Animal Behaviour 89 (2014) 191–198

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms

Irene K. Voellmy [a,*], Julia Purser [a], Douglas Flynn [a], Philippa Kennedy [a], Stephen D. Simpson [b], Andrew N. Radford [a]

[a] *School of Biological Sciences, University of Bristol, Bristol, U.K.*
[b] *Biosciences, College of Life and Environmental Sciences, University of Exeter, Exeter, U.K.*

ARTICLE INFO

Article history:
Received 11 September 2013
Initial acceptance 25 October 2013
Final acceptance 11 December 2013
Available online 8 February 2014
MS. number: 13-00755R

Keywords:
anthropogenic noise
environmental change
fish behaviour
Gasterosteus aculeatus
Phoxinus phoxinus
pollution
predation risk
species differences
starvation risk

Effective foraging behaviour is essential for animals to survive and reproduce, and depends on many intrinsic and environmental factors. There is increasing evidence that man-made (anthropogenic) factors can affect the behaviour of a wide range of taxa. However, few experimental studies have investigated how foraging behaviour is affected by exposure to increased noise levels, an issue of growing global concern. In our laboratory study, we examined how exposure to playback of noise originally recorded from ships, a prevalent source of human-generated underwater noise, affects the feeding behaviour of two sympatric fish species: the three-spined stickleback, *Gasterosteus aculeatus*, and the European minnow, *Phoxinus phoxinus*. Both species consumed significantly fewer live *Daphnia magna*, and showed startle responses significantly more often during playback of additional noise than during control conditions. However, whereas minnows showed a qualitative shift in activity away from foraging behaviour (greater inactivity, more social behaviour) under increased noise conditions, consistent with a classic stress- or fear-related defence cascade, sticklebacks maintained foraging effort but made more mistakes, which may result from an impact of noise on cognition. These findings indicate that additional noise in the environment can lead to reduced food consumption, but that the effects of elevated noise are species specific. It remains to be tested whether these interspecific differences translate into different ultimate impacts, but differential disruptions to foraging may have potential consequences for relative individual fitness and community structure.

Animals must minimize the risk of starvation if they are to survive and reproduce successfully. A wide range of morphological adaptations and behavioural techniques have therefore evolved to aid in the detection, acquisition and processing of food (Stephens, Brown, & Ydenberg, 2007). Foraging also involves constant decision making about when, where and on what to feed (Galef & Giraldeau, 2001), and how to optimize time allocation with other behaviours, such as reproduction and the avoidance of predators (Lima & Dill, 1990). Consequently, events that compromise any of these facets of foraging may have detrimental consequences for individual fitness.

It has long been established that foraging is affected by a range of internal and external factors, such as hunger level, health, quality and quantity of food sources, intra- and interspecific competition, and predation risk (Lima & Dill, 1990; Stephens et al., 2007). More recently, we have begun to realize the extent to which human activities such as habitat fragmentation, climate change, species introductions and the use of fertilizers and pesticides can affect food availability, predator–prey interactions and foraging behaviour (Blumstein & Fernández-Juricic, 2010; Candolin & Wong, 2012). In the last few decades, there has been increasing concern about how anthropogenic (man-made) noise, from such sources as urban development, resource extraction and transport, might affect individual species and community ecology (Blickley & Patricelli, 2010; Popper & Hastings, 2009; Slabbekoorn et al., 2010). However, while there is a growing literature demonstrating that anthropogenic noise can affect the behaviour of animals in a wide range of taxonomic groups, the primary focus has been on movement patterns and vocal communication (see Morley, Jones, & Radford, 2014); relatively few studies have experimentally considered foraging behaviour (for exceptions see Schaub, Ostwald, & Siemers, 2008; Siemers & Schaub, 2011; Wale, Simpson, & Radford, 2013a).

Elevated sound levels could affect foraging behaviour in three main ways, which are not mutually exclusive. First, noise could act as a stressor (Wright et al., 2007), decreasing feeding behaviour

* Correspondence: I. K. Voellmy, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K.
E-mail address: Irene.Vollmy@bristol.ac.uk (I. K. Voellmy).

0003-3472/$38.00 © 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.12.029

directly through reduced appetite (Charmandari, Tsigos, & Chrousos, 2005), or indirectly through a reduction in activity and locomotion (Mendl, 1999) or alterations to the cognitive processes involved in food detection, classification and decision making (De Kloet, Oitzl, & Joëls, 1999; Lupien & McEwen, 1997). Second, noise could act as a distracting stimulus, diverting an individual's limited amount of attention from their primary tasks to the noise stimuli that have been added to the environment (Chan & Blumstein, 2011; Mendl, 1999). This could impair foraging success if, for instance, suitable food sources are detected less often or more slowly, are assessed less accurately, or if prey items are mishandled (Purser & Radford, 2011). Third, noise could mask crucial acoustic cues (Brumm & Slabbekoorn, 2005). If cues produced by prey are masked, feeding opportunities may be missed (Schaub et al., 2008; Siemers & Schaub, 2011). If acoustic predator cues are masked and animals compensate by relying on visual information to a greater extent (Quinn, Whittingham, Butler, & Cresswell, 2006), then visually guided food searching and acquisition might be compromised.

Not only has there been a limited amount of research investigating the impact of anthropogenic noise on foraging behaviour, but noise studies in general also tend to consider the responses of only a single species in isolation (but for exceptions see Francis, Ortega, & Cruz, 2011a, 2011b; Ríos-Chelén, Salaberria, Barbosa, Macías Garcia, & Gil, 2012). However, it is likely that there will be stable interspecific differences in susceptibility and responses to elevated noise levels depending on variation in, for example, hearing ability (Fay, Popper, & Webb, 2008) and mechanisms of physiological stress response (Hofer & East, 1998). In sympatry, and particularly if there is overlap in ecological niches, these differences may alter the relative success of each species under scenarios of disturbance, and so potentially affect community composition and structure.

In this study we investigated how exposure to additional noise affected the feeding behaviour of two sympatric fish species. Numerous fishes use and produce sounds for a variety of reasons (Popper, Fay, Platt, & Sand, 2003), and there is increasing evidence that at least some species are susceptible to anthropogenic noise (see Popper & Hastings, 2009; Radford, Kerridge, & Simpson, 2014; Slabbekoorn et al., 2010). Hearing in fishes varies greatly (Fay et al., 2008; Fay & Popper, 2012), resulting in interspecific differences in vulnerability to anthropogenic noise. For instance, comparative studies have shown different masking effects of noise on a range of Mediterranean fish species (Codarin, Wysocki, Ladich, & Picciulin, 2009) and different behavioural thresholds for startle responses to pure tones in eight marine fish species (Kastelein et al., 2008). Fishes also differ greatly in their sensitivity to stress (Pottinger, 2010) and to risk in general. For instance, species with body armour remain longer in potentially dangerous feeding locations, initiate escape behaviour later at shorter flight distances and hide less than fish without such defensive adaptations (Abrahams, 1995; Krause, Cheng, Kirkman, & Ruxton, 2000; McLean & Godin, 1989); such relatively risk-tolerant species may conceivably also be more tolerant of other stressors such as novel anthropogenic noise.

In our laboratory-based experiments, we compared the foraging behaviour of three-spined sticklebacks, *Gasterosteus aculeatus*, and European minnows, *Phoxinus phoxinus*, when exposed either to silent-playback controls or to playback of noise originally derived from recordings of ships. With over 50 000 merchant ships carrying 90% of world trade around the globe (International Chamber of Shipping, 2013), shipping is a major contributor to marine anthropogenic noise (Hawkins & Popper, 2012). If increased noise induces a stress response, acts as a distraction or masks important cues, we predicted that fish might suffer a reduction in food intake arising from decreases in appetite, and thus in foraging effort and/or foraging performance (e.g. increased errors in detection, classification and handling). If noise acts as a stressor, we also expected increases in startle behaviour and/or inactivity during playback of additional noise. Interspecific differences in responses could arise if the species differ in their hearing capabilities and because minnows lack the morphological antipredator adaptations (bony plates and dorsal spines) of sticklebacks, and consequently show less bold behavioural patterns (Hoogland, Morris, & Tinbergen, 1957; Mathis & Chivers, 2003); they may therefore be more risk averse and show more stress-related behaviour in response to noise, at the expense of feeding activities.

METHODS

Ethical Note

All procedures were approved by the University of Bristol Ethical Committee (University Investigator Number: UB/10/034) and followed Association for the Study of Animal Behaviour and Animal Behavior Society Guidelines for the Use of Animals in Research. Fish were tested only once they were acclimated to the test set-up (i.e. when they did not hide or freeze in the test tank prior to trials). Data collected on stress-related behaviour during control conditions showed that fish were not disturbed to an unacceptable level by the test procedure. Moreover, fish showed only mild stress responses (such as brief startle responses) to playbacks of additional noise, and those responding to noise by decreasing their activity resumed pretrial activities within minutes of the playback stopping. All fish resumed normal pre-experimental behaviour (including feeding) in their holding tanks at the end of each test and training day. All fish used in this study were kept for future research.

Study Species and Holding Conditions

Three-spined sticklebacks and European minnows often coexist in freshwater habitats, such as ponds, streams, rivers and lakes, and brackish seashore and estuarine areas (Froese & Pauly, 2011; Joint Nature Conservation Committee and Centre for Ecology and Hydrolology, 2011). As a consequence, they can be exposed to a wide range of anthropogenic noise, from recreational boat traffic in lakes to shipping, pile driving and other industrial noise in major rivers and estuaries.

Thirty-six adult three-spined sticklebacks (30 for use as focal fish and six to act as familiar companions during experimental procedures to maintain normal behaviour) were caught using hand-held nets from a freshwater pond in southwest U.K. (51°30′4″ N, 2°38′13″ W; online stillwater associated with Hazel Brook/River Trym) with appropriate Environmental Agency permission. Fish were transported to the University of Bristol Aquarium Facility by car (journey time: 15 min) within 2 h after catching. For transport, a maximum of three fish were placed in transparent plastic bags (3 litres) that were filled with one-third pond water and two-thirds air; bags were placed in opaque black 10-litre plastic buckets, half-filled with pond water. Water conditioner (API stress coat, Mars Fishcare North America, Inc., Chalfont, U.S.A.) was added to the water to neutralize ammonia. All fish survived transport and were checked on arrival by the University Veterinary Officer, who had approved the transport process. After gradual acclimatization to the aquarium water, groups of up to 20 sticklebacks were transferred to three 100-litre glass holding tanks (90×36.5 cm; water depth: 30 cm; wall thickness: 4 mm). Tanks contained artificial plants for shelter, an external power filter and an airstone kept at low airflow