Short communication

Owl dusk chorus is related to the quality of individuals and nest-sites

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Dawn and dusk choruses represent one of the most investigated topics in avian vocal behaviour, but their underlying basis remains unclear. As with the dawn chorus in passerines, dusk chorus in owls seems to support the mate and rival assessment hypothesis and happens during the most constraining period, as individuals have not yet fed and, under the handicap principle, dusk chorus is likely to reveal inter-individual differences in competitive ability, body condition and/or habitat quality. Here, a study of vocal displays at dusk of 14 Eurasian Eagle Owls *Bubo bubo* revealed a temporal succession in the order in which males began their vocalizations. The vocalization order appeared to be related to both the quality of the nesting territory (based upon mean number of fledged young and proportion of rats in the diet) and the male's individual quality, as revealed by haematocrit values and the brightness of the white throat patch.

Keywords: calls, individual quality, vocal display.

Bird dawn and dusk choruses, the sunrise and sunset peaks in song output, represent one of the most investigated topics in vocal behaviour (Bradbury & Vehrencamp 2011). During choruses, various individuals are involved in interactive communication (Hardouin *et al.*

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2008, Foote *et al.* 2010, 2011); the frequency of interactions depends on the relationships among males (Foote *et al.* 2008), and the timing of vocal displays varies among individuals (Foote *et al.* 2011) and may be related to male quality (Otter *et al.* 1997, Murphy *et al.* 2008). However, the basis underlying twilight choruses remains unclear (Staicer *et al.* 1996, Burt & Vehrencamp 2005, Bradbury & Vehrencamp 2011) and studies have primarily focused on diurnal songbirds (but see Hardouin *et al.* 2008, Penteriani & Delgado 2009).

Eurasian Eagle Owls *Bubo bubo* perform dawn and dusk choruses, the dusk chorus being analogous in the daily cycle to the dawn chorus of diurnal birds. In a previous study of the dusk chorus of neighbouring males we detected a temporal succession in the order in which individuals start their vocalizations, a phenomenon not previously reported in avian choruses (Delgado & Penteriani 2007). Here, we characterize this pattern and identify factors that may determine this order. Our aim was to understand whether individuals living in high-quality sites and/or in better condition call earlier than individuals in low-quality sites and/or of worse condition, and whether those breeding on slopes exposed to sunlight for less time, start to vocalize earlier than those in sunnier places.

METHODS

Vocal behaviour

During 67 listening sessions, we documented the vocalizations of 14 breeding males (mean distance between neighbouring breeding sites: mean ± 1 sd, 1007 ± 480 m, range 250–1760 m) of a population in southwestern Spain (Sierra Morena). Listening sessions were conducted during 2011 and 2012, in the pre-laying period (September–January), the annual vocal activity peak of Eagle Owls (Delgado & Penteriani 2007). Vocal behaviour was monitored from 1 h before to 30 min after sunset (to ensure observation of the first owl vocalizations), one of the two daily peaks of Eagle Owl calls (Delgado & Penteriani 2007). During listening sessions we recorded time of the first and all subsequent calls of an individual and vocal display duration (minutes). We did not conduct observations on windy or rainy days because of interference with call displays and call detection by observers.

We arranged the 14 individuals into four neighbouring groups (two groups of three and two groups of four neighbours; sampling effort per group: group 1 = 22 nights; group 2 = 17; group 3 = 17; group 4 = 11). To avoid subjectivity when clustering the focus males, groups were identified on the basis of: (1) proximity: distances among the closest individuals of the same group (mean 964 ± 186 m) were shorter than distances

among the closest individuals of neighbouring groups (mean 1170 ± 309 m); and (2) location of suitable listening places from which it was possible to listen to the individuals of each group. The cluster made using proximity criteria and the location of suitable places for recording is mostly coincident with other methods of spatial segregation (Hernández & Navarro 2007).

To test whether the order in vocal displays differs from chance, we created a null model of emergence time to compare with real data. To do this, for all 67 nights we randomly sampled one male from each of the four groups repeatedly and calculated the frequency (%) with which each male would have started first.

Finally, we calculated (following Harper 1994): (1) repeatability of call order, which provides an additional indication of behavioural stability, and (2) repeatability of time to sunset of the first vocalization. This may help determine whether call order is a by-product of something internal (a fixed time to sunset, possibly based on individual quality independent of other birds) or external (interactions with neighbouring owls).

Breeding site quality and exposure

Quality of breeding sites was estimated by (1) mean egg laying date and mean number of fledglings; (2) the availability of Rabbits *Oryctolagus cuniculus*, the main prey of the population (mean biomass percentage in diet = 62.0 ± 19.1%), within the nest-site, estimated by the number of latrines per kilometre of transects within an area equal to the mean Eagle Owl home-range size in our population (more details in Campioni *et al.* 2013); and (3) the percentage biomass of rabbits and rats *Rattus* in the diet. Rats represent the second most common species in the Eagle Owl diet and increase with nesting site quality (Campioni *et al.* 2013).

Nest-site exposure is a categorical variable composed of the four cardinal and four ordinal compass directions, and corresponds to the amount of light illuminating the vicinity in which males started vocalizations. This represents the possible effect of ambient light in triggering the commencement of vocal displays.

Individual quality

The physiological condition of 10 of the 14 males that were trapped was estimated by Campioni *et al.* (2013): haematocrit (HT), an indicator of nutritional status, and body condition index (BCI, a reduced major axis regression using log of body mass and wing length; Delgado *et al.* 2010), with the highest values corresponding to the best individuals. We also measured the brightness (i.e. total reflectance) of the white feather patch on the male throat, which is positively correlated with individual quality (full details in Bettega *et al.* 2013).

Statistical analyses

To explain the frequency (%) with which each individual began the dusk chorus within a group (dependent variable), we ran three linear regression models (assuming that the residual variation follows a normal distribution with 0 mean and variance σ^2) related to the quality of the breeding site, the exposure of the nest-site and individual quality. First, we conducted a graphical analysis for the explanatory variables and checked for correlations (Spearman's rank correlation) among pairs of predictors: where $r_s \geq 0.6$ we retained those variables that we considered to have greater biological relevance. The frequency with which each individual began the dusk chorus was log-transformed and the response variables were normalized to zero mean and unit variance. Backward selection of variables was applied to the full model, and models were compared using likelihood ratio tests (Crawley 2007). Residuals of the final models were explored to verify the assumptions of normality and independence. Statistical analyses were performed using R 2.10.1 statistical software (R Development Core Team 2009) with the nlme (Pinheiro *et al.* 2009) package. Means are reported ± 1 sd.

RESULTS

The call starting time ranged from 56 to 1 min before sunset (mean = 22.8 ± 9.9 min). The earliest males to stop vocalizations did so 2 min after sunset (mean = 18.6 ± 3.5 min). Mean time of starting calls before sunset was different among the groups (41, 17, 30 and 31 min; $\chi^2 = 9.77$, df = 3, $P = 0.02$), whereas average ending time of calls after sunset was homogeneous (18, 22, 20 and 26 min; $\chi^2 = 1.63$, df = 3, $P = 0.65$). After the first individual of a group started calling, the second did not always begin vocalizing immediately (mean = 21.0 ± 4.2 min after the first individual started to call; min. = 1 min; max. = 69 min).

Order in vocal displays

Dusk choruses were usually initiated by the same individual of each group. For groups 1–4, the same individual started first in 93.8, 52.9, 50.0 and 36.4% of choruses, respectively, and in three of the four groups there was at least one individual that never called first. The order of vocal displays was different from the null model, in which the same individual for groups 1–4 started first in 34.6, 28.2, 35.9 and 30.0% of the simulated choruses, respectively; for the null model, the commencement of vocalizations was never started by the same individual. An ordered call sequence was also

evident for the individuals that occupied the second (53.9, 66.7, 40 and 36.4% of the cases) and third (45.5, 50.0, 64.7 and 42.9%) ranking in their respective groups. Repeatability for call order (0.80) was higher than that for time to sunset (0.52), suggesting that, independent of sunset, individual features appeared to play an important role in choruses.

When the 'usual early' caller was not first, the overall order did not change greatly, as the 'usually second' caller became first (the third and fourth individuals did not change their order). The habitual order typically changed because the 'usually first' owl started to vocalize later.

Nesting site and individual attributes

Males with the highest fecundity and proportion of rats in their diet (adjusted $R^2 = 0.33$, $F_{2,25} = 7.71$, $P = 0.003$; Table 1A) and those with the highest HT and brightness (adjusted $R^2 = 0.82$, $F_{2,7} = 20.96$, $P = 0.001$; Table 1B) started calling earlier. Nest-site exposure (adjusted $R^2 = -0.07$, $F_{2,25} = 0.15$, $P = 0.86$) did not affect calling order. The owl choruses thus determined the emergence of a hierarchical communication based on the characteristics of individual quality and the quality of the nest territory.

DISCUSSION

Our results support the contention that calls can carry information related to both the individual's state and habitat quality. The information contained in calls may be considered an honest signal of individual and territory quality (Hutchinson *et al.* 1993, Hoi-Leitner *et al.* 1995, Penteriani *et al.* 2002): as suggested by Montgomerie (1985) for the dawn chorus, energy reserves of nocturnal species should be lowest at sunset and may impose a handicap for the timing and amount of vocalizations. Experimental evidence supports the idea that birds in food-rich territories show higher call rates than

Table 1. Final linear regression models showing the effect of (A) breeding site quality and (B) individual features on Eagle Owl call order.

	Estimate	se	*t*	*P*
Log (call order)				
A				
Intercept	2.24	0.28	8.04	<0.0001
% rat biomass	0.82	0.29	2.88	0.008
Mean fecundity	0.68	0.29	2.39	0.025
B				
Intercept	27.02	3.03	8.91	<0.0001
Haematocrit	16.92	3.33	5.07	0.001
Badge brightness	17.67	3.33	5.30	0.001

individuals in poorer territories (Hoi-Leitner *et al.* 1995) and, more generally, that high display rates are associated with physiological costs (Oberweger & Goller 2001), which only individuals in better (body) condition are able to afford (Hardouin *et al.* 2007). The ability to maintain a high song output may reflect the ability of the male to acquire the resources needed to allow time for early/ longer vocal displays. This efficient resource acquisition is probably mediated by the occupation of high-quality territories (Reid 1987, Hutchinson *et al.* 1993).

A quality-mediated chorus might support the assertion that vocal displays arbitrate social relationships with territorial neighbours through interactive communication, as proposed by the social dynamics hypothesis (i.e. males sing to adjust their relationships with neighbours; Staicer *et al.* 1996, Foote *et al.* 2008), and also suggested for Little Owls *Athene noctua* (Hardouin *et al.* 2008).

The dusk chorus can thus emerge as a result of multiple external stimuli, such as time of sunset (Penteriani & Delgado 2009), a high density of conspecifics, and signals from early callers, where focal individuals orchestrate a sort of behavioural synchrony within the communication network.

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