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The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather

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Numerous attempts have been made to quantify ecological factors that affect the calling range of animal signals. The various processes leading signals to become distorted and embedded in background noise have been described in many habitats (ranging from forest to savannah) and the propagation path in these biomes has thereby been characterized. However, the impact of climatic factors on acoustic communication has been little studied. Surprisingly, to our knowledge, the importance of rain, a regular phenomenon occurring in all habitats except deserts, has never been investigated. Here, we describe a 69-fold advantage in area reached by the call of a territorial bird, the tawny owl (*Strix aluco*) in dry versus rainy conditions. In support of this, we found a marked reduction in the calling of tawny owls in rainy conditions. Constraints imposed by a rainy propagation path are likely to modify the reliability of acoustic information and thus calling behaviour of many animals.

Keywords: acoustic communication; rain; active space; tawny owl

1. INTRODUCTION

Communication is an association between an emitter's and a receiver's behaviour, as a consequence of a signal, a specific pattern of energy, transmitted between them (Shannon & Weaver 1949). In many animals, long-range calls are used to establish their relationships with members of their own and other species. The maximum transmission distance of the signal (i.e. calling range) determines the active space of the signal, one of the most important features of acoustic signals for a communicating animal (Marten & Marler 1977; Brenowitz 1982*b*). This feature is strongly affected by noise as this influences both detection and discrimination by the receiver (Wiley & Richards 1982).

Noise could result from the attenuation and degradation of signals during propagation, as all environments differ markedly from ideal homogeneous and non-scattering ones. Numerous studies have revealed characteristics of propagation in different habitats: forests with different types of foliage, fields with different densities of plants and pasture consisting of tall grasses or marsh where water forms a reflective surface (Aylor 1971; Morton 1975; Marten & Marler 1977; Brenowitz 1982*a*; Cosens & Falls 1984; Waas 1988). In these different habitats, a signal can be more or less extensively modified by various processes such as frequency-dependent attenuation, boundary interference, reverberation and amplitude fluctuation. In addition to attenuation and degradation of the signal, its mixing with irrelevant stimuli (background noise) is another important source of noise which affects, in particular, the effectiveness of acoustic signals (Wiley & Richards 1982; Dabelsteen *et al.* 1993; Holland *et al.* 1998). Ambient noise is ubiquitous in the natural environment, and its intensity and nature is characteristic of the particular habitats that species occupy. It can be generated by other animals (birds, mammals, frogs, insects...) or by other environmental sources such as rain, wind, flowing water and the breaking of waves. The intensity and nature of ambient noise are major determinants of the process of information discrimination, and many studies have dealt with the process whereby the listener's peripheral analysers extract the information contained in the signal from that noise (e.g. Brémond 1978; Brenowitz 1982*b*; Gerhardt & Klump 1988). However, the impact of climatic events on acoustic communication has been little studied (Larom *et al.* 1997). The importance of wind during propagation through the transmission channel has been suggested by Henwood & Fabrick (1979) and Brenowitz (1982*b*) while Lengagne *et al.* (1999*a*) demonstrated how wind makes call discrimination more difficult in penguins. Surprisingly, to our knowledge, the importance of rain on acoustic communication has never been studied. Rain is a regular phenomenon occurring in all habitats except deserts and is a major component of many climates. Thus, many animal species throughout the world are, potentially at least, affected by it.

This study deals with the relationship between heavy rain and acoustic communication. Calling is one of the principal mechanisms of communication for nocturnal birds such as the tawny owl (*Strix aluco*), for which the territorial call, or 'hoot', allows birds to maintain ownership on territories ranging from 15 to 22 ha (Appleby & Redpath 1996; Galeotti *et al.* 1996). By determining the calling range and the active space of the call in dry and rainy weather, it was possible to estimate the importance of rain on the acoustic communication process. We also determined whether the impact of the rain on acoustic information transmission affected the calling behaviour of the emitter.

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2. MATERIAL AND METHODS

(a) *Experimental procedures to measure calling range*

Determination of active space in rainy and dry conditions involves considering several parameters: call amplitude, background noise level, signal discrimination threshold and signal attenuation during propagation.

(i) *Electroacoustic and sound analysis material*

Forest ambient noise level and territorial call amplitude were measured using a Bruël & Kjaer sound-level meter type 2235 (linear scale, slow setting).

Male hoots and background noise were recorded using a Beyer dynamic M300 TG microphone (frequency range of 100–10 000 Hz ± 2 dB) mounted on a pole and connected to a Tascam DAT recorder (sampling frequency of 44.6 kHz, frequency response flat within the range of 20–20 000 Hz ± 1 dB).

To measure call attenuation during propagation, male hoots were broadcast from a Sony TCD5M tape recorder connected to an autonomous EAA amplifier loudspeaker (frequency range of 100 Hz to 8 kHz ± 2 dB). Propagated signals were recorded with a Tascam DAT recorder connected to a Beyer dynamic M300 TG microphone. Recorded tapes were digitized with a 16-bit Oros Au21 acquisition card equipped with an anti-aliasing filter (-120 dB octave^{-1}) at a sampling rate of 20 kHz.

(ii) *Meteorological conditions*

Investigations were conducted in two meteorological conditions. The dry condition consisted of a cloudy night without rain or wind, with a temperature of 7–9 °C measured at 1 m and 5 m above ground level. The rainy condition consisted of a night with heavy prolonged rain (23 mm of water in 12 h) without wind (except vertical displacement of air due to the rain), with a temperature of 8–12 °C.

(iii) *Amplitude of the territorial call*

The amplitude at which a territorial call was emitted was measured from 39 calls emitted by three birds. Measurements of sound pressure level were conducted at distances of 1–1.5 m from the bird in the aviary of the Wildlife Care Centre of Tonneins (Lot et Garonne, France) and expressed as mean and standard error of the mean.

(iv) *Ambient noise measurements*

In January and February, we measured the mean level of the forest ambient noise in dry and rainy conditions, at least 2 km from the nearest road in the forest of La Croix aux Bois (Ardennes, France). This is a large deciduous forest of mixed oak and beech with a canopy *ca*. 8–10 m above the ground. The sound-level meter was mounted on a pole at 1.8 m above the ground. In order to avoid drops falling on the microphone and sudden offset measurements, a sheet of muslin was placed 1.3 m above the recording equipment. To allow comparisons, the same procedure was followed for measurements conducted in dry conditions. To evaluate the intensity of the ambient noise levels, 20 instantaneous measurements were achieved in each of the two meteorological conditions and compared with a Mann–Whitney *U*-test. During winter nights, the background noise was very homogeneous, as most of the birds, mammals, anurans and insects remain silent at this time of year. Moreover, experiments were carried out at night when only nocturnal raptors are calling (mainly tawny owls in the French forest). Finally, we chose a place in a large forest, far away from human activities. To evaluate noise intensity in the perceptually relevant bands used by tawny owls (560–1080 Hz), a 1 min recording was made at 15 min intervals for 1 h. For each of the four recordings, five fast Fourier transforms (window size of 4096 points, $\Delta f =$ 4.9 Hz) were then calculated and intensity values were compared with a Mann–Whitney *U*-test.

(v) *Tests of sensory discrimination thresholds*

The discrimination threshold of the territorial call was estimated in rainy and dry conditions with six tawny owls kept in separate aviaries spread out over the 6 ha of the Wildlife Care Centre of Tonneins. When it hears a strange conspecific call, a tawny owl displays agonistic behaviour, usually in the form of a vocal response. Usually, the vocal activity of the test bird was more intense than that of the other captive tawny owls nearby, but in one case (out of 48), interactions between birds occurred and the test was repeated. The test sequence had nine hoots recorded on it, played at a natural rate over a period of 2.5 min. Birds were tested over two days in a random sequence with eight different values of signal-to-noise (S/N) ratio, a measure of the extent to which signal amplitude exceeds that of the background noise. We cannot control the natural background noise level in the aviary, fluctuating from 36 to 45 dB in dry conditions (58–62 dB in rainy conditions). Thus, to obtain a precise S/N ratio we used a computer to adjust the amplitude value of the test sequence to immediate background noise level (Brenowitz 1982*b*). For instance, to know if owls discriminated a call with an amplitude value 3 dB below the noise level (S/N = -3 dB), the test sequence played to birds had an amplitude value of 47 dB when the sound-level meter in the aviary showed a background noise level of 50 dB. For each S/N level, the proportion of positive responses (scored as any vocal response obtained during the 4 min following the last call on the test tape) and its 95% confidence limits were computed (function Binofit, MATLAB).

(vi) *Attenuation of the territorial call during propagation*

A propagation test was conducted in the forest of La Croix aux Bois during the period when the trees had no leaves, to measure amplitude attenuation of the call during propagation. The calculation took into account the absolute amplitude of the propagated call, but did not include the study of attenuation in rainy conditions because the amplitude values corresponding to the noise generated by rain could not be dissociated from the amplitude decrease of the propagated signal itself. The test tape consisted of typical territorial calls of tawny owls repeated 10 times at intervals of 15 s. The loudspeaker was suspended from a side branch of an oak, facing away from the trunk, 5 m above the ground. The sound recorded 1 m from the speaker was taken as the reference signal. The test tape was broadcast and the sound re-recorded at 16, 40, 130 and 200 m ranges. Call attenuation was assessed using the method described by Aubin & Jouventin (1998). Briefly, we compared the amplitude values (measured on signal envelope) of the propagated signals to the corresponding amplitude values of the reference signal. Thus, we obtained attenuation, in decibels, of the call for four distances of propagation: 15 m (16 − 1 m), 39 m (40 − 1 m), 129 m (130 − 1 m) and 199 m (200 − 1 m).

(b) *Calling behaviour of the tawny owl*

Observations were performed at the end of January during the period of greatest calling activity in the forest of La Croix aux Bois. The vocal activity (number of calls emitted in 10 min) of

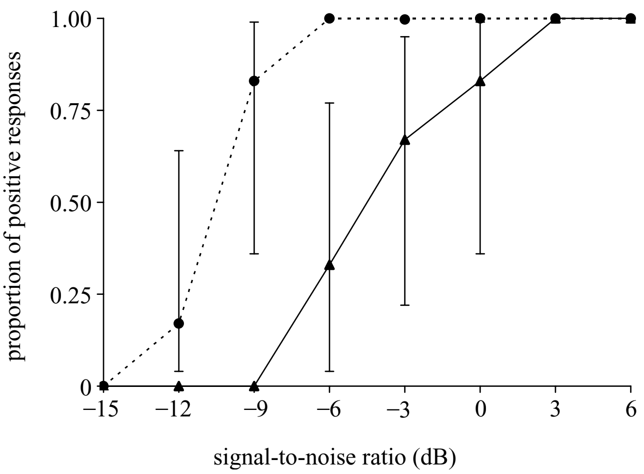

Figure 1. Discrimination by tawny owls of territorial calls masked by background noise generated by rain. Experimental calls with eight different values of S/N ratio were broadcast to six tawny owls. The figure shows the proportion of positive responses with 95% confidence intervals. Triangles represent rainy conditions, circles represent dry conditions.

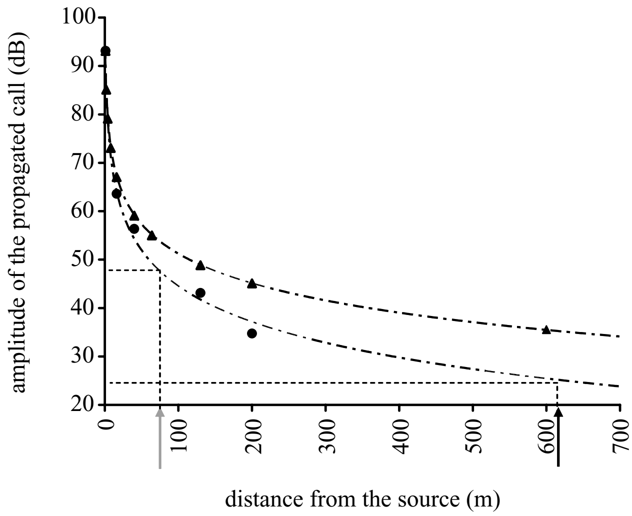

Figure 2. Attenuation of broadcast calls and the maximum distance at which they would be discriminated in dry and rainy conditions. Observed attenuation (circles; $n = 10$ for each distance) and the theoretical prediction (triangles) from the inverse square rule are shown. In rainy conditions, with 50.8 dB of background noise and a S/N ratio discrimination threshold of −3 dB, signal amplitude must be 47.8 dB to be discriminated by the birds. The grey arrow indicates the maximum discrimination distance under these conditions. The black arrow indicates the discrimination distance in dry conditions (with signal amplitude of 25.2 dB). The dashed and dotted lines represent the logarithmic curves.

a wild population of 22 pairs were studied during the first part of the night, on two dry and calm nights and two rainy nights. An ANOVA was carried out over squared values of vocal activity under a complete $2 \times 2 \times 6$ factorial design, i.e. dry or rainy conditions, day 1 or 2, and 6 h time-periods.

3. RESULTS

(a) *Amplitude of the territorial call*

The maximum sound pressure level of the 36 hoots recorded at 1 m was 93.1 ± 0.2 dB (range of 90.8–94.6 dB).

(b) *Ambient noise measurements*

The mean ambient noise level measured in the course of one hour in the dry condition was 33.4 ± 0.3 dB (range of 31.9–5.5 dB) whereas the level was 52.2 ± 0.4 dB in the rainy condition (range of 49.8–5.2 dB). The difference of 18.8 dB between the two meteorological situations was statistically different ($Z = 3.408$; $p < 0.001$).

At least 80% of the total energy of the call of the tawny owl is in the frequency band 560–1080 Hz. At this frequency, the background noise is 34.2 ± 0.3 dB in the dry condition and 50.8 ± 0.3 dB in rainy conditions ($Z = 6.451$; $p < 0.001$) (the difference of 16.4 dB is close to the difference of 18.8 dB found previously).

(c) *Sensory discrimination thresholds*

To estimate the discrimination threshold of the territorial call, experimental calls with different S/N ratios were broadcast to six tawny owls. The proportion of positive responses and their 95% confidence intervals shown in figure 1 allow testing for statistical differences between the two meteorological conditions studied. In the dry condition, five or six birds were able to discriminate the conspecific call with a S/N ratio of −9 dB. The recognition process still occurs at an emergence level well below the level of the noise. In rainy conditions, such a high frequency of discrimination (five or six birds) is obtained for an emergence level of 0 dB. In rainy and dry situations, there are no statistical differences in the discrimination process for a S/N ratio of 3, 6, and –15 dB (i.e. the confidence intervals overlap). The median values of the threshold on dry and rainy days were –9 and –3 dB, respectively.

(d) *Attenuation of the call during propagation*

Because of the spherical spread of sound energy radiating from a source in a homogeneous non-scattering medium, there is a theoretical attenuation of 6 dB for each doubling of the distance between source and receiver. All our propagation tests conducted in forest in dry conditions resulted in excess attenuation (attenuation above the theoretical prediction). Knowing the attenuation values and considering that the call was emitted at 93.1 dB, the theoretical and observed call intensity values after propagation can be calculated (figure 2). In forest, amplitude values of the call for a given propagation distance x could be obtained using the following formula: amplitude (dB) $= -10.475\ln(x) + 93.02$.

(e) *Calling range of the call*

Knowing the amplitude of the call at source, the background noise levels, the acuity of the receiver and signal attenuation during propagation allows the discrimination distance and the audible broadcast area to be determined for the two meteorological conditions. In dry conditions, with a background noise of 34.2 dB in the frequency band used by owls and with the median S/N ratio discrimination threshold of –9 dB, the territorial call will be discriminated until as low as 25.2 dB in amplitude. Using our formula for call attenuation in forest, a value down to 25.2 dB was reached beyond 614 m of propagation (figure 2). The same method applied to data for rainy conditions (50.8 dB of background noise and a discrimination threshold of –3 dB) gave a discrimination range for the call of 74 m. There is thus an approximately eightfold advantage in discrimination distance (614 versus 74 m) and a 69-fold advantage in audible broadcast area (118.4 versus 1.7 ha) to the individual calling in dry conditions over that in rainy ones.

(f) *Behaviour of the tawny owl*

The vocal activity of tawny owls was recorded during dry and rainy nights. ANOVA revealed a statistical effect of hour of observation on the vocal activity of the birds ($F = 5.2$; $p < 0.001$), but there is no interaction between hour and meteorological condition ($F = 1.9$; $p = 0.166$). The day of observation had no statistical influence on vocal activity ($F = 1.4$; $p = 0.246$) and there was no interaction between day of observation and meteorological condition ($F = 0.03$; $p = 0.873$). The observations point to a strong effect of the weather on the vocal activity of the tawny owl ($F = 118.8$; $p < 0.001$). Even during the courtship period, birds stop calling during nights with heavy rain. Of 22 wild pairs studied, 82% and 86% of birds called on two dry and calm nights, but only 14% and 5% called on two rainy ones.

4. DISCUSSION

(a) *Estimation of active space*

Efficiency in both mate attraction and territorial defence depend on how well the information is transmitted through the environment and discriminated by the receiver. Several attempts have been made to quantify the factors that affect the calling range of animals, primarily mammals and birds (Marten & Marler 1977; Waser & Waser 1977; Wiley & Richards 1978; Brenowitz 1982*b*; Brown 1989; Larom *et al.* 1997; Lengagne *et al.* 1999*b*). Early studies, avoiding song masking by background noise or using only physical sources of sound attenuation, have led to interesting estimations of broadcast areas (Marten & Marler 1977; Henwood & Fabrick 1979). Brenowitz (1982*b*) and Larom *et al.* (1997) presented quantitative estimates of active space for acoustic signals after assessment of call amplitude, background noise level, call attenuation and the discrimination threshold.

(b) *Efficiency of calling activity and weather conditions*

In dry and calm conditions in forest, the signal amplitude reached a level equal to the sensory discrimination threshold (25.2 dB) after propagation over 614 m (active space of 118 ha). In deciduous forest, average tawny owl territory sizes in Cambridgeshire, UK, are estimated to be 15 ha (Appleby & Redpath 1996). Thus, according to Brenowitz's prediction, information contained in the call will propagate efficiently across the emitter's own territory and remain effective across a large part of the adjoining territories. In rainy conditions, the signal amplitude reached a level equal to the sensory discrimination threshold beyond 74 m and consequently the audible broadcast area fell to 1.7 ha (12% of the emitter's own territory). There is a 69-fold advantage in audible broadcast area to the individual calling in dry conditions over that in rainy ones. In support of this, we found a marked change in the calling of tawny owls with the meteorological conditions. Even during the courtship period, birds stop calling during nights with heavy rain.

(c) *Maintenance of a given active space: predictions of the mathematical theory of information*

According to the mathematical theory of communication (Shannon & Weaver 1949), the amount of information V contained in a signal can be defined by $V = FT\gamma$ (where F represents frequency in Hz, T represents signal duration in s and $\gamma = \log_2 (1 + S/N)$). The channel of transmission can reduce the total amount of information that can be transmitted by its effects on one or several acoustic parameters. In a rainy environment, we observed a strong decrease of the S/N ratio and hence a reduced amount of information conveyed in the acoustic signal. To counteract this limitation, the theory suggests several possible ways in which an emitter could improve the efficiency of information transfer. Emitters could increase signal duration and so enhance the redundancy of the information. This phenomenon has been demonstrated in both underwater and terrestrial communication systems: both humpback whales (*Megaptera novaeangliae*) and king penguins (*Aptenodytes patagonicus*) adapt the temporal structure of their signals to such environmental constraints (Lengagne *et al.* 1999*a*; Miller *et al.* 2000). Although never described in any acoustic communication system, emitters could also modify the spectral composition of their acoustic signals to differ from that of the background noise and so keep the amount of information constant. A third, most obvious, possible solution is simply to broadcast signals at a high enough amplitude to overcome ambient noise. Studies on different mammal, bird and frog species suggest that amplitude regulation constitutes a widespread form of plasticity in vocal performance (Sinnot *et al.* 1975; Lopez *et al.* 1988; Manabe *et al.* 1998), but this solution is obviously only possible within physiological limits. To maintain the same active space in rainy conditions as in dry, tawny owls' calls would have to be emitted at 115.5 dB, an amplitude close to that of an aircraft taking off.

Rain is likely to constrain acoustic communication in many animals and habitats. There is a broad overlap between the spectrum of the noise generated by rain (frequency band of 0–5 kHz; mean amplitude of 55.8 dB, $n = 20$ measures) and the spectrum of acoustic signals used by birds: using published sonograms (Bergmann & Helb 1982), we found this overlap in 80% of 65 bird families and 94% of 412 European bird species. The same constraint will apply to many amphibian and mammal species that use low frequency sounds to communicate.

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