example, Masini et al. (2008) found that habituation was impaired by exposure to short intervals of loud noise in comparison to exposure to identical continuous loud noises. Moreover, Wysocki et al. (2006) showed that cortisol levels in four fish species increased when the fish were exposed to variable ship noise, but not when exposed to continuous Gaussian noise of similar intensities. The processes of habituation and sensitization to noise exposure are only just beginning to be explored (Masini et al. 2008;

Wale et al. 2013) and the implications are far from simple, so further research is certainly warranted. What is clear from our experiments is that even though the study fish have been kept in aquaria throughout their lives, this did not prevent a behavioural response to a different noise source.

Moving forward, there is a need for field-based experiments to consider the spatial scale of these demonstrated impacts (including consideration of the particle motion component of sound). Moreover, studies need to examine the effect of repeated and/or chronic noise exposure, as this represents the more ecologically realistic scenario in most circumstances. However, our study demonstrates that anthropogenic noise can affect social interactions, as well as essential individual behaviours, and provides the first indication that the impact can be context dependent. This highlights the need to look beyond the simple question of whether noise is having an effect, especially if we are to gain a full understanding of how this global pollutant influences individual fitness, population viability and community structure (see also Francis et al. 2009, 2012; Herrera-Montes & Aide 2011).

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Appendix

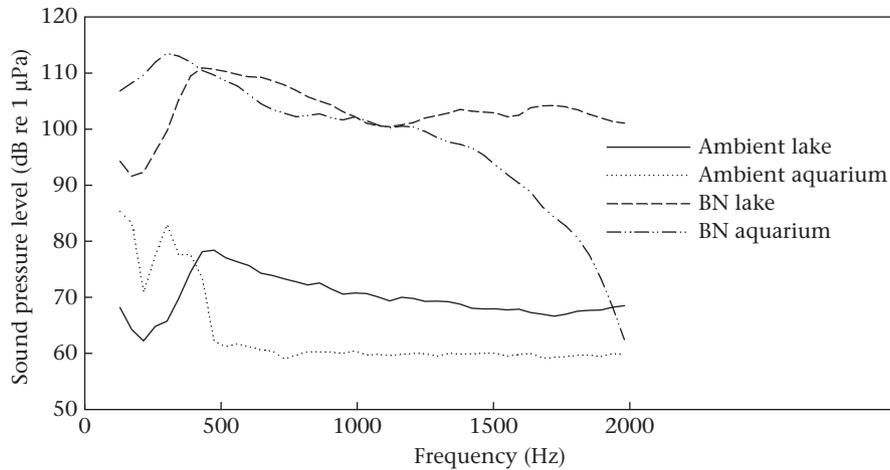


Figure A1. Sound pressure levels (SPL) in an experimental aquarium during boat noise playbacks (BN aquarium) and ambient control conditions (Ambient aquarium) as well as SPL from recordings made in Lake Tanganyika during boat passes (BN lake) and during ambient conditions (Ambient lake). The SPL shown (spectral density in dB/Hz re 1 μ Pa) were made from averaged power spectra of the recordings (FFT analysis: spectral level units, Hann evaluation window, 50% overlap, FFT size 1024).

Table A1

Data on boat sizes and engine types recorded in Bristol harbour (U.K.) and Mpulungu harbour in Lake Tanganyika (Zambia)

Boat number	Place	Boat size (m)	Engine
1	Bristol harbour	2.0	Outboard, 50 hp, Yamaha
2	Bristol harbour	3.0	Outboard, 25 hp, Mariner
3	Bristol harbour	4.5	Outboard, 50 hp, Yamaha
4	Bristol harbour	8.0	Inboard, 40 hp, unknown brand
5	Bristol harbour	11.0	Inboard, 40 hp, unknown brand
6	Bristol harbour	12.0	Inboard, 120 hp, unknown brand
7	Bristol harbour	12.0	Outboard, 25 hp, Mercury
8	Bristol harbour	12.0	Inboard, 70 hp, unknown brand
9	Bristol harbour	14.0	Inboard, 70 hp, Ford Fiesta
10	Bristol harbour	14.0	Inboard, 50 hp, Ford fsd marine diesel
11	Bristol harbour	14.0	Inboard, 50 hp, unknown brand
12	Bristol harbour	15.0	Inboard, 41 hp, Mitsubishi diesel
13	Bristol harbour	15.0	Inboard, 40 hp, unknown brand
14	Bristol harbour	18.0	Inboard, 60 hp, unknown brand
15	Bristol harbour	23.0	Inboard, 80 hp, unknown brand
16	Bristol harbour	28.0	Inboard, 75 hp, unknown brand
17	Bristol harbour	28.0	Inboard, 80 hp, unknown brand
18	Mpulungu harbour	3.5	Outboard, 25 hp, Mercury
19	Mpulungu harbour	20.0	Inboard, 40 hp, unknown brand
20	Mpulungu harbour	20.0	Inboard, 60 hp, unknown brand
21	Mpulungu harbour	26.0	Inboard, 40 hp, unknown brand