

## Variation in the male territorial hoot of the Tawny Owl *Strix aluco* in three English populations

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Little is known about owl song. We made sonagrams of the territorial calls of 50 male Tawny Owls *Strix aluco* from three different areas. Six temporal and four frequency measures of the calls were recorded from the sonagrams. The measures of the calls were then subjected to analysis to try to separate between individual owls and between owls from different areas. We also looked for similarities between calls of neighbouring owls and for any effect of habitat on owl hoots. Individual owls were separated on the basis of their hoots with a high degree of success (98.6% overall), and there were significant differences between areas. Differences were found between calls in woodland and farmland habitats, but these differences were not in the direction expected to increase sound transmission. Calls of neighbouring owls did not resemble each other more than calls from owls that were not in vocal contact, implying that if calls are learned by Tawny Owls, they are learned before dispersal.

When a bird sings, the two fundamental questions asked by behavioural researchers are (1) what advantage does the bird gain from singing? and (2) why should other birds respond to the signal in the way they do? In order to address these questions, it is necessary to know what information the song contains. In order to know this, it is useful to know whether the song was learned before or after dispersal. Song that developed before dispersal might be similar in closely related birds, giving information that may be used for kin recognition and mate choice. Song that developed after dispersal might result in local dialects and adaptation of song to habitat.

Much has been written about song development, dialects and environmental influences on song structure in passerines (e.g. Thorpe 1958, Marler 1970, Nottebohm 1975, Baptista & Johnson 1982, Mundinger 1982, Anderson & Connor 1985, McGregor & Thompson 1988, DeWolfe *et al.* 1989, Williams & Slater 1993). Few studies have addressed these issues in nonpasserines, possibly because song learning is not thought to be common in nonpasserine species. Song learning has been documented in only four families of nonpasserines compared with 33 families of passerines (Kroodsma 1982), and some nonpasserine species have been shown not to need learning to develop normal song (dove species: Lade & Thorpe 1964, Nottebohm & Nottebohm 1971; domestic fowl: Konishi 1963). However, song learning and dialects have been shown to occur in the Bobwhite Quail *Colinus virginianus* (Goldstein 1978, Bailey & Baker 1982). Another reason that nonpasserine song has received so little attention is that the emphasis in the past has been

towards qualitative description of syllable types, whereas the more simple song of nonpasserines requires quantitative analysis by sonagrams to investigate individual and population characteristics.

In this paper, we present the results of a quantitative study of the male territorial hoot of the Tawny Owl *Strix aluco*. Galeotti and Pavan (1991) showed that individual male Tawny Owls could be distinguished on the basis of temporal characteristics of this hoot, and Galeotti and Pavan (1993a) claimed that males respond more strongly to playback of territorial hoots of strangers than to hoots of neighbours. This implies that Tawny Owls make use of the information in the hoot to distinguish individuals.

We made recordings from Tawny Owls in three areas of southern England. Two of the areas were woodland habitat and one was farmland habitat. We made sonagrams of the hoots and took six temporal measures and four frequency measures from each one. We wanted to examine whether there were differences between the three areas and, if so, whether hoots in woodland were different than hoots in farmland. The acoustic adaptation hypothesis (Williams & Slater 1993) proposes that bird songs that are transmitted more effectively through a particular habitat are more likely to be heard and learned by other birds in that habitat, leading to song becoming adapted to the environment in which a bird lives. Adaptation of Tawny Owl song to the habitat could therefore be taken to be indirect evidence of post-dispersal song learning. The acoustic adaptation hypothesis would predict that owls in dense woodland should have calls at a lower frequency than those in open farmland because

lower frequencies travel better through obstacles such as leaves and branches. If post-dispersal learning is occurring in owl populations, then we would also expect the hoots of neighbouring birds to be more similar than the hoots of birds not in vocal contact.

## METHODS

### Study sites

Our three recording sites were in southern England at Wytham Woods, Oxfordshire (51°46'N, 1°2'W); Monks Wood, Cambridgeshire (52°24'N, 0°14'W) and the Fens, Cambridgeshire (52°29'N, 0°1'W). Wytham Woods is an area of 525 ha of mixed deciduous woodland surrounded by farmland. Monks Wood is an area of 148 ha of similar woodland, and the Fens study area is 16,000 ha of open farmland, with woods covering <0.5% of the area.

Average Tawny Owl territory sizes were 22 ha in Wytham Woods (B. Appleby, unpubl. data) and 15 ha in Monks Wood. Home range size in the Fens was 126 ha (S.M. Redpath, unpubl. data). The centre of the Monks Wood study site was about 20 km from the centre of the Fens study site. The centre of Wytham Woods was over 150 km from both the other sites.

Recordings were made of the hoots of 23 male owls from Wytham Woods, 10 from Monks Wood and 17 from the Fens. In all three sites, these accounted for nearly all the owls present in the study area.

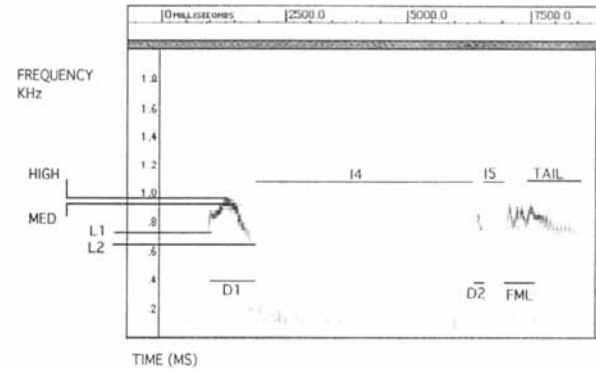
### Recording equipment and methods

Recordings were made using a Uher or Sony Walkman Professional tape recorder (TC-D5 PRO) with a Sennheiser MZW 816 microphone. Recordings were made on calm, dry nights from October to December 1992 and 1993 in Wytham Woods and in March 1993 in Monks Wood and the Fens. Birds were stimulated to hoot using playback of an unfamiliar male owl. Recordings were made as near to birds as possible, at 5–50 m.

### Sonagram production

Sonagrams were made on a Macintosh LCII computer. Sonagrams of the whole hoot were made using Soundedit Pro software (Macromind Paracomp, Inc., San Francisco, California, USA), and temporal measures were read off the screen. Soundedit Pro did not give accurate frequency measures, so sonagrams of the first note of each hoot were made with Canary software (Cornell Laboratory of Ornithology, Ithaca, New York, USA), and the frequency measures were read off the screen.

The temporal measures used were similar to those described by Galeotti and Pavan (1991). Six temporal measures were recorded for each call (Fig. 1): note 1 (D1), internote interval one (I4), note two (D2), internote interval two (I5) and note 3, which was split up into frequency mod-



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

ulated length (FML) and tail. 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, and all frequency measures were recorded in kilohertz.

### Analysis

Measures were taken from two to five hoots per owl (mean = 4). For all analyses, except the discrimination of individual owls, a mean was taken of the measures for each owl to give an average hoot for each owl.

Owls in the Fens were classed as out of vocal contact when their territories were over 5 km apart with at least two intervening territories between them. Owls in Wytham Woods were considered out of vocal contact if there were more than 2 km and three intervening territories between them and their territories were in different sections of the wood. Wytham Hill separates the three main sections of the wood, providing an acoustic barrier. Monks Wood is much smaller than the other two study sites, so we had to class owls as out of vocal contact if there were more than 1 km and two intervening territories between owls. Tawny Owls can hear and answer each other at a distance of 1.5 km over open land (Anderson 1961). Although sound does not travel as far in woodland, there was a slight chance that owls classed as out of vocal contact in Monks Wood might be able to hear each other occasionally. Because the three sites were analysed separately, any vocal contact between Monks Wood owls would not affect the results for the other two sites.

STATISTICA software (Statsoft, Inc., Tulsa, Oklahoma, USA) was used for discriminant analysis of individuals and populations and for ANOVA tests. SAS software (SAS Institute Inc., Cary, North Carolina, USA) was used for principal component analysis (PCA) to look for similarities between neighbours.

**Table 1.** Results of univariate ANOVA between individual Tawny Owls for each of the ten measures of the hoot

	F-ratio <sub>44,97</sub>	P-value
I5	27.3	<0.001
I4	26.4	<0.001
TAIL	14.5	<0.001
D1	18.2	<0.001
D2	5.1	<0.001
FML	21.1	<0.001
LOW1	7.7	<0.001
HIGH	36.2	<0.001
LOW2	10.4	<0.001
MED	44.3	<0.001

**Table 3.** Canonical coefficients of the first two discriminant functions separating individual Tawny Owls

	Root 1	Root 2
MED	-0.52	-0.23
I4	-0.19	0.71
I5	0.63	-0.61
FML	0.07	-0.05
D1	0.18	0.08
TAIL	0.31	-0.03
LOW2	0.23	0.25
D2	0.27	-0.37
HIGH	-0.39	-0.42
LOW1	-0.06	0.14

## RESULTS

### Discrimination of individual owls

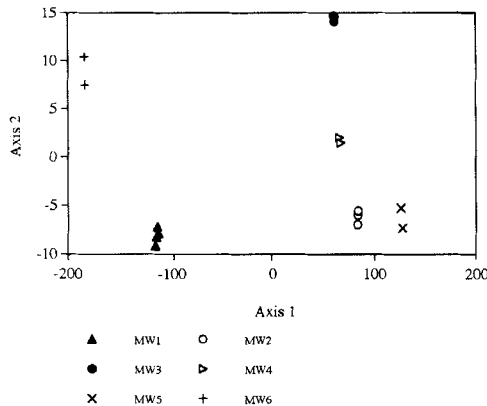
Analysis of variance showed that all the parameters differed significantly between individual owls (Table 1). Discriminant analysis on all ten measures allowed 98.6% of hoots to be attributed to the correct individual. There was some redundancy in parameter selection because several parameters were significantly intercorrelated (Table 2). All nine discriminant functions generated were statistically significant ( $P < 0.01$ ). MED and I5 contributed most to the first discriminant function, measures I4 and I5 to the second (Table 3). The first canonical axis was plotted against the second and shows a clear separation between owls (Fig. 2). When the three areas were considered separately, different measures were important in discriminating individuals in each, so no measure seemed to be consistently the most important in discriminating individuals.

### Discrimination of different areas

Univariate analysis of variance showed a significant difference between the areas only for the frequency measures LOW1, LOW2 and MED (Table 4). MANOVA between areas using all ten measures of the hoots showed the areas were significantly different (Wilks lambda 2.46,  $P < 0.001$ ). Discriminant analysis using five of the ten measures allowed owls to be classified into the correct area with 81.6% success. Both discriminant functions were statistically significant ( $P < 0.02$ ), with the first function accounting for most of the variance. LOW2, I5 and LOW1 contributed most to the first discriminant function, and MED and I4 contributed most to the second (Table 5). Figure 3 shows owls from the three areas plotted on a graph of the first canonical axis against the second canonical axis. The first axis weakly separates Wytham Woods from the other two sites, and the second axis separates the Fens from Monks Wood.

**Table 2.** Correlations between the different measures of the Tawny Owl calls. Underlined digits indicate a significant correlation between the two measures ( $P < 0.05$ )

	I5	I4	TAIL	D1	D2	FML	LOW1	HIGH	LOW2	MED
I5	1									
I4	<u>0.26</u>	1								
TAIL	<u>0.26</u>	<u>-0.22</u>	1							
D1	<u>0.19</u>	-0.13	<u>0.5</u>	1						
D2	<u>-0.24</u>	<u>-0.17</u>	0.12	<u>0.15</u>	1					
FML	<u>-0.2</u>	0.07	<u>-0.21</u>	0.16	0.1	1				
LOW1	<u>-0.28</u>	0.12	-0.06	-0.21	<u>-0.16</u>	<u>-0.15</u>	1			
HIGH	<u>-0.23</u>	-0.02	<u>-0.19</u>	<u>-0.22</u>	-0.09	0.09	<u>0.16</u>	1		
LOW2	<u>-0.25</u>	<u>0.2</u>	<u>-0.03</u>	<u>-0.17</u>	<u>-0.19</u>	-0.14	<u>0.67</u>	<u>0.5</u>	1	
MED	-0.28	0	<u>-0.18</u>	<u>-0.22</u>	-0.1	0.05	0.4	0.9	<u>0.31</u>	1



**Figure 2.** Six Monks Wood Tawny Owls plotted on first canonical axis against second canonical axis. Each dot, cross or triangle is a separate hoot. Hoots from the same owls fall close to each other.

**Habitat differences**

Multivariate pairwise MANOVAS between the three areas separately showed that, after Bonferroni adjustment for multiple testing, the Fens was significantly different from Wytham and Monks Woods but Wytham and Monks Woods were not significantly different from each other.

Because the Fens was of a different habitat type to Wytham and Monks Woods, *a priori* contrasts were included in univariate tests to compare the Fens (farmland site) with the two woodland sites. Four of the ten measures, FML, LOW1, HIGH and LOW2, were significantly different between the Fens and the woodland sites (Table 6). The frequency measures that showed a significant difference between woodland and farmland sites were not consistently lower in the woodland sites. HIGH conformed to the pattern expected and was significantly higher in the Fens, but LOW2 was lowest in the Fens and LOW1 was intermediate in the Fens. This implies the “shape” of the first note varied between habitat types, being more “curved” in the Fens. The same recording equipment was used at each site, so this difference was not an effect of the recording microphone.

**Table 4.** Results of univariate ANOVA between study sites for each of the ten measures of the Tawny Owl hoot

	F-ratio <sub>2,46</sub>	P-value
I4	1.10	n.s.
I5	1.96	n.s.
TAIL	0.72	n.s.
D1	1.34	n.s.
D2	2.88	n.s.
FML	3.07	n.s.
LOW1	16.0	<0.001
HIGH	2.97	n.s.
LOW2	19.5	<0.001
MED	4.38	<0.02

**Table 5.** Canonical coefficients of the two discriminant functions separating the three Tawny Owl study sites

	Root 1	Root 2
LOW2	0.78	0.41
I5	0.58	0.06
LOW1	0.53	0.33
MED	0.21	0.83
I4	0.06	0.61

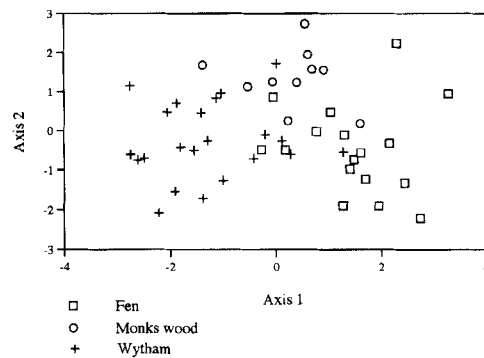
**Similarities between neighbours**

*Principal component analysis (PCA)*

The owl hoots from each area were plotted in multidimensional space using PCA of the temporal measures. More similar hoots are found closer together on the PCA map. The distance between hoots on the PCA plot was then calculated for every pair of owls that had adjoining territories and every pair of owls that was not in vocal contact according to the criteria stated in the Methods. In none of the three study sites were the plotted distances between hoots of neighbouring pairs significantly different from the plotted distances between pairs of males that were not in vocal contact (Table 7). This implies that the hoots of neighbouring owls are not more (or less) similar than hoots of owls that do not have vocal contact.

*Differences between pairs*

For each measure of the hoot, the magnitude of the difference was calculated between pairs of neighbouring owls and pairs of males that were not in vocal contact (strangers). Univariate ANOVA was performed to examine if the differences for the stranger pairs were larger. If so, it would imply neighbouring pairs had more similar hoots. There was no significant difference between the neighbour and stranger groups in any of the measures at any of the areas (Table 8).



**Figure 3.** Average hoot for each Tawny Owl plotted on first canonical axis against second canonical axis showing separation between the sites.

**Table 6.** Results of univariate ANOVAs on all measures of the Tawny Owl hoot between woodland sites and the Fens

	F-ratio <sub>1,46</sub>	P-value
I4	0.44	n.s.
I5	3.78	n.s.
TAIL	0.81	n.s.
D1	0.41	n.s.
D2	0.38	n.s.
FML	6.14	<0.02
LOW1	4.15	<0.05
HIGH	4.53	<0.04
LOW2	12.41	<0.01
MED	3.06	n.s.

### Variability of hoots in the three populations

The coefficient of variation was calculated for each measure in each area because this is a standardized measure of variability (Sokal & Rohlf 1981). A Friedman's test was performed on the ten coefficients of variation between areas to test whether any of the sites had a higher variability. The variation was significantly higher at the Fens (Friedman's  $\chi^2_2 = 6.2$ ,  $P < 0.04$ ) (Table 9).

### DISCUSSION

After we examined six temporal and four frequency measures of their hoots, we could distinguish Tawny Owls from each other with a high degree of accuracy. There was no indication that any part of the hoot that we measured consistently acted as an individual "identifier" for the owls. No measure was consistently important in discriminating individuals in all three areas; for example I5 was important in discriminating individuals in Wytham Woods and the Fens but was not important in Monks Wood. In addition, Galeotti and Pavan (1991) described FML as being very important

**Table 7.** Average distances between hoots on a PCA "map" for groups of neighbouring Tawny Owls and groups of Tawny Owl strangers from all three sites. A small PCA distance implies the hoots are similar to each other

Site	Owl group	n	Mean distance		P-value
			(cm)	s.e.	
Wytham Woods	Neighbour	32	2.65	0.25	n.s.
	Stranger	32	2.98	0.23	
Monks Wood	Neighbour	14	2.71	0.42	n.s.
	Stranger	9	3.31	0.55	
Fens	Neighbour	25	3.45	0.52	n.s.
	Stranger	53	3.02	0.27	

**Table 8.** Tables showing mean time differences in hoot measures for groups of neighbour pairs and groups of stranger pairs of Tawny Owls at the three sites, and results of an ANOVA between the two groups (none of the F-values was significant)

Variable	Mean difference		d.f.	F
	Neighbours	Strangers		
<b>Wytham Woods</b>				
D1	116.6	123.02	1,63	0.07
I4	662.82	553.7	1,63	1.16
D2	32.04	41.57	1,63	2.1
I5	68.08	58.63	1,63	0.5
FML	126.07	125.64	1,63	0
TAIL	169.42	142.31	1,63	0.82
LOW1	54.8	51.8	1,24	0.04
HIGH	45.3	80.8	1,24	3.4
LOW2	41.3	54	1,24	0.88
MED	38.7	64.8	1,24	2.76
<b>Monks Wood</b>				
D1	83.8	76.7	1,21	0.06
I4	605.6	719	1,21	0.36
D2	28.2	35.8	1,21	0.38
I5	66.8	64.6	1,21	0.01
FML	43	35.1	1,21	0.35
TAIL	116.9	136.7	1,21	0.43
LOW1	41.7	74	1,9	1.04
HIGH	70.8	90.5	1,9	0.28
LOW2	56.3	49.6	1,9	0.03
MED	64.3	94	1,9	0.67
<b>Fens</b>				
D1	171.9	128.8	1,77	3.32
I4	925.6	791.8	1,77	1.03
D2	21.3	22.1	1,77	0.05
I5	107.5	99.3	1,77	0.15
FML	143.5	158.9	1,77	0.19
TAIL	177.2	143.1	1,77	1.77
LOW1	59.4	41.6	1,19	0.73
HIGH	81.6	76.8	1,19	0.03
LOW2	52.6	57.4	1,19	0.04
MED	80.6	69.9	1,19	0.13

in discriminating individuals in their Italian study sites because it was highly variable between owls but very constant in the hoots of each individual owl. Amongst the English study sites, FML was important only in discriminating individuals in Monks Wood.

Hoots from the three areas we studied could be distinguished with a high degree of accuracy using multivariate measures. There was some evidence that habitat influenced hoot structure. Hoots from the Fens were significantly different from hoots from each of the two woodland sites, and hoots from the woodland sites were not significantly different from each other. In addition, four of the ten measures differed significantly between the Fens and the woodland sites. Three of the four measures which were significantly different between the Fens and woodland sites were fre-

**Table 9.** Mean of the coefficients of variance for all ten measures at each of the three study sites for Tawny Owl hoots

Site	Coeff. var.	n
Fens	0.142	10
Monks Wood	0.101	10
Wytham Woods	0.125	10

quency measures. The acoustic adaptation hypothesis would predict that these frequencies would be lower in woodland because low frequencies travel better through obstacles such as branches and leaves. This was the case for only one of the three frequencies that differed. There might be a confounding factor in that the owls in the Fens were much farther apart than owls in the woodland areas. Low frequencies travel farther than high frequencies, so they might also be favoured in the Fens. It is therefore difficult to be certain that acoustic adaptation was not taking place.

We found no evidence that owls with neighbouring territories had more similar hoots. It is possible that if post-dispersal learning was taking place, owls would learn from only one neighbour. Because each owl was compared with each of its neighbours, groups of neighbours in our analysis would then contain some similar hoots and some hoots that were no more similar than those of owls that were not in vocal contact. Because our sample sizes were large, however, we would still expect to see reduced differences between hoots in groups of neighbours if learning was taking place. No such trend was found, so we concluded there was no evidence for learning from neighbours.

If owls were learning their hoots after dispersal, we would expect to find that the three areas were distinguishable and that there were differences between hoots in different habitats. We would also expect that, on average, neighbours had more similar hoots than owls with no vocal contact and that hoots in the Fens were more variable because the owls have less vocal contact. We did find that the populations were distinguishable and there were habitat differences, although these were in the "shape" of the first note rather than simply the frequency, and we did find hoots in the Fens were more variable. However, the most direct measure of post-dispersal learning was whether owls with territories close to each other had more similar hoots. There was no evidence for this, despite a thorough analysis using two different approaches, so we concluded post-dispersal learning was not taking place.

If Tawny Owls do not learn their hoots after dispersal, they might inherit or learn their hoots from their fathers or learn their hoots from a neighbouring male before dispersal. Fledged owls remained on the natal territory for approximately 4 months after fledging, so they had ample time to learn their calls. Owl chicks perform squeaky hootlike calls before leaving their natal territories (B.M. Appleby & S.M. Redpath, pers. obs.). If owls acquire their hoots before leav-

ing the natal territory and then disperse short distances before setting up territories, this behaviour could lead to a number of owls in an area having similar hoots. Over 83% of the young Tawny Owls in one British population dispersed under 10 km before setting up territories (Cramp *et al.* 1985). The increased similarity of hoots within areas that we revealed could have arisen in this way. The different shape of the first note in the Fens could also be simply a result of a local variant of the first note. The increased variability in farmland could occur if owls acquired their hoots before dispersal and there was increased dispersal in farmland habitat. Unfortunately, no information on dispersal distances of Tawny Owls in different habitats is available.

Radio-tagging juveniles before dispersal and comparing sonagrams of their hoots once they have established territories with the hoots of their fathers and males with neighbouring territories to their fathers would show whether the young acquire their calls before dispersing, and from where they acquire them. However, because of the high mortality of young Tawny Owls (G. Hirons 1974, unpublished DPhil thesis, Oxford University), the amount of time they might live and the uncertainty of the influences they might encounter before establishing a territory, this field experiment would be very difficult. Rearing captive owls to investigate if they will learn song would be preferable, but hand-reared Tawny Owl chicks do not develop a hoot when kept in captivity (P. Galeotti, unpubl.).

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