

A dusk chorus effect in a nocturnal bird: support for mate and rival assessment functions

Loïc A. Hardouin · Dominique Robert ·
Vincent Bretagnolle

Received: 18 December 2007 / Revised: 2 June 2008 / Accepted: 5 June 2008 / Published online: 24 July 2008
© Springer-Verlag 2008

Abstract The dawn chorus is a striking feature of spring mornings and a characteristic behaviour of many bird species, particularly the passerines. Dawn singing has been considered a reliable signal of male quality for mate and rival assessment. Singing is presumed to be relatively costly at dawn both because air temperatures are relatively low and because birds have not fed overnight. Models of optimal daily routine predict the existence of a “dusk chorus” in nocturnal birds, although this prediction has received little empirical attention. Nocturnal birds at dusk may be energy-limited because of a lack of daytime feeding, and singing at dusk may thus ensure signal reliability. Here, we used an observational and experimental approach to study vocal behaviour at dusk and dawn in a nocturnal raptor, the little owl *Athene noctua*. We assess whether male little owls adjust their vocal behaviour according to feeding stage (i.e. period of the night), ambient air temperature and territorial context (i.e. spontaneous calling behaviour vs elicited calling by intrusion). Across different temperatures, we find that both spontaneous vocal

activity and inter-individual variability in call duration increased at dusk, clearly indicating a dusk chorus phenomenon. Results from playback presentations suggest that food, rather than air temperature, is likely to be more constraining at dusk. We discuss how comparing dusk and dawn choruses in nocturnal and diurnal species can provide insights into both mechanistic and functional aspects of signalling behaviour.

Keywords Dawn chorus · Owls · Proximal factors

Introduction

Sexual signals and displays are used by males for the purpose of persuading females to mate or to repel rival males from their territories (Anderson 1994; Maynard-Smith and Harper 2003). In such contexts, the time and effort individuals are able to allocate for display depends partly on proximal environmental factors, such as time of the day and ambient light, as well as on available energy reserves (Bradbury and Vehrencamp 1998). Individuals are therefore expected to experience trade-offs between displaying and other mutually exclusive behaviours such as foraging. Hutchinson et al. (1993) applied stochastic dynamic programming (SDP) to model this trade-off. SDP is appropriate for modelling decisions made by an individual according to its current state (e.g. energy reserves) and its environment. Applied to signalling theory, SDP models assume that signals are costly and that the effects of energetic costs on an animal's subsequent behaviour are mediated by its current energetic state (Hutchinson et al. 1993; Hutchinson and McNamara 2000; Hutchinson 2002; Thomas and Cuthill 2002). One type of prediction of SDP models is the daily routines of

Communicated by J. Podos

L. A. Hardouin · V. Bretagnolle
Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934,
Villiers-en-Bois 79360, France

D. Robert
Grande rue,
Montchauvet 78790, France

L. A. Hardouin (✉)
Centre for Mammal Vocal Communication Research,
Department of Psychology, School of Life Sciences,
University of Sussex,
Pevensey Building,
Falmer BN1 9QH, UK
e-mail: loic.hardouin@gmail.com

behaviour that provide an optimal solution to the trade-off between the changing costs and benefits of signalling and other competing behaviours such as foraging and resting.

Optimal daily routines (ODR) have been used to explain the bird dawn chorus, a striking behaviour that occurs in spring in temperate and tropical latitudes. The dawn chorus occurs in many bird species but is particularly prevalent in the passerines (Kacelnik and Krebs 1983; Slagsvold et al. 1994; review in Staicer et al. 1996). It is characterised by a peak in vocal activity at dawn, followed by a lull later in the day, then a smaller peak of vocal activity at dusk. The ODR model makes the assumption that, during daytime, a male bird has to choose between singing and foraging and that the decision is mediated by his current energy reserves (e.g. Barnett and Briskie 2007). Energy reserves should be lowest at dawn, because they have not been built up overnight, and because nighttime is typically colder and associated with higher metabolic energy expenditure. In addition, singing activity is typically considered to deplete energetic reserves and, therefore, to be costly (Oberweger and Goller 2001). However, this latter point has been debated because actual measurements of the energetic cost of singing have led to contradictory results. Whilst some studies found slight or no differences in metabolic rate when birds were singing as opposed to when they were not (e.g. Ward et al. 2004), others found metabolic rate to be higher during singing in comparison to any other activity except flying (Oberweger and Goller 2001). Indirect evidence of the impact of metabolic state, based on measurements in the wild of proxies for energetic reserves such as foraging activity, body mass or ambient air temperature, is more convincing (though alternative explanations are possible: see Gaunt et al. 1996). Birds generally sing less when their body reserves are low (Reid 1987; Godfrey and Bryant 2000; Thomas 2002a; Thomas et al. 2003), when foraging success is low (Kacelnik 1979; Mace 1989; Cucco and Malacarne 1997) or when ambient conditions are too metabolically demanding (Garson and Hunter 1979; Thomas 2000). Energy reserves constitute a buffer against the risk of starvation, and thus, the allocation of time for singing vs feeding results from a trade-off taking into account both overnight and daily energy requirements (Mace 1989; Thomas et al. 2003). As pointed out by Staicer et al. (1996), singing requires not only an important energetic input, but there is also a further cost to individuals in reduced foraging time.

For these reasons, several authors have suggested that singing at dawn may provide a particularly honest signal of male quality (Zahavi 1975; Grafen 1990). Singing rates during the dawn may reveal differences among males in relation to energetic reserves accumulated the previous day, thus giving some indication of a males' ability to acquire resources (Thomas and Cuthill 2002). Therefore, differ-

ences in quality between individuals should be most obvious at dawn in diurnal birds, as males are expected to differ with regard to energetic reserve states, hence potentially providing females and rivals with efficient cues for assessing male quality from the perspective of the handicap principle (Hutchinson et al. 1993). Indeed, at least in the passerines, dawn chorus parameters such as duration of song output and chorus onset have been shown to correlate with aspects of male quality (Welling et al. 1997; Otter et al. 1997; Murphy et al. 2008). Cold temperatures are expected to increase individual basal metabolic rate for thermoregulation and, as a consequence, both reduce song output and increases inter-variability between males (see Garson and Hunter 1979; Strain and Mumme 1988). However, because, at dawn, temperatures are coldest while, simultaneously, males have not fed, it has not been possible so far to disentangle these two proximate factors (Kacelnik and Krebs 1983).

Studying daily patterns of singing activity in nocturnal birds may provide novel insights. ODR models predict the occurrence of a large dusk chorus and smaller dawn chorus in nocturnal birds that can sing and forage effectively by night (Hutchinson et al. 1993) because energy reserves at dusk should be relatively depleted given a lack of recent foraging, which would make dusk signalling comparatively reliable. This prediction, however, has received little attention in free-ranging animals (Godfrey and Bryant 2000), particularly for night singers (but see Amrhein et al. 2002; Thomas 2002b for studies on the nightingale *Luscinia megarhynchos*). Whereas diurnal passerines face both adverse temperature and low body reserves at dawn, in nocturnal birds, the situation is shifted. At dawn, air temperature is minimal but birds will have already fed. On the other hand, at dusk, air temperature is milder but they have not fed. The effect of this shift has never been investigated, and it is difficult to produce a priori predictions about when signal output should be favoured.

Here, we use both observational and experimental evidence to study the dusk and dawn vocal behaviour of the little owl *Athene noctua* to assess how males may adjust their vocal behaviour according to the stage of the night, ambient air temperature and territorial context (i.e. spontaneous calling behaviour vs elicited calling by intrusion). We quantify calling behaviour of males at dusk and at dawn, both in natural (spontaneous) and simulated aggression (playback) contexts. Then, by contrasting calling activity in these contexts at dawn and dusk, we investigate how ambient air temperature and stage of the night (a proxy for cumulative food intake) affect vocal output. Finally, because the stage of the night and ambient air temperature may differently affect males' body fat reserves, we also documented inter-individual variability in call output both

in spontaneous calling and playback responses at dusk and at dawn.

Materials and methods

Study area and species

The little owl (family Strigidae) is a territorial, resident, philopatric and monogamous nocturnal raptor (Génot 1992a; Exo 1992; Génot et al. 1997), usually inhabiting open fields (Génot 2005). Little owls make extensive use of acoustic communication for territory maintenance, as well as for attracting mates (Schönn et al. 1991). Moreover, like many owl species, little owls' vocal activity is characterised by a peak at both dusk and dawn and an overnight lull (Exo and Scherzinger 1989). During the breeding season, two call types predominate: the chewing call, produced by both males and females, and the hoot, produced only by males (Exo 1984; personal observation). The hoot is usually produced in strophes over the entire breeding season, peaking in March (Génot 1992b; 2001). Both chewing calls and hoots are used by males in territorial contests. Although the chewing call can be given in response to playback, the hoot is predominantly used in response to playback from February to April (90% of the vocalizations uttered; unpublished data). We thus focused on hoots because they are used by males to defend their territories (Schönn et al. 1991), although territorial responses that begin with hoots may sometimes end with chewing calls.

Fieldwork was conducted from 11 February to 30 March 2003 and from 20 February to 23 March 2004 in two agricultural plains situated in western France (46°N, 00°24' W, site 1) and in northern France (48°54'N, 01°37'E, site 2). In both localities, little owls are mainly restricted to villages where they can find nest cavities. Densities of little owls are 0.49 pairs/km² in site 1 (Bretagnolle et al. 2001) and 0.30 pairs/km² in site 2. Local density, however, can reach up to 1.53 pairs/km².

Environmental conditions

Air temperature was measured using a thermometer with an external temperature sensor (Oregon Scientific N°TA113, precision ±1°C). During the whole study, we took air temperature at dusk and at dawn. We used the current temperature rather than the temperature prevailing during the previous 24 h. While it has been shown that past temperature reflects an animal's ability to optimise storage of fat reserves, current temperature may constrain the bird's ability to achieve this optimum, and a positive correlation has been found between fat reserves and current temperature (Gosler 2002). Local sunrise and sunset times were

found at <http://lychnis.imcce.fr/cgi-bin/levcou.cgi> (Institut de Mécanique Céleste/Observatoire de Paris).

Measures of spontaneous calling activity

We placed three Sony TCM-20DV cassette recorders and two Panasonic cassette recorders RQ-L31 near male singing posts (see Hardouin et al. 2006) for 3 h after sunset and 3 h before sunrise. Those male singing posts were checked before and during the whole study to ensure the placing of the recorders. Because we did not have two consecutive nights without a response from a given male at the same period, we could infer that, for each male, there was no systematic pattern of non-response. Ten individuals from site 1 were used for the natural song output recording and were tape-recorded between 5 and 30 March 2003. Each male was recorded during five nights. One hundred recording sessions (five nights at dusk and dawn for 10 males) were then conducted, which resulted in 30 h of recordings for each male (15 h at dusk and 15 h at dawn). From recordings, we established the probability for each male to spontaneously call at dusk and at dawn (from here on referred to as "presence of spontaneous vocal activity") and then extracted the following vocal activity parameters: duration of spontaneous vocal activity, onset of first calling after sunset, and time elapsed between last calling and sunrise.

Playback design and methodology

For our experimental analysis, we simulated rival male intrusion by broadcasting hoot playbacks. The experimental design involved broadcasting one category of stimulus (i.e. unfamiliar hoot) to each individual, from a single location, at dusk and then again at dawn of the same night. We used the 10 males from site 1 for which we also recorded spontaneous activity. Measures of recorded spontaneous activity and playback trials of a given male during a given night were always separated by at least 2 days. In addition, 12 males from site 2 were also selected: therefore, in total, playback trials were carried out on 22 males. Males were tested from sunset to 3 h after dusk and from 3 h before dawn to sunrise. Each male received a different playback stimulus (22 different playback stimuli total), assigned at random. Because the time of day at which males were tested may introduce a temporal bias in our study, given that the probability of feeding increases as time passes, a circuit was established to minimise travel time between territories. To limit a potential order effect, the first male of the circuit was determined randomly each night.

The 22 stimuli used in this playback experiment had been recorded in previous years from 22 different males at locations away from the two study sites. Male calling had

been elicited by the playback of hoots from unfamiliar individuals and recorded with a Sennheiser MKH-815T directional microphone, connected to a Sony TC-D5M tape recorder. The recordings were always made at a short distance from the owls (10–50 m) between 8:00 p.m. and 4:00 a.m. in good recording conditions. Stimuli were selected to have comparable recording quality. Thus, we limited the potential influences of pseudoreplication (Kroodsma 1989) and execution errors (McGregor et al. 1992).

Playback tapes were prepared using Audacity freeware (D.M. Mazzoni, Canada, <http://audacity.sourceforge.net/>) to reduce background noise and normalise each recording at the same maximum amplitude (−3 dB). Hoots were played back in the field using an AIWA TP-18 tape reader connected to a Barthe EDUVOICE loudspeaker (frequency response 50–6,000 Hz±3 dB) that was pointed towards the territory centre of the individual to be tested. From the centre of their territory, and up to 500 m away, males remained similarly reactive to playback (response ratio: mean ± SE=0.90±0.06, unpublished data). Moreover, males move on average 420 m from the centre of their home range (Génot 2005). We can therefore confidently assume that tested males always heard our playbacks. All playbacks were played at a fixed volume, which was set to approximate the perceived loudness of natural hoots. The 22 playback tapes each contained 12 hoots (mean duration ± SE of 61±9 s). In site 1 and site 2, each male was presented with 10 and 5 trial repetitions, respectively. Each trial consisted of one playback of 12 hoots followed by a silent period of 5 min, during which the following vocal behaviour was quantified: latency (time elapsed between onset of playback and first vocal response), duration of response and hoot rate. The duration and latency were estimated using a chronometer. We considered that more than 30 s of silence after the last hoot constituted the end of the response. Moreover, silences lasting more than 10 s and up to 30 s were subtracted from the total duration of the vocal response. Latency and duration of response were significantly correlated ($r=-0.31$, $t=-5.1$, $df=244$, $P<0.001$). We thus focused only on latency and hoot rate to quantify the vocal response of our subjects. We also assessed the “response ratio” as the number of responses given to playback divided by the total number of playback stimuli presented. This was done both across the entire sample (“global response ratio”) and for each individual male.

Statistical analysis

Mixed models are particularly useful when the experimental design involves spatial replication (e.g. nested designs) (Crawley 2002). We used linear mixed effect models with three error distributions: a binomial distribu-

tion (logistic regression) when analysing the presence of spontaneous vocal activity and response ratio (call spontaneously/respond to playback: coded as 1; or do not call spontaneously/do not respond to playback: coded as 0); a Poisson distribution when analysing the latency of response to playbacks and a normal distribution when analysing the duration of spontaneous vocal activity or hoot rate. Period (dusk vs dawn; see “Materials and methods”), air temperature and interaction between period and temperature were the fixed effects in the models. Time of day (i.e. the two recordings of spontaneous vocal activity involving the same night on each subject or the two replicated playbacks) was nested within subjects and treated as a random effect in the models.

The duration of spontaneous vocal activity was log-transformed to achieve an approximately normal distribution ($D=0.11$, $P=0.29$, Kolmogorov–Smirnov test, $N=70$). Hoot rate was normally distributed ($D=0.10$, $P=0.12$; $N=246$). Finally, we assessed the validity of the models by checking that residuals did not show any trends nor were correlated with fitted values (Venables and Ripley 2002). The R 2.6.1 freeware (R development Core Team 2007) with lme4 package (Bates 2007) was used for all statistical analyses.

Results

Environmental conditions

During the whole study, temperature averaged $3.8\pm 4.3^\circ\text{C}$ (range -6 – 17°C). We compared temperatures between sites, months and periods (three-factor nested ANOVA with site, month within site and period –dusk and dawn– within month as factors: $R^2\text{Adj.}=0.48$, $F_{7, 312}=0.05$, $P<0.001$, $N=320$) and found that temperatures between sites did not differ significantly ($F_{1, 312}=0.57$, $P=0.45$). Temperatures were significantly warmer in March ($F_{2, 312}=11.2$, $P<0.001$), but most variation in temperature was accounted for by period (i.e. dusk vs dawn). As expected, the coldest temperatures were recorded at dawn ($F_{4, 312}=37.4$, $P<0.001$).

Spontaneous calling activity

Calls were produced significantly more often at dusk than at dawn (occurrence of spontaneous vocal activity at dusk: mean ± SE=0.84±0.05, $N_{\text{calling}}=42$ out of 50; at dawn: mean ± SE=0.56±0.07, $N_{\text{calling}}=28$ out of 50; see Table 1 and Fig. 1). At least one hoot was emitted in 70 of the 100 recording sessions (global spontaneous vocal activity ratio: mean ± SE=0.70±0.05). On average, males began to call 79 ± 47 min after dusk and ceased 113 ± 45 min before dawn. Males that began to sing earlier at dusk did not tend to stop later at dawn (linear regression: $R^2\text{Adj.}=0.13$, $F_{1,9}=2.4$, $P=$

Table 1 Results for analysis of observations of spontaneous calling

	N	Fixed effects						Random effects	
		Period		Air temperature (T)		Period*T		Subjects	Time of day within subjects
		Est. ± SE	P	Est. ± SE	P	Est. ± SE	P		
Spontaneous calling rate	100	2.3±0.9	0.01*	0.02±0.10	0.86	-0.01±0.20	0.96	4.9±2.2	~0
Duration of song output	70	1.3±0.7	0.1	0.10±0.09	0.26	-0.23±0.11	0.049*	0.4±0.6	~0

Sample size, estimate and standard error and *P* values for the terms in the model. For random effects, the variance and the standard deviation of the random effects (intercept) are provided. “Period*T” refers to the interaction between period and air temperature. For the random effect, Est. ± SE are given. * <0.05

0.15). The occurrence of spontaneous vocal activity was not affected by ambient air temperature (mean ± SD=6.7±3.9°C, range: -1.6–16.8°C; see Table 1) whatever the period of night (see interaction period*temperature in Table 1, Fig. 1).

In contrast to the occurrence of spontaneous vocal activity, the duration of response did not vary significantly between the two periods of the night (at dusk: mean ± SD=291±366 s vs at dawn: 235±201 s; Table 1). However, inter-individual variance was significantly higher at dusk than at dawn (Bartlett’s *K* squared=10.1, df=1, *P*=0.001).

When air temperature increased, dusk call output decreased, whereas dawn call output increased (interaction period*temperature: Table 1). Ambient air temperature alone had no overall net influence on the duration of spontaneous vocal activity (Table 1).

Territorial response to playback

Owls in the two study populations behaved similarly in response to playback with regard to period, i.e. dusk vs

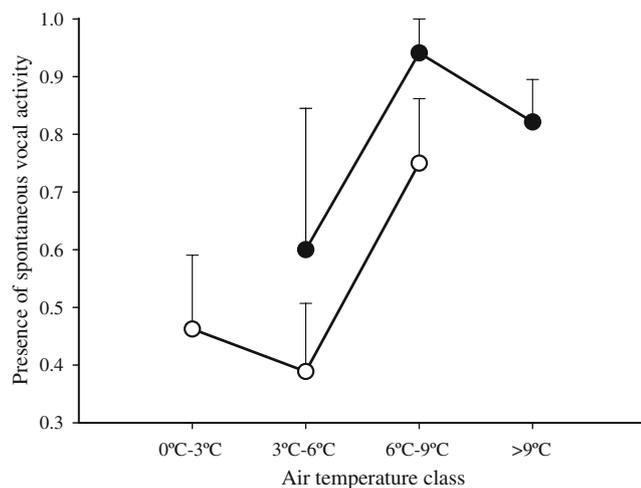


Fig. 1 Occurrence of spontaneous vocal activity (mean ± standard error) according to air temperature (presented here in class, whereas temperatures have been used as continuous variables in statistical analysis) contrasted with the period of the night. Black circles indicate dusk period and white circles dawn period

dawn: we did not identify site differences in either response ratio (logistic regression: site effect, $F_{1,316}=2.88$, $P=0.09$, power test=0.97; site*period effect: $F_{1,316}=0.85$, $P=0.35$) or response intensity (latency: site effect, $F_{1,244}=2.0$, $P=0.16$; site*period: $F_{1,242}=0.4$, $P=0.53$; hoot rate: $F_{1,244}=2.95$, $P=0.09$; site*period: $F_{1,242}=0.24$, $P=0.61$). Therefore, data from the two sites were pooled for subsequent analyses. We did not detect any temporal/playback presentation order effect on response ratio (at dusk: estimate ± SD=0.09±0.10, $P=0.36$; at dawn: estimate ± SD=0.17±0.21, $P=0.42$; $N=320$), latency (at dusk: estimate ± SD=-0.05±0.06, $P=0.4$; at dawn: estimate ± SD=-0.08±0.12, $P=0.47$; $N=246$) or hoot rate (at dusk: estimate ± SD=0.002±0.004, $P=0.58$; at dawn: estimate ± SD=0.0003±0.0060, $P=0.9$; $N=246$).

The global response ratio to playback was high, with 246 responses against 74 non-responses (global response ratio: mean ± SE=0.77±0.02). The main parameter affecting individual response ratios was the interaction between ambient temperature and time of day: males responded less strongly to playbacks at dusk when temperatures were coldest, yet more strongly to playbacks at dusk when temperatures were highest (Table 2, Fig. 2). The response ratios of individual males to playbacks was less for cold temperatures at dusk than at dawn (interaction period*temperature, Table 2), but the reverse was true when ambient temperature was warmer (Fig. 2). This interaction was less pronounced when analysing response intensity: when males responded to playback, the latency increased for cold temperatures and at dusk (Table 2), while hoot rate remained unaffected (Table 2). There was no effect of the interaction between period (dusk vs dawn) and ambient temperature (interaction period*temperature, Table 2). When temperature was $<3^{\circ}\text{C}$, response ratios were particularly low at dusk; this could be considered as a “threshold” temperature, below which calling is much reduced ($<3^{\circ}\text{C}$: 44% at dusk against 85% at dawn; $>3^{\circ}\text{C}$: 82% at dusk against 80% at dawn): in fact, the overall response ratio was significantly reduced when $T<3^{\circ}\text{C}$ ($W=11,104$, $P=0.01$, Mann–Whitney test). By comparing dawn and dusk male response ratios when air temperature was <3 vs $>3^{\circ}\text{C}$, we

Table 2 Results for analysis of playback trials

	N	Fixed effects						Random effects	
		Period		Air temperature (T)		Period*T		Subjects	Time of day within subjects
		Est. ± SE	P	Est. ± SE	P	Est. ± SE	P		
Response ratio	320	-2.4±0.4	<0.001***	-0.18±0.09	0.03*	0.41±0.10	<0.001***	0.85±0.92	0.09±0.31
Latency	246	0.38±0.12	0.01**	-0.05±0.01	0.02*	0.004±0.020	0.86	0.17±0.42	0.11±0.33
Hoot rate	246	0.001±0.009	0.9	-0.0007±0.0010	0.56	0.002±0.001	0.11	0.001±0.030	~0

Estimate and standard error and *P* values for the terms in the model. For random effects, the variance and the standard deviation of the random effects (intercept) are provided. “Period*T” refers to the interaction between period and air temperature. For the random effect, Est. ± SE are given. ***<0.001, **<0.01, *<0.05

found that male’s response ratio was more variable at dusk (linear regression: $R^2\text{Adj.}=0.22$, $F_{1, 21}=7.0$, $P=0.01$, power test=0.68, $N=22$, Fig. 3) than at dawn ($R^2\text{Adj.}=0.46$, $F_{1, 21}=18.9$, $P<0.001$, power test=0.96, $N=22$, Fig. 3). In general, males which responded less when the temperature was $<3^\circ\text{C}$ were also those which responded less strongly overall to playbacks at any temperature. Hence, lower ambient air temperatures induced higher variability in male response ratios at dusk than at dawn.

Relationship between natural and provoked calling activity

We examined spontaneous vocal activity and response ratio to playback for the 10 individuals from site 1 (Fig. 4). There was no significant association among males (simple regression: $R^2\text{Adj.} \sim 0$, $F_{1,9}=0.2$, $P=0.7$), i.e. males with higher spontaneous vocal activity at dusk were not necessarily those that responded more to playbacks during the same period.

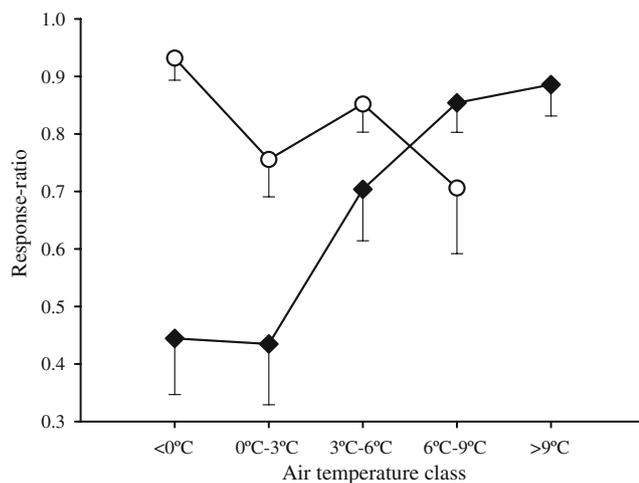


Fig. 2 Response ratio (mean ± standard error) to playbacks according to air temperature (presented in class, whereas temperatures have been used as continuous variables in statistical analysis) contrasted with the period of the night. Filled diamonds indicate dusk period and circles dawn period

Discussion

The main result of this study is that male little owls’ spontaneous vocal activity was higher at dusk than at dawn, even though the duration of the period of vocal activity did not differ between these two periods. This reversed nightly pattern of singing was expected from theoretical models of daily routines of singing and foraging (Hutchinson et al. 1993) and has also been observed in some nocturnal singers (e.g. marsh warbler *Acrocephalus palustris* and Blyth’s reed warbler *Acrocephalus dumetorum* Toivari and Lindqvist 1962; thrush nightingale *Luscinia luscinia* Sorjonen 1977; common nightingale Thomas 2002b). However, unlike fully nocturnal birds, such as owls, these species are unable to forage during darkness and, therefore, their vocal activity during darkness differs qualitatively by featuring high song rates during the middle of the night (Thomas 2002b). Thus, predictions made by SDP models for birds that both sing and forage effectively at night might not apply to these species.

We also observed higher inter-individual variability in vocal activity at dusk than at dawn. This could reveal inter-individual differences in energetic reserves (Staicer et al. 1996) or, alternatively, differences in the way males allocate singing and foraging activities (Wright and Cotton 1994; Atienza and Illera 1997; Thomas et al. 2003). Other factors that might influence spontaneous vocal activity are worth further investigation. Since little owls are sometimes able to forage and vocalise during daylight (to a much lesser extent than at night; personal observation), the effect of daytime singing and foraging (in refuelling energy reserves, for example) may contribute to a singing/foraging trade-off. Other factors that might influence spontaneous vocal activity include the presence of conspecifics (neighbour, mate: see Finck 1990 on little owl *A. noctua*) or seasonal variation in territorial activity (e.g. Amrhein et al. 2004 on nightingales).

At least three environmentally based hypotheses proposed so far to explain the existence of the dawn chorus in passerines (see Kacelnik and Krebs 1983; Slagsvold et al.

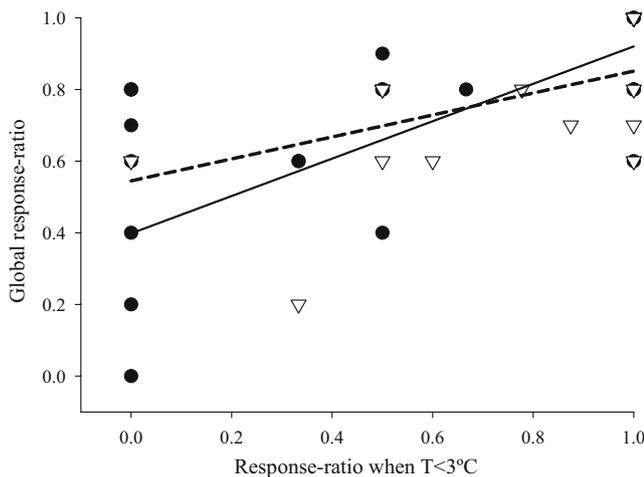


Fig. 3 Correlations of response ratio to playback experiments at dusk (black circles and plain line) and dawn (triangles and dotted line), contrasting response ratio when air temperatures were inferior to 3°C to the global response ratio of each male

1994; Staicer et al. 1996) might be applicable to the dusk chorus observed here. First, one could argue, as in the case for passerines, that foraging is less efficient at dusk because of lower prey activity. We believe, however, that it is unlikely that foraging is less efficient at dusk than at dawn in little owls. The little owl is an opportunistic feeder with a wide range of prey (i.e. passerines, small mammals, insects, earthworms, molluscs and crustaceans, Juillard 1984; Bavoux et al. 2000; Blache 2001) characterised by varying periods of activity. Our study was conducted during early spring and hunting activity is known to peak at dusk between May and June (Juillard 1984). Dusk is the second peak of singing activity for many passerines (Hutchinson et al. 1993), making them more likely to be preyed upon by nocturnal raptors such as little owls.

Second, the acoustic transmission of signals might presumably be favoured at dusk relative to other times of day. Dawn in passerines is supposed to be favourable for singing because the environmental conditions are expected to limit sound degradation and echoes (Brown and Handford 2003 but see, Dabelsteen and Mathevon 2002). It is not clear to us, however, how acoustic transmission properties for owl calls might be favoured at dusk.

Third, the risk of predation may be less severe at dusk than at dawn or overnight. Since little owls have no known major predators (although tawny owls *Strix aluco* have been recorded as preying upon this owl: Zabala et al. 2006), this hypothesis is unlikely to be applicable to dusk chorus in little owls. Nevertheless, it would be interesting to test if the presence of forests, the tawny owl's specific habitat, close to little owl territories affects their nocturnal vs diurnal vocal behaviour. Perhaps owls living near forests

would favour daytime or early dusk singing to avoid tawny owl predation.

We propose instead that the dusk chorus in little owls most likely has evolved in the context of social functions (Staicer et al. 1996). First, spontaneous vocal activity was higher at dusk, as was the variance between males in the duration of vocal activity. Second, the duration of spontaneous vocal activity tended to decrease at dusk when temperatures were milder. These results suggest that the assessment of male quality by rival males and potential mates would be improved in these more constraining situations, and are consistent with the handicap principle of honest signalling (Zahavi 1975; Grafen 1990; Staicer et al. 1996). Whether dusk chorusing in this species serves a mate-guarding or a mate attraction function, or both, is more speculative. The female attraction hypothesis would predict that dusk chorus should be more intense during the breeding season. Moreover, unpaired males would be expected to exhibit a higher dusk chorus than paired males. However, this prediction has received poor empirical support and even contradictory evidence in passerines (Staicer et al. 1996). Whether the pairing status affects song output in little owl also remains to be investigated. In this species, pairing usually occurs in autumn, and singing activity has been reported during autumn when new males usually establish their territory and attract females. However, during our experiments (in February and March), subjects were likely already paired. Indeed, in each tested male, at least once during our experiments, we could hear a female calling. Therefore, it is unlikely that mate attraction alone would explain our results.

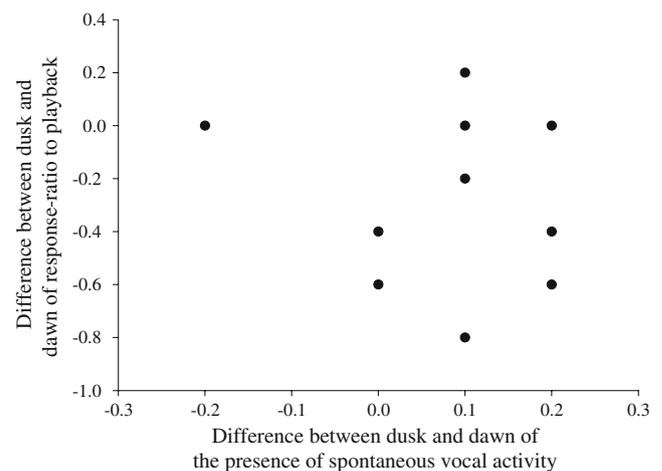


Fig. 4 Comparison of the difference between dusk and dawn response ratio and presence of spontaneous vocal activity. Positive values correspond to males which responded more or had higher vocal activity at dawn and negative values to those responding more or having higher vocal activity at dusk

The mate-guarding hypothesis suggests that dawn chorusing allows males to repel other males, thus reducing the chances of extra-pair copulations (Welling et al. 1997; Staicer et al. 1996). However, extra-pair copulations are extremely rare in owls and genetic monogamy is the norm (Wendt et al. 2001; Hsu et al. 2006; Saladin et al. 2007); hence, the mate-guarding hypothesis appears to have no strong support in this species.

While dusk chorusing in owls may be directed towards inter-sexual assessment, it is also possible that singing at dusk is crucial to advertise territory ownership and allow male–male assessment. Experimental evidence has shown that, at dawn, male European robins (*Erithacus rubecula*) with high overnight energy expenditures were less likely to initiate vocal behaviour and less likely to respond to calls or songs from conspecifics than those with low overnight expenditures (Godfrey and Bryant 2000). Carolina wren males (*Thryothorus ludovicianus*) also seem to respond more strongly to playback during the day than at dawn (Shy and Morton 1986). Our playback experiment is fully consistent with these results, as male little owls responded less to playback at dusk than at dawn, especially when environmental conditions were more stressful (i.e. cold air temperatures).

Indeed, this result suggests an increase of food and air temperature constraints at dusk when males faced a new rival. Little owls from both study sites seemed to respond similarly to environmental constraints, in our case, the stage of the night and the ambient air temperature, occurring at dusk and dawn.

Our results further suggest that, while ambient air temperature directly affects metabolic rate, males may be in a lower energetic state at dusk. Although a food supplementation experiment and actual data on male body condition would be necessary to test this hypothesis, it is supported by the increase of male response ratio at dawn, even when temperatures were coldest, a possible consequence of the fact that males have fed. We also found that males which responded less at $<3^{\circ}\text{C}$ were those which generally responded less to playbacks, which suggests that male foraging or hunting efficiency may be another factor involved in male ability to refuel energy reserves during the night and for the next day. When males responded to playback, we found that the period and temperature (but not the period*temperature interaction) had an effect on the latency. Cold air temperatures reduced the territorial response but less than the response ratio. Consequently, the decision to respond or not for a male facing an intrusion may firstly be limited by a physiological threshold, assuming some cost of territorial conflict. Therefore, when a male responds, he shows that he is willing to fight. Even though there was no difference in behavioural response between dusk and dawn, male inter-individual variation in

territorial responses was higher at dusk with less intra-individual variation. We therefore cannot reject the possibility that the degree of behavioural response may reflect male's body condition (Maynard-Smith and Harper 2003). In addition, this could also suggest that the motivation and the quality-related cues transmitted by the intruder could be additional factors affecting the responses of territory owners (Hardouin et al. 2007).

By comparing the individual nightly pattern of spontaneous vocal activity and the responses to playback, we first found that, in general, males at dusk were more likely to spontaneously call than to respond to playbacks. This suggests that there may be additional costs that males face when an intrusion occurs (Grafen 1990). When we recorded spontaneous vocal activity, males were typically surrounded by their neighbours, and therefore, their calling activity did not incur the costs usually associated with calling in the context of an intrusion by a new rival. Conversely, when a new rival is simulated by playback, the receiver may be urged to transmit honest information on his willingness to fight and protect his territory and/or female (Grafen 1990; Zahavi and Zahavi 1997). This hypothesis is reinforced by the fact that owls are able to discriminate between neighbour and stranger rival males (Hardouin et al. 2006). Finally, we did not find any association among the 10 males studied both for spontaneous vocal activity and playbacks as males that had higher spontaneous vocal activity at dusk did not tend to respond more to playback. We suggest that these two vocal activities (i.e. spontaneous calling and response to playback) may have different functions and/or involve different selection pressures (Liu 2004).

In conclusion, our results indicate that little owls have a defined dusk chorus that features increased inter-individual variation among males and, thus, seems likely to function as a cue to male quality for female or rival assessment. Indirectly, this study also suggests that hoots may be costly to produce for owls. Consistent with the ODR model, our results suggest that food, rather than air temperature, could be more constraining at dusk, although alternative hypotheses or the involvement of further factors are possible, e.g. the effect of daylight air temperature, foraging efficiency, etc. Finally, by comparing dusk and dawn vocal behaviour in two different groups of birds with opposite patterns of daily activity, i.e. owls and passerines, this study has provided new insights into the possible functions of dusk/dawn chorusing, and a platform for further investigations.

Acknowledgements We greatly thank “GEC78 Chevêche” for their valuable help with fieldwork. We are especially indebted to Dr. Ben Charlton, Dr. David Reby, Anna M. Taylor and two anonymous referees for constructive comments on the earlier drafts of the manuscript. L.A.H. was supported by a French ministry of research grant from the University Louis Pasteur, Strasbourg, France.

References

- Amrhein V, Korner P, Naguib M (2002) Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Anim Behav* 64:939–944
- Amrhein V, Kunc HP, Naguib M (2004) Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* 121:110–117
- Anderson M (1994) Sexual selection. In: Krebs JR, Clutton-Brock T (eds) *Monographs in behaviour and ecology*. Princeton University Press, New Jersey
- Atienza JC, Illera JC (1997) Tree species selection to perform singing and foraging behaviour by great and blue tits: a trade-off between food gathering and territorial behaviour. *Bird Study* 44:117–119
- Barnett CA, Briskie JV (2007) Energetic state and the performance of dawn chorus in silvereyes (*Zosterops lateralis*). *Behav Ecol Sociobiol* 61:579–587
- Bates D (2007) lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.99875-9
- Bavoux C, Burneleau G, Seguin N (2000) Consommation de crabes par la Chevêche d'Athéna *Athene noctua* dans l'île d'Oléron (Charente-Maritime). *Alauda* 68:329–330
- Blache S (2001) Etude du régime alimentaire de la Chevêche d'Athéna (*Athene noctua*) en période de reproduction en zone agricole intensive dans le sud-est de la France. *Ciconia* 25:77–94
- Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer, Sunderland
- Bretagnolle V, Bavoux C, Burneleau G, Van Nieuwenhuyse D (2001) Abondance et distribution des chevêches d'Athéna: approche méthodologique pour des enquêtes à grande échelle en plaine céréalière. *Ciconia* 25:173–184
- Brown TJ, Handford P (2003) Why birds sing at dawn: the role of consistent song transmission. *Ibis* 145:120–129
- Crawley MJ (2002) *Statistical Computing: An introduction to Data Analysis using S-plus*. Wiley, New York
- Cucco M, Malacarne G (1997) The effect of supplemental food on time budget and body condition in the black redstart *Phoenicurus ochruros*. *Ardea* 85:211–221
- Dabelsteen T, Matheson N (2002) Why do songbirds sing intensively at dawn? A test of the acoustic transmission hypothesis. *Acta Ethol* 4:65–72
- Exo KM (1984) Die akustische unterscheidung von steinkauzmännchen und -weibchen (*Athene noctua*). *J Ornithol* 125:94–97
- Exo KM (1992) Population ecology of little owls *Athene noctua* in central Europe: a review. In: Galbraith CA, Taylor IR, Percival S, Davies SM (eds) *The ecology and conservation of European owls*. Joint Nature Conservation Committee, Paisley, pp 64–75
- Exo KM, Scherzinger W (1989) Voice and inventory of call-notes of the little owl (*Athene noctua*): description, context and habitat adaptation. *Ecol Birds* 11:149–187
- Finck P (1990) Seasonal variation of territory size with the little owl (*Athene noctua*). *Ecologia* 83:68–75
- Garson PJ, Hunter ML Jr (1979) Effects of temperature and time of the year on the singing behaviour of wrens *Troglodytes troglodytes* and great tits *Parus major*. *Ibis* 121:481–487
- Gaunt AS, Bucher TL, Gaunt SLL, Baptista LF (1996) Is singing costly? *Auk* 113:718–721
- Génot J-C (1992a) Biologie de reproduction de la chouette chevêche *Athene noctua scop*, en bordure des Vosges du nord. *Ciconia* 16:1–18
- Génot J-C (1992b) Contribution à l'écologie de la chouette chevêche, *Athene noctua* (scop) en France. PhD thesis Université de Dijon, France
- Génot J-C (2001) État des connaissances sur la chevêche d'Athéna, *Athene noctua*, en bordure des Vosges du nord de 1984 à 2000. *Ciconia* 25:109–118
- Génot J-C (2005) La Chevêche d'Athéna, *Athene noctua*, dans la réserve de la Biosphère des Vosges du Nord de 1984 à 2004. *Ciconia* 29:1–272
- Génot J-C, Juillard M, Van Nieuwenhuyse D (1997) Little owl. In: Hagemeyer WJM, Blair MJ (eds) *The EBC atlas of European breeding birds: their distribution and abundance*. T. & A. D. Poyser, London, pp 408–409
- Godfrey JD, Bryant DM (2000) State-dependent behaviour and energy expenditure: an experimental study of European robins on winter territories. *J Anim Ecol* 69:301–313
- Gosler AG (2002) Strategy and constraint in the winter fattening response to temperature in the great tit *Parus major*. *J Anim Ecol* 71:771–779
- Grafen A (1990) Biological signals as handicap. *J Theor Biol* 144:517–546
- Hardouin LA, Tabel P, Bretagnolle V (2006) Neighbour-stranger discrimination in little owl *Athene noctua*. *Anim Behav* 72:105–112
- Hardouin LA, Reby D, Bavoux C, Burneleau G, Bretagnolle V (2007) Communication of male quality in owl hoots. *Am Nat* 169:552–562
- Hsu Y-S, Li S-H, Lin Y-S, Philippart MT, Sevenringhaus LL (2006) High frequency of extra-pair copulation with low level of extra-pair fertilization in the Lanyu scops owl *Otus scops botelensis*. *J Avian Biol* 37:36–40
- Hutchinson JMC (2002) Two explanations of the dawn chorus compared: how monotonically changing light levels favour short break from singing. *Anim Behav* 64:527–539
- Hutchinson JMC, McNamara JM (2000) Ways to test stochastic dynamic programming models empirically. *Anim Behav* 59:665–676
- Hutchinson JMC, McNamara JM, Cuthill I (1993) Song, sexual selection, starvation and strategic handicaps. *Anim Behav* 45:1153–1177
- Juillard M (1984) La chouette chevêche. Nos oiseaux, Prangins
- Kacelnik A (1979) The foraging efficiency of great tits (*Parus major*) in relation to light intensity. *Anim Behav* 27:237–241
- Kacelnik A, Krebs JR (1983) The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* 83:287–309
- Kroodsma DE (1989) Suggested experimental design for song playbacks. *Anim Behav* 37:600–609
- Liu W-C (2004) The effect of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Anim Behav* 68:39–44
- Mace R (1989) The relationship between daily routines of singing and foraging: an experiment on captive great tits *Parus major*. *Ibis* 131:415–420
- Maynard-Smith J, Harper DGC (2003) *Animal signals*. Oxford University Press, New York
- McGregor PK, Catchpole CK, Dabelsteen T, Falls JB, Fusani L, Gerhardt HC, Gilbert FS, Horn AG, Klump GM, Kroodsma DE, Lambrechts MM, McComb KE, Nelson DA, Pepperberg IM, Ratcliffe LM, Searcy WA, Weary DM (1992) Design and interpretation of playback: the Thornbridge Hall NATO ARW consensus. In: McGregor PK (ed) *Playback and studies of animal communication*. Plenum, New York, pp 1–9
- Murphy MT, Sexton K, Dolan AC, Redmond LJ (2008) Dawn song of the eastern kingbird: an honest signal of male quality? *Anim Behav* 75:1075–1084
- Oberweger K, Goller F (2001) The metabolic cost of birdsong production. *J Exp Biol* 204:3379–3388
- Otter K, Chruszcz B, Ratcliffe L (1997) Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behav Ecol* 8:167–173
- R Development Core Team (2007) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL <http://www.R-project.org>.

- Reid ML (1987) Costliness and reliability in the singing vigour of Ipswich sparrows. *Anim Behav* 35:1735–1743
- Saladin V, Ritshard M, Roulin A, Bize P, Richner H (2007) Analysis of genetic parentage in the tawny owl reveals extra-pair paternity is low. *J Ornithol* 148:113–116
- Schönn S, Scherzinger W, Exo K-M, Ille R (1991) Der Steinkauz. Neue Brehm-Bücherei, pp 120–136
- Shy E, Morton ES (1986) The role of distance, familiarity, and time of day in Carolina wrens responses to conspecific songs. *Behav Ecol Sociobiol* 19:393–400
- Slagsvold T, Dale S, Sætre G-P (1994) Dawn singing in the great tit (*Parus major*): mate attraction, mate guarding, or territorial defence? *Behaviour* 131:115–138
- Sorjonen J (1977) Seasonal and diel patterns in the song of the Thrush Nighthales *Luscinia luscinia* in SE Finland. *Orn Fenn* 54:101–107
- Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signalling. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca, pp 426–453
- Strain JG, Mumme RL (1988) Effects of food supplementation, song playback, and temperature on vocal territorial behaviour of Carolina wrens. *Auk* 105:11–16
- Thomas RJ (2000) Strategic diel regulation of body mass in European robins. *Anim Behav* 59:787–791
- Thomas RJ (2002a) The cost of singing in nightingales. *Anim Behav* 63:959–966
- Thomas RJ (2002b) Seasonal changes in the nocturnal singing routines of common nightingales *Luscinia megarhynchos*. *Ibis* 144:E105–E112
- Thomas RJ, Cuthill I (2002) Body mass regulation and the daily singing routines of European robins. *Anim Behav* 63:285–295
- Thomas RJ, Cuthill IC, Goldsmith AR, Cosgrove DF, Lidgate HC, Proctor SLB (2003) The trade-off between singing and mass gain in a daytime-singing bird, the European robin. *Behaviour* 140:387–404
- Toivari L, Lindqvist O (1962) Daily singing rhythmic of the marsh warbler (*Acrocephalus palustris*) and Blyth's reed warbler (*Acrocephalus dumetorum*). *Orn Fenn* 39:151–154
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 2nd edn. Springer, New York
- Ward S, Lampe HM, Slater PJB (2004) Singing is not energetically demanding for pied flycatchers *Ficedula hypoleuca*. *Behav Ecol* 15:477–484
- Welling P, Koivula K, Orell M (1997) Dawn chorus and female behaviour in the willow tit *Parus montanus*. *Ibis* 139:1–3
- Wendt M, Jörg TE, Thomas L (2001) Genetic paternity analyses in little owls (*Athene noctua*): does the high rate of parental care select against extra-pair young? *J Ornithol* 142:195–203
- Wright J, Cotton PA (1994) Song versus food: trade-off decisions in a breeding colony of European starlings *Sturnus vulgaris*. *Bird Study* 41:95–101
- Zabala J, Zuberrogoitia I, Martinez-Climent JA, Martinez JE, Azkona A, Hidalgo S, Iraeta A (2006) Occupancy and abundance of Little owl *Athene noctua* in an intensively managed forest area in Biscay. *Orn Fenn* 83:97–107
- Zahavi A (1975) Mate selection—a selection for handicap. *J Theor Biol* 53:205–214
- Zahavi A, Zahavi A (1997) The handicap principle: a missing piece of Darwin's puzzle. Oxford University Press, New York