# Notes and Comments

## Communication of Male Quality in Owl Hoots[*]

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abstract: The evolution of communication through intrasexual selection is expected to lead signalers to transmit honest information on their fighting ability. Here we studied the information encoded in the acoustic structure of the territorial calls of a nocturnal raptor. During territorial contests, male scops owls give hoots composed of a downward frequency shift followed by a stable plateau. We found that the frequency of the hoot was negatively correlated with the body weight of the vocalizer. We shifted the frequency contour of natural hoots in order to create resynthesized calls corresponding to individuals of varying body weight and used these stimuli in playback experiments simulating an intrusion into the territory of established breeders. Territory owners responded less intensely when they heard hoots simulating heavier intruders, and males with heavier apparent weight tended to give hoots with a lower plateau in response to playbacks simulating heavier intruders.

Keywords: scops owls, vocal communication, acoustic coding, male competition, frequency alteration.

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Animal sexual displays result from a combination of inter- and intrasexual selection pressures (Andersson 1994). Receivers of both sexes are expected to attend to broad features (such as the rate of calling or the diversity of call types) as well as more detailed acoustic parameters in order to extract information on the quality and resource holding potential (RHP; Parker 1974) of signalers (Bradbury and Vehrencamp 1998). While receivers should be selected to discriminate between honest and dishonest signalers, thereby ensuring the reliability of signals, signalers can get a selective advantage by giving the maximum impression of their RHP or, when possible, by exaggerating their signaled quality (Maynard-Smith and Harper 2003). This conflict of interest suggests that while sexual signals should be mostly honest, they are likely to contain a limited amount of deceptive information (Grafen 1990; Adams and Mesterton-Gibbons 1995).

Empirical studies of vocal communication in vertebrates have shown that broad features of signaling such as call or syllable repetition rate (Clutton-Bock and Albon 1979; McComb 1987; Galeotti 1998; Illes et al. 2006) have the potential to provide information on the quality of the signalers during sexual interactions. High display rates are typically associated with physiological costs (e.g., Prestwich 1994; Oberweger and Goller 2001; Ward et al. 2003; but see Ward et al. 2004) and can also lead to increased levels of aggression (e.g., Vehrencamp et al. 1989) and predation (e.g., Mougeot and Bretagnolle 2000). Because only better-condition individuals can afford these associated costs, display rate is expected to transmit honest information about quality to receivers in both intra- and intersexual contexts (e.g., Clutton-Bock and Albon 1979; Alatalo et al. 1990; Castellano and Giacoma 1998; Illes et al. 2006; Leitão et al. 2006). Quality-related variation has also been identified in the acoustic structure of amphibian (common toads *Bufo bufo*: Davies and Halliday 1978; bullfrogs *Rana catesbeiana*: Bee 2002), reptile (Hermann tortoises *Testudo hermanii*: Galeotti et al. 2005; marginated tortoises *Testudo marginata*: Sacchi et al. 2003), bird, and mammal sexual calls. In terrestrial mammals, recent studies have identified important acoustic components—vocal tract resonances

(also known as formants)—as reliable cues of body size in the calls of a wide range of species (rhesus macaques *Macaca mulatta*: Fitch 1997; dogs *Canis familiaris*: Riede and Fitch 1999; red deer *Cervus elaphus*: Reby and Mc-Comb 2003), and the role of formants as assessment cues has been confirmed in red deer in the context of male-male agonistic interactions (Reby et al. 2005).

In songbirds (passerines), it is well established that the call rate or the diversity of the song repertoire has the potential to provide information on male quality during inter- and intrasexual interactions (Catchpole and Slater 1995; Searcy and Yasukawa 1996), and relatively few studies have revealed equivalent roles for individual acoustic components of the songs (with the exception of Vallet et al. 1998; Drăgănoiu et al. 2002; Forstmeier et al. 2002; Leitão and Riebel 2003; Ballentine et al. 2004). In contrast, the vocal repertoire of nonpasserine birds is typically characterized by the absence of complex songs (Catchpole and Slater 1995), and male sexual calls tend to be limited to a small number of highly stereotyped call types (Bretagnolle 1996; Miller 1996). The more stereotypical nature of vocal signals means that quality-related information is more likely to be coded in the variation of the acoustic components that compose the acoustic structure of the calls (e.g., fundamental frequency, vocal tract resonances, amplitude, etc.), reflecting anatomical or physiological constraints associated with the production of these specific components (as shown in mammals; e.g., Reby and Mc-Comb 2003). However, this area remains underinvestigated, and while several correlations between attributes and acoustic parameters have been identified (Genevois and Bretagnolle 1994; Beani and Dessì-Fulgheri 1995; Leonard and Horn 1995; Martìn-Vivaldi et al. 1998, 2000; Barbraud et al. 2000), only a handful of studies have demonstrated that the particular acoustic parameters identified are actually used by listeners in either female choice or male-male competition contexts (as evidenced in a recent review by Ten Cate et al. [2002]). One such example is found in collared doves *Streptopelia decaocto*, where the proportion of frequency-modulated elements versus non-frequency-modulated elements in the coos is positively correlated with body weight and where males respond significantly more strongly to playbacks that contain coos with modulated elements (Slabbekoorn and Ten Cate 1997, 1998).

Nocturnal raptors have extraordinarily acute auditory senses (Mikkola 1983) and are likely to rely predominantly on acoustic communication for mutual assessment. In all species, males are territorial (König et al. 1999) and give calls (hoots) in the context of mate attraction and territory acquisition and maintenance (little owl *Athena noctua*: Schönn et al. 1991; Japanese brown masked owls *Ninox scutulata japonica*: Oba 1996; tawny owls *Strix aluco*: Gale-

otti 1998). Studies investigating whether hoots provide information on caller quality in tawny owls *S. aluco* have shown that the interhoot interval indicated male RHP, while the duration of the hoot and the frequency range of its first note appeared to reflect territory quality and parental ability (Galeotti 1998). Another study on the same species has shown that the highest frequency of hoots was negatively correlated with parasitic loads (Redpath et al. 2000). However, neither study investigated whether male owls effectively perceived these quality-related cues during territorial contests.

In this study, we provide a detailed description of the acoustic structure of hoots given by male scops owls *Otus scops* in the context of territorial contests. Hoots are short, high-pitched, and highly stereotyped calls given in long series by both intruders and territorial males (Koenig 1973; Galeotti et al. 1997*a*). We investigate whether the temporal structure and/or the frequency structure of owl hoots conveys information on the phenotypic attributes of the callers. We then use playback of resynthesized hoots in order to assess whether males perceive this information during territorial contests. We hypothesized that when they hear hoots representative of males of varying quality, territorial males should adapt their territorial response to the apparent quality of the male conveyed in the playback. We also predicted that when males hoot in response to the playback, they should vary the acoustic parameters of their responses in relation to the apparent quality advertised by the caller in the playback.

## Relationships between Acoustic Parameters and Physical Attributes

### Study Area and Animals

Our study was conducted on the Isle of Oléron (area, 175 km²; 45°57′N, 01°18′W, western France), as part of a long-term study of scops owls started in 1981 by C.B. and G.B., under a license administered by the Centre de Recherches sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle (Bavoux et al. 1991; Bavoux 1999). The island's habitat is very heterogeneous, with three principal habitats: marshes (24.6%; mainly old saltwater marshes), wooded zones (21.1%; mainly pine forests), and residential areas (18.3%). The population size, estimated using a standardized playback protocol on 185 plots, ranges between 128 and 252 singing males between 2000 and 2005 (where local density can reach 6 males/ km²). The study species is present on the island from April to September. Hatching occurs from June to July, and fledging occurs around 24 days after hatching. The territorial activity starts as soon as males arrive on the breeding sites, decreases during the rearing period (between July

and August, males sing less spontaneously but remain quite reactive to playbacks), and occasionally resumes when chicks are dispersing until migration in October.

Seventeen breeding pairs were caught in nest-box traps in June and July of 2003 and 2004, during the reproductive period (approximately 10 days after hatching). Males were identified by the absence of a brood patch (always present in breeding females; Bavoux et al. 1993) and weighed with 0.1-g precision. Their wing lengths were measured with 1-mm precision. They were ringed, equipped with a VHF transmitter (Biotrack Pip; 2.1% of bird body weight) and released on average 20 min after catching. Male body weight ranged between 69.9 and 86.1 g, (mean $\pm$ SD = 77.1 $\pm$ 4.1 g, $N = 17$). The regression of body weight on wing length was not significant ($F = 1$, df = 1, 15, adjusted $R^2 \sim 0$, $P = .3$), and the residuals remained highly correlated to body weight ($F = 225.2$, df = 1, 15, adjusted $R^2 = 0.93$, $P < .001$). Body weight is therefore likely to directly reflect fat reserves and will be considered as an index of body condition, while wing length will be interpreted as an index of body size.

### Sound Recording and Analysis

We recorded 31 series of 5–50 hoots from 19 males (total: 897 hoots) between 2003 and 2004, including the 17 males for which we had biometrical data. These 17 males were recorded at night and identified using a Yaesu FT817 VHF transceiver and a flexible Yagi antenna to ensure that we did not incorrectly identify recordings of males. We elicited hooting by broadcasting a series of territorial hoots from an unfamiliar male, recorded 75 km away from the study site in 2002. Calls were recorded on CrO2 tapes using a Sennheiser MKH-815 T shotgun microphone and a Sony TCD 5M recorder, digitized (22 kHz sampling rate, 16 bits amplitude resolution) using a Maestro 3 CC SoundBlaster-compatible card in a Dell Inspiron 8100 PC, and edited and bandpass filtered (Hann band: min = 1,000 Hz, max = 2,200 Hz) using PRAAT, version 4.3.04 (P. Boersma and D. Weenink, University of Amsterdam). For each hoot series, we measured the interval between consecutive hoots (*intH*) directly on the waveform using the cursors in PRAAT (fig. 1*a*). The frequency contour of calls from each individual was extracted using the "to pitch cc" command with the following settings: time step, 0.01; silence threshold, 0.10; minimum $F$ = 1,000 Hz; and maximum $F$ = 2,000 Hz (accuracy of frequency discrimination: $\pm 0.01$ Hz). The output files were exported to an Excel spreadsheet. Hoots are modulated calls composed of a downward frequency shift followed by a stable plateau (fig. 1*b*, 1*c*). The following parameters were extracted from the frequency contour: the maximum frequency of the contour *maxF* (achieved at the onset of the downward shift), the minimum frequency of the contour *minF* (achieved at the beginning or at the end of the plateau), the median frequency of the plateau *medF*, the duration of the downward shift *d1*, and the duration of the plateau *d2* (fig. 1*c*) and are reported in table 1. In order to assess the relationship between the biometric measures associated with the quality of the males and the variables characterizing the temporal and frequency structure of their vocalizations, we used between 11 and 50 hoots (mean $\pm$ SD = 36.5 $\pm$ 11.9 hoots) for each of the 17 males for which we had biometrical data, recorded as close as possible to the capture date (range 0–12 days). We ran simple and multiple linear regressions (weighted least square) using acoustic characteristics (*minF*, *medF*, *maxF*, *d1*, *d2*, and *intH*) as predictor variables and the body weight of the caller as the outcome variable. All statistical analyses were conducted using R, version 2.2.0 (Ihaka and Gentleman 1996).

### Results: Physical Correlates of Acoustic Parameters

There were highly significant individual differences in the acoustic structure of hoots between males (MANOVA: $F = 52.3$, df = 18, 878, $P < .001$, $N = 897$; see table 1 for univariate ANOVAs). The multiple regression showed that the model based on a linear combination of the acoustic parameters was a good predictor of body weight ($F = 7.5$, df = 6, 10, adjusted $R^2 = 0.71$, $P = .002$) but not of body size ($F = 1.5$, df = 6, 10, adjusted $R^2 = 0.15$, $P = .27$). Body weight was negatively correlated with each of the frequency parameters, with *maxF* being the best predictor of male body weight (multiple regressions, table 1). Using simple regressions, we found that when considered separately, all of the frequency contour parameters (*minF*, *maxF*, and *medF*) but none of the duration parameters (*d1*, *d2*, and *intH*) were significant predictors of the weight of the caller (simple regressions, table 1). These results show that the frequency parameters reflect body weight (interpreted as an index of body condition), with males in better condition giving vocalizations with an overall lower frequency contour.

### Playback Experiments

#### Resynthesis of Playback Stimuli

In order to investigate whether territorial males perceive (and use) body weight–related variation in the height of the frequency contour, we resynthesized hoot sequences in which the frequency contour was shifted by $\pm 20\%$ or $\pm 5\%$. We resynthesized naturally occurring sequences from 10 different males. Each sequence contained 20 hoots and had an average duration of 54 $\pm$ 5 s (range 45–61 s;
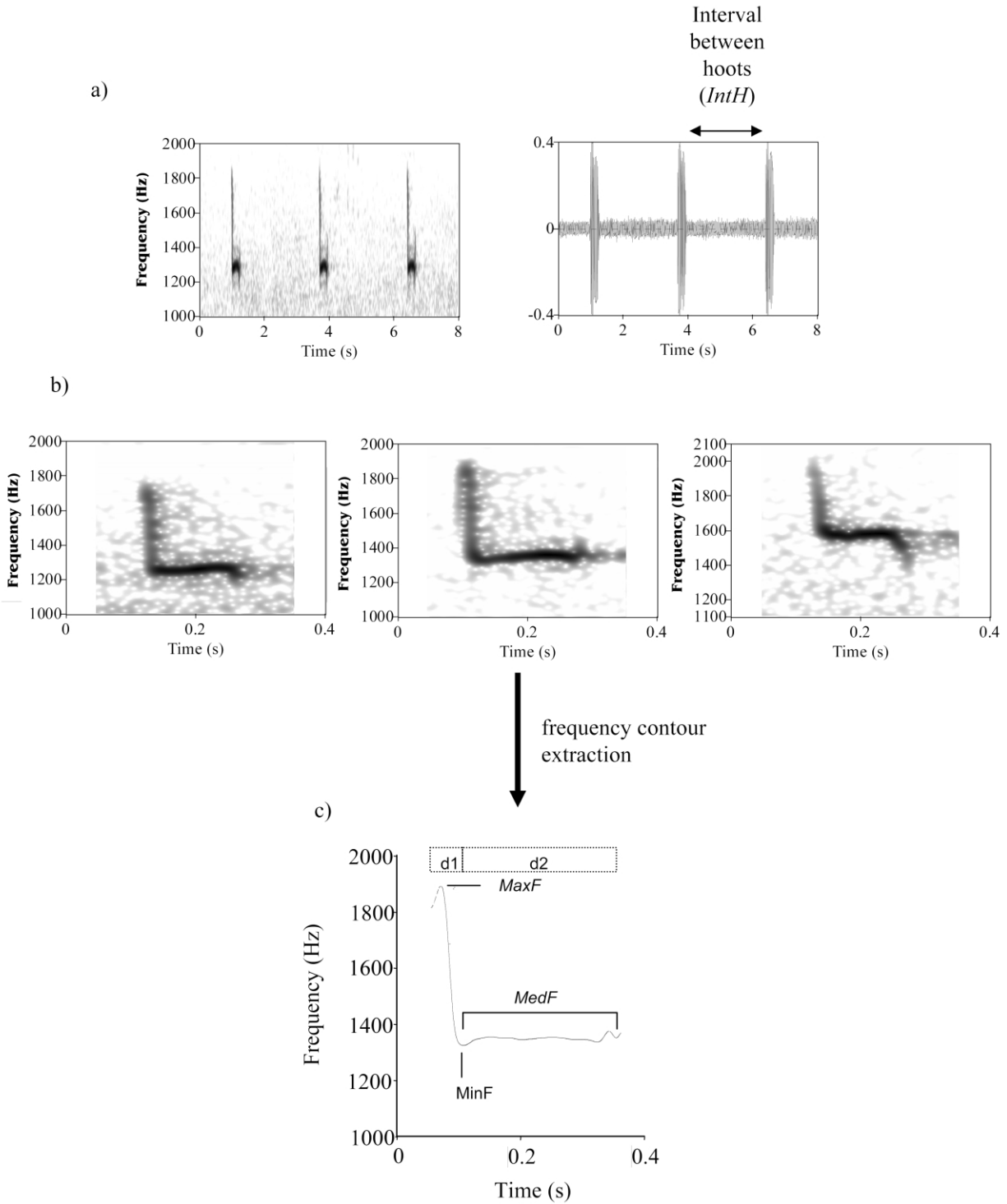
**Figure 1:** *a*, Waveform and spectrogram of three hoots from a series given by a male scops owl. *b*, Spectrograms of hoots from three different males, illustrating the natural variation in the height of the frequency contour. *c*, Extracted frequency contour with measured parameters.

**Table 1:** Interindividual differences (ANOVA) and relationship with body weight and wing length in multiple and simple regressions for each of the six acoustic parameters

| | | ANOVA | | Body weight | | | | | Wing length | | | | |
| | | | | Multiple regression | | Simple regression | | | Multiple regression | | Simple regression | | |
| | Mean ± SD | F (df 18, 87) | P | t value | P | $R^2$ | t value | P | t value | P | $R^2$ | t value | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Frequency parameters (Hz): | | | | | | | | | | | | | |
| MaxF | 1730.4 ± 93.9 | 60.4 | <.001 | −2.42 | .03 | .68 | −5.9 | <.001 | 1.5 | .15 | −.05 | .4 | .7 |
| MedF | 1358.0 ± 93.3 | 250.6 | <.001 | −2.33 | .04 | .41 | −3.5 | .003 | −1.4 | .17 | −.05 | −.4 | .7 |
| MinF | 1311.7 ± 76.2 | 138.6 | <.001 | −2.22 | .05 | .31 | −2.9 | .01 | 1.2 | .23 | −.06 | .1 | .9 |
| Temporal parameters: | | | | | | | | | | | | | |
| d1 (ms) | 41.1 ± 11.7 | 2.9 | <.001 | .59 | .56 | .07 | −1.5 | .15 | −.6 | .5 | .07 | −1.5 | .14 |
| d2 (ms) | 197.6 ± 27.6 | 2.9 | <.001 | .77 | .45 | −.03 | −.7 | .47 | −.4 | .7 | −.06 | −.2 | .8 |
| intH (s) | 2.46 ± .23 | 25.8 | <.001 | −1.23 | .24 | −.02 | −.8 | .42 | −.04 | .9 | −.01 | .9 | .4 |

Note: Adjusted $R^2$ values are shown.

all of these sequences originated from our 2003/2004 database; see details of recording and digitizing procedures in "Sound Recording and Analysis"). Using PRAAT, we extracted the frequency contour ("PitchTier") and the intensity envelope ("IntensityTier") of each hoot and then multiplied its frequency contour by a factor $k$ (leaving the frequency ratio unchanged). Since we used maximum frequency (*maxF*), the best predictor of body weight, as a reference for our resynthesis, $k$ was calculated as the ratio of the intended maximum frequency over the maximum frequency of the exemplar. Intended maximum frequency values were 1,500 Hz (−20%), 1,620 Hz (−5%), 1,780 Hz (+5%), and 1,900 Hz (+20%). These values represent the range of natural variation of the frequency contour in our population and mimic very heavy individuals (−20%), individuals slightly heavier than average (−5%), individuals slightly lighter than average (+5%), and very light individuals (+20%), corresponding to males with predicted body weights of 85.5, 81.6, 76.3, and 72.4 g, respectively. A sine wave signal was resynthesized on the basis of the rescaled frequency contour ("To sound [sine]" command), and the original intensity envelope was reapplied to the signal, creating a rescaled, natural-sounding stimulus. This resulted in four variants for each exemplar in which only the frequency contour had changed (the intensity, the duration, and the interhoot spacing remained unchanged).

### Playback Protocol

The playbacks consisted of two independent trials (20% and 5% trials), in which pairs of body weight variants from the same exemplar were contrasted (very heavy [−20%] and very light [+20%] variants contrasted in the 20% trial, and slightly heavier than average [−5%] and slightly lighter than average [+5%] variants contrasted in the 5% trial). The 20% trial was carried out on 30 individuals May 25–June 1, 2005, and the 5% trial was carried out on 17 individuals June 2–4, 2005. Both experiments were performed in the same weather condition (i.e., windless and warm night). Playbacks of natural calls were used to locate males between 1 and 2 days before the actual playback experiment. All playbacks were done during the night, between 2100 and 0400 hours. Within each trial, the two variants of the same exemplar were played 8 min apart to the same territorial male from the same location within its territory. The order of presentation of both size variants and exemplars was systematically balanced in order to control for possible order effect and to limit pseudoreplication (as a result, the same exemplar was not played more than three times in the 20% trial or more than twice in the 5% trial). Stimuli were played using an Anchor Audio Liberty LIB-6000 HC loudspeaker with a response frequency of 60 Hz–15 kHz ± 3 dB, positioned at approximately 20 m (10–30 m) from the expected location of the male, thereby simulating a close-range intrusion in its territory.

### Response Analyses

Males typically responded to the playback stimuli by calling back and occasionally by flying toward the source. We did not record any female response to the playbacks. While females sometimes hoot in duet with males, female calls are easily identifiable as they are more modulated and higher pitched, and they lack the synchrony and repeat-

ability that characterizes male calls (Koenig 1973; Galeotti et al. 1997*a*). We recorded the response of the subjects for 5 min after each playback and measured the response latency and the duration of the vocal response, as well as the number of approaches toward the speaker and the closest distance at which males approached the speaker (approximated by sound using a four-category scale: <10, 10–30, 30–50, >50 m). In order to quantify the behavioral response using uncorrelated variables, we performed a principal component analysis based on the correlation matrix (McGregor 1992). The subsequent statistical analyses were performed on the scores of the first two principal components (PC1, PC2; see "Results: Behavioral Response").

Up to 5 min of response hoots were recorded using a Sennheiser MKH 418 P48 shotgun microphone and a Marantz PMD 670 solid-state recorder on 512-Mb Compact flash cards (file format: WAV, 22 kHz, 16 bits). The acoustic parameters (see fig. 1) of the first 10 hoots of each response were quantified following the same procedure as described above (see "Sound Recording and Analysis"). Because the scores of all of our response variables were normally distributed, we analyzed the variance of our response variables (*PC1*, *PC2*, *minF*, *maxF*, *medF*, *d1*, *d2*, and *intH*) using paired *t*-tests. Two males who responded to both 20% playbacks, but for which only one response was recorded, were excluded from the acoustic analyses of the response hoots. Finally, we used the multiple regression equation obtained in "Results: Physical Correlates of Acoustic Parameters" to estimate the body weight of the subjects, using the frequency and temporal parameters of the hoots they gave in response to the playbacks (averaged over the two playback treatments).

## *Results: Behavioral Response*

The rate of vocal response to the playbacks was very high, with 96% of males calling back. Two males failed to respond to a −20% treatment and one to a +5% treatment. The principal component analysis performed on the four response variables generated four uncorrelated components, of which the first two accounted for 38.7% and 28.7% of the variance, respectively. The variables quantifying vocal behavior (latency and length of response) were loaded on the first principal component (latency: $r = 0.83$, length of response: $r = -0.79$) while the variables characterizing the behavioral response (i.e., closest distance and flights) were correlated with the second principal component (flights: $r = 0.79$; closest distance: $r = -0.70$). In the 20% trial, there was a strong difference for both components 1 and 2 between the −20% and +20% treatments (*PC1*: $t = -5.2$, $P < .001$; *PC2*: $t = 3.9$, $P < .001$; df = 29). Individuals gave stronger responses, characterized by shorter latency and longer duration, a closer

distance to the speaker, and more approaches when played back hoots with high frequency contour (indicating a lightweight signaler). There were no significant differences for both components between the +5% and −5% treatments (*PC1*: $t = 0.12$, $P = .89$; *PC2*: $t = -0.3$, $P = .70$; df = 16; fig. 2). In both trials, the variation in vocal (*PC1*) or behavioral responses (*PC2*) between the paired treatments was not correlated with the estimated body weight of the subject. This suggests that the territorial response of the males is not affected by their own body condition but mainly by the apparent body weight of the intruder.

## *Results: Alteration of Acoustic Characteristics in Response Hoots*

In both trials, the paired *t*-tests showed that there were no significant differences between the treatments for any of the acoustic parameters (−20% vs. +20% treatments, $N = 26$; *d1*, $t = -0.59$; *d2*, $t = 0.4$; *intH*, $t = 0.1$; *minF*, $t = 0.23$; *medF*, $t = 0.8$; *maxF*, $t = -0.7$; all $P > .39$, df = 25; −5% vs. +5% treatments, $N = 16$; *d1*, $t = 0.7$; *d2*, $t = -0.5$; *intH*, $t = -0.01$; *minF*, $t = 0.1$; *medF*, $t = 0.1$; *maxF*, $t = 0.2$; all $P > .46$, df = 15). However, 20 of the 26 males (binomial test, binary variable: increase = 0, decrease = 1, $P = .009$; with lowered $\alpha = 0.01$ after Bonferonni's adjustment) gave calls with lower *medF* frequency in response to hoots with lower frequency contours (indicative of heavier males). When we plotted the variation of *medF* (the difference in *medF* between hoots given in response to treatment −20% and hoots given in response to treatment +20%) against the estimated body weight of the subjects, we found that there was a significant negative correlation ($F = 5.1$, df = 1, 25, adjusted $R^2 = 0.14$, $P = .03$; fig. 3).

## Discussion

In the first part of this study, we show that the height of the frequency contour of male scops owl hoots conveys information on body weight and therefore potentially reflects the RHP of the caller. As mentioned in the introduction to this article, negative correlations between fundamental frequency contour and body size have been documented in a wide range of species and are likely to be a consequence of an acoustic allometry between the size of the vocal apparatus and the frequency of the sound signal (see Fitch and Hauser 2002 for a review). Here we have identified an overall correlation between hoot frequency and body weight that is independent of body size. Body weight and condition exert particularly limiting constraints in small (Hutchinson et al. 1993; Thomas et al. 2003) and migratory (Kokko 1999) birds and would therefore be expected to affect the outcome of physical contests.
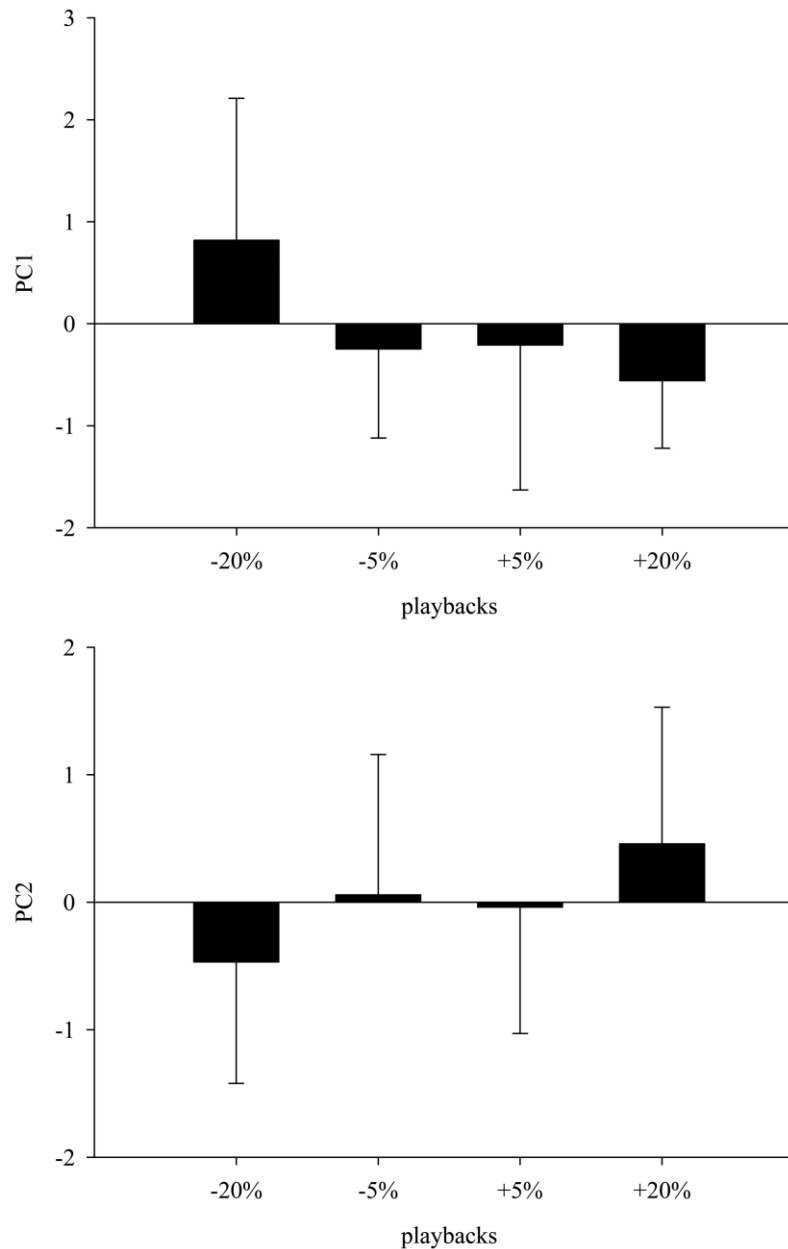
**Figure 2:** PC1 and PC2 scores (*Y*-axis, mean ± SD) of the principal component analysis computed on the four response measures for each trial (*X*-axis). Note that positive values of PC1 represent lower vocal responses, while positive values of PC2 represent stronger behavioral responses.

For this reason, indicators of body weight and condition are likely to have evolved in the sexual communication signals of these species (e.g., Martìn-Vivaldi et al. 1998; Ten Cate et al. 2002).

Although the current lack of understanding of the mechanisms of voice production in owls limits our ability to discuss the bases of this relationship, one possibility is that it may result from physiological constraints that op-erate during sound production. For example, lower-pitch hoots may be more costly to produce and/or reflect su-perior muscular or respiratory abilities. The relationship between pitch and body weight may reflect the fact that heavier, better-condition males are also characterized by higher testosterone levels, which in turn affect the fre-quency of their vocalizations. Indeed, male condition and testosterone levels have been shown to positively correlate
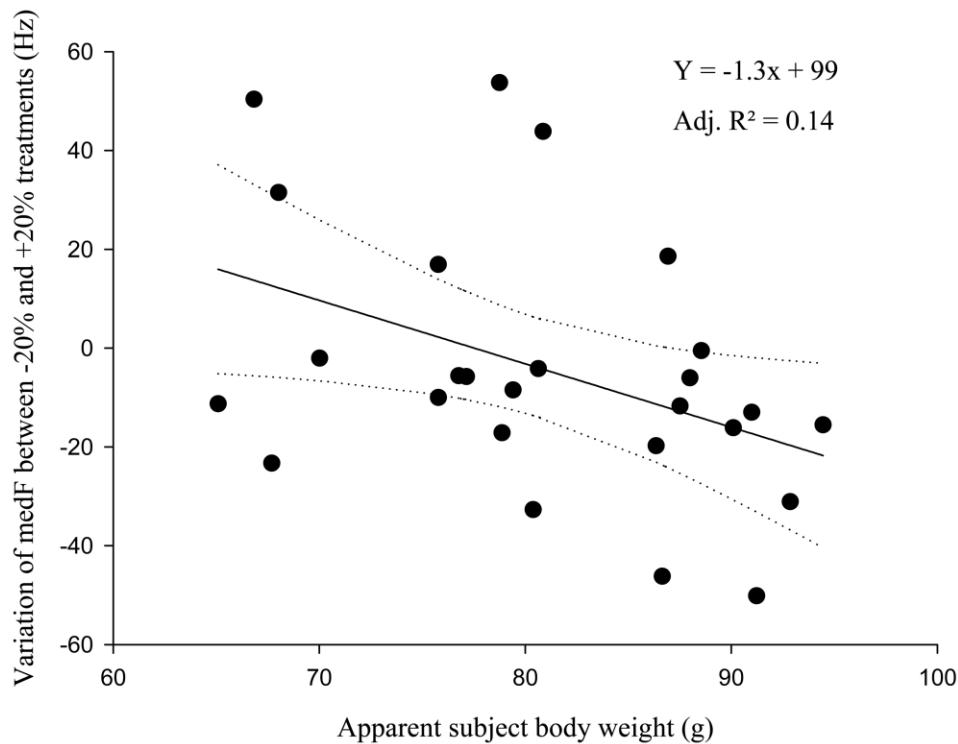
**Figure 3:** Scatterplot and trend line illustrating the correlation between Δ*medF* (median frequency of the plateau) corresponding to the differences in *medF* in response hoots between treatment −20% and +20% against the estimated weight of the subjects, as predicted from the frequency contour of their response hoots, averaged over the two experiments. The solid line represents the predicted regression, and the dotted lines represent the confident interval (5% and 95%) of the regression. Note that negative values of Δ*medF* indicate that the subject gave a lower *medF* in response to the −20% treatment (mimicking a very heavy intruder) than to the +20% treatment (mimicking a very light intruder).

(Chastel et al. 2005), and higher testosterone levels are typically associated with more intense sexual displays (Galeotti et al. 1997*b*; Chastel et al. 2005). Moreover, experimental studies have demonstrated that injections of testosterone lower the frequency of male calls in birds (gray partridges *Perdrix perdrix*: Beani et al. 1995; zebra finches *Taeniopygia guttata*: Cynx et al. 2005).

When we played back resynthesized hoots in which the frequency contour had been rescaled to mimic males of varying body weight, we found that territorial males tended to respond less intensely to hoots reflecting heavier individuals. Interestingly, whereas there were no differences in the intensity of vocal and behavioral response between the two 5% variants, the intensity of response was intermediate to that observed in the +20% or −20% variants, indicating that the intensity of the territorial responses is positively correlated to the frequency of the rival hoots (and therefore negatively correlated to the apparent body weight; fig. 2). These playback experiments unambiguously demonstrate that territorial males perceive the height of the frequency contour in their opponents' hoots.

Moreover, the way males adapt their territorial behavior in response to this strongly suggests that they use the height of the frequency contour as an indicator of their opponents' body weight.

While territory owners might be expected to reserve strong responses for heavier intruders as they usually represent a bigger threat, empirical support for this expectation is more mixed, with some studies on vertebrate territorial species supporting it (collared dove: Slabbekoorn and Ten Cate 1997; willow warbler *Phylloscopus trochilus*: Järvi et al. 1980; great reed warbler *Acrocephalus arundinaceus*: Catchpole 1983), while others provide contradictory evidence (Australian frog *Uperoleia rugosa*: Robertson 1986). In this study, it was impossible to predict with certainty which variant represented a bigger threat and whether receivers would have a greater or lesser reaction to a bigger threat. As a consequence, the results of our playback experiment do not allow us to infer which of our stimuli variants represents a bigger threat for receivers, only that they react differently to the variants and therefore perceive this variation as meaningful. However,

we suggest that the most parsimonious explanation is that established territorial scops owl males might benefit from avoiding unnecessary escalations against heavier individuals at an early stage in a vocal contest, explaining why resident males gave a more cautious response to playback of hoots mimicking heavier intruders. Moreover, at this stage of the breeding season, lower-quality intruders may cause a more serious threat to resident males than higher-quality intruders that are more likely to have already established a territory. This interpretation is supported by the fact that in this population, both male hoot frequencies are significant predictors of egg-laying dates, with males with lower-frequency hoots pairing with females that lay eggs earlier, independently of the female's body weight (Hardouin 2006). This playback experiment could be replicated at different stages of the breeding season in order to examine whether males respond differently in the early stages of territoriality.

A comparable function of the call frequency has been identified in common toads *Bufo bufo*, where the fundamental frequency is negatively correlated with body size and used by males to assess the size of competitors during contests over females (Davies and Halliday 1978). Subsequent studies in a range of anuran species (Arak 1983; Wagner 1992) have confirmed that the fundamental call frequency was indicative of caller size. However, while in certain species (e.g., green frogs *Rana clamitans*: Bee et al. 1999) males alter their behavior in response to these cues in assessment situations, males from other species do not appear to use this information (bullfrogs: Bee 2002). To our knowledge, our study provides the first experimental evidence that birds respond differentially to weight-related variation in the frequency contour of the hoots of their rivals. When we analyzed the pitch contour in the hoots that were given in response to the playbacks, we found that although there were no overall differences between the −20% and +20% treatments, a significant proportion of territorial males lowered the median frequency of the plateau (but not their *minF* and *maxF*) in response to stimuli mimicking the heavier individuals. This shows that males can modify the frequency of the plateau part of their hoots by a small amount (21 ± 16 Hz) relative to the observed interindividual differences existing between light and heavy males (interindividual variation of *medF*: range 1,192–1,605 Hz). We suggest that this differential frequency alteration may reflect an attempt by territorial males to increase their apparent weight after hearing hoots indicative of heavier individuals. Similar small-scale modulation of "static" frequency components in sexual signals has been observed in anurans (dominant frequency in Blanchard's cricket frogs *Acris crepitans blanchardi*: Wagner 1989, 1992; and green frogs: Bee 2000) and deer (Reby et al. 2005) and interpreted as a means used by males to exaggerate apparent RHP during vocal contests. In red deer, harem holders extend their vocal tract further, decreasing vocal tract resonances (formants) in their roars and increasing their apparent size when they respond to playbacks indicating larger opponents (Reby et al. 2005).

Finally, it appears that the extent to which individuals differentially vary their plateau can be predicted from the estimated body weight of the callers (as measured from the average of their responses to the extreme size variants). More specifically, heavier males perform a differential decrease of the frequency of their plateau, whereas lighter males tend not to decrease (or even increase) the frequency of their plateau. Signaler-dependent frequency alteration has also been identified in green frogs (Bee 2000), where small males decrease their dominant frequency in response to playbacks corresponding to the largest male. The frequency alteration we have identified here appears to fall into the category of "signal of size-independent fighting ability" (Wagner 1992), where the frequency alteration provides information on the male condition (motivation, experience, or, in our case, body weight) independently of its body size. However, we prefer to view this observation as a preliminary result calling for further research. Actual data on the body weight of the territorial subjects would be preferable to the indirect indications that we use here, and playbacks of resynthesized hoots independently shifting the extreme frequency values (*minF* and *maxF*) of the hoots from the frequency of the plateau are needed to disentangle the relative role of these different elements of the frequency contour. It is also necessary to test whether small variations of these elements (of the order of those observed in response to our paired playbacks) are actually perceived and used by receivers.

In conclusion, this study shows that the acoustic coding of sender-specific attributes in nonpasserine bird vocalizations can be complex, involving components with both static and dynamic dimensions. It reinforces the view that the fine-scale structure of sexual signals is not arbitrary but reflects interindividual differences in quality that may result from selection through male-male competition (Ten Cate et al. 2002).

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