Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality

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Vocal displays are supposed to be an honest signal of the phenotypic and genetic quality of individuals and their territory. Moreover, signal interactions are nearly always associated with individuals in aggregations, and their function could in part be explained as social behaviour. Conspecific density has been shown to be a particularly strong proximate and ultimate factor acting on several individual/population features; thus, it may be expected to affect vocal behaviour too. Here, I investigate the hypothesis that, in long-lived, territorial species, density affects the vocal displays of mated males, masking their honesty as a possible signal of male/territory quality. Each month I listened to the dusk calls of 17 breeding male Eurasian Eagle Owls *Bubo bubo* during their prelaying period. Nine males bred in a low-density situation, the other eight in a high-density one. Conspecific density was found to affect the honesty of call features as signals of male and/or territory quality. The call display as a reliable predictor of male fitness measured as productivity persisted only in situations of high breeding owl density, where male–male competition was stronger. Accommodation of call activity allows individuals to minimize the costs of aggressive calling by adjusting the territoriality threshold to local conditions. The results of this study emphasize the importance, when investigating the evolution and maintenance of honest territorial or sexual signals, of considering the environmental and social context experienced by the individual, thereby corroborating the idea that male–male competition contributes to the maintenance of honest signalling.

It is widely accepted that many vocal displays have evolved through intersexual (e.g. mate attraction and stimulation, mate-guarding, extra-pair copulations [EPCs]) and intrasexual selection (e.g. conspecific repulsion, delineation of territorial boundaries; e.g. Krebs *et al.* 1978, Catchpole 1982, Ritchison 1983, McDonald 1989). Moreover, they are generally supposed to be costly, because of the time spent in this activity instead of others relevant to individual fitness and energy demands for song production (e.g. Zahavi 1977, Brackenbury 1980, Alatalo *et al.* 1990, Cuthill & MacDonald 1990, Eberhardt 1994, Catchpole & Slater 1995, Gaunt *et al.* 1996, Kroodsma & Miller 1996), although the energetic costs of singing (e.g. oxygen consumption) are controversial (Chappel *et al.* 1995, Horn *et al.* 1995) and the possibility that birds are sometimes not giving honest signals cannot be excluded. Several authors (e.g. Hutchinson *et al.*

1993, Eberhardt 1994, Hoi-Leitner *et al.* 1995, Johnstone 1995; see also reviews in Catchpole & Slater 1995, Kroodsma & Miller 1996) have therefore proposed that the duration of vocalizations represents an honest signal of the phenotypic and genetic quality of individuals (and of the quality of their territories), because high-quality males (or males in high-quality territories) can bear singing costs better than low-quality individuals (or individuals in low-quality territories). Although data on the relationship between male quality (or that of its territory) and call displays are scarce for non-passerine birds, vocalization patterns of birds of prey and owls seem also to be related to individual and/or territory quality (Appleby & Redpath 1997, Galeotti 1998, Penteriani *et al.* 2002).

Starting from the assumption that calling can be considered an honest signal of the quality of a male and/or its territory, there is an impressive body of scientific literature on the factors influencing and

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modulating song production and, more generally, call behaviour. Song displays have been reported to depend upon individual health and nutritional condition (e.g. Møller 1991a, Saino *et al.* 1997), food availability (e.g. Gottlander 1987, Reid 1987, Strain & Mumme 1988), hormones (e.g. Balthazart 1983, Marler *et al.* 1988), habitat constraints (e.g. Garson & Hunter 1979, Higgins 1979, Klump 1996) and social context (e.g. Kroodsma 1979, Galeotti *et al.* 1997). In the latter case, most of the interest has been directed at matched countersinging (e.g. Krebs *et al.* 1981, Falls 1985, Simpson 1985), mate and neighbour recognition (e.g. McGregor & Avery 1986, Brindley 1991, Stoddard *et al.* 1991, Galeotti & Pavan 1993, Temeles 1994, O'Loghlen & Beecher 1999), song structure (e.g. Galeotti *et al.* 1997) and temporal patterning (e.g. Popp 1989). Moreover, male songs have typically been explained in the context of sexual selection, e.g. females choose males that sing more because they are likely to be in better condition (e.g. Payne & Payne 1977, Greig-Smith 1982, Beani & Dessì-Fulgheri 1995, Catchpole & Slater 1995, Johnstone 1995, Kroodsma & Miller 1996). Most of the above cited studies have been carried out on oscines (songbirds), species characterized by weak pair-bonds, low territoriality and relatively frequent EPCs. In long-lived 'quite monogamous' species, in which pair bonds and territories are maintained year-round and persist over several years, we can hypothesize different patterns and functions of call behaviour (Penteriani 2002).

Despite the great interest in avian vocalizations, few data have been published as yet on the possible effects of conspecific density on bird call displays (Penteriani *et al.* in press), and no consideration has been given to the effect of density pressure on the honesty of call behaviour as a predictor of individual and/or territory quality. In many cases, the collective pattern of signal interactions can be reduced to a summation of interindividual stimuli and responses (Alexander 1975). There is evidence that males of many species adjust their vocal activity to signal at the same time as their neighbours: this type of collective display has been referred to as a temporal equivalent of a (spatial) lek (Walker 1983).

Conspecific density is an important factor affecting several individual and population features including territorial behaviour, evolution of species characters, species distribution, EPC and cuckoldry rate, fecundity (e.g. Fretwell & Lucas 1970, Parker 1974, Møller 1991b, Danielson 1992, Møller & Birkhead 1993, Ferrer & Donázar 1996, Stamps *et al.*

1997, Ruxton *et al.* 1999, Doutrelant *et al.* 2000), and possibly vocal behaviour.

The aim of this work was to investigate the hypothesis that, in long-lived, territorial species such as Eurasian Eagle Owls *Bubo bubo*, density affects the vocal displays of mated males and, consequently, may disrupt the honesty of call behaviour as a possible signal of male and/or territory quality. The vocal displays of Eagle Owls have both territorial and sexual functions (Penteriani 2002), and the main territorial defence is performed by males, which are generally more vocal than females (Penteriani 1996). For individuals that breed several times during their life, signalling could be affected by their life history experience, and by the trade-off between territorial and sexual pressures (Penteriani 2002), in turn affected by local condition and needs. Thus, an individual's signalling behaviour may depend on whether it is surrounded by conspecifics or is relatively isolated. If we accept the general assumption that call displays are costly, we should predict that males without neighbours invest in such displays relatively less than those in high-density situations, making it difficult to evaluate correctly, by the characteristics of call displays, their individual quality or that of the territory that they occupy. Males in low-density situations would derive less advantage from paying the socially imposed costs of signalling.

METHODS

Study area and data collection

The study was conducted from October 1999 to July 2000 on the Luberon mountain in Southern France (43°53′N, 5°24′E). Elevation ranged from 160 m in the Durance river valley to 1125 m on the Grand Luberon ridge. The study area was characterized by a mosaic of cliffs, shrub vegetation (*Quercus coccifera*, *Thymus vulgaris* and *Rosmarinus officinalis*), Mediterranean forest (*Quercus ilex*, *Q. pubescens* and *Pinus halepensis*), croplands, pastures and fallow fields.

Before carrying out the study, a census was made of breeding pairs throughout the massif (Penteriani *et al.* 2001), and I had previously observed the calling behaviour of the species (1997–1999). I chose 17 nest-sites distributed over the study area and monitored the dusk activity of males. I was able to collect data on dusk movements related to call activity of each individual, calling behaviour, location and use of call perches (Penteriani 2002). In addition, to avoid

possible confusion in the attribution of recorded calls to a specific male, I made tape-recordings of the Eagle Owl at each listening session and determined from sonograms whether the recorded birds were always the same (V. Penteriani unpubl. data). Actually, the hooting of Eagle Owls shows great constancy, is specific to the individual and allows unequivocal identification of an individual (Lengagne 2001). This allowed me to identify each individual by the sonogram features of its hooting.

During the breeding season of 2000, I systematically checked all the breeding sites of the males for which I recorded the call activity to obtain data on egg-laying dates, productivity (number of fledged young per breeding pair) and diet, all of which were subsequently tested as possible predictors of call duration (see Statistical analyses).

Within the study area, two main situations of different breeding pair density were identified, associated with a difference in cliff availability (Penteriani *et al.* 2001, 2002). On the basis of this it was possible to discriminate two subsamples of the investigated population: males breeding in a high-density situation (31.6 nest-sites/100 km^2), where the distance between two nearest neighbours was frequently less than 1 km, and males breeding in a low-density situation (19.6 nest-sites/100 km^2), where the distance between two nearest neighbours often exceeded 3 km (Penteriani *et al.* 2001). The two subsamples are parts of a continuously occupied landscape that have relatively high and low densities.

Each month from early October, when calling resumed, to mid-February, when egg-laying generally started (Penteriani *et al.* 2000, 2001), I listened to the 17 breeding males. Nine males bred in situations of low density (distance to nearest neighbour more than 2 km), the other eight in situations of high density (distance to nearest neighbour not more than 1 km). My passive auditory sessions (Penteriani *et al.* 2000) started 1 h before sunset and ended 2 h after sunset, when the males left their song-posts for foraging trips and temporarily ceased their vocal displays. During each listening session, I collected the following data for the deep and booming *oohu*, the main call type of adult males (Penteriani 1996): (1) time of all calls from the first to the last; (2) duration of each vocal event (a series of single calls), hereafter referred to as 'call duration' (timed using a stopwatch; a series was judged to have ended if more than 60 s of silence elapsed before the next call). A value of 1 s was arbitrarily ascribed to one isolated call (Penteriani 1999); (3) number of

calls in each series; (4) number of series per sunset session.

I did not conduct observations on windy, cloudy or rainy days because of their potential interference with call displays, and I always recorded the vocalizations from the same locations and from within 500 m of the nesting cliffs.

Statistical analyses

To test the hypothesis that density affects call displays, masking honest signalling of male and/or territory quality, the analysis was organized in successive steps. First, I explored the features of the call period of the 17 Eagle Owls to detect possible differences between high- and low-density situations.

Secondly, I used a Generalized Linear Model (GLM; McCullagh & Nelder 1989) to obtain a mathematical description of the predictors of mean call duration (log-transformed dependent variable with normal error and logit link function), in an attempt to avoid covariance of explanatory variables. Among the variables describing bird call performance, the duration of vocalizations (see point [2] above) seems to be among the most significantly correlated with male quality (Catchpole & Slater 1995, Welch *et al.* 1998). Moreover, I only used the mean call duration in the GLM because I had identified previously a strong correlation between mean call duration and (a) mean number of calls per series (Spearman rank correlation: $r^S = 0.97$, $n = 17$, $P < 0.0001$), and (b) mean number of series ($r^S = 0.81$, $n = 17$, $P < 0.0001$).

GLMs allow for the use of appropriate error formulations from the exponential family distribution, avoiding the restrictions of traditional regression models. Each explanatory variable and all possible interactions were fitted to the observations using the GENMOD procedure of the SAS package (SAS Institute 1996). The statistical significance of each variable was tested in turn in the model (forward stepwise procedure according to Forero *et al.* 2002), retaining those that contributed to the largest significant change in deviance. The best model was selected by likelihood ratio tests for Type I analysis (SAS Institute 1996). The variables were incorporated into the model only when they explained more than 5% of the deviance.

I used a set of 10 possible predictors of the mean call duration. I used three landscape structure features within 1 km of the nest cliff (percentage of open land, distance to the nearest open land, Shannon

index for landscape diversity). These parameters represent the most common and useful ones used to describe the structure and quality of Eagle Owl nesting habitat (Penteriani *et al.* 2001, 2002). I used one parameter of density (the nearest-neighbour distance – NND – between occupied nests), and four variables related to diet (percentage biomass of mammals and birds in diet, diet richness, Shannon index for diet diversity), which explained most of the variation in the diet of individual pairs (Penteriani *et al.* 2002). Finally, I used two variables related to reproduction (egg-laying date and productivity), which have also been used to define individual male quality (see reviews in Catchpole & Slater 1995, Kroodsma & Miller 1996).

The GLM attempted to explain call duration as a function of the chosen predictors, whereas the interactions between all the variables were tested to detect whether strong levels of male–male competition promote honesty in vocal displays, in comparison to males without close neighbours. That is, if call duration results were related to some parameters of individual or territory quality in high-density situations only.

Thirdly, I used Mann–Whitney *U*-tests and Spearman's correlations to investigate: (a) the possible impact of conspecific density on the time of the first call at sunset, and (b) the possible differences in individual/territory quality between the high- and low-density samples. I hypothesize that in the absence of a difference in quality between the two samples, possible significant differences in mean call duration within the sample are unlikely to be ascribed to differences in male individual and/or territory quality, supporting an influence of conspecific density on call behaviour. Five parameters were used to assess and compare the quality of males and their territories: reproductive success, three features of the territory (percentage of open land, distance to the nearest open land, Shannon diversity index for landscape) and diet richness (see Penteriani *et al.* 2002 for more

details). All the landscape and diet parameters have been shown to be good predictors of Eagle Owl territory quality in Mediterranean landscapes (Penteriani *et al.* 2001, 2002). To avoid pseudoreplications, when multiple measurements were collected from the same individual, I used their mean for analysis. All the tests were two-tailed.

RESULTS

Call behaviour during the prelaying period

The sample of 17 males exhibited high variability in call behaviour. This variability was explained by the differences between males breeding in the high-density situation ($n = 8$) and those breeding in the low-density situation ($n = 9$; Table 1). These differences were significant in terms of mean call duration (Mann–Whitney *U*-test: $z = -3.368$, $P = 0.001$), mean number of calls per series ($z = -3.464$, $P = 0.001$) and mean number of series per sunset session ($z = -2.953$, $P = 0.003$).

Density affected (Mann–Whitney *U*-test: $z = -1.828$, $n_1 = 8$, $n_2 = 9$, $P = 0.05$) the time of the first call at sunset: males in the high-density situation started their first dusk call earlier (11.2 ± 19.8 min after sunset, range = $14–68$ min) than males in the low-density one (19.6 ± 19.1 min after sunset, range = $10–73$ min).

GLM of the mean call duration

For the GLM of the logarithm of mean call duration I obtained a model accounting for 64.0% of the original deviance (Table 2). One explanatory variable (NND) and its interactions with productivity and percentage biomass of mammals in the diet entered the GLM model with call duration as the dependent variable. NND alone accounted for 41.0% of the deviance in the null model. The model showed that call duration increased with density of conspecifics,

Table 1. Characteristics of Eagle Owl calls during the prelaying period (early October to mid-February): all males ($n = 17$), males at high-density ($n = 8$) and males at low-density ($n = 9$).

	Call duration (s)		Number of calls in each series		Number of series in each sunset session	
	Min.–max.	$\bar{x} \pm$ sd	Min.–max.	$\bar{x} \pm$ sd	Min.–max.	$\bar{x} \pm$ sd
Overall sample	30.0–4472.0	884.7 ± 1105.4	5.0–387.0	82.7 ± 97.2	1.0–8.0	3.1 ± 2.0
High-density	174.7–4472.0	1182.6 ± 1018.2	59.1–387.0	96.2 ± 96.2	3.5–8.0	3.7 ± 3.7
Low-density	30.0–497.2	257.4 ± 180.7	5.0–48.2	33.2 ± 30.5	1.0–2.6	2.1 ± 2.0

Table 2. Generalized Linear Model (GLM) for the predictors of mean call duration of male Eagle Owls (*n* = 17), using normal error and logistic link. The variables were fitted to the model according to the degree of change in deviance when the variable was added to the model and when it explained more than 5% of deviance. The model accounted for 64.03% of the original deviance.

Explanatory	Estimate	se	χ^2	*P*
Intercept	791.76	68.36		
NND	−0.17	0.03	8.98	0.0027
NND × productivity[a]	0.03	0.01	4.53	0.0333
NND × mammal biom[b]	−0.0001	0.00	3.87	0.0490
Residual deviance	274946.37			

[a]Number of fledged young per breeding pair.
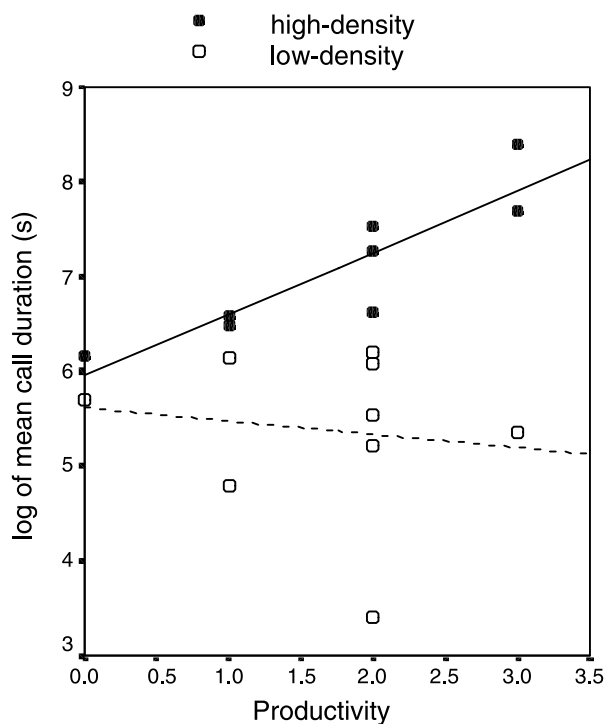[b]Percentage biomass of mammals in the diet.

Figure 1. Mean call duration by male Eagle Owls in relation to distance to the nearest neighbour and number of fledged young (productivity, employed as a measure of male/territory quality). The increase in the duration of vocal displays was positively correlated with productivity in the males nesting in high-density situations only, where male–male competition was higher.

and that the increase in the duration of vocal displays was positively correlated with productivity for males with short nearest-neighbour distances only (males in high-density situations; Fig. 1). A further and less significant effect of mammal biomass in diet on call duration was detected. A high percentage

of mammals in the diet of some pairs in the low-density situation was directly correlated with call duration, owing to a scattered distribution of Rabbits *Oryctolagus cuniculus* in the study area, mostly being a passive outcome of local habitat dynamics and dietary responses to such changes (see Penteriani *et al.* 2002).

Individual/territory quality in high- vs. low-density sample

Additional support for the hypothesis that density can affect vocal displays, masking their honesty as a signal of individual and/or territory quality, was found in the fact that the number of young fledged per breeding pair (Mann–Whitney *U*-test: $z = -0.437$, $n_1 = 8$, $n_2 = 9$, $P = 0.662$), percentage of open land ($z = -0.770$, $P = 0.441$), distance to open land ($z = -1.170$, $P = 0.242$), Shannon index for landscape diversity ($z = -0.722$, $P = 0.470$) and diet richness ($z = -1.276$, $P = 0.202$) did not differ significantly between males in high- and low-density situations. That is, the detected differences in mean call duration for the overall sample are unlikely to be ascribed to differences in male individual or territory quality.

DISCUSSION

The analysis of the dusk call displays of male Eurasian Eagle Owls during the prelaying period highlighted the influence of conspecific density on call activity: the shorter the NNDs, the higher the call duration of males. NNDs as a predictor of mean call duration explained approximately two-thirds of the overall variability in call duration. Excitation or stress due to conflict situations is reported to increase call frequency in a number of passerine species (Brémond 1968, Van der Elzen 1977, Ueda 1993), not necessarily to communicate something, but perhaps because of a broader motivational context (Owings & Morton 1998). The density effect masked the honesty of call duration as a possible signal of male and/or territory quality in the whole population: the analysis of my sample showed that call duration was related to productivity only for the males in the high-density situation. Moreover, the absence of significant differences in individual and territory quality between males in high- and low-density situations supports the hypothesis that the variation in mean call duration for the overall sample is unlikely to be ascribed to differences in male quality.

This study, to my knowledge, represents the first evidence that conspecific density can produce such an effect on honest signalling of individual and/or territory quality. The call display as an honest indicator of male fitness persists only in situations of strong male–male competition; that is, high breeding owl density. For the males in this situation, one parameter of individual fitness was related to call duration: males calling for longer had higher productivity. This call pattern is similar to those of songbirds, for which the cost of vocal displays is an increasing function of the time spent calling and a decreasing function of male quality (e.g. Møller 1991c, Catchpole & Slater 1995, Kroodsma & Miller 1996). In the low-density situation, no correlation was detected between call duration and male or territory quality: high productivity owls were relatively silent. In several other studies, researchers have failed to find reliable evidence for good singers (and their mates) having better than average breeding success (e.g. Catchpole & Slater 1995, Welling *et al.* 1997): in these cases density could be one of the confounding factors causing extra variation and making it difficult to detect an effect of male quality.

A high investment in vocal signalling in the absence of competition would be a waste of time and resources: accommodation allows a male to minimize the costs of aggressive calling by adjusting his territoriality threshold to local conditions. Assessment forms the foundation upon which communication systems are built, and individual behaviour depends in part on the evaluative reactions due to experience and source of feedback sustaining or disrupting activities that produce it (Owings & Morton 1998). Such flexibility allows males to balance the costs and benefits of territorial behaviour and maximize their fitness. Communication can itself be considered a social behaviour (McGregor & Peake 2000): when a species is not homogeneously distributed over the landscape (e.g. some patches have a high concentration of individuals, while other patches have a few, relatively isolated individuals), is strongly territorial and has well-established communication networks, we need to be careful with regard to the possible impact of conspecific density on call displays. As underlined by Galeotti (1998), males that sing longer are not only likely to be in better condition, but also more strongly motivated than others. The difference in density between males in my study and the associated differences in call behaviour between individuals living within the same area emphasize the importance of considering each population not as a homogeneous grouping, but as a heterogeneous assemblage of individuals, subject to heterogeneous pressures and showing heterogeneous responses. Among owls, an increase in call activity has been associated with high conspecific density for the Tawny Owl *Strix aluco* (Galeotti 1994) and the Long-eared Owl *Asio otus* (Tome 1997).

One might expect male Eagle Owls in high-density situations to adopt a mechanism that would reduce the effort expended in competitive behaviour towards neighbours, because it appears to involve considerable time and energy. This scenario might reflect a habituation process, that is the waning of a response because of repeated stimulation (Fisher 1954). This does not seem to occur in neighbouring Eagle Owls, despite the considerable cost, in terms of time, that males incur in their vocal activity (e.g. interference with courtship and feeding). If we accept habituation as a widespread phenomenon conducive to the reduction of aggression among neighbours (Rowland 1988), we can hypothesize that the recorded high call intensities are maintained because of frequent intrusions by floaters and/or neighbours into high-density territories, in which it is easier to engage in copulations (Smith & Arcese 1989), and whose potential nesting cliffs are very attractive because they are abundant, clearly visible and homogeneously distributed within such territories (Penteriani *et al.* 2001). Finally, in situations of high density when the social environment calls for longer vocal displays, the earlier starting time of vocalizations might be a strategy to save the night time for other vital activities (e.g. foraging).

The results of the present study stress the importance of taking into account the environmental and social conditions experienced by the individuals when investigating the evolution and maintenance of honest territorial and/or sexual signals. At the same time, male–male competition ensures honesty. The observed behaviour represents a further element consolidating the idea that male–male competition contributes to the maintenance of honest signalling, because in the absence of strong competition (i.e. for the males in the low-density situation) the call behaviour was not related to male or territory quality.

My results also highlight the need to approach the study of call behaviour from a wider perspective than that of birdsong alone. We therefore run the risk of making a biased interpretation of song function and evolution if our vision of call displays is limited

only to birdsong. A mate-attracting function of song does not seem generally applicable to species such as Eagle Owls, which usually call when already mated. More research is needed on 'permanently' paired and territorial species, for which mate attraction is an event that occurs once or a few times in an individual's life, and where the major selective forces affecting song evolution are not necessarily those related to mate acquisition. Birdsong is not a peculiarity of songbirds.

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