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Review

Attention, noise, and implications for wildlife conservation and management

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A B S T R A C T

Anthropogenic stimuli are often viewed as disturbances that directly interfere with signal processing or communication, or directly harm animals. However, such sounds may also distract individuals and thus potentially interfere with their ability to make biologically important decisions about food selection, mate selection, and predator detection. This is because all of these decisions require animals to focus their attention on these tasks and the attention allocated to perceived stimuli is limited. We review the ways that attention is studied, the diversity of taxa in which this cognitive process has been studied, and how stimuli from one modality may interfere with attentional processes in another modality. Such distraction may increase the vulnerability of prey to predators and thus influence predation rates and, ultimately, both the population size, and the effective population size (through differential mortality). Recognizing that distraction is likely to be widespread is the first step towards managing it for wildlife conservation and the management of problem animals.

Contents

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1. Introduction

Anthropogenic noise is present throughout the ocean (Hatch and Wright, 2007) and on land (Jabben et al., 2001). This creates a problem for animals that use sounds to conduct a variety of biologically important tasks (Lein, 1981; Gerhardt et al., 2002; Brumm and Slabbekoorn, 2005; Surlykke and Kalko, 2008). And, although they may adapt to living with certain urban characteristics (Luniak, 2004; Hunter, 2007), studies have shown that prominent ambient noise can mask acoustic signals (e.g., Slabbekoorn and Peet, 2003; Warren et al., 2006; Woods and Yezerinac, 2006), change population distributions (e.g., Reijen et al., 1998; Bejder et al., 2006; Bayne et al., 2008), increase vigilance (e.g., Delaney et al., 1999; Karp and Root, 2009), and create physiological stress (e.g., Campo et al., 2005). Indeed, anthropogenic sounds have been shown to even affect avian community structure and the nature of interspecific interactions (Francis et al., 2009). Despite rare adaptations to extraneous noise, such as modifying call structure to avoid acoustic masking (Foote et al., 2004), anthropogenic noise generally causes deleterious consequences. For example, beaked whale strandings (e.g., Frantzis, 1998) may be a direct result of extremely loud anthropogenic sounds (Cox et al., 2006). A deeper knowledge of the ways animals respond to anthropogenic sounds may help us understand, and hence manage, our impacts, or, if desired, use anthropogenic sounds to interfere with “problem” animals.

One little-examined impact of anthropogenic noise is that it may draw attention and thus distract animals. While animals can perceive stimuli in many modalities, they generally respond to a very narrow range of stimuli because attention filters out irrelevant information (Shettleworth, 2010). Attention is finite and limits the total amount of information that can be processed (Dukas, 2004). Thus animals become distracted when attention is reallocated to peripheral and irrelevant perceived stimuli, leaving them less able to attend to a stimulus important for survival or reproductive success. Anthropogenic sounds can be peripheral stimuli. Importantly, as long as stimuli can be perceived (even those from another modality), attention may be compromised.

An example of the consequences of compromised attention is seen in a study demonstrating that loud boat motor sound reduced a hermit crab’s (*Coenobita clypeatus*) ability to properly assess a simulated predation risk (Chan et al., 2010). We proposed “the distracted prey hypothesis”, which asserts that extraneous and relatively continuous stimuli (of any modality that is perceived) are capable of reallocating attention and distracting animals from performing biologically important task (e.g., predator detection, foraging, sleeping). What was surprising about this study was that an invertebrate—a hermit crab—not only possessed attention, but also was capable of being distracted. Most (but not all) previous studies have studied attentional processes in vertebrates (see below), and those that have studied attentional processes in invertebrates have not focused on how sounds may distract them.

Attentional processes occur after stimulus perception and stimulus filtering (Blumstein and Bouskila, 1996), and attention is a cognitive process. Importantly, attentional processes can be influenced by stimuli from multiple modalities (Driver and Spence, 1998). Distraction by a stimulus of one modality can affect performance in a task of another. For example, the presence of a continuous white noise impaired the ability of Norway rats (*Rattus norvegicus*) to perform a visual discrimination task (Maes and de Groot, 2003), showing that while they had focused their attention upon stimuli in their visual field, an irrelevant stimulus from another modality was capable of drawing attention away from the visual discrimination task. This finding, along with those of Chan et al. (2010), has important consequences for wildlife conservation because it implies that anthropogenic stimuli may broadly influence an animal’s performance visual tasks, even if the stimuli are not visual.

2. How attention is studied

Animals must divide their attention between various activities (e.g., playing, foraging, grooming) while simultaneously assessing predation risk (Blumstein, 1998). The study of attention can involve allocation of attention under certain conditions. For example, it has been shown that elk (*Cervus elaphus*) spend less time on vigilance and focus more attention on feeding when predation risk is low (Wolff and Van Horn, 2003). The allocation of attention may also be dependent on foraging behaviour. Bernays and Funk (1999) speculated that animal specialists that focus attention on a specific food source likely have higher foraging efficiency, which may give them an advantage over generalists because they spend less time on foraging and more attention can be allocated to assessing predation risk. It is possible that too many stimuli can be overwhelming; certain predators may become confused by swarming prey because they are unable to focus their attention on a specific individual (Jeschke and Tollrian, 2007). This confusion could be a direct result of divided attention (Shettleworth, 2010).

Attentional capabilities can also be studied in a more direct manner. One way is to investigate performance in visual discrimination tasks (e.g., Sagi and Julesz, 1986; Corbetta et al., 1991). The goal of such studies is to see how visual distractors influence the ability to identify a target from the background. Studies capitalize on the need to forage for cryptic prey or detect predators from a complex background. Treisman and Gelade (1980) suggested that attention is focused serially towards different features of the target and then integrated into a unified percept (i.e., feature integration theory). Such serial examination is required in visual searching (VanRullen et al., 2004), whereby the desired target is selected from the surrounding distractors (Wolfe, 2010). A study on visual searching tests attention by distracting the animal from identifying the target quickly and accurately (Shettleworth, 2010). In addition, possessing a ‘search image’ (i.e., focusing attention on specific visual features—Tinbergen, 1960; Langley, 1996) and employing ‘area restricted searches’ (i.e., restricting attention to a small and specific area—Curio, 1976; Kareiva and Odell, 1987; Fauchald and Tveraa, 2003) can further help identify a desired target. Many taxa have been subjected to visual discrimination tasks that test their attentional abilities.

3. Taxa in which attentional processes have been described

Here we review (the mostly) experimental studies demonstrating the variety of taxa that possess attentional abilities. Each study is intended to show the prevalence of attentional processes, regardless of the precise experimental procedures or findings. The diversity of species demonstrates that attention is a widespread, perhaps universal, cognitive ability that allows animals to cope with exposure to irrelevant stimuli. Compromised attention thus could have potentially important implications for conservation and management.

3.1. Primates

Studying attentional abilities in primates is an area of much interest. Chimpanzees (*Pan troglodytes*) (Tomonaga, 2001), baboons (*Papio papio*) (Deruelle and Fagot, 1998; Fagot et al., 1998), capuchin monkeys (*Cebus apella*) (Spinozzi et al., 2003), and macaques (*Macaca mulatta*) (Bichot et al., 1996; Bichot and Schall, 1999) are capable of focusing their attention to identify a target among a variety of distractors. In addition to visual discrimination tasks, joint attention (i.e., the ability to focus attention where another is looking via nonverbal communication) is an example of how attention is utilized and has been studied in a number of primates (e.g., chimpanzees—Povinelli and Eddy, 1996; macaques—Tomasello et al., 1998; olive baboons (*Papio anubis*)—Vick and Anderson, 2003; pileated gibbons (*Hylobates pileatus*)—Horton and Caldwell, 2006; orangutans (*Pongo pygmaeus*)—Itakura and Tanaka, 1998; lemurs (*Eulemur fulvus* and *Eulemur macaco*)—Ruiz et al., 2009). While these studies are experimental and direct evaluations of attentional processes, there is evidence from observational studies suggesting other primates are capable of attentional processes as well. For example, female mountain gorillas (*Gorilla gorilla beringei*) often shift their attention away from foraging to approaching adult males more often than when there are approaching females (Watts, 1998). In this case, it is logical to assume that adult males distract foraging females (implying the existence of attentional processes).

3.2. Rodents

There are many studies of attentional processes in rodents, mostly in rats and mice. For example, it has been shown that Norway rats possess the ability for sustained attention (i.e., vigilance) (e.g., Granon, 1998; Mirza and Stolerman, 1998), divided attention (i.e., being able to divide attention between different stimuli) (e.g., McGaughy et al., 1994; Jentsch and Taylor, 2003), and selective attention (i.e., focusing attention at a specific target) (e.g., Piser and Fibiger, 1983). These three terms are examples of how attention is described in practice. Mice (*Mus musculus domesticus* and *Mus musculus musculus*) have also been used as a model species in a variety of attention studies (e.g., Gaalen et al., 2003; Young et al., 2004; Greco and Carli, 2006). The study of attention is not limited to rats and mice though; Mongolian gerbils (*Meriones unguiculatus*) focus attention on novel stimuli presented in their visual field (Cheal, 1980). Also, California ground squirrels (*Spermophilus beecheyi*) have been shown to shift their attention to fast moving stimuli in a study conducted on their directional selectivity (Paolini and Sereno, 1998). And, Blumstein (1998) studied golden marmots (*Marmota caudata aurea*) and suggested that limited attention enhanced predation risk for individuals distracted by being engaged in social behaviours such as play and aggression.

3.3. Mammals (excluding primates and rodents)

Attentional processes have been studied in other mammals—mostly through visual discrimination tests (e.g., sea lions (*Zalophus californianus*)—Schusterman, 1966; Schusterman, 1967; elephants (*Loxodonta africana*)—Savage et al., 1994; red deer (*C. elaphus*)—Reby et al., 2008). Although attention has been studied in dolphins (e.g., Pack and Herman, 2004, 2006), the attentional processes of other cetaceans have not been as well investigated, most likely because of the logistical constraints in working with them.

3.4. Birds

Birds have also been the focus of many visual discrimination studies. For example, extensive work has been done on pigeons (family *Columbidae*) involving visual searches for cryptic food or specific patterns on complex, distracting backgrounds (Bond, 1983; Plaisted and Mackintosh, 1995; Langley et al., 1996). The ability to selectively focus attention to discover cryptic targets has also been shown in fowl (*Gallus gallus domesticus*) (Dawkins, 1971). Pigeons have been used to study the ‘attention threshold hypothesis’, which argues that the latency to discover a desired target within a backdrop of distractors is minimized by shifting between selectively focusing attention upon one stimulus type at a time and performing a slower search by becoming receptive to a full spectrum of stimuli (Bond, 1983). Blue jays (*Cyanocitta cristata*) and other species that have to find food against complex visual backgrounds may be more vulnerable to predation when searching for cryptic prey due to a compromised ability to detect predatory stimuli (Dukas and Kamil, 2000; Dukas, 2002).

3.5. Amphibians and reptiles

Studies involving attentional processes have been conducted on a variety of amphibians and reptiles, such as frogs (e.g., Ingle, 1975; Greenfield and Rand, 2001) and lizards (Fleishman, 1986). An example is an anole (*Anolis auratus*), which has a visual reflex that is drawn by moving and relevant objects. Fleishman (1992) speculated that there must be an attentional process that prevents distraction from ambient environmental motions (e.g., vegetation movement due to wind) that allows the lizards to discriminate relevant from irrelevant motions (i.e., visual search capabilities). In addition, Prechtl (1994) observed cortical oscillations that are linked to attentional processes in a species of pond turtles (*Pseudmys scripta*). The oscillations were also observed in response to salient (i.e., attention capturing) stimuli, such as sudden movements made by the experimenter.

3.6. Invertebrates

Attentional processes have been studied in honeybees (*Apis mellifica*), which have been shown to pay attention to a particular space occupied by different landmarks indicating the position of a sugar source (Anderson, 1977). This use of attention allows them to optimize their foraging patterns. The attention has also been suggested in spiders (e.g., Hebets, 2004; Nakata, 2010), hermit crabs (e.g., Jackson and Elwood, 1990; Chan et al., 2010), and nematodes (e.g., Hills et al., 2004). For instance, it has been shown that hermit crabs (*Pagarus bernhardus*) can be distracted during investigation of potential shells (Jackson and Elwood, 1990). Distraction in hermit crabs has been suggested in a variety of other studies (e.g., Elwood, 1995; Elwood et al., 1998; Neil and Elwood, 1986). We expect that given the diversity of invertebrate taxa in which attention has been studied, that most/all species have limited attentional abilities.

4. The conservation and management relevance of attentional processes

We have shown that attentional processes are widespread among animals. It is possible that distraction by anthropogenic noise might affect the population dynamics of many species through its impacts on survival and the later responses of adaptive behaviour. Many populations of amphibians (Collins and Storfer, 2003), reptiles (Gibbons et al., 2000), marine mammals (e.g., Turvey et al., 2007; Estes et al., 2009), birds (see Pimm et al., 2010) and most primates (see Mittermeier et al., 2009) are either declining, threatened, or endangered in at least some of their range. Despite dominating the planet's biodiversity, invertebrates have rarely been the focus of conservation (Dingle et al., 1997), even though they play a crucial role in a variety of different ecosystems (e.g., Lavelle et al., 2006; Mysterud et al., 2010; Riipinen et al., 2010). All of these taxa rely on attention to select which stimuli are most relevant to their survival and reproduction (Shettleworth, 2010). This realization, combined with the observation that humans produce anthropogenic sounds (and other stimuli) throughout the world, suggests that conservation biologists and wildlife managers should understand how attention can be manipulated for management, and understood for conservation.

Studying attentional deficits would be useful in situations where anthropogenic disturbances have negatively affected target species populations. For example, California ground squirrels have been shown to change their behaviour by increasing their vigilance in the presence of electricity generating wind turbines (Rabin et al., 2006). Because we know these populations are already affected by anthropogenic noise, it would be useful to investigate whether distraction plays a role as well. Compressor stations that assist in maintaining flow through gas pipelines in the boreal forest create a constant noise year round that can be heard within a 1 km radius. The effect of this noise has been studied in birds (Bayne et al., 2008), but there has not been as much work done investigating the effect on the mammals that live there (e.g., hares, ungulates, bears). They too may be distracted by the noise, which could affect population sizes of target species. In addition, a large portion of the literature on anthropogenic noise investigates its effect on avian populations (see Slabbekoorn and Ripmeester, 2008; Warren et al., 2006) and we speculate that distraction could be a prominent mechanism for increased predation risk, which may reduce population size.

Determining whether anthropogenic noise is distracting is particularly important for those populations where evidence suggests that there may not be energetic costs to living with noise or other potential distractors. For instance, Bisson et al. (2009) found that white-eyed vireos (*Vireo griseus*) suffered no significant energy cost resulting from the presence of anthropogenic disturbance (including noise) and, that activities such as parental care continued uninterrupted. However, it is conceivable that while the birds continued to perform these tasks, their proficiency decreased due to distraction and thus they suffered a fitness cost. For instance, distraction does not eliminate, but rather reduces blue jays '(*C. cristata*) ability to detect predators in their periphery (Dukas and Kamil, 2000). Thus, lack of evidence of energetic costs does not necessarily mean that there are no fitness costs to potentially distracting stimuli.

To properly conserve biodiversity and to manage wildlife populations, we should consider anthropogenic noise as not only a mechanism for masking communication, but also one that may distract animals. We have shown that such attentional capabilities are taxonomically widespread and, importantly, that the distraction can come from stimuli in any modality (e.g., auditory—Berti and Schroger, 2003; visual—Visser et al., 2004; olfactory—Bunsey and Strupp, 1995). The majority of the examples we have outlined examine mostly the visual attentional capacity of these taxa, but with respect to risk assessment, predator detection likely involves more than visual cues. Chemosensory cues are also used in risk assessment by certain prey to avoid predation (Kats and Dill, 1998). For example, certain species of skinks (*Carlia rostralis* and *C. storri*) use odors to detect predators and assess the level of risk depending on the predator species (Lloyd et al., 2009). Therefore, anthropogenic noises may also distract animals from detecting predator sensory cues as well. The opposite theoretically works as well; anthropogenic stimuli of other modalities could distract animals from auditory cues necessary for biologically important tasks.

We speculate that noise could be strategically used to distract, and thus disrupt 'overabundant' animals. If, by doing so, we are able to reduce their reproductive success or survival, we have a potentially effective management tool. Noise has already been shown to deter some problem species away from a particular space. For example, ongoing research conducted by Dr. Richard Holstetter shows that altering the noise made by bark pine beetles (*Dendroctonus ponderosae*) and playing it back to them can effectively disrupt their mating and tunneling behaviour (Anon., 2010).

Additionally, ultrasonic noise has been found as a deterrent for certain nuisance animals (e.g., Nelson et al., 2005). Animals may, however, habituate to such chronic sound exposure (Bomford and O'Brien, 1990). If, despite habituation, the noise still distracts animals, the intended effect may persist. More research into how animals habituate to such sounds is needed.

5. Conclusions

We need studies that aim to better understand the population consequences of distraction on wildlife populations. In some cases, we may wish to reduce the effect of distraction while in other cases we may wish to increase it (i.e., to repel problem animals or invasive species). One key future question will be to understand how animals habituate to distracting stimuli over time. While Chan et al. (2010) speculated that continuous stimuli could result in habituation, more empirical evidence is necessary to test this hypothesis. In humans, continuous noises of even low intensity can impair cognitive performance (Beaman, 2005). It is possible that although animals may habituate to the stimuli, it may not always result in recovered risk assessment.

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