biology
letters
Animal behaviour

Biol. Lett. (2012) **8**, 913–916
doi:10.1098/rsbl.2012.0676
Published online 12 September 2012

On the evolution of noise-dependent vocal plasticity in birds

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Signal plasticity is considered an important step in the evolution of animal communication. In acoustic communication, signal transmission is often constrained by background noise. One adaptation to evade acoustic signal masking is the Lombard effect, in which an animal increases its vocal amplitude in response to an increase in background noise. This form of signal plasticity has been found in mammals, including humans, and some birds, but not frogs. However, the evolution of the Lombard effect is still unclear. Here we demonstrate for the first time the Lombard effect in a phylogentically basal bird species, the tinamou *Eudromia elegans*. By doing so, we take a step towards reconstructing the evolutionary history of noise-dependent vocal plasticity in birds. Similar to humans, the tinamous also raised their vocal pitch in noise, irrespective of any release from signal masking. The occurrence of the Lombard effect in a basal bird group suggests that this form of vocal plasticity was present in the common ancestor of all living birds and thus evolved at least as early as 119 Ma.

Keywords: acoustic communication; Lombard effect; phenotypic plasticity; noise; signal masking

1. INTRODUCTION

Noise is a major constraint on any form of communication. In particular, animals that use sound to communicate must deal with various biotic and abiotic noises in their habitats. Solutions to the problem of acoustic signal masking involve special adaptations in the receiver as well as in the sender [1–3]. On the sender's side, one mechanism to increase the signal-to-noise ratio in a noisy environment is the Lombard effect, an involuntary vocal phenomenon in which a calling animal increases its vocal amplitude in response to an increase in background noise [4]. This noise-dependent vocal plasticity requires a neural feedback loop between vocal production and perception [5], two systems that are often viewed in isolation. The Lombard effect is well known in human speech and it has also been reported in several other mammalian species, as well as some phylogentically derived bird groups, but is absent in frogs [4].

Signal plasticity is considered an important step in the evolution of animal communication systems [6]. Thus, elucidating the phylogenetic origins of vocal flexibility is important for understanding the diversification and versatility of animal signals in general [7]. However, our understanding of the evolution of the Lombard effect in birds is still incomplete, as only members of the more derived neognath lineage have been studied. Therefore, it is ambiguous whether the Lombard effect is a derived trait of the Neognathae or a shared trait of all birds. Here we investigated for the first time vocal plasticity in one of the most 'ancient' living groups of birds, tinamous, members of the Palaeognathae [8]. Specifically, we tested (i) whether the elegant crested tinamou, *Eudromia elegans* (figure 1*a*), exhibits the Lombard effect and (ii) whether a noise-dependent amplitude adjustment affects call frequency, as demonstrated in humans [4] and suggested for neognath birds [9,10].

2. MATERIAL AND METHODS

(a) *Experimental set-up*

Very little is known about the repertoire and function of elegant crested tinamou calls [11]. We monitored our captive group of three females (F1, F2 and F3) and two males (M1 and M2) for six months in a housing room (4.3 × 3.5 m and 2.2 m high, 12 L : 12 h cycle with a 10 min artificial dawn and dusk) during which time all their vocalizations were automatically recorded. For the Lombard experiments, we tested each of the tinamous singly in an aviary (1 × 1 m and 2 m high) in a sound-shielded room monitored by five video cameras. Digital sound recordings (44.1 kHz sample rate, 16-bit accuracy) were made with an omnidirectional microphone (Sennheiser ME62) suspended 1.6 m above the centre of the cage floor to a computer through an external sound card (Edirol UA-101). White noise in the frequency band from 0.01 to 10 kHz was played from a computer through an amplifier (Dynavox CS-PA1) to two loudspeakers (JBL pro III) (see the electronic supplementary material, figure S1). The speakers were mounted opposite each other at the approximate height of a tinamou's head (30 cm), 1.3 m from the centre of the cage. We broadcast the noise at two levels, varying their order systematically between birds. The playback amplitude was set at 45 dB(A) sound pressure level (SPL) for the low-noise condition and at 65 dB(A) for the high-noise condition (measured at the position of the birds' heads at the centre of the cage). Depending on the bird's exact position the received noise level varied by up to 5 dB. To elicit calling, we played a male tinamou call at 75 dB(A) at the beginning of each session using a digital playback device (Foxpro Scorpion X1-A). The noise amplitude was changed when the tested bird had called at least 12 times.

(b) *Acoustic analyses and statistics*

The sound analyses were carried out using the software Avisoft-SASLab Pro (v. 5.1.17) (see the electronic supplementary material). Briefly, for each call, the maximum SPL was measured (integration time 50 ms) and then the background noise value was subtracted [4]. Peak frequencies were measured in power spectra with a resolution of 0.7 Hz. Individual differences in call amplitude and frequency between the noise conditions were tested with two-sided Mann–Whitney *U*-tests. All statistically significant differences retained significance at $p < 0.01$ after Bonferroni–Holm correction. The relationship between amplitude and frequency across birds was investigated with a general linear mixed model. Sex was included in the model as a fixed factor, and individual as a random effect. We used a Wald-χ^2 test to investigate the link between call amplitude and frequency.

3. RESULTS

We identified at least 12 different call types in our recordings (see the electronic supplementary material, figure S3). One of the most common vocalizations were hoo-weet and chee-weet calls (figure 1*b*,*c*), which were also the only calls that were repeatedly elicited by our playback. Females responded to the playbacks with hoo-weets, whereas males responded with chee-weets, which were considerably higher in amplitude

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2012.0676 or via http://rsbl.royalsocietypublishing.org.

Received 19 July 2012
Accepted 17 August 2012

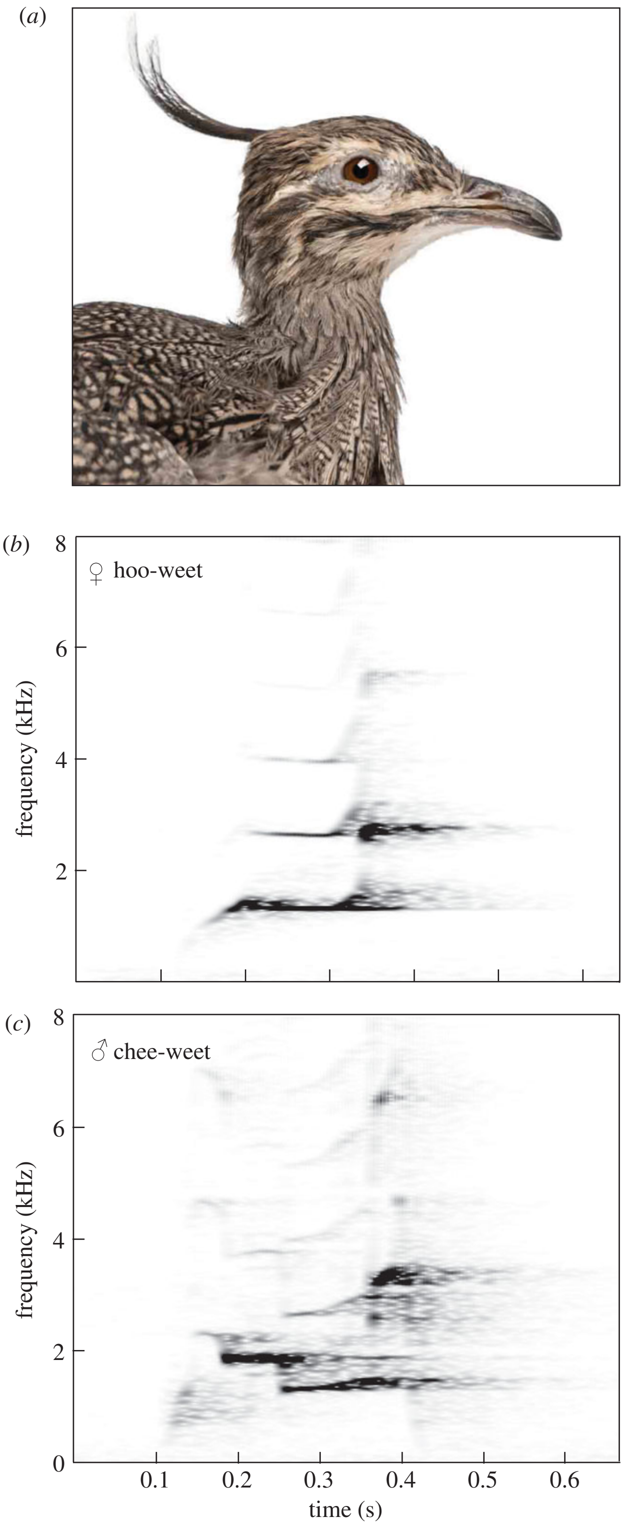

Figure 1. (*a*) Elegant crested tinamou (photo by Eric Isselée/Shutterstock.com). (*b*) Female *hoo-weet* and (*c*) male *chee-weet* call (see the electronic supplementary material, Audio S11, S12).

than the female calls (figure 2). All females increased the amplitude of their hoo-weet calls in response to the increase in the noise (Mann–Whitney U-tests: F1: $U = 46$, $n_1 = 12$, $n_2 = 77$, $p < 0.001$; F2: $U = 0$, $n_1 = 17$, $n_2 = 42$, $p < 0.001$; F3: $U = 43$, $n_1 = 21$, $n_2 = 17$, $p < 0.001$; figure 2*a*). The increase in amplitude was associated with a rise in peak frequency (F1: $U = 72.5$, $n_1 = 12$, $n_2 = 77$, $p < 0.001$; F2: $U = 87$, $n_1 = 17$, $n_2 = 42$, $p < 0.001$; F3: $U = 65.5$, $n_1 = 21$, $n_2 = 17$, $p = 0.001$; figure 2*a*). On average, call amplitudes increased by 14 ± 8 dB (mean ± s.d.) in noise, and frequencies rose by 161 ± 92 Hz. In contrast, the males neither changed the amplitude of their chee-weet calls with increased background noise (M1: $U = 371$, $n_1 = 25$, $n_2 = 32$, $p = 0.641$; M2: $U = 230$, $n_1 = 21$, $n_2 = 27$, $p = 0.266$; figure 2*b*) nor their call frequency (M1: $U = 399$, $n_1 = 25$, $n_2 = 32$, $p = 0.987$; M2: $U = 267.0$, $n_1 = 21$, $n_2 = 27$, $p = 0.732$; figure 2*b*). However, we found a strong link between call amplitude and peak frequency across all males and females, irrespective of the level of background noise (Wald test: $\chi^2_1 = 315.53$, $p < 0.001$).

4. DISCUSSION

We present the first evidence for the Lombard effect in a palaeognath bird. Moreover, we also found that tinamous use a large repertoire of call types that vary in structure and usage. As such, our results demonstrate that a basal bird exhibits a degree of vocal complexity and plasticity that had only been described in mammals and more derived birds. Interestingly, only the female tinamous increased their call amplitude in response to increased in background noise. The absence of a similar response in the tested males may be due to the considerably higher call amplitude of males. Males may have called closer to their physical upper limit and may therefore have had no capacity to increase their call amplitude, at least for the chee-weet call. A sex difference in the Lombard effect was also reported in a songbird, the Bengalese finch *Lonchura striata* [12]. Although both male and female finches exhibited the Lombard effect, the effect was weaker in females, probably because, like male tinamous, they called at higher amplitudes.

Our study also demonstrated a coupling of vocal amplitude and pitch in tinamou calls, which has previously been suggested for vocalizations of more derived birds (reviewed in [13]). Most probably this association is the result of a physical coupling during vocal production [14]. This biophysical link may have led to a frequency increase when the tinamous raised their call amplitude in elevated noise. It is important to note that the increase in call pitch did not yield an increase in the signal-to-noise ratio, as the vocalizations were masked by the broad spectrum background noise. Thus, we conclude that the noise-dependent increase in peak frequency in the tested birds is a passive response that occurs irrespective of any release from signal masking. This finding in a bird resembles the Lombard effect in humans, as speakers also involuntarily raise their vocal pitch in noise even when it would not improve signal detection [15]. Birds exposed to intense anthropogenic noise often vocalize at higher frequencies, which has been interpreted as an adaptation to mitigate masking from low frequency noise [16,17]. This frequency shift can be achieved either by using different call types [18] or by modifying the same call [17,19] similar to the Lombard effect. Higher song frequencies can be beneficial in terms of receiver responses in noise [20–22], but whether the increases in pitch are indeed the outcome of selection processes is debated

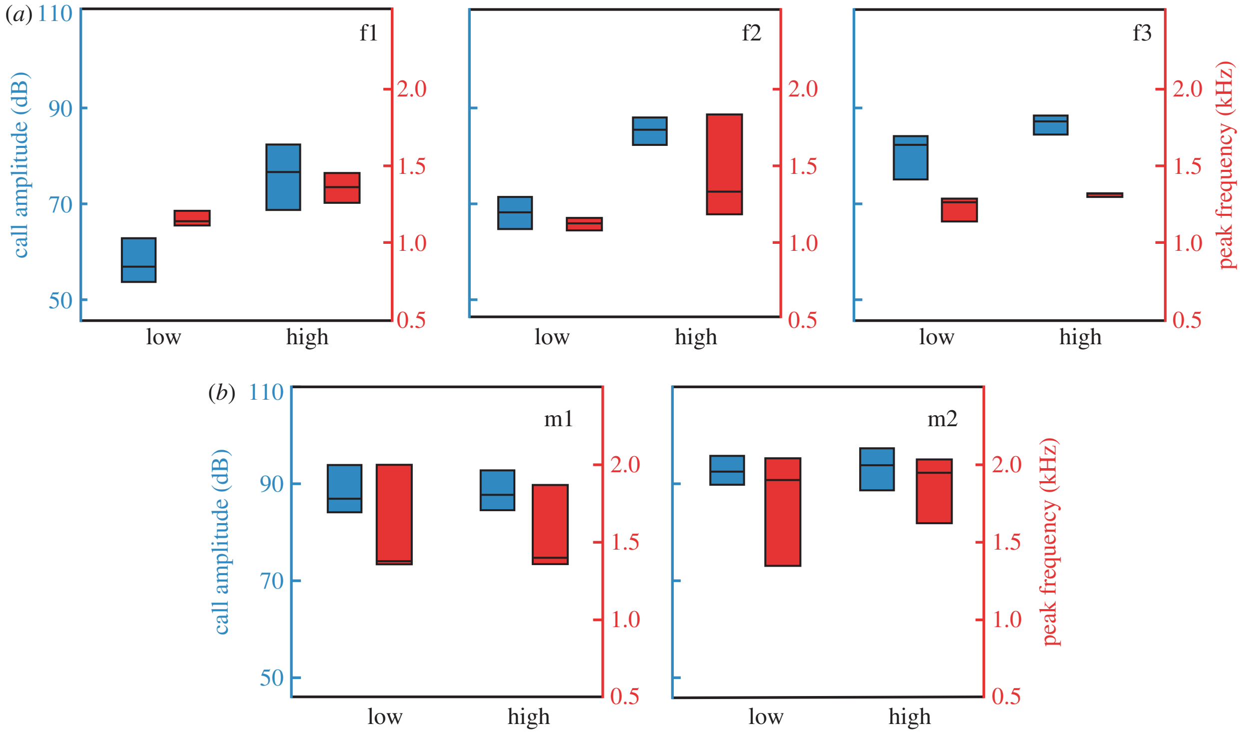

Figure 2. Noise-dependent changes in call amplitude and peak frequency. Medians and interquartile ranges are given for (*a*) females and (*b*) males. Low: 45 dB(A) noise, high: 65 dB(A) noise (re. 20 μPa).

[13,23]. Our data show that a noise-related increase in vocal frequency can occur irrespective of any release from signal masking, supporting the notion that the observed changes in urban bird vocalizations may be a by-product of the Lombard effect that creates a fortuitous masking release in low-frequency noise [24].

Our findings suggest that the Lombard effect may be a shared trait of extant birds, and may therefore have evolved more than 119 Ma [25]. Presuming it is also an ancestral trait in mammals, one can put forward at least two alternative phylogenetic hypotheses: (i) the Lombard effect evolved independently in the most recent common ancestor to mammals and again in ancestral birds or (ii) it is a trait shared through common descent. If the latter is true, then the common ancestor of birds and mammals, i.e. an early amniote, must have exhibited the Lombard effect. The neuronal circuits essential for the Lombard effect in mammals are located in the brainstem [5], the phylogenetically oldest part of the vertebrate brain. Moreover, given that many amphibians vocalize but do not seem to show a Lombard response [26], it is conceivable that this form of vocal plasticity might have evolved in an early amniote. To test these two hypotheses, the closest living relative of birds, the crocodilians and other members of the Sauropsidae need to be studied.

We thank Wolfgang Kunz for bird care, and Niels Rattenborg and two anonymous reviewers for comments. Financial support was provided by the Max Planck Society and the DFG (award BR 2309/6-1).

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Electronic Supplementary Material

On the evolution of noise-dependent vocal plasticity in birds

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A-weighted noise levels were measured with a precision sound level meter (CEL-500 Sound Analyzer) using an integration time of 125 ms. Due to the frequency response of the amplifier and the loudspeakers (and to a lesser degree to the acoustic properties of the test room), the received noise at the position of the bird slightly deviated from a completely flat frequency spectrum (figure S1). However, within the range of the examined tinamou calls (1-3 kHz), the noise spectrum varied less than 2.1 dB (minimum call frequency 1.01±0.12 kHz (mean±SD), maximum call frequency: 2.89±0.81 kHz, measured 20 dB below the peak).

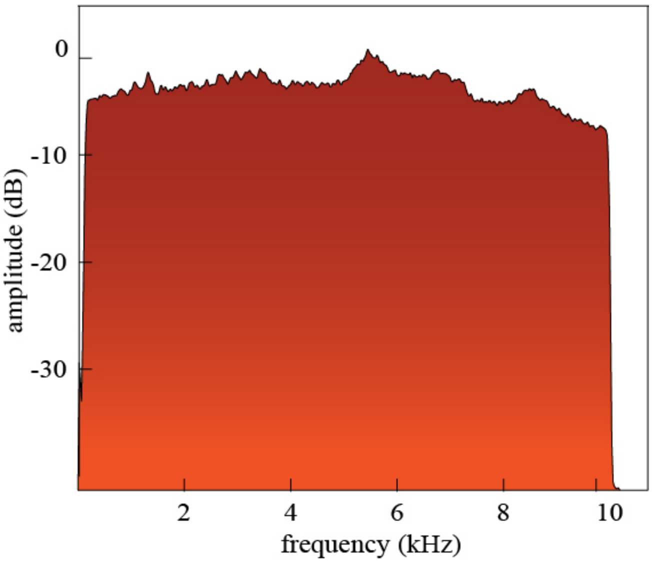

Figure S1: Power spectrum of the experimental noise after amplification and playback through the loudspeaker. The averaged spectrum was created in Igor Pro 5.0 (Wavemetrics Inc., Portland, OR, USA) from a 15-s long segment of noise, using a 1024-point FFT with a Hamming window and a 95% frame overlap.

To calibrate the sound pressure level (SPL) measurements of the tinamou calls, we selected a 2-s high-amplitude noise from each recording session and the SPL of the noise was set to the value measured with the SPL meter at the position of the microphone. To account for variation in distance between the bird and the microphone and for differences in the birds' orientation two corrections were made [1]. (1) The distance between the bird and the microphone was measured in the video recordings, and in cases where the bird was not exactly below the microphone, a correction according to the inverse square law of sound spreading was made. These corrections were less than 1.2 dB. (2) We measured the sound radiation pattern around a birds head and corrected the measured SPL values accordingly. These corrections were less than 4 dB.

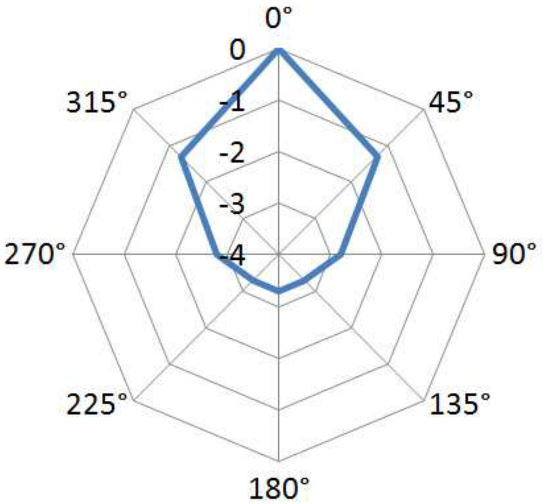

Figure S2: Sound radiation pattern of tinamou hoo-weet calls in the horizontal plane around the bird’s head. Average sound pressure levels are given relative to the sound pressure level at frontal incidence (azimuth angle 0°). Simultaneous measurements with four microphones, where one of them happened to be within the frontal ± 20° azimuth angle are displayed. N denotes the number of analysed call.

The sound radiation pattern was measured with an array of seven microphones, each of which was positioned at 1m distance from the head of the test bird (c.f. [2]). Four microphones were placed in the horizontal plane at the height of the bird’s beak at 0°, 90°, 135° and 180° (figure S2). The other three microphones were positioned at 45°, 90°, and 135°on the surface of an imaginary sphere above the horizontal plane around the bird’s head. The microphones were fed into a pre-amplifier (SM Pro Audio PR8E) and then through an external multi-channel soundcard (Edirol UA-101) to a PC that simultaneously recorded the seven channels with a sampling rate of 44.1 kHz and 16 bit accuracy. The call amplitudes in each recording channel were measured in hoo-weet calls that were produced in different directions in the horizontal plane. To calibrate the array, we first recorded a sine tone (f = 1 kHz) with a constant amplitude and measured the amplitude of the tone with the precision sound level meter at the position of each of the seven recording microphones. The values taken at each position were then used to calibrate the seven respective recording channels prior to the analysis of the tinamou calls.

Elegant crested tinamou (*Eudromia elegans*) calls

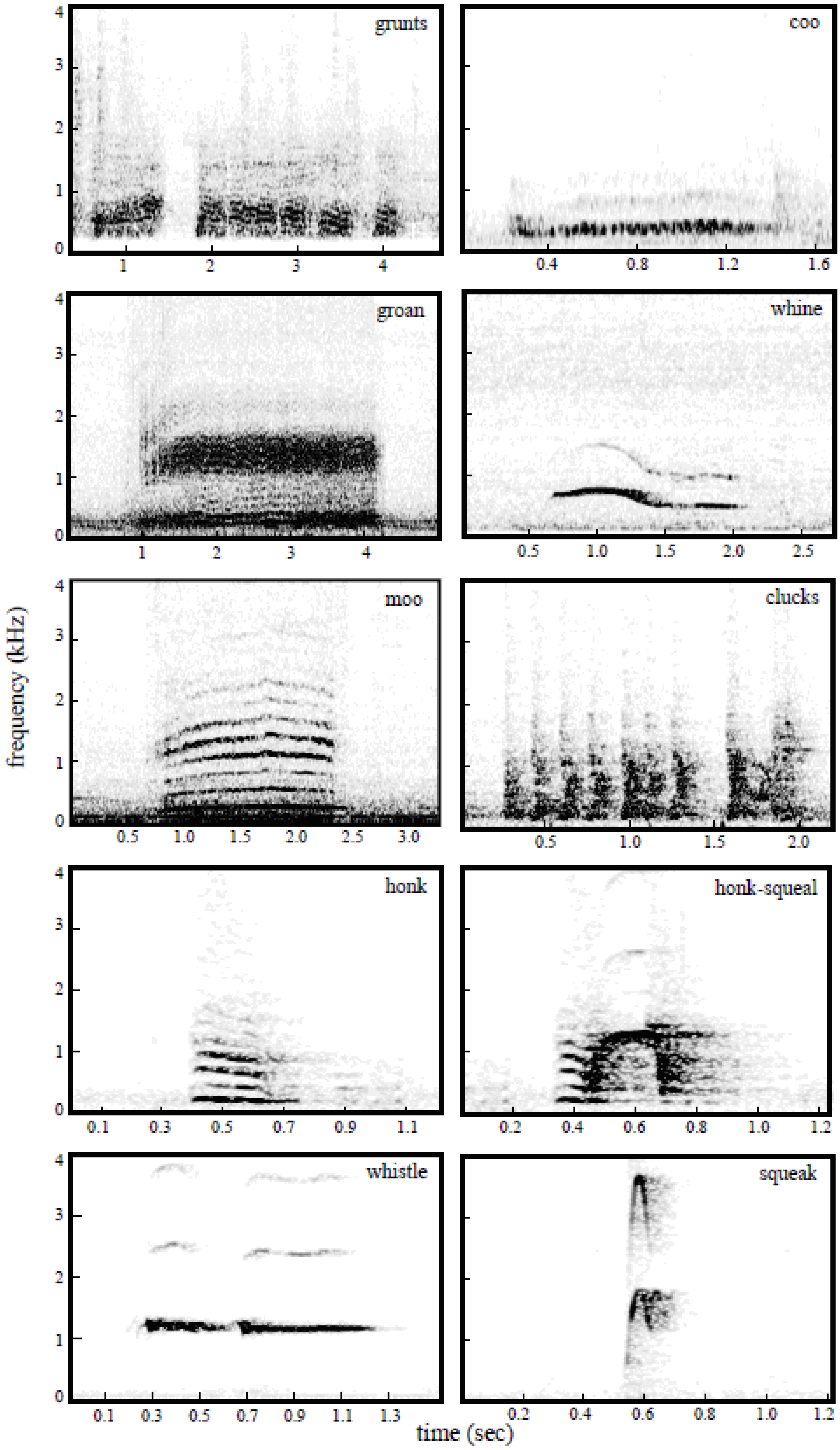

Figure S3: Typical examples of elegant crested tinamou call types (ordered by increasing average call amplitude, with softest calls at the top and loudest at the bottom).

Grunts (supplementary Audio S1): A very rare call type only observed in females after egg laying (the same day of egg laying or the next day). Grunts were very low amplitude and uttered in bouts of up to 30 s.

Coo (supplementary Audio S2): A soft (low amplitude) vocalization that was always produced in bouts of several calls and accompanied by a flaring of the crest. Outside the time when females were laying eggs, male and female coo bouts were only a few seconds long. During the egg-laying period, however, females, but not males, produced very long continuous coo bouts, sometimes lasting for several hours.

Groan (supplementary Audio S3), ***whine*** (supplementary Audio S4), and ***moo*** vocalizations (supplementary Audio S5) were among the calls of longest duration and all were produced in situations of increased vigilance, e.g. in response to disturbance or by single individuals that were isolated from the group.

Clucks (supplementary Audio S6): A low to intermediate amplitude call type that was produced by both sexes. Clucks only occurred during agonistic interactions and were produced by dominant animals while displacing or chasing another bird. Clucking was always accompanied by a full erection of the crest.

Honk (supplementary Audio S7): Produced by both sexes, most often in series together with honk-squeals.

Honk-squeal (supplementary Audio S8): One of the most common call types, regularly produced by both sexes. Honk-squeals were common and could be produced during agonistic interactions. They were accompanied by a peculiar head-bobbing posture, in which the erect neck is quickly drawn to the chest and then raised again.

Whistle (supplementary Audio S9): This call was only observed in males, mostly during the hour before the lights turned on in the holding room. When whistling before “dawn”, the calling male was sitting in his roost bowl on the ground where it had spent the night (elegant crested tinamous are ground-roosting birds and each individual usually digs a roost bowl every night [3]). In response to playback of whistles, males produced many different call types, including chee-weets, squeaks, honk-squeals, and whistles, whereas in females whistle playbacks elicited no calling.

Squeak (supplementary Audio S10): Produced by both sexes, but males squeaked more often and at higher amplitudes than females. In males, but not females, squeaks could be elicited by a playback of whistles and honk-squeals.

For ***hoo-weet*** and ***chee-weet*** calls see figure 1 (supplementary Audio S11, S12). Like the male whistle call, the female hoo-weet was often produced before dawn from the roosting bowl. Females occasionally produced hoo-weet calls in the middle of the night. During the light phase of the photoperiod, females often responded to male chee-weets with hoo-weets. Chee-weets were uttered very often during months preceding egg laying, but males ceased producing this call type after females started laying eggs. As in squeaks, the sound pressure level of chee-weets varied considerably, whereas hoo-weets were always produced at high amplitudes. Both hoo-weets and chee-weets could be elicited by the playback of chee-weet calls.

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