



## Increased amplitude and duration of acoustic stimuli enhance distraction

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Extraneous sounds have a variety of effects on animals; they may interfere with communication, cause physical harm, increase wariness, influence settlement decisions, or they may cause distractions in ways that increase vulnerability to predation. We designed a study to investigate the effects of changing both the amplitude and duration of an acoustic stimulus on distraction in a terrestrial hermit crab (*Coenobita clypeatus*). In experiment 1, we replicated the key findings from a field result: crabs hid more slowly in response to a silent visual stimulus when we simultaneously broadcast a white noise than they did when in a silent condition. In experiment 2, we altered the noise duration and found that a long noise generated greater latencies to hide than a short noise. In experiment 3, we increased the noise amplitude and found that hide latency increased with higher-intensity auditory stimuli. These experiments demonstrate a variety of stimulus factors that influence distraction. Our results suggest that prey animals could be in greater danger from predators when in an environment with auditory distractions.

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Many animals rely on either producing or perceiving biologically important auditory stimuli. These sounds have been implicated in sexual selection (Searcy & Andersson 1986), spatial navigation (Simmons & Stein 1980) and hunting (Goerlitz et al. 2008), amongst other adaptive behaviours. Because many species can perceive a large variety of stimuli (see Shettleworth 2010), extraneous noises may compete with biologically meaningful stimuli and this competition may have behavioural consequences. Anthropogenic noises may interfere with animal calls, forcing them to change their vocalization rates (Morisaka et al. 2005; Parris et al. 2009). Extraneous noise may also increase vigilance (Karp & Root 2009) and can interfere with the ability to detect auditory cues associated with approaching predators (Quinn et al. 2006).

Distraction is a phenomenon well documented in primates (Grueninger & Pribram 1969; Van Essen et al. 1991; Escera et al. 2003; Berti 2008; Parmentier et al. 2008), rats (*Rattus norvegicus*: Riddell et al. 1969; Thorpe et al. 2002) and corvids (Dukas & Kamil 2000; Dukas 2004). A recent study in an invertebrate species showed that auditory distractors affect the escape response to a visual threat. Chan et al. (2010) demonstrated that in the presence of a loud noise, a simulated predator could get closer to terrestrial hermit crabs (*Coenobita clypeatus*) before they withdrew into their

shells than when the crabs were approached in silence. Chan et al. (2010) suggested that distraction influences the ability to properly respond to risk, potentially exposing animals to greater risk of predation. This mechanism is consistent with prior research on hermit crab attentional processing, albeit for different tasks. For example, Jackson & Elwood (1990) suggested that differences in attentional processing might occur at distinct portions of shell assessment behaviour in an aquatic hermit crab, resulting in the modulation of distractibility (for other examples, see also Neil & Elwood 1986; Elwood 1995; Elwood et al. 1998).

To further investigate the stimulus factors that influence distraction, we conducted three experiments in a laboratory setting with captive, terrestrial Caribbean hermit crabs. First, we created a captive assay that replicated the primary finding of the Chan et al. (2010) field study. Then, we performed a pair of experiments to investigate the effects of modifications to the acoustic stimulus on the crabs' escape response. The results of these three experiments illuminate the mechanisms underlying acoustic distraction and have implications for the effects of anthropogenic noise on the susceptibility of animals to predators.

### GENERAL METHODS

#### Subjects

We used 40 medium sized (3–4 cm shell length, measured as the longest length on the shell) Caribbean hermit crabs obtained

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from an Internet source ([live-hermitcrabs.com](http://live-hermitcrabs.com)) or a local aquarium store (Apex Aquariums, Culver City, CA, U.S.A.) as our subjects. We selected this species partly because they have good visual ability (see Cronin & Forward 1988). Additionally, although the mechanism is not well understood, hermit crabs use acoustic and/or vibrational stimuli in social behaviour (Burggren & McMahon 1988). The animals inhabited shells from marine snails (genus *Turbo*). Crabs were housed in groups of five and were maintained on a 14:10 h light:dark cycle to simulate the testing hours of Chan et al. (2010). Their daily diet consisted of one piece of dried tropical fruit per crab and approximately 5 g of commercially produced hermit crab meal (United Pet Group Hermit Crab Meal, United Pet Group, Cincinnati, OH, U.S.A.) per housing cage. We randomly assigned each crab to one home cage where it was housed during testing. The home cage contained dirt substrate, a small cup for water consumption, a paper plate and a water-soaked sponge (rewetted every 24 h) to maintain high humidity in the home cage.

Subjects were distinguished by one of five colours (one unique colour for each crab within the cage) of nontoxic OPI nail enamel (N. Hollywood, CA, U.S.A.) painted on their largest claw, and another mark on their shell.

While no permits are required to work with nonthreatened or nonendangered invertebrates in the United States, we were sensitive to the welfare of our subjects and followed ASAB/ABS research guidelines.

#### Apparatus

The experiment was conducted in  $2.5 \times 1.5$  m soundproof room. We used one speaker (Sony SRS 77G) that was adjacent to a 17-inch (43 cm) Dell LCD monitor and broadcast white noise at a fixed 82 dB SPL when measured 1 m with a RadioShack sound meter (CAT 33-2055). This distance between the speaker and the subject was 0.25 m. The speaker was on the ground, but the crab was elevated off the ground and the crab-holding apparatus (see below) likely attenuated substrate-borne vibrations. We used the LCD monitor to display a visual stimulus, a hawk with its wings spread. This image began as a single pixel at the top and centre of the screen, and then expanded and descended at a constant rate for 17 s until it reached a maximum size of screen width (approximately 30 cm or 900 pixels wide) at the bottom of the screen (Fig. 1). Our primary concern was finding a visual stimulus that reliably elicited the crabs' withdrawal response. Pilot work with a variety of visual stimuli indicated that this stimulus effectively elicited the response.

We designed an automated withdrawal detector (AWD) that was situated 15 cm in front of the LCD monitor (Fig. 2). The AWD consisted of two 20 cm sliding metal levers elevated 5 cm above the ground at its base, with an adjustable C-clamp attached to the same end on both levers. The levers were attached to a  $20 \times 20$  cm wooden platform and allowed us to adjust the clamp's position to an individual crab's shell size by enabling both vertical (to raise or lower the crab) and horizontal (to move the crab closer or further from the monitor) adjustment. We positioned an infrared photobeam emitter and receiver such that an infrared beam ran parallel to the clamp's spine. We designed its position so that, when a crab emerged while in the clamp of the AWD, its legs disrupted the beam. The break in beam detection was scored by the computer as 'emergence' and measured to the nearest hundredth of a second. Then, with the same precision, it measured the time when the crab withdrew back into its shell (i.e. when the crab removed its legs and the beam was restored).

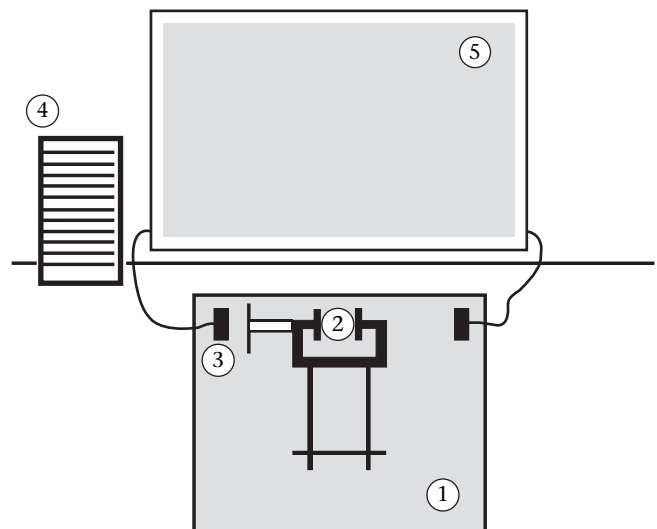
#### Statistical Analysis

For each experiment, we used paired two-tailed *t* tests to compare the latency to hide between each treatment. We also



**Figure 1.** Photograph of the silent visual predator presented to Caribbean hermit crabs on our LCD monitor.

calculated effect sizes using Cohen's *d* scores and the pooled variance. In our statistical analysis, we eliminated crabs that did not respond at all to the visual stimulus in any condition. This occurred in both experiments 1 and 3; in both, there were two crabs (out of 20) that did not respond at all to the visual stimulus. If the crab responded in one condition, but not the other, we used the maximum latency to hide (17 s) for the condition without a response. This only occurred in experiment 2, where five crabs in the loud sound duration condition and two crabs in the short duration condition failed to respond.



**Figure 2.** A schematic of our experimental set-up. (1) Automated withdrawal detector, (2) crab holder (modified C-clamp), (3) photobeam sensors (one on each side of the clamp; one emitter and receiver), (4) Sony speaker and (5) LCD monitor.

## EXPERIMENT 1: DEVELOPING A CAPTIVE ASSAY

### Methods

Twenty crabs were exposed to both a white noise and silent treatment during each experimental session (i.e. a within-subjects design). In each session, a crab received a single trial of one acoustic treatment first, which was followed by a trial with the other treatment. The order of the treatments was counterbalanced across subjects. We began each session by placing the crab in the AWD on its back so the aperture of its shell faced the ceiling, because preliminary investigation demonstrated that this position resulted in the crabs emerging quickly (see also Nolan 2004). Once the crab fully emerged (as detected by the interruption of the infrared beam) for a continuous 30 s interval, we broadcast either silence or the white noise (i.e. the acoustic treatment). After 30 s of the acoustic treatment had elapsed, the visual stimulus was presented. The auditory and visual stimuli co-terminated when the visual stimulus reached its maximum size on the monitor. The latency to hide for each subject was recorded by computer.

### Results

The crabs took significantly longer to hide when noise was present (mean  $\pm$  SD =  $12.48 \pm 4.08$  s) compared to no noise ( $7.67 \pm 4.19$  s;  $t_{17} = 4.652$ ,  $P < 0.001$ ,  $d = 0.478$ ; Fig. 3a). This represents a successful laboratory replication of the Chan et al. (2010) field results and thus provides a laboratory assay to study attentional processes in the hermit crab.

## EXPERIMENT 2: DOES NOISE DURATION INFLUENCE DISTRACTION?

### Methods

Methods were similar to experiment 1 with two exceptions. The first adjustment was that we broadcast the white noise for 10 s or 90 s after the crab's emergence prior to initiating the visual stimulus presentation. The second was that each session consisted of only one trial instead of two. Thus, each crab received two sessions, with one duration of noise in the first session and the other duration in the next session. The order of duration conditions was counterbalanced across crabs. The time interval between the first experiment and the second was 1.5 weeks and we used the same 20 subjects as in the first.

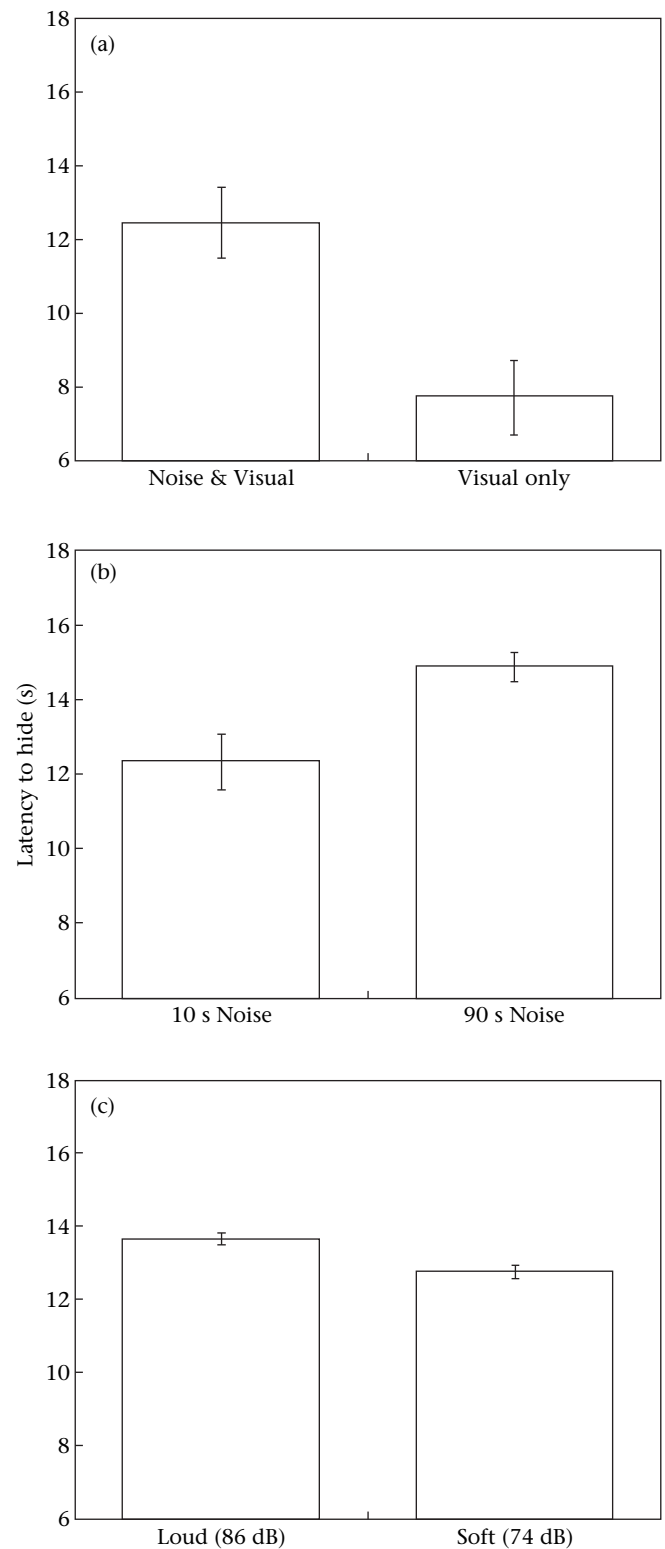
### Results

The crabs took significantly longer to hide during the visual stimulus when they experienced the 90 s noise (mean  $\pm$  SD =  $14.88 \pm 1.78$  s) compared to the 10 s noise ( $12.33 \pm 3.35$  s;  $t_{19} = 2.615$ ,  $P < 0.05$ ,  $d = 0.452$ ; Fig. 3b).

## EXPERIMENT 3: DOES NOISE AMPLITUDE INFLUENCE DISTRACTION?

### Methods

This experiment was similar to the prior two, except we used an entirely new set of 20 crabs as subjects in this experiment. We held the noise duration before exposure to the visual stimulus constant at 30 s (as in experiment 1) and manipulated the amplitude of the two treatments. Trial types consisted of either an 86 dB SPL or a 74 dB SPL broadcast to the crabs. Also, as with experiment 2, each session had only one trial as opposed to two. The order of intensity conditions was counterbalanced across crabs.



**Figure 3.** Latencies to hide (average  $\pm$  SE) to silent simulated approaching predators. (a) Experiment 1: simulated predator presented with noise (at 82 dB SPL, measured at 1 m) or silence. (b) Experiment 2: simulated predator initiating after 10 s or 90 s noise. (c) Experiment 3: simulated predator presented with noise at 86 dB SPL or 74 dB SPL.

## Results

The crabs took significantly longer to hide in the presence of the louder white noise (mean  $\pm$  SD = 13.68  $\pm$  0.72 s) relative to the quieter one (12.76  $\pm$  0.75 s;  $t_{17}$  = 4.830,  $P$  < 0.001,  $d$  = 0.529; Fig. 3c).

## GENERAL DISCUSSION

Louder and longer white noise enhanced distraction and resulted in longer latencies to produce a withdrawal response. We determined that the noise distracted the crabs, and thus, we conclude that the magnitude of an auditory stimulus has a direct relationship with the amount of distraction it produces. Chan et al. (2010) tested whether noise associated with some experimental approaches had a masking or distracting effect on a hermit crab's ability to respond to threat, and their results provisionally refuted the masking hypothesis. We can fully refute the masking hypothesis in these studies because the addition of noise inhibited the crabs' response with a completely silent simulated predator.

The effect of the white noise on the crabs' ability to perform a simple biologically important task is probably a reflection of the effect of extraneous stimulation on protective behaviour in general. We should expect that other animals can be similarly distracted, and that this process ought to adversely affect risk assessment. There is ample empirical evidence to suggest that this is the case. For example, when rats are trained in silence to perform a discrimination task involving appetitive reinforcement, they show reduced performance when their subsequent testing sessions are accompanied by white noise (Maes & de Groot 2003).

Similar effects have been found in other invertebrates. For example, Moorhouse et al. (1987, 1990) found that ambulatory behaviour in locusts was interrupted by the presentation of extraneous noise; Elwood and colleagues have reported that an aquatic hermit crab can be distracted from ongoing activity by extraneous visual stimuli (Neil & Elwood 1986), by potentially dangerous visual stimuli (Jackson & Elwood 1990), and by multimodal, startle-inducing stimulation (Elwood et al. 1998).

Distraction is not a binary phenomenon: the effect of distraction varies directly with the strength of the distractor (Berti et al. 2004). We would expect that the effect of distraction on an organism's ability to perform important biological tasks would increase with the intensity of the distracting stimulus. Our results demonstrate that increasing the potency of the distracting auditory stimulus (e.g. amplitude and duration) enhanced the distraction effect (i.e. longer latencies to hide). These results have potential ramifications for the behaviour and survival of wildlife exposed to anthropogenic sounds. Certain disturbances caused by high-intensity anthropogenic noise have already been shown (e.g. Jepson et al. 2003; Slabbekoorn et al. 2010). An additional effect of high-energy noises is the potential for increased predation due to impaired risk assessment.

Chan et al. (2010) suggested that animals may not ultimately suffer a deficit in self-protective responding if they habituate to a distracting stimulus over time. Habituation is described behaviourally as the decrease of responsiveness to repeated stimulation (Groves & Thompson 1970; Rankin et al. 2009). While we did not test for habituation directly, our second experiment provides evidence that longer-distracting stimuli can compromise, rather than recover, an animal's ability to engage in self-protective behaviour. Long-term exposure to anthropogenic stimuli has been shown to permanently alter other types of behaviour, including changing a population's distribution (Lusseau 2004; Bejder et al. 2006). These sorts of evidence suggest that habituation may not occur in all instances of exposure to persistent stimuli. We conclude that we should not

assume that animals will adapt to the presentation of anthropogenic noise, and that their fitness may be compromised.

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