

## Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*

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Background noise should in theory hinder detection of auditory cues associated with approaching danger. We tested whether foraging chaffinches *Fringilla coelebs* responded to background noise by increasing vigilance, and examined whether this was explained by predation risk compensation or by a novel stimulus hypothesis. The former predicts that only inter-scan interval should be modified in the presence of background noise, not vigilance levels generally. This is because noise hampers auditory cue detection and increases perceived predation risk primarily when in the head-down position, and also because previous tests have shown that only interscan interval is correlated with predator detection ability in this system. Chaffinches only modified interscan interval supporting this hypothesis. At the same time they made significantly fewer pecks when feeding during the background noise treatment and so the increased vigilance led to a reduction in intake rate, suggesting that compensating for the increased predation risk could indirectly lead to a fitness cost. Finally, the novel stimulus hypothesis predicts that chaffinches should habituate to the noise, which did not occur within a trial or over 5 subsequent trials. We conclude that auditory cues may be an important component of the trade-off between vigilance and feeding, and discuss possible implications for anti-predation theory and ecological processes.

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An important principle of foraging theory is that vigilance and therefore predator detection is compromised when foraging (Lima and Bednekoff 1999). Consequently animals may have to rely on the sounds of a predator approaching, the sounds of other prey responding to a predator or alarm calls of con- and heterospecifics as early warning of a predator's approach when either looking for or handling food, especially in the 'head-down' position (Harvey and Greenwood 1978, Smith 1986). In species that feed socially, for example, and in which alarm calls are used, it is likely that early warnings for most group members will be mainly auditory and especially important when an individual is not scanning for predators itself (Klump and Shalzer 1984, Gyger et al. 1986). Indeed, an individual's benefit

gain from the commonly observed decline in vigilance in large groups relies on transmission of information about a predator's approach from a vigilant individual to a non-vigilant individual (Lima 1995), and this may frequently be via an auditory signal (Alatalo and Helle 1990, Cresswell 1994). Even if animals do not feed socially, heterospecific alarm calls can give an indication of the presence of a predator, and this is perhaps very important for many small bird species that use alarm and mobbing calls to monitor the location of hawks and manage their predation risk accordingly (Forsman et al. 1998, Forsman and Monkkonen 2001). Similarly, feeding animals may rely on detecting any other sound associated with a predator, such as that made by the predator's approach.

Sound detection is influenced by a variety of environmental factors (Wiley and Richards 1996). One of these is the level of background noise and the signal-to-noise ratio plays an important role in the detection and recognition of signals (Klump 1996). Some studies suggest that vocalizing animals compensate for increased levels of natural and unnatural background noise by increasing the strength, or by modifying the frequency and nature of, their vocalizations (De la Torre and Snowdon 2002, Slabbekoorn and Peet 2003, Brumm 2004, Brumm et al. 2004). Fewer studies have considered the effects of noise on behaviour with respect to the reception of auditory signals. Use of safe versus unsafe habitat in gerbils *Gerbillus* spp. was not influenced by background noise, suggesting that auditory cues were not important as a predator detection mechanism (Abramsky et al. 1996). However, while two studies explained increased vigilance levels in the presence of noise by a 'novel stimulus' hypothesis (Krebs et al. 1997, Dyck and Baydack 2004), we could find none that did so in the context of elevated perceived predation risk. One study showed that two Australian parrot species *Psittaciformes* increased vigilance levels in noisy locations but it was unclear whether the response was caused by the noise itself or the confounding effect of human activity which was responsible for the noise (Westcott and Cockburn 1988).

We tested if chaffinches *Fringilla coelebs*, a species that occurs alone and in flocks throughout the year (Cramp and Perrins 1994), increased their vigilance behaviour when foraging in the presence of background white noise. Foraging chaffinches search for food in a head-down posture, peck at the food item when found and handle the item in the head-up position (Cresswell et al. 2003, Whittingham et al. 2004, Butler et al. 2005). Scanning surroundings can occur when handling food or independently at any time during foraging. It follows that chaffinches can increase vigilance by decreasing interscan interval and by increasing scan duration, so that time spent in the head-down position when searching for food decreases when interscan interval increases. We discriminated between the novel stimulus and predation risk compensation hypotheses on the basis of three predictions. Prediction 1: If the predation risk compensation hypothesis explains the response, chaffinches should modify the various components of vigilance behaviour only if they are compromised by lack of auditory information. That is, they should decrease the amount of time spent in the head-down position, or interscan interval; scan duration should be less affected, if at all, because the chaffinch is less reliant on auditory cues when scanning in the head-up posture. If the novel stimulus hypothesis applies, then all aspects of vigilance should be affected. Prediction 2: Predation risk compensation predicts that chaffinches should modify vigilance only if doing so is adaptive in the

context of predation, that is, if it helps to detect predators. Previous work on the current system showed that the ability to detect an approaching model sparrowhawk *Accipiter nisus*, the major predator of passerine birds in Eurasia (Newton 1986), was correlated with interscan interval but not with scan duration (Cresswell et al. 2003). To compensate for the masking of auditory cues, chaffinches should decrease interscan interval, but not scan duration as was also the case for Prediction 1. In contrast, vigilance patterns again should increase generally if chaffinches were simply responding to a novel stimulus. Prediction 3: Predation risk compensation predicts no habituation with repeated tests on the same individuals because the threat of predation has not altered. The novel stimulus hypothesis predicts habituation as novelty declines over time.

## Methods

Twenty-nine chaffinches were caught under license from English Nature between November 2002 and February 2003 and kept in captivity for a maximum of one week at the Wytham Field Laboratory, Oxford. On capture, birds were aged and sexed (see Svensson 1984). Chaffinches were housed individually in standard small-bird keeping cages in a natural temperature- and light-controlled aviary. Cages were stacked together so that chaffinches were in close sight and sound of each other: chaffinches were kept in separate cages for ease of catching and transfer from the keeping aviary to the experimental cage. Lighting followed the natural light-dark cycle and included 30 minutes of twilight in the mornings and evenings. In practice this meant about 8 hours of light midwinter. Birds were fed *ad libitum* wild birdseed mixture and water. Prior to experiments, birds were food deprived for 2–3 hours to encourage foraging during trials. Experiments were conducted on all individuals within four days of capture (mean 1.92 days  $\pm$  0.14).

## Experimental set-up

Each chaffinch was transferred from its keeping cage in the aviary to an experimental cage 30 m away in a large greenhouse with whitewashed sides. The experimental cage was a cubic wire box (dimensions, 0.5  $\times$  0.5  $\times$  0.5 m) placed over a substrate of artificial wheat stubble with peat compost spread thinly between the stubble (see Butler et al. 2005). Two wheat stubble types were available in the cage for the purposes of another experiment to investigate patch choice by chaffinches (see Butler et al. 2005): one half of the substrate was covered in straws 13 cm in height (the long stubble) and the other half of the board was covered in straws 3 cm in

height (the short stubble). Any trial in which the chaffinch moved between patches during data collection was disregarded: analysis in this paper is at the level of change within individuals during a trial so the presence of variation in the feeding substrate between individuals did not add a bias to the results (see Results).

Prior to each trial, the peat was replaced and a number of canary grass *Phalaris canariensis* seeds were scattered over the 0.5 m<sup>2</sup> basal area of the cage. Four seed density combinations were used to investigate the effect of seed density on patch choice in another experiment (see Butler et al. 2005) but there was always sufficient seed available so that a bird could feed close to its maximum intake rate (see Cresswell et al. 2003). Analysis in this paper is at the level of change within individuals within a trial so the presence of variation in the seed density between individuals or between successive trials on individuals (see below) did not bias the experiment in any way (see results).

A single chaffinch was introduced into the cage and its feeding and vigilance behaviour were recorded by a video camera for several minutes. The experimenter sat out of sight in a separate room in the greenhouse and viewed the chaffinch's behaviour through a direct video feed to a computer monitor. Background white noise was played 2 m from the experimental cage for two to four periods of 30 s interspersed with 30 s periods of silence until the chaffinch had fed during a period. The noise was gently faded up and down over 5 s at the start and end of each noise period to avoid startling the bird. For each individual, we collected foraging data from one noise-on and one noise-off period (i.e. a total of 60 s). The order in which the data were collected for each of these noise states was randomised. Data were always collected from: a) the first noise-on period in which the birds foraged, and from b) the noise-off data from the period immediately preceding or following the noise-on period. The noise itself was a synthetic white noise with sound energy equally distributed across the frequencies (e.g. equally up to 22.1 kHz, including between 6–8 kHz that encompasses chaffinch "see" alarm calls: Heinrich Brumm, pers. comm.). The white noise was played from two standard personal computer speakers (Time Computers Ltd. UK). This gave a stereo effect which we assume simulated a general increase in background noise levels; a single speaker would give a point of focus for the noise source, giving the appearance of an approaching threat. The noise level was measured with a standard hand-held decibel meter, placed in the same location as the feeding chaffinch, with a standard A-filter (20 µPa). The maximum noise level recorded was 68 dB (A) and this was independent of the time constant used to measure the sound. These levels are similar to those experienced by birds in the wild. Brumm (2004) shows that some nightingales *Luscinia megarhynchos* sing close to normal when living near motorways where the noise

levels reach 65 dB. Brumm and Todt (2002) used white noise levels up to 75 dB as an acoustic mask and found that some nightingales also sang. Similarly great tits *Parus major* nest in urban areas where noise levels reach 63 dB (Slabbekoorn and Peet 2003). Background noise levels reach 74 dB in King Penguin colonies (Aubin and Jouventin 1998) and 65 dB when raining in French forests (Lengagne and Slater 2002). Finally, to control for the possibility that any detected behavioural response to the noise was simply a response to a novel stimulus, the foraging behaviour of each chaffinch was recorded in single trials on four subsequent days. During these trials, white noise was played continuously. If the chaffinches perceived the noise as a novel stimulus, a decline in the response with repeated exposure would be expected as they gradually habituated to the stimulus. We assumed that trials over 4 subsequent days were sufficient exposure to achieve habituation. This seems reasonable because in a similar experiment rats had habituated to substantially higher white noise levels of 95 dB by the fourth trial (Krebs et al. 1997).

Our experimental design was more complicated than necessary to address the hypotheses tested in this paper because two other independent experiments were carried out simultaneously. This approach was taken for practical as well as ethical reasons; that is, to minimise the number of wild birds that needed to be caught and the length of time they were kept in captivity. Nevertheless, all potential confounding effects of variation in treatment due to these alternative experiments were controlled for by randomising the incidental treatments for other experiments with respect to the background white noise treatment for the current experiment, so that the former were simply another source of unbiased variation acting on the birds, and by including the treatments in all relevant models.

## Analysis

Video from each trial was analysed frame by frame (25 frames s<sup>-1</sup>) from which several variables were recorded. Previous research has shown that the chaffinches were effectively vigilant when handling seeds in the head-up posture (Whittingham et al. 2004). A head-up period, when the bird was assumed to be vigilant, was defined as when the chaffinch had its head above the level of its back and a head-down period was defined as when the chaffinch had its head below its body level, when the bird was assumed to be searching for food.

For each foraging bout, head-up period, head-down period and peck rate were recorded; mean values were calculated for each foraging bout and then means of these means were calculated for the noise-on and noise-off treatments separately. A foraging bout is defined here as at least 5 consecutive pecks, each separated by less

than 10 s. Data was collected from foraging bouts because we were interested in measuring background levels of vigilance, rather than vigilance levels during periods of alarm, when alert or when not foraging. For example, if individuals became startled for any reason, measurements of vigilance during this time would not tell us anything about how birds allocate time to vigilance to detect predators when feeding, only how birds allocate time to vigilance when they believe there is a potential danger actually present. Variables measured were mean duration of the head-down period (henceforth shortened to head-down period) and the mean duration of the head-up period (henceforth head-up period) during all foraging bouts within the noise-on or off period. The mean number of head-up periods and, hence, head-up rate, the mean proportion of time with the head-up (henceforth, proportion time spent vigilant), the mean number of pecks and hence peck rate during all foraging bouts within the noise-on or off period were also recorded.

The various measures were inter-correlated. For example, using feeding data from the noise-off treatment, head-down period was correlated with peck rate ( $R = -0.45$ ,  $P = 0.038$ ,  $n = 22$ ) and with proportion of time spent vigilant ( $R = -0.73$ ,  $P < 0.001$ ,  $n = 22$ ). Mean head-up period was correlated with peck rate ( $R = -0.56$ ,  $P = 0.007$ ,  $n = 22$ ), head-up rate ( $R = -0.90$ ,  $P < 0.001$ ,  $n = 22$ ) and proportion of time spent vigilant ( $R = 0.76$ ,  $P < 0.001$ ,  $n = 22$ ). Mean head-down period was not correlated, however, with mean head-up period ( $R = -0.13$ ,  $P = 0.56$ ,  $n = 22$ ). The probability of visual predator detection in animals (and therefore predation risk for the purposes of our study) depends on both the proportion of time spent vigilant and how this is split into head-up and head-down periods (Pulliam 1973, Roberts 1994). Therefore we used both the proportion of time spent vigilant and duration of head-down and head-up periods to determine if vigilance that determines probability of predator detection was affected by noise. Furthermore we also used peck rate to determine whether any changes in vigilance as a consequence of noise led to reduced intake rate.

Analysis was restricted to 22 individuals because 4 birds moved between stubble types within the cage during the course of a trial, and in 3 other trials feeding data was inadvertently collected in an unbalanced way, so that the noise was played much less than 50% of the duration of the trial. Removal of these individuals did not affect the conclusions drawn from the results. Analysis was carried out at the level of the individual, comparing the mean for any given variable between the noise-on and noise-off treatment in a matched pair format using a t-test. Possible confounding effects of age, sex, body condition (mass/wing length<sup>3</sup>) or experimental conditions (days in captivity prior to the trial, the stubble type or the seed density) on any significant

changes due to the experimental treatment were explored by testing the dependence of any change with these variables in a General Linear Model.

We tested whether the chaffinches habituated to the noise over subsequent trials by examining whether the proportion of time spent vigilant decreased with repeated exposure to the white noise: number of previous trials (0–4) was a dependent continuous variable in the model and the model included bird identity ( $n = 22$  birds) as a random factor to control for the repeated measures design. The model also included experimental treatment type to control for experimental variation because stubble type varied as part of the second experiment (as above) with order of treatment randomised for the four subsequent repeated white noise exposures. Some individuals did not feed in subsequent trials and so on average there were  $3.6 \pm 0.3$  effective trials per bird even though all were given the same number of trials in the first instance (range 1–5, median and mode = 4). This analysis was also repeated omitting data from the first trial because white noise was played continuously in all subsequent trials rather than in 30 second periods on and off, and being faded up and down at the start and end of each noise-on period.

We tested whether chaffinches habituated to the noise within a trial by examining whether the proportion of time spent vigilant decreased with continued exposure to the white noise. We compared the proportion of time spent vigilant in the first half of the first noise on period of the first trial with the second half of the first noise on period of the first trial. We predicted that if habituation occurred within a trial then there would be a decline in proportion of time spent vigilant in response to the onset of the noise through the trial so that the proportion of time spent vigilant would be less in the second half of a noise on period.

We analysed data using the SPSS statistical programs (Norusis 1990) and according to Sokal and Rohlf (1981). All probabilities quoted are two-tailed. Means and standard errors are quoted in the form mean  $\pm$  1 standard error.

## Results

The total percentage of time spent vigilant during foraging bouts was greater during noise-on than during noise-off treatments ( $71 \pm 1\%$  and  $66 \pm 1\%$  respectively,  $t_{21} = 2.9$ ,  $P = 0.007$ ). Mean head-up period was the same during noise-on and noise-off treatments ( $5.9 \pm 0.3$  s,  $t_{21} = 0.1$ ,  $P = 0.89$ ), but mean head-down period was shorter during the former (mean difference =  $-0.6 \pm 0.2$  s,  $t_{21} = -2.8$ ,  $P = 0.011$ ; noise on  $2.4 \pm 0.1$  s and noise off  $3.0 \pm 0.2$  s). Head-down periods were correlated between treatments within individuals (Fig. 1) suggesting consistent differences between individuals in this beha-

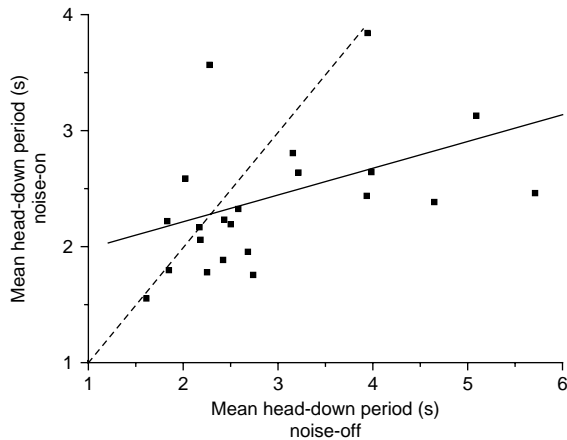


Fig. 1. The relationship between head-down period duration in noise-on and noise-off treatments for individual chaffinches ( $n=22$ ). The solid line indicates the regression relationship between the two treatments for the same individual ( $P=0.03$ ) and the dashed line the expected 1:1 relationship if there was no effect of noise on duration of the head-down period (most points lie below the line indicating that head-down periods were longer in the absence of loud white noise).

viour. The difference in head-down period between noise-on and noise-off treatments was not dependent on the initial head-down period for an individual ( $R=0.06$ ,  $n=22$ ,  $P=0.80$ ). The difference in head-down period duration was also not significantly affected by age ( $F_{1,13}=0.08$ ,  $P=0.78$ ), sex ( $F_{1,13}=2.1$ ,  $P=0.17$ ), mass-correcting for size (mass/wing length<sup>3</sup>,  $F_{1,13}=0.7$ ,  $P=0.43$ )-number of days in captivity before the experiment ( $F_{1,13}=0.04$ ,  $P=0.85$ ), stubble type ( $F_{1,13}=1.5$ ,  $P=0.24$ ) or seed density ( $F_{3,13}=0.9$ ,  $P=0.48$ ).

The number of pecks during a head-down period was significantly lower during the noise-on compared to noise-off treatment (noise present  $0.80 \pm 0.04$  pecks, noise absent  $0.96 \pm 0.06$  seeds,  $t_{21} = -2.6$ ,  $P=0.016$ ).

There was no evidence for habituation in response to the white noise during repeated trials because the proportion of time spent being vigilant actually increased slightly with repetition of the treatment, rather than the strength of response declining (number of repeats  $F_{1,53}=11.6$ ,  $P=0.001$ , strength of effect =  $0.023 \pm 0.007$ ) controlling for bird identity and stubble treatment. This result was similar if the first trial was omitted from the data (number of repeats  $F_{1,33}=25.6$ ,  $P<0.001$ , strength of effect =  $0.024 \pm 0.005$ ) controlling for bird identity and stubble treatment. There was no significant change, however, in the peck rate with repetition of the treatment (number of repeats  $F_{1,53}=0.01$ ,  $P=0.91$ ).

There was no strong evidence for habituation in response to continued exposure to the white noise within a trial. There was no significant difference between the proportion of time spent vigilant in the first half of the first noise on period of the first trial with the second half

of the first noise on period of the first trial (matched pairs t-test,  $t_{21}=1.2$ ,  $P=0.23$ ; first half mean proportion of time spent vigilant =  $0.70 \pm 0.02$ , second half mean proportion of time spent vigilant =  $0.67 \pm 0.02$ ).

## Discussion

### Predation risk compensation or novel stimulus?

Predation risk compensation predicts that inter-scan interval should be the main vigilance behaviour modified in the presence of background noise in chaffinches because hampered detection of auditory cues compromises predation risk primarily when in the head-down position when probability of predator detection will be increased by increasing head up rate, but not when already visually scanning surroundings because there is nothing further a scanning chaffinch can do to increase probability of detection whether it is noisy or not: previous tests with this system have shown that only interscan interval is correlated with predator detection ability (Cresswell et al. 2003, Whittingham et al. 2004). Chaffinches in the current experiment only modified interscan interval, supporting this adaptive hypothesis. If the novel response hypothesis applied, vigilance levels generally should have increased. Polar bears, for example, increased head-up frequency, scan duration and inter-scan interval when in the presence of tourist vehicles which act as a novel stimulus to which the bears have become habituated, though in this case the bears were resting and not foraging (Dyck and Baydack 2004). Apparently few other studies have explored the influence of noise on vigilance or even on other forms of anti-predation behaviour. One field study showed that neither thermal nor non-thermal aspects of the environment, the latter including wind and associated noise, had any effect on the vigilance of dark eyed juncos *Junco hyemalis* (Boysen et al. 2001). This was against expectations and was explained by the fact that the juncos lived in a non-time-limited environment. In another study, Krebs et al. (1997) invoked a novel, or stressor stimulus hypothesis, to explain changing vigilance patterns in laboratory rats during loud (95 dB) and control (65 dB) white noise (discussed further below). However, a 'no-noise' treatment was absent so it is unclear whether vigilance levels were already heightened in the 65 dB control treatment. Another study related noise levels to use of safe habitats but found that two gerbil *Gerbillus* spp did not modify the use of safe and risky habitats in the presence of white noise (Abramsky et al. 1996). The only other study we could find showed that two Australian parrot species *Psittaciformes* increased vigilance levels in noisy locations but the effect was likely confounded by human activity (Westcott and Cockburn 1988). Therefore, apart from a handful of studies, including the current one, there remains little evidence to support the hypothesis

that background noise affects vigilance specifically and anti-predation behaviour generally, despite strong theoretical grounds for predicting that any interference with a specific predator-detection process should result in compensation (Lima 1987).

Chaffinches in our study showed no sign of habituating to the noise both within and between trials, again supporting the predation risk compensation hypothesis. It is possible that insufficient time had passed for the birds to have habituated. However, results from (Krebs et al. 1996) give reasonable grounds to believe that this was not the case. They found that after an initial increase in vigilance among laboratory rats in the high white noise treatment (95 db) relative to the control noise treatment (65 db), complete habituation had occurred by the 4th trial. This initial increase in vigilance followed by habituation was taken as evidence for a novel or stressor stimulus hypothesis. Furthermore, their control noise level (60 dB) was similar to our experimental level and did not change consistently over subsequent trials, further supporting the likelihood that the 65 dB our chaffinches were exposed to was insufficiently high to invoke a stress response. It should be noted, however, that Krebs et al. (1996) used domesticated rats and also exposed them to constant noise over a four day period, whereas we use wild animals with probably much less exposure to unusual noises before capture and to the noise during their four day experimental period. Though we did not directly discount the novel response hypothesis, for example by habituating the birds to the sound before the trials, the lack of habituation and the predicted way in which vigilance changed collectively suggest that the predation risk compensation hypothesis was a more likely explanation for our results. Furthermore, there was no detectable startle or behavioural response when the noise was gradually faded in and out during trials, with birds simply continuing to forage.

### Potential fitness consequences

Observations from populations suggest that environmental noise has important fitness consequences for birds. High noise levels are associated with declines in bird populations, which is especially evident in the context of road traffic (Reijnen and Foppen 1991, Reijnen et al. 1995, 1996, 1997, Klump 1996, Wiley and Richards 1996, Forman and Alexander 1998, Forman and Deblinger 2000) although some species are not affected by road noise (Junker-Bornholdt et al. 1998) and the degree to which traffic noise constrains non-predation related intraspecific acoustic communication (e.g. bird song) possibly plays an important role in determining which species are more affected by traffic noise (Rheindt 2003). The mechanisms underlying these declines are barely understood but vigilance in the

framework of the predation-starvation trade-off could play an important role in a number of ways. Elevated noise levels could affect habitat profitability by reducing intake rate. In our experiment intake rate suffered because of the change in vigilance pattern. Whether this occurs in the wild and has a direct effect on fitness is unknown. Similarly, certain types of food or feeding methods that are incompatible with heightened vigilance may be ruled out when noisy because they are too dangerous or unprofitable (see Hilton et al. 1999, Yasué et al. 2003 for possible examples). The extent to which individuals are plastic in their vigilance response may also be important, as has been suggested for the ability to modify vocalisations in noisy environments (Slabbekoorn and Peet 2003). 'Personality' related differences between individuals have been shown to explain variation in plasticity when responding to predation risk in low and high risk situations (Quinn and Cresswell 2005). Personality could also influence the ability to adapt to noisy environments. Some individuals may be able to compensate for increased noise levels by foraging in groups, though their ability to do so may be dependent on their likelihood of incurring a cost through interference competition. The preceding arguments relate to individual differences but may equally relate to species differences, and there is evidence that species differ in their sensitivity to noise, though the underlying causes for these differences are unknown (see discussion in Brumm 2004).

Potential negative effects of elevated noise levels on fitness could be offset by negative effects on predator behaviour. Predators must also rely on auditory cues for detecting prey (Krams 2001) and, for example, the hunting success among long-eared owls *Asio otus* decreased with windspeed (Willem 2001), though in this case the relative importance of sound or the movement of vegetation in concealing prey was unclear. Even if the noise associated with wind does not affect the predator, any increased vigilance among prey could be offset by other correlated effects on predators. Redshanks *Tringa totanus*, for example, forage further from predator-concealing cover when windy (Hilton et al. 1999) even though the hunting success of sparrowhawks when attacking redshanks decreases with windspeed independently of distance from cover (Quinn and Cresswell 2004). In this case noise was probably unimportant to the hawk and instead the effect of wind was thought to be explained by differential effects on aerodynamic performance and flight stability when hunting in an open habitat. Clearly, disentangling the effects of noise from other correlated effects at the same time as predicting concurrent responses by predator and prey remains a challenging prospect.

Though the noise levels in our experiment were relatively high they were nevertheless similar to those found in many natural and unnatural systems, for

example those close to shorelines, running water, on wind swept landscapes and in urban environments (Aubin and Jouventin 1998, Cynx et al. 1998, Jouventin et al. 1999, Lengagne et al. 1999, Lengagne and Slater 2002, Slabbekoorn and Peet 2003, Brumm 2004, Brumm et al. 2004). The nature of the sound we used may be less representative of those experienced in the wild. Further experiments and field observation will test the generality of our results. As noise levels are likely to continue increasing across the landscape, the extent to which the starvation predation trade-off determines whether and how animals can adapt may become an increasingly important topic.

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