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INDICATORS OF MALE QUALITY IN THE HOOTS OF TAWNY OWLS (*STRIX ALUCO*)

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Abstract.—The number of songs in a male's repertoire, and the amount of time he spends singing, have been shown to correlate with territory size and quality, reproductive success, parental care and parasite load in some passerine species. In addition, females of some species use song rate and complexity as a cue to mate choice and are more responsive to more frequent and complex songs. Few studies, however, have examined the influence of body size and parasitic infections on the sound frequency (pitch) and structure of vocalizations of birds. The Tawny Owl (*Strix aluco*) hoot is important in communication between birds at night when visual information is limited, and is simple enough to allow a quantitative analysis of its structure. Six temporal and four frequency measures of the hoots of 50 Tawny Owls were taken, and compared to body mass, wing length, breeding success and number and intensity of parasitic infections of the singers. There was a decrease in call frequency with increasing body mass and the vibrato tail of the last note was longer in larger birds, but there was no part of the call that correlated with breeding success. There was an increase in call frequency as the number of parasitic infections increased, and there was a decrease in the length of calls as the intensity of parasitic infections increased.

Key Words: Strix aluco; *hoot structure; body weight; body size; breeding success; blood parasites; female choice; assessment.*

Indicadores de calidad del macho en ululatos de *Strix aluco.*

Resumen.—La cantidad de canciones en el repertorio del macho, y la cantidad de tiempo que dedica cantando, han mostrado una correlación entre el tamaño del territorio y la calidad del éxito de reproducción, preocupación paterna, y carga parasítica en especies *passerinus.* En suma, hembras usan la velocidad y complicación de la canción como señal para escoger su pareja están mas interesadas en canciones complicadas y de mas frecuencia. Pocos estudios, sin embargo, han examinado la influencia del tamaño corporal y infeccion parasítica en la frecuencia modulada del sonido (tono) y estructura de vocalización en pájaros. El ululato de *Strix aluco* es importante en comunicación entre los pájaros por la noche cuando información visual es limitada, y es lo suficientemente como simple para dejar un análisis cualitativo de su estructura. Seis temporal y cuatro frecuencias moduladas de los ululatos de 50 *S. aluco* fueron tomados, y comparados al tamaño corporal, largo de ala, éxito de cría, y numeros e intensidad de infección parasítica de los cantadores. Hubo reducción en frecuencia de llamadas y aumento de el tamaño corporal y la cola *vibratus* de la ultima nota fue mas larga en los pájaros grandes, pero no hubo ninguna parte de la llamada que hizo correlación con el éxito de cría. Hubo un aumento en la frecuencia de llamadas cuando la cantidad de infeccion parasítica aumentaron, y hubo una reducción en la duración de llamadas cuando la intensidad de infeccion parasítica aumento.

[Traducción de Raúl De La Garza, Jr.]

Some bird species can recognize their offspring (Tschanz 1968, Beer 1969, Beecher et al. 1981), mates (White 1971, Brooke 1978, Jouventin et al. 1979) and territorial neighbors (Falls 1992, Galeotti and Pavan 1993) through their vocalizations. Song can also give information on the position and orientation of the signaler (Richards 1981, Mcgregor and Falls 1984, McGregor and Krebs 1984).

Song appears to also be important in sexual selection in many species and females have been shown to be more responsive to males with higher song output (Houtman 1992, Payne and Payne 1977) whether song output was increased by lengthening songs or reducing intersong intervals (Wasserman & Cigliano 1991). In Willow Warbler (*Phylloscopus trochilus*) males, there was a link between high song output and good territories (Radesater et al. 1987, Radesater & Jakobsson 1989), and Houtman (1992) showed that Zebra Finch (*Poephila guttata*) males with higher song output produced heavier offspring. Females of some species have also been shown to prefer males with more complex repertoires (Searcy & Marler 1984, Baker et al. 1986, Catchpole et al. 1984, Eens et al. 1991a). The complexity of song has been found to correlate with territory size, survival and reproductive success (Hiebert et al. 1989, McGregor et al. 1981, Catchpole 1986).

As song is used by males to attract females, it has been hypothesized that song may give information on the parasite infections of male singers. Hamilton & Zuk (1982) found bird species with more complex songs were more likely to have blood parasite infections, but this correlation disappeared when phylogeny was taken into account (Read & Weary 1990). Møller (1991) studied the effect of parasites within a population of Barn Swallows (*Hirundo rustica*) and found that males infected with mites produced less song.

Despite the implications for mate choice, little is known about how the size and weight of a bird affects its vocalizations, and whether parasite infections affect the structure or frequency of a bird's call. This is particularly relevant for nocturnal birds, which may not have detailed visual information about a potential mate or rival. In this paper, we present an analysis of the information contained in the "hoot" vocalization of the Tawny Owl (*Strix aluco*). Tawny Owls are nocturnal woodland birds, so visual information transferred between territorial rivals or potential mates at night is probably very limited. The hoot is individually distinct and constant with time and is thought to function in communication between the sexes as well as territorial defense (Galeotti & Pavan 1991).

METHODS

Recordings of Tawny Owls were made at Wytham Woods, Oxfordshire (51.46° N 1.2° W), Monks Wood, Cambridgeshire (52.24° N 0.14° W), a farmland area, (The 'Fens') Cambridgeshire (52.29° N 0.1° W) and Kielder Forest, Northumberland (55° 15'N 2° 35'W). Recordings were made using a Uher or Sony Walkman Professional tape recorder (TC-D5 PRO) with a Sennheiser MZW 816 microphone. Recordings were made of male birds on calm, dry nights from October–December 1992–93 in Wytham Woods, and in March 1993 in Monks Wood and the Fens. Recordings of birds at Kielder Forest were made in November 1994. Birds were stimulated to hoot using playback of an unfamiliar male owl. The hoots of male owls can be distinguished from hoots of female owls by the squeaky grating quality of the female hoot. In the case of the Wytham owls, the sex of the birds was confirmed using radiotags. Recordings were made as near to birds as possible, at distances between 5–50 m.

Sonograms were produced on a Macintosh LCII computer. Tawny Owl hoots have a basic structure of three notes (Fig. 1) that can be clearly determined in owls from all areas. Sonograms of the whole hoot were made using Soundedit Pro software (Macromind Paracomp, Inc., 600 Townsend, San Francisco, CA 94103 U.S.A. 1992) and temporal measures were recorded. Soundedit Pro did not give accurate frequency measures, so sonograms of the first note of each hoot were made with Canary software (Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850 U.S.A.), and the frequency measures were recorded.

Temporal measures used were similar to those described by Galeotti and Pavan (1991). Six temporal measures were recorded for each call. These were: note 1 (D1), internote interval one (I4), note two (D2), internote interval two (I5) and note 3 was split up into frequency modulated length (FML) and tail (Fig. 1). Frequency measures used were the highest and two lowest frequencies of the first note (HIGH, LOW1 and LOW2) and the middle of the highest part of the first note (MED). All time measures were recorded in milliseconds (ms) and all frequency measures were recorded in KHz. Only clear recordings with little background noise were used for making sonograms. Any sonograms where all call parameters could not be determined were discarded. An "average" sonogram was calculated for each owl by taking the mean of a minimum of 3 calls from each owl.

Breeding success of owls was measured at Wytham Woods, Monks Wood and the Fens in 1993. Breeding success was defined as the total number of owlets fledged/-breeding area and was found by monitoring nests or by locating calling chicks in June and July before mortality of fledged chicks has occurred. Fledged young can be located in June and July when they call loudly and continuously for food (Muir 1954, Southern 1970).

Males were caught in spring 1993 and 1994 using nest-box traps (Petty et al. 1994). Males were weighed, measured for wing length and blood slides were prepared by placing a drop of blood from the branchial vein directly onto a glass slide and smearing it with a second slide to produce a blood layer one cell thick. The smear was then air dried and fixed in absolute ethanol and stained with Giemsa's stain. Parasite species were identified by M. Anwar at Oxford University and the number of each species was quantified by counting the number of parasites in 10 000 blood cells. The two measures of parasite infection used were the number of parasite species present and the total number of blood cells containing parasites (all parasite species pooled). For some owls, the blood parasite counts and body measurements were taken at differ-

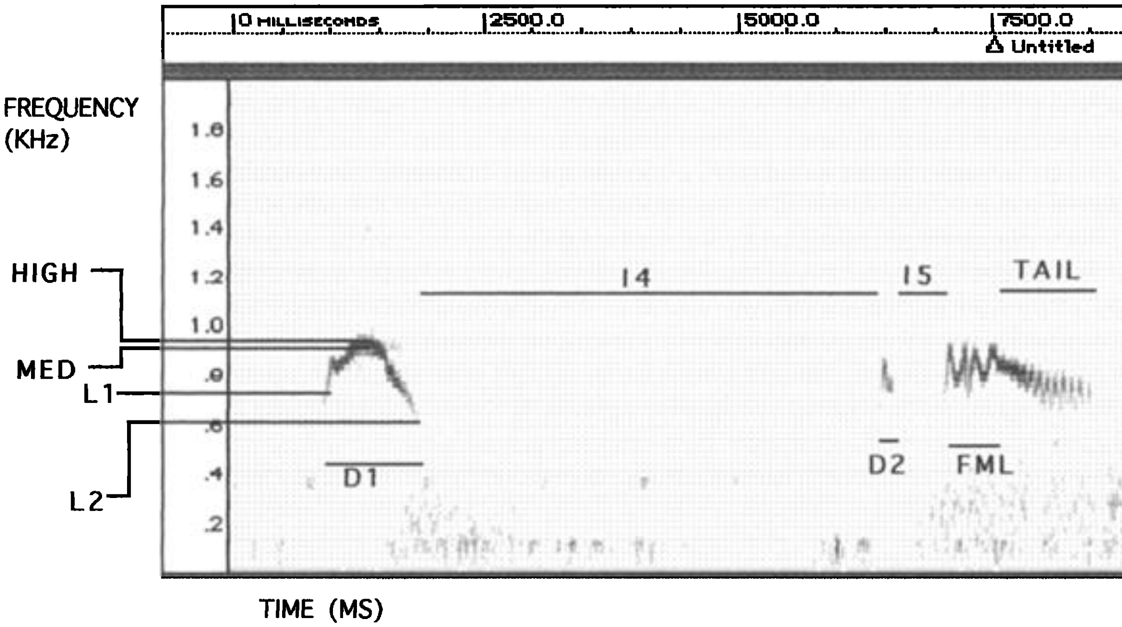

Figure 1. Sonogram of Tawny Owl hoot showing time and frequency measures.

ent times of year than recordings of their hoots. In this case, the identity of the owl was confirmed using radiotags or by confirming that the same male was present the following breeding season.

The data were examined visually using histograms and no evidence was found for a significant deviation from the normal distribution. Parametric tests were therefore used.

RESULTS

The hoots of 50 male Tawny Owls were recorded at the four study sites (Table 1). Although none of the temporal measures of call varied significantly among the four sites (ANOVA, $P > 0.05$), there was a significant difference between the sites in all of the frequency measures (LOW1 $F_{3,46} = 17.03$, $P < 0.0001$; LOW2 $F_{3,46} = 12.58$, $P < 0.0001$; MED $F_{3,46} = 4.63$, $P = 0.007$; HIGH $F_{3,46} = 6.08$, $P = 0.001$). The Kielder owls were lighter than those of the other populations ($F_{3,15} = 3.25$, $P = 0.051$), but this was based on only 4 birds from Kielder and there was no significant difference among the sites for wing length and the breeding success of pairs ($P > 0.05$).

Table 1. The number of Tawny Owls from the four study sites for which data on both call parameters and body measurements, breeding success and parasite loads were available.

STUDY SITE	# OWLS	BODY MASS	WING LENGTH	FLEDGING SUCCESS	# INFECTIONS	PARASITE LOAD
Wytham	20	5	5	20	4	4
Monks Wood	9	4	4	9	0	0
Fens	16	6	6	16	0	0
Kielder	5	4	0	0	4	4

Pearson Rank Correlations were not significant for body mass, wing length, breeding success and parasite number and load for any of the owls used in the analysis; however, there was a significant correlation between number of parasites and breeding success ($r = 1$, $P < 0.001$) which was based on only four Wytham owls.

There was no significant correlation between the body mass of a bird and the length of any of the notes or the internote intervals of its call, but there was a negative correlation between the highest frequency of the song and body mass (Fig. 2, $r = -0.48$, $P < 0.05$). There was no significant correlation between wing length and any of the frequency measures of the call. The only time measure of the call that correlated significantly with wing length was the tail of the third note ($r = 0.71$, $P < 0.003$). Likewise, there was no significant cor-

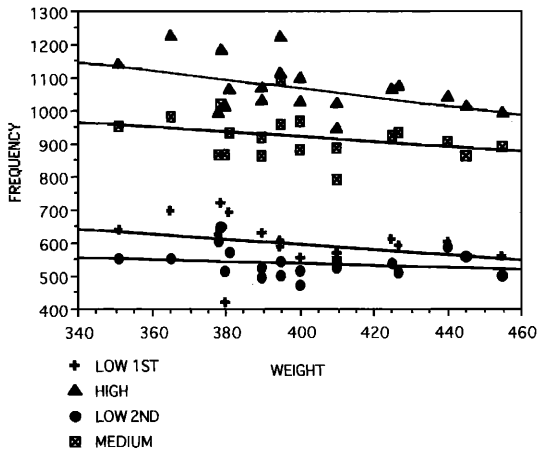

Figure 2. Effect of body mass of Tawny Owls on the four frequency measures of their hoots.

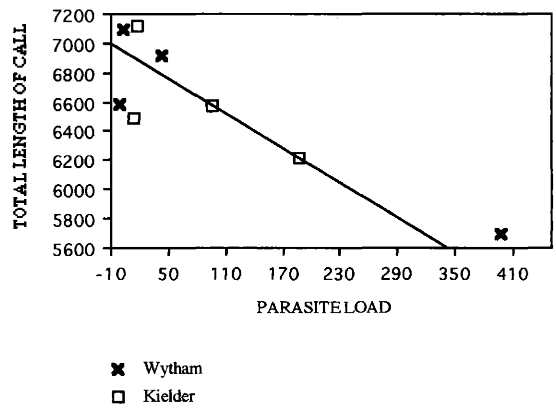

Figure 4. Effect of parasite load on the total length of Tawny Owl hoots.

relation between average breeding success in 1993 and any of the call parameters. All four frequencies were entered into a regression model as independent variables to try to predict breeding success as the dependent variable, however the model did not significantly predict breeding success ($F_{4,40}$ = 0.29, P = 0.88).

The number of parasite species present in an individual ranged between one and four. The parasites found were *Leucozytozoon ziemanni, Haemoproteus syrnni, H. noctuae* and *Trypanosoma*. All frequency measures increased with increasing numbers of parasites (Fig. 3), but this was only significant for the lowest frequency at the start of the first note. The Kielder birds had higher numbers of parasites and higher frequency calls, but due to the small sample size it was not possible to analyze the data by site to see if the relationship held in each case.

There was a significant negative correlation between the length of the internote interval ($r = -0.75$, $P < 0.05$), gaps in the song ($r = -0.76$, $P < 0.05$), and the total length of the song (Fig. 4, $r = -0.87$, $P < 0.05$) and the parasite load, but there was no significant correlation with any of the frequencies measured ($P > 0.05$).

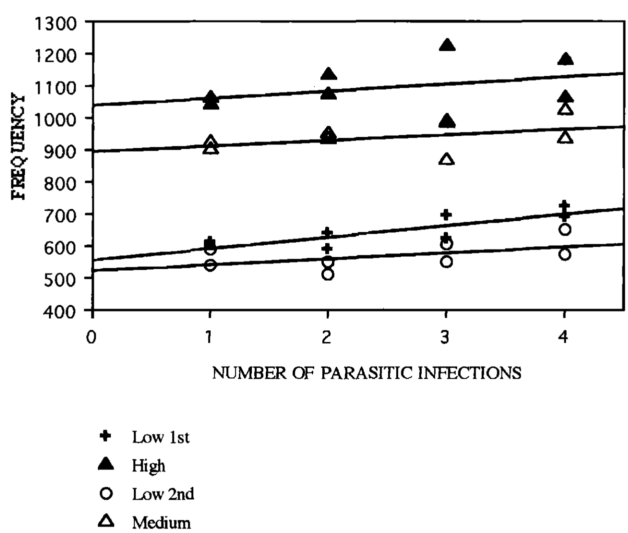

Figure 3. Effect of parasitic infections of Tawny Owls on the four frequency measures of their hoots.

DISCUSSION

For a bird embarking on a territorial dispute, assessing the size of the opponent is important in predicting the probable outcome of a fight. This is especially true for an aggressive bird like a Tawny Owl, where vocal disputes are often fierce and prolonged. For a female assessing a potential mate, the body mass of a male might give information on resources available in his territory. The size of the syrinx is likely to affect the frequency of the call and could vary with the size of a bird. We found that the highest frequency of Tawny Owl calls to be more closely correlated with body mass than the lowest frequency. This decrease in highest note frequency with size implies that birds might be emitting their highest note to advertise their small size. Newton (1988) found that smaller sparrowhawk males had a higher lifetime reproductive success than large males. Although the selective pressures favoring reduced size in Tawny Owl males are probably different to those in sparrowhawks, reversed sexual dimorphism implies there might be selection for smaller males in Tawny Owls. Females might, therefore, favor small males and be using male hoots to assess this.

The only call parameter that correlated significantly with wing length was the length of the vibrato tail of the third note, which increased with wing length. Wing length is an indication of body size of birds. It is possible that a larger bird might be able to sustain the last note for a longer time, perhaps due to increased lung volume. Data on more birds would be needed to ascertain whether the length of the last note was a reliable signal of body size.

None of the measures of the call were significantly correlated with breeding success, so there is no detectable signal that females could reliably use to assess the breeding capability of a potential partner. As there was only one year's breeding data available, and this varies with food supply and site (Petty 1992), it is possible that a correlation does exist between reproductive ability and call parameters, but it was obscured by other factors.

All measures of frequency increased with increasing number of parasitic infections and this was significant for the lowest frequency at the start of the first note. Males that are able to give low frequency calls might therefore be indicating a resistance to parasites. Birds with higher parasite loads gave significantly shorter calls. Physiological reasons that might cause this are obscure, but it might imply that long calls are costly to give and are therefore an indication of good health. In frogs, heavily infested males have also been shown to have below average call durations (Read 1988), and long calls in frogs are more effective in attracting females (Rand and Ryan 1981, Wells and Schwartz 1984, Ryan 1985). Lengths of owl hoots are fairly constant with time (Hirons 1976) so it is possible that call length could be utilized to signal parasite burdens and potential breeding capabilities.

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