

FACTORS AFFECTING THE VOCAL BEHAVIOUR OF EAGLE OWLS *BUBO BUBO*: EFFECTS OF SEX AND TERRITORIAL STATUS

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SUMMARY.—*Factors affecting the vocal behaviour of Eagle Owls Bubo bubo: effects of sex and territorial status.* We performed a playback experiment in order to assess the efficiency of two methods for detecting Eagle Owls *Bubo bubo* and to assess factors affecting detection rates. On each experimental visit we recorded the number and sex of the responding owls, the calling rate and the corresponding type of voice during three periods: spontaneous calls (SC; 30 min), elicited calls (PB, by broadcasting male territorial hoots; 30 min) and post-challenge period (PPP; 15 min). We conducted a survey of 17 territories in Spain, and found 10 unpaired males, six paired males and seven paired females (one male attended two females). Paired males delivered territorial hoots during the SC period and continued hooting during the PB period, while most unpaired males became silent in the PB period, and the calling rate of those that continued on hooting was lower than that for paired males. When hearing the intruding male's voice, females increased their call rate. Most puzzling, females responded to male playbacks with mating-begging calls, not with territorial or alarm calls. During the PPP period, paired males delivered significantly more territorial calls than unpaired males. Thus, mating status may have an effect on male Eagle Owl response to male playback. We suggest that: (1) the exclusive use of playbacks may bias surveys towards paired owls, (2) the combined use of recording spontaneous calling owls and the broadcast of male territorial voices may improve survey methods by revealing floaters, and (3) paired males tried to defend aggressively both mate and territory and unpaired males hooted primarily to attract females, but they tried to avoid territorial disputes with other males.

Key words: *Bubo bubo*, Eagle Owl, floaters, polygyny, survey methods, territorial behaviour.

RESUMEN.—*Factores que afectan el comportamiento vocal del Búho Real Bubo bubo: efectos del sexo y el estatus territorial.* Hemos realizado un experimento vocal para determinar la eficacia de dos métodos de detección de Búhos Reales *Bubo bubo*, así como los factores que condicionan las tasas de detección. En cada visita experimental se registró el número y sexo de las aves que fueron detectadas y la tasa de canto de cada tipo de voz emitida durante tres periodos: cantos espontáneos (SC; 30 min), llamadas inducidas (PB, emitiendo cantos territoriales de un macho; 30 min) y periodo de post-intrusión territorial (PPP; 15 min). Los muestreos se realizaron en 17 territorios en España, y encontramos 10 machos no emparejados, seis machos emparejados y siete hembras emparejadas (un macho atendió a dos hembras). Los machos emparejados emitieron cantos territoriales durante el periodo SC y continuaron así durante el periodo PB, mientras que la mayoría de los machos no emparejados se callaron durante el periodo PB. Además, la tasa de canto de los machos no emparejados que continuaron emitiendo voces durante el periodo PB fue inferior a la de los machos emparejados durante el mismo periodo. Ante la voz de un macho intruso, las hembras incrementaron la tasa de emisión de cantos. Sorprendentemente, las hembras respondieron al reclamo con voces de solicitud de cópula y de alimento, en lugar de con voces territoriales o de alarma. Durante el periodo PPP los machos emparejados emitieron más voces territoriales que los no emparejados. Por lo tanto, el estatus territorial podría tener efectos sobre la respuesta del Búho Real a los reclamos de un macho. Sugerimos que: (1) el uso exclusivo de reclamos grabados podría sesgar los resultados de los censos en favor del número de machos emparejados, (2) el uso combinado de la escucha de cantos espontáneos y cantos inducidos podría mejorar la eficacia de los muestreos al revelar la presencia de individuos flotantes, y (3) los machos emparejados intentaron defender de manera agresiva tanto a sus parejas como a sus territorios, mientras que los machos no emparejados cantaron principalmente para atraer hembras, y evitaron conflictos territoriales cesando su actividad vocal ante la intrusión simulada.

Palabras clave: *Bubo bubo*, Búho real, comportamiento territorial, individuos flotantes, métodos de muestreo, poliginia.

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INTRODUCTION

The song of many bird species is a sexual signal that conveys information about individual qualities that play a relevant role in advertising territory ownership and mate attraction (Galeotti & Pavan, 1993; Catchpole & Slater, 1995; Appleby & Redpath, 1997; Galeotti, 1998). The hoots of some owl species have been shown to confirm this assertion and, furthermore, there is evidence that individual recognition and variation among populations exists (Galeotti & Pavan, 1991; Galeotti *et al.*, 1993; 1996). Males and females react in a variety of ways to the hooting of intruders. Thus, while territory defence is cooperative for some species (Galeotti *et al.*, 1997; Appleby *et al.*, 1999), males and females of other species respond exclusively to intruders of their own sex (Wiklund & Village, 1992; Slagsvold, 1993).

Taking advantage from such behavioural responses, several studies have used tape recordings of conspecific calls to perform census work on owls (Sarà & Zanca, 1989; Ward *et al.*, 1991; Haugh & Didiuk, 1993; Kavanagh & Peake, 1993; Redpath, 1994; Viada, 1994; Debus, 1995; Zuberogoitia & Campos, 1998; Martínez *et al.*, 2002). Although the use of recordings has not proved successful at enhancing the detection of all owl species (Kavanagh & Peake, 1993; Enríquez & Salazar, 1997; Evans, 1997; Francis & Bradstreet, 1997; Takats & Holroyd, 1997), hypotheses to explain why the target individuals did not respond to the broadcast of conspecifics have been very seldom proposed. Rohner (1997) found differences in detectability between floaters and paired male territorial owners in the Great-horned Owl *Bubo virginianus*. Floaters were not vocal at all, thus studies based on the recording of spontaneous or elicited calls will not detect floaters in this species (Rohner, 1997).

Although there is no complete consensus on the definition of floaters, they are frequently identified as young, dispersing individuals or as vagrant adults that have failed to obtain a territory («the floating population», «surplus birds»). Some authors, however, have suggested that the concept of «floater» goes far beyond defining a group of transient animals ready to take over vacancies in territories as soon as they encounter them. They define floating as a complex life history trait that involves deci-

sions about settlement (where and when to settle in a territory), mating (with whom to mate) and reproduction (when, how and how much to invest in reproduction; Smith & Arcese, 1989; Heg, 1998). Furthermore, most floaters have a their own home ranges (Smith & Arcese, 1989; Ens, 1992; Ens *et al.*, 1995; Rohner, 1997; Heg, 1998). Smith & Arcese (1989) suggested that when the reproductive success of unpaired territorial males and floater males is equal, it would be better for unpaired males to behave as floaters, thus eluding the costs of defending a territory. It is important to reveal the presence of this «shadow population» (Rohner, 1997), since the pool of non-established birds can mask population declines when census results are based on breeding pairs (Wilcove & Terborgh, 1984; Franklin, 1992).

Information on the suitability of the playback method to census Eagle Owl *Bubo bubo* populations is scant, and it has even been suggested that this could not be an effective method (Penteriani & Pinnchera, 1990; 1991). In contrast, Martínez *et al.* (1992) used playback with apparent success. Since owl census is a time consuming activity (Duncan (Duncan, 1997; Francis & Bradstreet, 1997), standardised, labour-efficient survey techniques should be made available for managers in order to maximize detection rates. The aims of this study are: (1) to determine the efficiency of the playback method relative to census based on spontaneous calls and (2) to determine factors that may influence the response of Eagle Owls to conspecific recordings.

METHODS

Study area and period

The study was conducted in 17 territories previously known to be occupied by one male (eight territories in Madrid, central Spain, and five in Alicante and four in Valencia, both in eastern Spain). The experimental period was set between 19/11/98 and 24/1/99 in order to include the seasonal peaks in vocal behaviour of the species. Previous surveys of breeding of the Eagle Owl in the selected territories showed that there was variation in the start of laying between eastern and central Spain (*pers. obs.*). Thus, the dates of the vocal experiment were

adjusted so that it was conducted prior to laying in each territory (eastern Spain: 1/11/98-26/12/98; central Spain: 7/11/98-24/1/99). Accordingly, the start of each experimental visit (see below) varied 1 h and 23 min between point-count stations (range = 17 h 20 min-18 h 43 min). The experiment was performed once in each territory. Counts were performed only during dry, windless nights. Territories were visited between six and nine times throughout the breeding season (November to June) in order to ascertain if they were occupied by a pair or by single owls (Olsson, 1997).

Experimental visits

Each experimental visit to a territory included the following phases:

Spontaneous calls (SC): Starting 5 minutes before dusk and after an initial 2-minute settling period, we recorded the following data during a 30-min period: date, hour, sex of the owl according to its vocalisations (Saurola, 1997), calling rate (number of vocalisations), and agonistic response, if any could be noticed. Sex differentiation by voice is possible for the Eagle Owl because the sonorous, low pitched booming of the male territorial call is easily distinguishable from the harsh, higher pitched territorial call of the female (Cramp & Simmons, 1980; Mikkola, 1983; Saurola, 1997). The functional meaning of the different calls was assessed according to Saurola (1997). If the target individuals were hooting at the time of our arrival to the point count, the experimental visit was cancelled and repeated the next day. The length of the observation periods in owl surveys is usually short and is set arbitrarily. However, Redpath (1994) showed that a 30-min period is advisable when censusing Tawny Owls *Strix aluco*. Thus we conservatively determined a 30-min interval for each experimental period.

Playback (PB): Immediately after SC, a territorial intrusion was simulated by broadcasting male territorial calls during 30 minutes using cassette players. Broadcast volume was adjusted to ensure clear vocal rendition. The same data as in SC were recorded, plus latency (i.e. time elapsed from the onset of the period to the first vocalisation of the focal owl). During the playback sessions we broad-

casted the territorial call of a male Eagle Owl recorded far from the study area. Each broadcast period consisted of 5 periods (bouts) of 4 min each, when a male territorial call was broadcasted at a rate of 14 calls/min. Bouts were separated by periods of silence lasting 2 min. By using such a rate and period we imitated those recorded during spontaneous male encounters in the same study areas in 1996, 1997 and 1998 (mean calling rate for five different pairs of contesting males = 13.9 territorial calls/min, SD = 1.74, range = 11.6-14.91; mean duration of bouts = 3.8 min, SD = 0.23; mean duration of pauses between bouts = 1.7 min, SD = 0.29). The only difference between experimental territorial intrusions and spontaneous owl encounters was the total interaction time, because spontaneous disputes ranged from 3 min to 3.2 hours.

Unfortunately, we had not a sample of 17 different Eagle Owl voice recordings (i. e. stimuli) to generate a distribution of responses. Therefore, the playbacks made on the different territories can be considered as pseudoreplicates (Kroodsma, 1989). This does not represent a problem when assessing the efficiency of survey methods, but restricts the outreach of inference about behaviour because we cannot be sure that the average response of the owls to another type of recordings would be the same (Kroodsma, 1989). In agreement with Kroodsma (1989), our suggestions about behaviour of the Eagle Owl must be approached conservatively.

Post-playback period (PPP): After the playback session we recorded again the same data during 15 min., with the exception of latency time. Counting stations were located between 150 and 250 m from the cliffs in which Eagle Owls were frequently heard delivering territorial hoots. Only in one territory, where a pair of owls was detected, was the station located 300 m away due to poor accessibility of the cliff. A territory was classified as occupied if an Eagle Owl was detected between November and June. A male was classified as unpaired if no female was recorded during the study period.

The distribution of the number of vocalisations per 30 min was skewed, thus we log-transformed original data and used t-tests for comparisons of means. We used non-parametric tests for the rest of the analyses.

RESULTS

Number of territories

Table 1 shows the number of Eagle Owls of each sex found in each survey period. Only in one out of the 17 territories were Eagle Owls not found at all. Six territories were classified as occupied by paired males and 10 territories as occupied by unpaired males. In one territory we found that the male attended two different females by singing alternatively with each other in two different cliffs located 300 m apart. The two females were considered as two different focal individuals (hence $n = 7$ for females), but only the response of the male with the first female that we detected was used in the analysis of male behaviour. Surveying the territories throughout the breeding season confirmed the results obtained during the experimental periods as to territories being occupied by a pair or by single owls.

Efficiency of broadcasts

Male response

As the PB period was performed after the SC period, it could be argued that differences in the number of territories found between the SC and PB periods could be due to variations in the timing of hooting, i.e. our results would just mirror peaks in hooting. Thus, before testing for differences in the number of territories found in each period, we tested if time of day (min. after sunset) when experiments were conducted had any effect on the probability of assessing territory occupancy. First we tested if calling rates (number of vocalisations of the male territorial call per 30 min) varied with time, but we found no significant correlation between the time on which the SC and PB periods started and calling rates (SC: $r = 0.080$, $P = 0.760$, $n = 17$; PB: $r = -0.242$, $P = 0.350$, $n = 17$; Spearman rank correlations). Since all males were detected during the SC period (see below), we only tested if the probability of detecting a hooting male varied with the time of the day on which the playback experiment started (min. after sunset). We performed a Logistic Regression Analysis (Hosmer & Lemeshow 1989) using time as independent variable and the detection (code 1) or not (code 0) of an oc-

cupied territory as the dependent variable. The probability of detecting a singing male (i.e., an occupied territory) did not vary with the time of day on which the PB periods started (Likelihood Ratio test, $G_1^2 = 22.795$, $P = 0.398$).

All males were hooting during the SC period, while only 10 of them continued vocally active during the PB period (Table 1). The six paired males were detected both during the SC and PB periods, while out of ten unpaired males detected in the SC period only three remained producing the territorial hoot also during the PB period, and one male delivered alarm calls. Thus, the proportion of hooting males that became silent after hearing the voice of an intruder differed between paired (0%) and unpaired (60%) males ($G_1 = 7.71$, $P = 0.005$). Moreover, the proportion of unpaired males that stopped producing territorial hoots (70%) was also larger than for paired males ($G_1 = 9.71$, $P = 0.001$). During the PPP period only one out of the six paired males became silent, while five out of the ten unpaired males were detected (Table 1), but the difference was not significant ($G_1 = 1.90$, $P = 0.168$).

Territorial hoots were the most frequent call uttered in all experimental periods. It was the only sound delivered during the SC period both by paired and unpaired males, but the 30% of males of both types detected during the PB and PPP periods delivered also alarm calls (Table 1).

The mean number of territorial calls emitted per 30 min during the SC period was very similar for both paired and unpaired males (Table 2). However, the territorial calling rate was larger for the paired than for the unpaired males (Table 2), both during the PB period ($t_7 = 2.23$, $P = 0.061$) and during the PPP period ($t_7 = 2.38$, $P = 0.049$), although the differences were only marginally significant. However, only four out of six paired males increased their calling rate during the PB period with respect to the SC period, which represents a non significant change (paired-samples t test, $t = -0.44$, $P = 0.51$, $n = 6$).

The length of the latency period did not differ between paired and unpaired males (paired: mean = 7.9 min, SD = 10.2, $n = 6$; unpaired: mean = 6.8, SD = 7.4, $n = 4$, Mann-Whitney test, $U = 1.42$, $P = 0.273$). Since surveys were conducted at dusk, we could not thoroughly evaluate agonistic responses. However, one

TABLE 1

Number of Eagle Owls found in each survey period in relation to sex, mating status and type of call delivered. «Other call» mean alarm calls in the case of males, and mating-begging calls in the case of females. SC: spontaneous calls period, PB: playback period, PPP: post-challenge period.
 [Número de Búhos Reales encontrados durante cada periodo experimental en relación al sexo, emparejamiento y tipo de voz emitida. «Otras voces» se refiere a llamadas de alarma en el caso de los machos y llamadas de cópula y solicitud de alimento en el caso de las hembras. SC: periodo de cantos espontáneos, PB: periodo de respuesta a voces grabadas, PPP: periodo de post-intrusión territorial.]

Status [Estado]	Males [Machos]						Females [Hembras]		
	SC		PB		PPP		SC	PB	PPP
	Paired [Emparejado]	Unpaired [Sin pareja]	Paired [Emparejado]	Unpaired [Sin pareja]	Paired [Emparejado]	Unpaired [Sin pareja]			
Territorial hoot [Canto territorial]	6	10	5	2	4	3	3	0	1
Other call [Otras voces]	0	0	0	1	1	1	0	2	2
Both [Ambos]	0	0	1	1	0	1	2	3	1

TABLE 2

Mean call rate of male (territorial call) and female (T.call: territorial call. Mating: mating-begging call) Eagle Owls in each survey period in relation to mating status (all females paired). SC: spontaneous calls period, PB: playback period, PPP: post-challenge period.
 [Tasa media de cantos de machos —canto territorial— y hembras —voces de cópula y solicitud de alimento— en relación a si los individuos estuvieron emparejados o no. SC: periodo de cantos espontáneos, PB: periodo de respuesta a voces grabadas, PPP: periodo de post-intrusión territorial.]

	Males [Machos]						Females [Hembras]					
	SC		PB		PPP		SC		PB		PPP	
	Paired [Con pareja]	Unpaired [Sin pareja]	Paired [Con pareja]	Unpaired [Sin pareja]	Paired [Con pareja]	Unpaired [Sin pareja]	T.Call [Canto territorial]	Mating [Canto de cópula]	T.Call [Canto territorial]	Mating [Canto de cópula]	T.Call [Canto territorial]	Mating [Canto de cópula]
Mean [Media]	54.6	48	104.6	35.3	116	45.2	12.7	46	13.3	105.6	42.3	24.2
SD	43.1	56.9	83.4	56.8	61.6	77.2	9.3	16.9	4.6	99.5	47.4	15.7
Range [Rango]	6	10	6	3	5	4	4	2	3	5	3	4

paired male flew over the broadcast station, almost dive-bombing over the cassette player.

Female response

Only four out of seven females were detected during the SC period, while most of them (six out of seven) were detected during the SC and PB periods altogether (Table 1) and the last female was only detected during the PPP period. Table 2 shows the mean call rate per 30 min of the females detected in each period. To test for differences in the calling rates between contiguous experimental periods we compared the number of calls produced by each of the seven females. Between the SC and PB periods, females significantly increased the mating-begging call rate (Wilcoxon matched-pairs test, $Z = -2.02$, $P = 0.043$, $n = 7$), while there were no significant changes in the emission of territorial calls between experimental periods (paired-samples t test, $t = -0.18$, $P = 0.901$, $n = 7$).

DISCUSSION

The use of recorded conspecific calls has proved to be an effective census technique for many owl species (Sara & Zanca, 1989; Ward *et al.*, 1991; Haugh & Didiuk, 1993; Kavanagh & Peake, 1993; Redpath, 1994; Viada, 1994; Debus, 1995; Zuberogoitia & Campos, 1998; Martínez *et al.*, 2002). However, the use of taped calls did not enhance our ability to detect Eagle Owl territories. Listening to spontaneous vocalisations of the owls yielded 16 territories (i.e. singing males) out of 17 counting stations, while the use of playback yielded 10 territories. Seven out of 16 of the territories would have been wrongly classified as unoccupied by a male when taped calls were broadcasted.

The onset of the SC period varied for each territory. If the Eagle Owls' hooting behaviour would have peaked in the very first minutes of the evening and then decreased, the PB period would most certainly not have been conducted during the maximum in hooting behaviour, and this would explain the low probability of detecting a male during the PB period. However, we did not find any relationship between the time when the recording of spontaneous calls started and the number of territorial hoots delivered in 30 min, despite a range of variation of SC starting time between territories of 1 h and

23 min, much greater than the difference between SC and PB starting time.

The probability of detecting a male Eagle Owl during the PB period was greater for paired (all were detected) than for unpaired males (4 out of 10 were detected). In addition, the hooting rate of paired males tended to be higher than for unpaired males in the PB and PPP periods. Thus, these results suggest that the male reaction to an intruder may depend on its mating status: paired males kept on advertising their presence while most unpaired owls became silent or reduced their hooting rate. This accounts for the lower number of males detected during the PB period.

Rohner (1997) found a different pattern for the Great-Horned Owl: while almost all paired owls delivered spontaneous calls and 70% of them responded to playback, floaters were not vocally active at all. Floaters had larger home ranges than paired males, and although their home ranges overlapped with occupied territories of pairs, they were located along territorial boundaries more often than expected by chance (Rohner, 1997). Thus, it appears that the behaviour of paired owls, which are territory owners, may restrict the use of space by floaters (see also Ens *et al.*, 1995), and that floaters could remain secretive to avoid direct fighting with such territory owners. Eagle Owls are reported to have larger territories (typically between 12 and 20 km²; Cramp & Simmons, 1980) than paired Great-horned Owls (estimated average territory size: 4.83 km²; Rohner, 1997). The larger territories of the Eagle Owl would reduce the probability of direct fighting between contestant males, but at the same time it would increase the chances of successful encounters with neighbouring females. It is unclear if the unpaired males found in this study were floaters or not. However, in the light of our results, it is still reasonable to suggest that they followed the strategy of floaters suggested by Smith & Arcese (1989). If the reproductive success of unpaired territorial males and floater males were equal, then it would be better for unpaired males to behave as floaters, thus eluding to pay the costs of defending a territory. This is supported by our finding that unmated Eagle Owls became silent at the hearing of a male. One likely explanation for such behaviour is that they tried to engage in extra pair copulations with paired females.

Females also increased the call rate in response to male playback, but altogether they were less vocal than males. One astonishing result is that they responded to playback by increasing the mating-begging call rate, not any other call rate. It has been recently suggested that polygyny may be a common mating system for the Eagle Owl (Dalbeck *et al.*, 1998). Whether females in this study were seeking extra-pair copulations remains an open question that falls out of the scope of this study due to design limitations. The tendency for members of the Eagle Owl pair to respond together to playback does not necessarily imply that territorial defence is cooperative in Eagle Owls, as it is in Scops Owls *Otus scops*; Galeotti *et al.*, 1997) and Tawny Owls (Appleby *et al.*, 1999). In order to test this suggestion we would have to carry out a further, more complicated test of the sex-specific response to intruders of their own sex (Galeotti *et al.*, 1997; Appleby *et al.*, 1999).

In conclusion, our results show that by just hearing spontaneous hooting males we would record a higher number of males but we would have doubts about the mating status of most of them, while if we only broadcasted the voice of territorial males we would detect mainly the paired fraction of the population. Thus, the combined use of both methods is a better strategy than the use of any of these methods alone. Our results need validation from experimental studies using larger sample sizes under a wide array of environmental conditions. This study leaves several open questions for further research regarding relationships between the probability of detection and the mating systems of the Eagle Owl, habitat quality and owl and prey density. The influence of such factors should be accounted for in further studies in order to provide managers with a labour-efficient survey method for this species.

ACKNOWLEDGEMENTS.—Pertti Saurola, Heiki Lokki and Pekka Pouttu shared with us their expertise on the Eagle Owl's vocal array. We are most indebted to Toni Bolea and members of BRINZAL, who performed an amazingly good fieldwork. Pertti Saurola, David Serrano, Vincenzo Penteriani, José Enrique Martínez Torrecilla and Alejandro Izquierdo provided valuable comments on the manuscript. Germán López worked very hard on a previous version of the manuscript. José Antonio Donázar and

Diego Gil reviewed the submitted manuscript and provided valuable comments. We thank Andrea Gardiábal for translating the references from German into Spanish.

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[Recibido: 25-9-01]
[Aceptado: 30-10-01]

