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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.

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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McPeek 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; Bruintjes & 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; Bruintjes 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; Bruintjes & 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 (Bruintjes & 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 ± 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 (Bruintjes 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 ± 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/μPa; frequency range 2–30 000 Hz) and a solid-state recorder (Roland Edirol