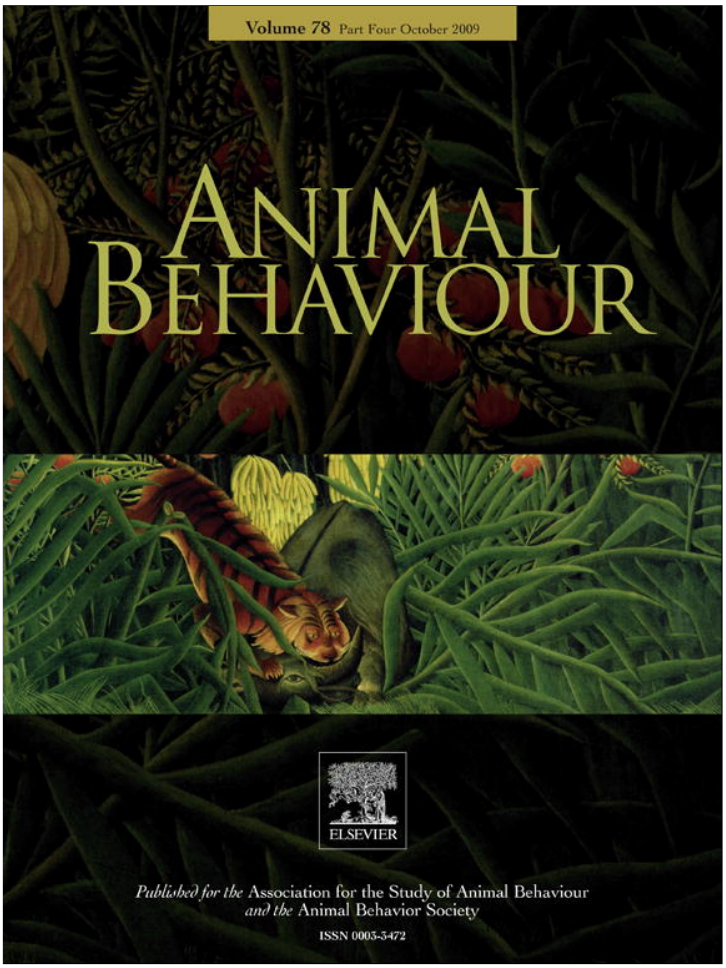
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Animal Behaviour 78 (2009) 907–913

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Acoustic cues to reproductive success in male owl hoots

Loïc A. Hardouin [a,b,*], V. Bretagnolle [a,1], P. Tabel [a,1], C. Bavoux [c,2], G. Burneleau [d,3], D. Reby [b,4]

[a] Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934
[b] Centre for Mammal Vocal Communication Research, School of Psychology, University of Sussex
[c] Le Marais aux Oiseaux
[d] Mauzac, Saint-Just-Luzac

ARTICLE INFO

Article history:
Received 21 January 2009
Initial acceptance 18 February 2009
Final acceptance 17 July 2009
Published online 15 August 2009
MS. number: 09-00044R

Keywords:
fitness
male–male competition
Otus scops
scops owl
sexual call

Previous research on hooting in male scops owls, *Otus scops*, has shown that heavier males produce overall lower-frequency hoots, and that males alter, and attend to, hoot frequency during territorial contests. We examined how hoot frequency relates to, and possibly affects, male fitness. We quantified the reproductive success of 20 breeding pairs, and documented the phenotypic attributes of both the female and the male, including acoustic variables characterizing male hoots. We investigated whether male body condition, skeletal size and hoot frequency are predictors of the pair's reproductive success. Paired males in good condition did not breed earlier or produce more and heavier fledglings; however, paired males with lower-frequency hoots did breed earlier and produce more and heavier fledglings, even when the effect of interindividual variation in body condition on hoot characteristics was controlled for. Since males with lower-pitch hoots did not have access to better females, we suggest that this relationship might be a product of their increased competitive ability during territorial establishment, where males with lower-pitch hoots acquire better territories, leading to the production of fitter offspring. This also suggests that, in scops owls, males with lower-pitch hoots than expected from their body condition are currently under positive selection from intrasexual competition pressure.
© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Sexual selection theory has proved extremely successful in explaining male ornaments and/or armaments (Andersson 1994; Forrest & Raspet 1994; Kokko et al. 2002). Males can exhibit elaborate vocal and visual signals of which size and or intensity may depend on body condition, body size, age or all of these (Andersson 1994). These signals serve both in competition between males and mate choice, thus giving some males a reproductive advantage over others (reviewed in Berglund et al. 1996). Signals that serve a dual function are likely to have evolved first in the context of male–male competition as an indicator of male competitive ability, only later becoming subject to female choice (Berglund et al. 1996; ten Cate et al. 2002). The handicap principle theory predicts that the same signal has a role in both intra- and intersexual selection (Zahavi & Zahavi 1997). Territorial males able to produce a signal that indicates strong phenotypic quality (body condition and size or other qualities) should suffer fewer territorial intrusions, injuries or conflicts (Maynard Smith & Harper 2003). Such males are in turn likely to be preferred by females, with potentially a direct impact on reproductive performance (ten Cate et al. 2002; Maynard Smith & Harper 2003).

In several taxa, quality-related variation is typically coded in the acoustic structure of sexual calls (amphibians: Davies & Halliday 1978; Bee 2002; reptiles: Galeotti et al. 2005; Sacchi et al. 2003; nonpasserine birds: Genevois & Bretagnolle 1994; Martìn-Vivaldi et al. 1998; passerine birds: Forstmeier et al. 2002; Leitão & Riebel 2003; Ballentine et al. 2004; mammals: Riede & Fitch 1999; Reby & McComb 2003), rather than in the diversity or complexity of signals as illustrated by the complex vocal repertoires of some passerine birds. For instance, negative correlations between fundamental frequency (F0) and static attributes such as skeletal size (directly reflecting the acoustic allometry between the size of the vocal apparatus and the frequency) or dynamic attributes such as condition or dominance rank (reflecting the physiological or indirect social costs of producing these signals) have been documented in amphibians, birds and mammals (birds: Leonard & Horn 1995; amphibians: Bee 2002; mammals: Vannoni & McElligott 2008; reviewed in Fitch & Hauser 2002). Playback experiments have

* Correspondence and present address: L. A. Hardouin, Emirates Center for Wildlife Propagation, BP 47, 33250 Missour, Morocco.
E-mail address: loic.hardouin@gmail.com (L.A. Hardouin).
[1] V. Bretagnolle and P. Tabel are at the Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Villiers-en-Bois, France.
[2] C. Bavoux is at Le Marais aux Oiseaux, Les Grissotières, 17550 Dolus-d'Oléron, France.
[3] G. Burneleau is at Mauzac, 17320 Saint-Just-Luzac, France.
[4] D. Reby is at the Centre for Mammal Vocal Communication Research, School of Psychology, University of Sussex, Falmer BNI 9QH, U.K.

0003-3472/$38.00 © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2009.07.016

Author's personal copy

shown that in some species, F0 variation actually functions as an index of resource-holding potential during contests over females or territories (amphibians: Davies & Halliday 1978; Grafen 1990; birds: ten Cate et al. 2002; Hardouin et al. 2007). Also, some studies have shown that females use F0 variation when assessing mating partners (amphibians: Ryan 1980; birds: Beani & Dessì-Fulgheri 1995). However, few studies have investigated whether size- or condition-related variation in fundamental frequency correlates with and/or affects male reproductive success.

We investigated the relationship between reproductive success and vocal characteristics in European scops owls, *Otus scops*, a small migratory, mainly monogamous and territorial nonpasserine species. Male scops owls defend multipurpose territories and use a long series of short, high-pitched and highly stereotyped vocalizations, called hoots, while they establish, advertise and maintain their territorial boundaries, and also when challenging other territorial males and attracting females (Koenig 1973; Galeotti et al. 1997). In such a small and migratory species of bird, where body condition is a particularly limiting constraint (Hutchinson et al. 1993; Kokko 1999; Thomas et al. 2003) and should affect the outcome of physical contests, indicators of body condition are expected to play a substantial role in intrasexual communication. Previous research on this species has shown that the frequency of male hoots conveys information on body weight (but not on skeletal size), with lower-frequency hoots indicating heavier (but not bigger) males and hence reflecting the condition of the caller (Hardouin et al. 2007). Moreover, the way males adapt their territorial behavioural response (including the frequency of their own hoots) to the playback of resynthesized hoots strongly suggests that they use the frequency of the hoot as an indicator of their opponent's fighting ability (Hardouin et al. 2007).

However, whether this correlate of quality actually predicts male reproductive performance remains to be investigated. Using a sample composed of all the males used in our previous study (Hardouin et al. 2007), plus three other individuals, we tested for a relationship between hoot frequency and mating performance by comparing male hoot frequency and female body condition across mated pairs. We also investigated whether male hoot frequency and both male and female body condition and skeletal size are significant predictors of the pair's reproductive performance and their nestling growth rates. Finally, as we confirmed that hoot frequency and male body condition (but not body size) were related, we used a measure of hoot frequency independent of body condition (condition-independent frequency component, CIFC), and tested the relationship between CIFC and traits related to reproductive success and female body condition.

METHODS

Study Area and Species

Our study was conducted from 2002 to 2004 on the Isle of Oléron (175 km^2, Saint-Pierre d'Oléron: 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. (Bavoux et al. 1991) under a licence administered by the Centre de Recherche sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle de Paris, France. Our study area (28.5 km^2) was restricted to sites situated in the northwest and southeast of Saint-Pierre d'Oléron. These sites are characterized by three principal habitats: fields and meadows (26.7%), wooded zones (22.9%; mainly broadleaved forests) and marshes (17.5%; mainly old saltwater marshes).

Scops owls are present on the island from April to September. Their density on the island can reach up to 2.25 males/km^2 (C. Bavoux & G. Burneleau, unpublished data). The laying period occurs from mid-May to mid-June and eggs are incubated for 24–25 days. Each pair produces only one clutch per year, hatching occurs from mid-June to mid-July and fledging around 24 days after hatching. Vocal territorial activity starts as soon as males arrive on the breeding sites and decreases during the rearing period (from July to August), occasionally resuming when chicks are dispersing until migration in September. In this species, the female does all the incubation and brooding (where brooding normally occurs until 10 days after hatching, Bavoux et al. 1993) while the male provides all the food during this period.

Data Collection

All nestboxes (from 72 to 91) were inspected early in the season for any signs of occupancy, and occupied nestboxes (from 12 to 18) were checked at the end of the laying period. Eggs were counted, measured and weighed; the mean number of eggs per pair ± SD was 4.5 ± 1.0 ($N = 31$ nests). Occupied nestboxes were visited every 3 days until hatching. Hatching date was determined for each chick at 2 days accuracy (3.6 ± 1.8 hatchlings/brood, $N = 31$). Nestlings were identified by a coloured mark applied with a felt-tip pen on the top of the head (approximately 6 mm large and 1 cm long using water-based markers, Uni PROCKEY PM-126, Mitsubishi Pencil Co., Ltd, Tokyo, Japan) and ringed at 10–15 days of age. There is no evidence that the coloured marks affected either chicks' or parents' behaviour as there were no significant differences in the ratio of hatchlings and fledglings and the growth rate of marked and unmarked chicks (C. Bavoux & G. Burneleau, unpublished data).

Sixty chicks were weighed (±0.1 g) and their wing lengths were measured (±1 mm) every 2 days until they fledged (2.9 ± 1.5 fledglings/brood and 11.8 ± 1.6 measurements/chick, $N = 32$). Observations involved different pairs each year, except for two males that bred in 2 consecutive years but for which we considered the 2 years as independent samples. In addition, one male in 2004 was polygamous with two breeding females in the same nestbox; as it was not possible to disentangle the relative contribution of each female, we calculated an average of the two females' body conditions.

Twenty breeding males for which we had hoot recordings (17 from a previous study in 2003 and 2004, Hardouin et al. 2007) and all but one of their mates were caught in nestbox traps in June and July from 2002 to 2004 (2002: $N = 3/3$; 2003: $N = 5/5$; 2004: $N = 12/11$ males/females). Males were caught at the same stage of the reproductive period (approximately 10 days after hatching) and females on average 28 ± 5 days after the laying date. They were sexed using the presence/absence of a brood patch (Bavoux et al. 1993), weighed (±0.1 g), and their wing lengths measured (±1 mm; males: weight = 77.3 ± 4.6 g, wing length = 158 ± 4 mm, $N = 20$; females: weight = 106.2 ± 12.7 g, wing length = 161 ± 4 mm, $N = 19$). All captured males and females were ringed. In 2003 and 2004, male scops owls were ringed and equipped for radiotracking and identification purposes with a VHF transmitter (model PIP, weight = 0.6 g, Biotrack Ltd, Wareham, Dorset, U.K.) fixed on a thin leather strip (weight = 1 g) that was hand-sewn round the right tarsus. The leather strip and the transmitter weighed 1.6 g which corresponded on average to 2.08 ± 0.12% of the weight of male scops owls (range 1.85–2.29%) and did not exceed 3% of the animal's total body mass (Withey et al. 2001). It was not necessary to recapture the males as the fitted transmitters were self-detachable (personal observation).

Females lost weight during the breeding season ($F_{1,203} = 32.9$, $R^2_{adj} = 0.13$, $P < 0.001$, based on the total number of captured females from 2002 to 2004, $N = 32$, linear mixed-effect models with female identity as a random factor). Over the capture events (6.4 ± 3.5 capture events/female on 14.8 ± 7.2 days), we recorded

Author's personal copy

a weight loss of 18.8 ± 10.2 g. Accordingly, an index of female body condition ($N = 19$ females) was calculated using the residuals of the regression of body weight on wing length and the relative date of capture. We used the single measurement for females caught once, and the last measurement for females caught several times. For males, for which we had only one capture event (at a similar stage of the reproductive period), we used the residuals of the regression of body weight on wing length as an index of body condition (Jakob et al. 1996).

Estimation of Growth Rate

From the biometric data collected on nestlings during rearing, we fitted growth curve models (Ricklefs 1983; Zach et al. 1984) using a program written on the statistical package SAS 8.0 with PROC NLIN (SAS Institute, Cary, NC, U.S.A.). The use of nonlinear least-square regression assumes that residuals are randomly distributed, independently of chick age (Zach et al. 1984). We compared two models (logistic and Gompertz), and chose the best model with regard to residual distribution, estimated visually by plotting residuals versus age. The Gompertz model was chosen and three growth curve parameters were extracted: the inflexion of the sigmoid (I), the asymptotic value (A) and the growth rate (GR).

Sound Recording and Analysis

Twenty males were tape-recorded at night. In 2003 and 2004, male identities could be verified using radiotags (Hardouin et al. 2007). Three males that were recorded around their nestbox during capture sessions in 2002 were added to our sample and included in our analyses. As calling owls were invisible, false identification may be a problem when several males were calling simultaneously around a nestbox. We determined the owner of the nest after capture, assigning the recordings to the captured male (which stopped calling). We stimulated male hooting by broadcasting a series of territorial hoots from an unfamiliar male recorded in 2002, 75 km from the study site. Calls were recorded on CrO2 tapes using a Sennheiser MKH 815T shotgun microphone and a Sony TCD 5M recorder, and digitized using a Maestro 3 CC soundblaster compatible card onto a Dell Inspiron 8100 PC, before being edited, bandpass filtered and analysed (Hann Band: minimum = 1000 Hz, maximum = 2200 Hz) using PRAAT 4.3.04 (P. Boersma & D. Weenink, University of Amsterdam, The Netherlands). The fundamental frequency contour was extracted using a procedure previously detailed in Hardouin et al. (2007) and the following parameters were measured (Fig. 1): the maximum frequency of the contour (achieved at the onset of the downward shift; maxF = 1734 ± 108 Hz), the minimum frequency of the contour (achieved at the beginning or at the end of the plateau; minF = 1300 ± 4 Hz) and the median frequency of the plateau (medianF = 1349 ± 84 Hz). The relationships between the morphometric measures and variables characterizing the temporal and frequency structure of the 17 male vocalizations have been already investigated, and showed that 67% of the variance was explained by hoot frequency components (Hardouin et al. 2007). We reanalysed the relationship between male body condition and hoot frequency ($PC1_{hoot}$) on our extended sample ($N = 20$). We used 8–50 hoots (33.5 ± 14.7 hoots) for each of the 20 males, recorded as close as possible to the capture date (range 0–12 days).

Statistical Analyses

To reduce the number of variables in our analyses, three principal component analyses (PCA) were performed on the reproductive performance, growth rate and hoot frequency data.

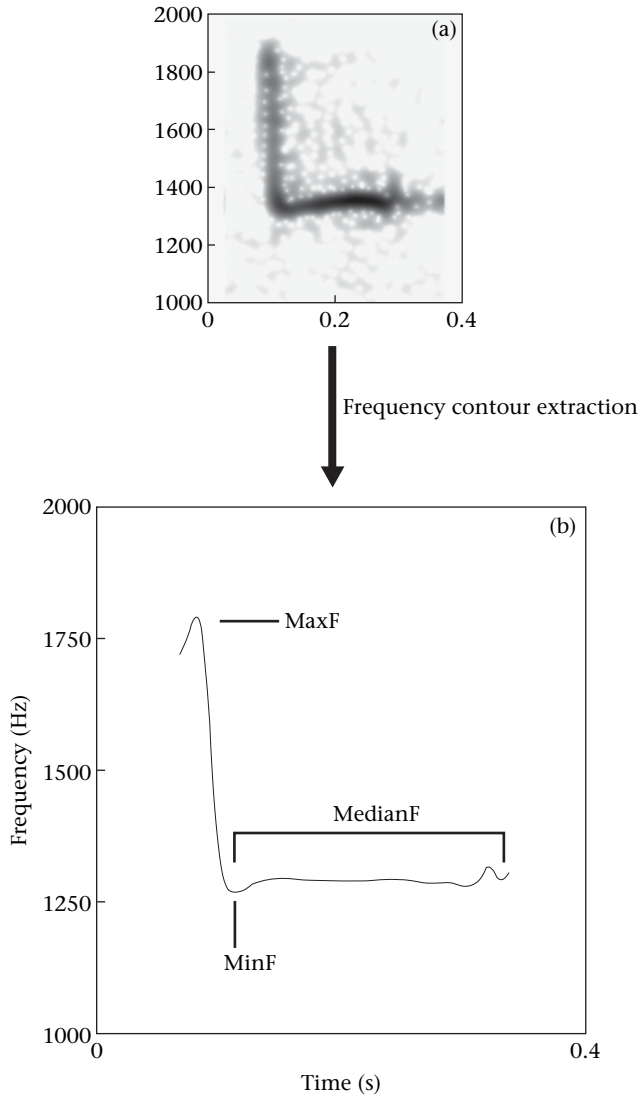


Figure 1. (a) Spectrogram of a hoot and (b) extracted frequency contour with measured parameters.

For reproductive performance we used four reproductive variables: relative laying date, clutch size, number of hatchlings and number of fledglings. To remove the effect of annual variation in reproductive performance, we used relative rather than absolute reproductive variables. These were obtained by subtracting individual reproductive variables from the corresponding annual means of the population. The four parameters were strongly correlated with each other, for example, the relative number of hatchlings was correlated with the relative clutch size ($F_{1,18} = 22.8$, $R^2_{adj} = 0.53$, $P < 0.001$), the relative number of fledglings was correlated with the relative number of hatchlings ($F_{1,18} = 20.1$, $R^2_{adj} = 0.50$, $P < 0.001$) and the laying date was negatively correlated with fledgling output, pairs breeding earlier producing significantly more fledglings ($F_{1,18} = 7.6$, $R^2_{adj} = 0.26$, $P = 0.01$). We therefore summarized reproductive performance by using the first component ($PC1_{RP}$) of a PCA performed on the four parameters, which accounted for 60.8% (eigenvalue = 1.56) of the total reproductive performance variance. $PC1_{RP}$ was negatively correlated with the relative laying date (−0.70) and positively correlated with the relative clutch size (0.78), and the relative numbers of hatchlings (0.80) and fledglings (0.81). Therefore, higher values of $PC1_{RP}$ represent higher reproductive performance.

Author's personal copy

For chick growth the first component ($PC1_{GR}$) derived from the PCA and based on the three growth curve parameters (*I*, *A* and GR) explained 63% of the total variance. This component had an eigenvalue of 1.38. GR was positively correlated with the $PC1_{GR}$ (0.3). In addition, *I* and *A* were negatively correlated with $PC1_{GR}$ (0.90 and 0.94, respectively) and, hence, positive $PC1_{GR}$ characterized heavier and (to a lesser extent) faster-growing chicks.

For hoot frequency a PCA was used to investigate the covariance between frequency contour parameters and to reduce the number of dependent variables ($PC1_{hoot}$). All measured components of the frequency contour were positively correlated (Table 1). The first principal component derived from the correlation matrix explained 67.3% of the total variance: only this component had an eigenvalue greater than 1 ($PC1_{hoot} = 1.42$). As $PC1_{hoot}$ was positively correlated with all hoot frequency components (Table 1) positive values of $PC1_{hoot}$ represented higher-frequency hoots.

From the regression between body condition and hoot frequency ($PC1_{hoot}$), the residuals (CIFC) were extracted for subsequent analysis. Positive residuals represented males that produced higher-frequency hoots than predicted by their body condition.

Using simple linear regressions, we investigated (1) the relationship between female body condition/skeletal size, $PC1_{hoot}$, male body condition/skeletal size and CIFC and (2) the relationship between reproductive components ($PC1_{RP}$), $PC1_{hoot}$, male and female body condition and size and CIFC.

The relationship between chick growth rate ($PC1_{GR}$), male body condition, female body condition, $PC1_{hoot}$ and CIFC were analysed using generalized linear mixed-effect models with brood as a random factor. Since $PC1_{GR}$ strongly reflects chick final body weight and since this trait is likely to be heritable (e.g. Lukefahr et al. 1996), the average body condition of the parents was added as a fixed factor when we tested the relationship between chick growth rate, $PC1_{hoot}$ and CIFC. This factor is removed from the model when a negative slope is observed. All the data were normally distributed. All statistical analyses were conducted using R 2.6.1 (R Development Core Team 2007) with the nlme package (Pinheiro et al. 2005). Means are given ±SD.

RESULTS

Hoot Frequency and Male Condition

Hoot frequency ($PC1_{hoot}$) was negatively correlated with male body condition ($F_{1,18} = 7.1$, $R^2_{adj} = 0.24$, $P = 0.01$) but not with male body size (using wing length as an index of body size: $F_{1,18} = 1.0$, $R^2_{adj} \sim 0$, $P = 0.32$), meaning that males in better condition produced lower-frequency hoots, confirming results previously obtained on a subsample (Hardouin et al. 2007).

Hoot Frequency, Reproductive Performance and Female Body Condition

There was no significant relationship between male body condition, $PC1_{hoot}$ or CIFC and female body condition (Table 2), indicating that females in better condition did not mate with males in better body condition or with lower-frequency hoots. In addition, larger females did not prefer to mate with larger males or those with lower-frequency hoots (Table 2). Moreover, the reproductive component $PC1_{RP}$ did not vary significantly with male or female body size and condition (Table 2).

In contrast, hoot frequency ($PC1_{hoot}$) and CIFC were negatively correlated with reproductive performance ($PC1_{RP}$), indicating that males with lower-frequency hoots had overall better reproductive performance even when the effect of male body condition on hoot frequency was controlled for (Fig. 2, Table 2). Taken independently, the number of fledglings was negatively correlated with hoot frequency and CIFC ($PC1_{hoot}$: Estimate ± SE = −0.38 ± 0.17, $P = 0.03$; CIFC: Estimate ± SE = −0.41 ± 0.18, $P = 0.03$).

Hoot Frequency and Chick Growth Rate

There was no significant relationship between female body size or condition and chick growth rate (body size: estimate ± SE = −0.023 ± 0.049, $P = 0.6$; body condition: estimate ± SE = −0.011 ± 0.034, $P = 0.7$). In contrast, males with low-frequency hoots produced heavier and faster-growing nestlings ($PC1_{hoot}$: estimate ± SE = −0.22 ± 0.10, $P = 0.051$; with the average parent's body condition: estimate ± SE = 0.013 ± 0.019, $P = 0.6$; Fig. 3), even when we controlled for male body condition (CIFC: estimate ± SE = −0.27 ± 0.10, $P = 0.01$; with the average parent's body condition: estimate ± SE = 0.02 ± 0.02, $P = 0.3$; Fig. 3). However, no relationships were observed between chick growth rate and male body condition or size (body condition: Estimate ± SE = −0.03 ± 0.03, $P = 0.3$; body size: Estimate ± SE = −0.01 ± 0.03, $P = 0.7$).

Table 1
Pearson Correlation coefficients between hoot frequency parameters and $PC1_{hoot}$ resulting from the three parameters

	MaxF	MinF	MedianF	$PC1_{hoot}$
MaxF	1.00			0.47
MinF	0.24	1.00		0.94
MedianF	0.26	0.89	1.00	0.95

DISCUSSION

In the scops owl, we found that while body condition was not a significant predictor of reproductive performance, the frequency of the hoot, which is itself correlated with body condition, was a good predictor of reproductive performance as well as nestling growth rate, even once F0 was corrected for the variation in body condition. Males with low-pitch hoots, or lower-pitch hoots than predicted from their body condition, tended to mate with females that laid earlier and larger clutches, and tended to raise more fledglings that grew faster. It may be surprising that while male body condition is correlated with hoot frequency (see Hardouin et al. 2007), only the latter was correlated with reproductive performance, suggesting that hoot frequency is a more reliable predictor of male phenotypic quality than male body condition. Similar results have been found in human hunter-gatherers where men with lower-pitch voices father more children than men with higher-pitch voices (Apicella et al. 2007). In scops owls, only heavier males in good condition can afford to decrease their hoot frequency during territorial contests (Hardouin et al. 2007), and therefore selection for lower pitch is likely to be constrained (or stabilized) by the physiological cost of cheating (Maynard Smith & Harper 2003).

While the relationship between hoot frequency and fitness might reflect a direct advantage of producing lower-pitch hoots during male–male competition, it might also reflect a common underlying factor affecting both hoot frequency and reproductive success. For example, in several taxa, lower-pitch vocalizations are associated with higher circulating levels of testosterone (birds: Fusani et al. 1994; Cynx et al. 2005; humans: Evans et al. 2008), a hormone that is also known to determine arrival date in birds (Berthold 2001), that is, males with lower-pitch hoots might arrive earlier than those with higher-pitch hoots. The absence of any relationship between male body weight and reproductive performance may also be the result of a trade-off, mediated by testosterone levels, between hoot pitch and body condition. Indeed,

Author's personal copy

Table 2
Results of the linear models with parameter estimates, approximate SEs and *P* values from a *t* distribution (*t* values were obtained by the ratio between the estimates and their SEs) for the fixed-effects table

Independant variables	Male								Female			
	Body condition		Body size		$PC1_{hoot}$		Residuals of $PC1_{hoot}$ on body condition		Body condition		Body size	
	Estimate±SE	*P*	Estimate±SE	*P*	Estimate±SE	*P*	Estimate±SE	*P*	Estimate±SE	*P*	Estimate±SE	*P*
Female body condition	0.09±0.11	0.4	—	—	−0.44±1.53	0.77	0.11±0.11	0.3	—	—	—	—
Female body size	—	—	0.19±0.19	0.3	−0.06±0.57	0.9	−0.30±0.60	0.6	—	—	—	—
Reproductive performance ($PC1_{RP}$)	−0.03±0.09	0.7	−0.09±0.08	0.3	−0.60±0.22	0.01*	−0.64±0.24	0.01*	−0.02±0.04	0.6	−0.17±0.10	0.1

$N = 20$, except for 'Female body condition' $N = 19$.
*$P < 0.05$.

experimentally increased testosterone levels result in enhanced sexual ornamentation but also in a greater loss of condition in red grouse, *Lagopus lagopus scotica* (Mougeot et al. 2004). In scops owls, males with higher testosterone levels might suffer greater loss of body weight during the breeding season (e.g. they might be more active in competing with rivals); hoot pitch might therefore more directly reflect male quality and reproductive performance. Moreover, since hoot pitch is used during male territorial contests in scops owls (Hardouin et al. 2007), it could play a direct role in territory establishment: males with lower-pitch hoots could acquire and secure their territory earlier, and might therefore benefit from acquiring higher-quality territories, in terms of either nest site availability or food resources (Martìn-Vivaldi et al. 1999). In that case, advantages in terms of intrasexual competition for resources would be the basis for the observed relationship (Przybylo et al. 2001; Lampe & Espmark 2003).

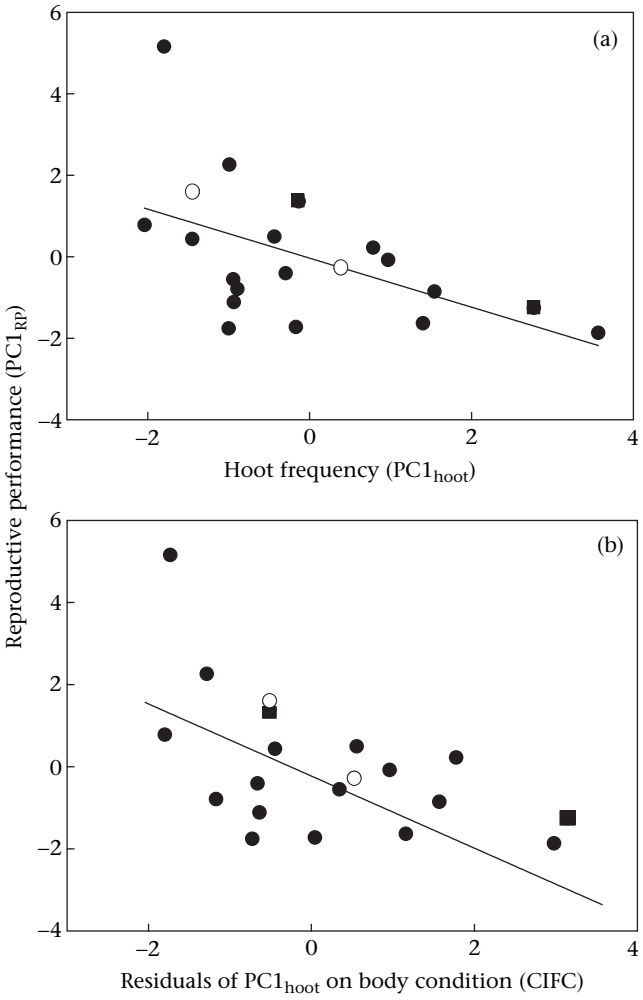


Figure 2. Scatterplots illustrating the negative relationship between $PC1_{RP}$ (i.e. relative laying date, relative clutch size, relative numbers of hatchlings and fledglings) and (a) $PC1_{hoot}$ and (b) CIFC. Positive values of $PC1_{hoot}$ indicate higher-pitch hoots; positive values of $PC1_{RP}$ indicate a stronger reproductive performance. The relationships remained significant even when removing the polygamous male (upper left points: $PC1_{hoot}$, estimate ± SD = −0.41 ± 0.17, $P = 0.02$; CIFC: estimate ± SD = −0.40 ± 0.18, $P = 0.04$). The two males followed in 2 successive years are labelled differently (white circle and black square).

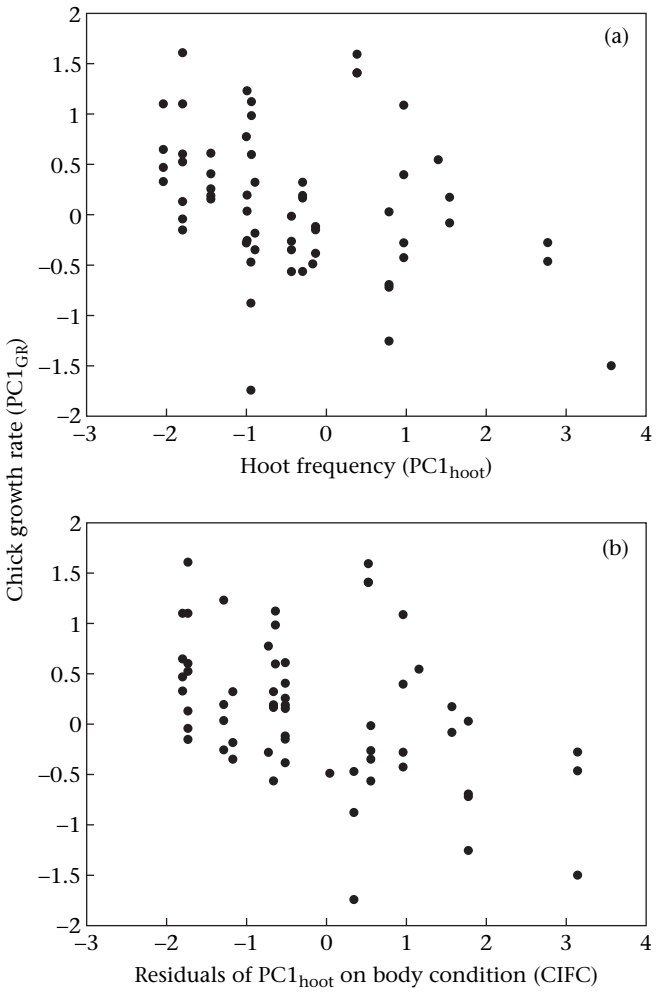


Figure 3. Scatterplots illustrating the relationship between the first axis of the principal component based on the three components of chick growth $PC1_{GR}$ and (a) $PC1_{hoot}$ and (b) CIFC. Positive values of $PC1_{hoot}$ indicate higher-pitch hoots and positive values of $PC1_{GR}$ indicate faster growth rate and heavier chicks at fledging.

Author's personal copy

We also found that males producing lower-frequency hoots than predicted by their body condition have an overall higher reproductive success. This relationship suggests that there is currently sexual selection for males to produce lower-pitch hoots in scops owls (see also Møller & Thornhill 1997). This reinforces the idea that hoot frequency could be driven by additional physiological constraints rather than just body weight and condition. However, the role of androgens in determining hoot frequency is yet to be investigated in our study species.

Our results did not reveal any relationship between female body condition and hoot frequency, male body condition or the residuals of hoot frequency over male condition. Females in better condition did not appear to mate with lower-frequency (i.e. better-quality) males. While this observation cannot be used to infer how pairs are formed in this species, it would be consistent with a 'lottery model' of mate choice, where females obtain the best available territory even without choosing mate or territories (Aebischer et al. 1996). Since male scops owls are likely to occupy territories sequentially and in order of decreasing quality (at least using hoot frequency as a proxy of male quality), the few unpaired males available at any moment also occupy the best available territory (Aebischer et al. 1996). Future studies should investigate the timing of female arrival from the wintering areas, as well as the possible use by females of male hoot frequency as a signal of male quality.

In our study, we found no relationship between reproductive performance and female body condition, at least as measured using the indexes available to us. In fact, none of the traits or indexes of reproductive performance (relative laying date, relative clutch size, hatchlings and fledglings) were correlated with either female or male body condition. Although a similar result (i.e. female body condition uncorrelated with fecundity or survival) has been reported in some species (e.g. blue petrels, *Halobaena caerulea*: Chastel et al. 1995), in many others, heavier females produce larger clutches and heavier males achieve higher reproductive success and survival rates (e.g. Newton 1986; Velando et al. 2003). Finally, in migratory birds, prior ownership is also likely to affect arrival date, and males may invest differentially in regaining the territory they owned in the previous year, depending on the quality of their territory rather than on their own quality or condition (Forstmeier 2002).

Our results therefore suggest that, in scops owls, the phenotypic quality of the male, as reflected in its ability to secure/defend a territory, might be key to the pair's reproductive performance. This is consistent with similar observations in several species of birds (e.g. Korpimäki 1992) and amphibians (Wells 1977). In this respect, scops owls are comparable to many migrating passerines, and we note that the population of scops owl studied here migrates to Africa in winter. One possible interpretation would be that better-quality males are ready for spring migration earlier than other males, and therefore secure better breeding territories, enabling them to mate first with females. As we did not observe any significant correlation between indexes of female quality and reproductive performance, the role of female quality, as we measured it, is less obvious. However, we cannot exclude the possibility that other indexes of female quality might affect the brood's success. Finally, further studies are needed to establish whether reproductive success is directly determined by male quality or indirectly via the quality of male territories.

In conclusion, while in a previous study we demonstrated that, during territorial contests, male scops owls adapted their behaviour according to the frequency contour of their opponent's hoots (Hardouin et al. 2007), here we have shown that males with lower hoot frequencies have an overall better reproductive success. This constitutes the first evidence in a nonpasserine species that the fundamental frequency of a sexual call advertises individual fitness. This result calls for further playback experiments to investigate whether hoot frequency determines, or merely reflects, male reproductive success.

Acknowledgments

We thank Véronique Gosson for her valuable help with fieldwork and Dr Sébastien Descamps for his contribution to the recordings in 2002. We are grateful to Catherine Lemarchand, Loïc Mimaud and the students of 'Le Marais aux Oiseaux' for their help with fieldwork. We are particularly indebted to Drs Gwénaël Beauplet, Ben Charlton, Karen McComb and Alexandre Millon for their helpful advice and comments at different stages of the manuscript. We greatly thank Drs Andrea Pilastro, Wolfgang Forstmeier and an anonymous referee for their helpful comments. L.A.H was supported by a grant from the University Louis Pasteur of Strasbourg.

References

Aebischer, A., Perrin, N., Krieg, M., Studer, J. & Meyer, D. R. 1996. The role of territory choice, mate choice and arrival date on breeding success in Savi's warbler *Locustella luscinioides*. *Journal of Avian Biology*, **27**, 143–152.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Apicella, C. L., Feinberg, D. R. & Marlowe, F. W. 2007. Voice pitch predicts reproductive success in male hunter-gatherers. *Biology Letters*, **3**, 682–684.

Ballentine, B., Hyman, J. & Nowicki, S. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology*, **15**, 163–168.

Bavoux, C., Burneleau, G. & Nicolau-Guillaumet, P. 1991. Aspects de la biologie de reproduction du Hibou petit-duc, *Otus scops*. *Alauda*, **59**, 65–71.

Bavoux, C., Burneleau, G., Juillard, M. & Nicolau-Guillaumet, P. 1993. Le petit-duc, *Otus scops*, sur l'île d'Oléron: régime alimentaire des poussins. *Nos Oiseaux*, **42**, 159–170.

Beani, L. & Dessì-Fulgheri, F. 1995. Mate choice in the grey partridge, *Perdix perdix*: role of physical and behavioural male traits. *Animal Behaviour*, **49**, 347–356.

Bee, M. A. 2002. Territorial male bullfrogs (*Rana catesbeiana*) do not assess fighting ability based on size-related variation in acoustic signals. *Behavioral Ecology*, **13**, 109–124.

Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, **58**, 385–399.

Berthold, P. 2001. *Bird Migration: a General Survey*. New York: Oxford University Press.

Chastel, O., Weimerskirch, H. & Jouventin, P. 1995. Influence of body condition on reproductive decision and reproductive success in the blue petrel. *Auk*, **112**, 964–972.

Cynx, J., Jay Bean, N. & Rossman, I. 2005. Testosterone implants alter the frequency range of zebra finch songs. *Hormones and Behavior*, **47**, 446–451.

Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.

Evans, S., Neave, N., Wakelin, D. & Hamilton, C. 2008. The relationship between testosterone and vocal frequencies in human males. *Physiology and Behavior*, **93**, 783–788.

Fitch, W. T. & Hauser, M. D. 2002. Unpacking 'honesty': vertebrate vocal production and the evolution of acoustic signals. In: *Acoustic Communication* (Ed. by A. M. Simmons, R. R. Fay & A. N. Popper), pp. 65–137. New York: Springer.

Forrest, T. G. & Raspet, R. 1994. Model of female choice in acoustic communication. *Behavioral Ecology*, **5**, 293–303.

Forstmeier, W. 2002. Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology*, **71**, 1–9.

Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. 2002. A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal Society B*, **269**, 1479–1485.

Fusani, L., Beani, L. & Dessi-Fulgheri, F. 1994. Testosterone affects the acoustic structure of the male call in the grey partridge (*Perdix perdix*). *Behaviour*, **128**, 301–310.

Galeotti, P., Sacchi, R. & Pirani, E. 1997. Cooperative defence and intrasexual aggression in scops owls (*Otus scops*): responses to playback of male and female calls. *Journal of Raptor Research*, **31**, 353–357.

Galeotti, P., Sacchi, R., Pelliteri Rosa, D. & Fasola, M. 2005. Female preference for fast-rate, high-pitched calls in Hermann's tortoises *Testudo hermanii*. *Behavioral Ecology*, **16**, 301–308.

Genevois, F. & Bretagnolle, V. 1994. Male blue petrels reveal their body mass when calling. *Ethology Ecology & Evolution*, **6**, 377–383.

Grafen, A. 1990. Biological signals as handicap. *Journal of Theoretical Biology*, **144**, 517–546.

Author's personal copy

Hardouin, L. A., Reby, D., Bavoux, C., Burneleau, G. & Bretagnolle, V. 2007. Communication of male quality in owl hoots. *American Naturalist*, **169**, 552–562.
Hutchinson, J. M., McNamara, J. M. & Cuthill, I. C. 1993. Song, sexual selection, starvation and strategic handicaps. *Animal Behaviour*, **45**, 1153–1177.
Jakob, E. M., Marshall, S. D. & Uetz, G. W. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*, **77**, 61–67.
Koenig, L. 1973. Das Aktionssystem der Zwergohreule *Otus scops scops* (Linné 1758). *Zoologische Tierpsychologie*, **13**, 1–124.
Kokko, H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**, 940–950.
Kokko, H., Brooks, R., McNamara, J. M. & Houston, A. I. 2002. The sexual selection continuum. *Proceedings of the Royal Society B*, **269**, 1331–1340.
Korpimäki, E. 1992. Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's owls. *Journal of Animal Ecology*, **61**, 103–111.
Lampe, H. M. & Espmark, Y. O. 2003. Mate choice in pied flycatchers *Ficedula hypoleuca*: can females use song to find high-quality males and territories? *Ibis*, **145**, E24–E33.
Leitão, A. & Riebel, K. 2003. Are good ornaments bad armaments? Male chaffinch perception of songs with varying flourish length. *Animal Behaviour*, **66**, 161–167.
Leonard, M. L. & Horn, A. G. 1995. Crowing in relation to status in roosters. *Animal Behaviour*, **4**, 1283–1290.
Lukefahr, S. D., Odi, H. B. & Atakora, J. K. 1996. Mass selection for 70-day body weight in rabbits. *Journal of Animal Sciences*, **74**, 1481–1489.
Martìn-Vivaldi, M., Palomino, J. J. & Soler, M. 1998. Song structure in the hoopoe (*Upupa epops*): strophe length reflects male condition. *Journal für Ornithologie*, **139**, 287–296.
Martìn-Vivaldi, M., Palomino, J. J., Soler, M. & Martinez, J. G. 1999. Song strophe-length and reproductive success in a non-passerine bird, the hoopoe *Upupa epops*. *Ibis*, **141**, 670–679.
Maynard Smith, J. & Harper, D. 2003. *Animal Signals*. New York: Oxford University Press.
Møller, A. P. & Thornhill, R. 1997. A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology*, **10**, 1–16.
Mougeot, F., Irvine, J. R., Seiwright, L., Redpath, S. M. & Piertney, S. 2004. Testosterone, immunocompetence, and honest sexual signaling in male red grouse. *Behavioral Ecology*, **15**, 930–937.
Newton, I. 1986. *The Sparrowhawk*. London: T. & A.D. Poyser.
Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. 2005. nlme: Linear and nonlinear mixed effects models. R package version 3.1-65. http://cran.r-project.org.
Przybylo, R., Wiggins, D. A. & Merilä, J. 2001. Breeding success in blue tits: good territories or good parents? *Journal of Avian Biology*, **32**, 214–218.
R Development Core Team 2007. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. http://www.R-project.org.
Reby, D. & McComb, K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, **65**, 519–530.
Ricklefs, R. E. 1983. Avian postnatal growth. In: *Avian Biology* (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 1–83. New York: Academic Press.
Riede, T. & Fitch, W. T. 1999. Vocal tract length and acoustics of vocalization in the domestic dog *Canis familiaris*. *Journal of Experimental Biology*, **202**, 2859–2867.
Ryan, M. J. 1980. Female mate choice in a neotropical frog. *Science*, **209**, 523–525.
Sacchi, R., Galeotti, P., Fasola, M. & Ballasina, D. 2003. Vocalizations and courtship intensity correlate with mounting success in marginated tortoises *Testudo marginata*. *Behavioral Ecology and Sociobiology*, **55**, 95–102.
ten Cate, C., Slabbekoorn, H. & Ballintijn, M. R. 2002. Birdsong and male–male competition: causes and consequences of vocal variability in the collared dove (*Streptopelia decaocto*). *Advances in the Study of Behavior*, **31**, 31–75.
Thomas, R. J., Cuthill, I. C., Goldsmith, A. R., Cosgrove, D. F., Cosgrove, D. F., Lidgate, H. C. & Burdett Proctor, S. L. 2003. The trade-off between singing and mass gain in a daytime-singing bird, the European robin. *Behaviour*, **140**, 387–404.
Vannoni, E. & McElligott, A. G. 2008. Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. *PLoS One*, **3**, e3113, doi:10.1371/journal.pone.0003113.
Velando, A., Lessells, C. M. & Márquez, J. C. 2003. The function of female and male ornaments in the Inca tern: evidence for links between ornament expression and both adult condition and reproductive performance. *Journal of Avian Biology*, **32**, 311–318.
Wells, K. D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour*, **25**, 666–693.
Withey, J. C., Bloxton, T. D. & Marzluff, J. M. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. In: *Radio Tracking and Animal Populations* (Ed. by J. J. Millspaugh & J. M. Marzluff), pp. 43–75. San Diego: Academic Press.
Zach, R., Liner, Y., Rigby, G. L. & Mayoh, K. E. 1984. Growth curve analysis of birds: the Richards model and procedural problems. *Canadian Journal of Zoology*, **62**, 2429–2435.
Zahavi, A. & Zahavi, A. 1997. *The Handicap Principle: a Missing Piece of Darwin's Puzzle*. Oxford: Oxford University Press.