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## Article

### Activity patterns at the Arctic Circle: nocturnal eagle owls and interspecific interactions during continuous midsummer daylight

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Circadian rhythms result from adaptations to biotic and abiotic environmental conditions that cycle through the day, such as light, temperature, or temporal overlap between interacting species. At high latitudes, close to or beyond the polar circles, uninterrupted midsummer daylight may pose a challenge to the circadian rhythms of otherwise nocturnal species, such as eagle owls *Bubo bubo*. By non-invasive field methods, we studied eagle owl activity in light of their interactions with their main prey the water vole *Arvicola amphibius*, and their competitor the white-tailed eagle *Haliaeetus albicilla* during continuous midsummer daylight on open, treeless islands in coastal northern Norway. We evaluated circadian rhythms, temporal overlap, exposure, and spatial distribution. The owls maintained a nocturnal activity pattern, possibly because slightly dimmer light around midnight offered favourable hunting conditions. The eagles were active throughout the 24-h period as opposed to the strictly diurnal rhythm reported elsewhere, thus increasing temporal overlap and the potential for interference competition between the two avian predators. This may indicate an asymmetry, with the owls facing the highest cost of interference competition. The presence of eagles combined with constant daylight in this open landscape may make the owls vulnerable to interspecific aggression, and contrary to the available literature, eagle owls rarely exposed themselves visually during territorial calls, possibly to avoid detection by eagles. We found indications of spatial segregation between owls and eagles reflecting differences in main prey, possibly in combination with habitat-mediated avoidance. Eagle owl vocal activity peaked in the evening before a nocturnal peak in visual observations, when owls were active hunting, consistent with the hypothesis of a dusk chorus in nocturnal bird species. The owls may have had to trade-off between calling and foraging during the few hours around midnight when slightly dimmer light reduced the detection risk while also providing better hunting conditions

Keywords: activity, *Arvicola amphibius*, avian apex predators, *Bubo bubo*, circadian rhythms, eagle owl, *Haliaeetus albicilla*, interference competition, interspecific killing, midnight sun, non-invasive, predators, prey, vocal activity, water vole, white-tailed eagle



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## Introduction

Animal activities often follow cyclic patterns, which are adaptations to predictable changes in the biotic and abiotic environment (Kronfeld-Schor et al. 2017). Interspecific interactions can be major factors shaping such temporal activity cycles (Kronfeld-Schor et al. 2017). Animals may e.g. increase their access to food by increasing temporal overlap with prey species (Jenny and Zuberbuhler 2005, Penido et al. 2017) and decreasing overlap with competitors (Halle 2000, Gerber et al. 2012), and they may reduce predation risk by minimizing overlap with predators (Nelson and Vance 1979). To adjust their activity patterns to cyclic environmental conditions, animals have evolved internal biological clocks that are set to environmental synchronizers (or Zeitgebers) the major of which is the light-dark cycle (Daan and Aschoff 1975, Halle 2000, Nouvellet et al. 2012, Kronfeld-Schor et al. 2017). Using light as a major synchronizer of the biological clock may cause problems if light no longer is a reliable cue, which may in turn affect interspecific interactions (Kronfeld-Schor et al. 2017). The majority of diel activity studies have been conducted in systems in which daylight hours are followed by dark hours on a daily basis (but see Daan and Aschoff 1975, Reierth and Stokkan 1998, Speakman et al. 2000, Ruby et al. 2002, Nouvellet et al. 2012, Penteriani et al. 2013). However, in areas of high latitude, uninterrupted daylight forms a basis for highly productive food webs during summer (Street et al. 2012), but may be a challenge to the circadian rhythms of species that are normally nocturnal. The activity patterns of such species during the Arctic summer may depend on the plasticity of the internal timing system, both of the species in question and of species with which it interacts (Speakman et al. 2000, Kronfeld-Schor et al. 2017).

The Eurasian eagle owl *Bubo bubo* is a nocturnal and crepuscular 'sit and wait' hunter (Cramp and Simmons 1985, Penteriani et al. 2000, 2008, Campioni et al. 2010). Although nestlings and fledglings can be active during the day (Penteriani et al. 2000), adult eagle owls normally start their hunt immediately after sunset (Cramp and Simmons 1985). With a wingspan of 160–188 cm, eagle owls are apex predators and have been recorded to take prey as large as young roe deer *Capreolus capreolus* or fully grown greylag geese *Anser anser*, and they frequently kill diurnal raptors and other owl species (Mikkola 1976, Cramp and Simmons 1985, Lourenco et al. 2011a, Dahl 2015). However, their main prey are small mammals and birds (Cramp and Simmons 1985). At the Arctic Circle in coastal northern Norway, European water voles *Arvicola amphibius* are the main prey of nesting eagle owls, constituting > 95% of frequency and > 75% of the prey biomass (Bichsel 2012). The activity of water voles is reported to be polyphasic with activity peaks both during bright and dark hours (Erkinaro 1973a, Airolidi 1979), but contrary to most rodents (Blumstein 2008), the overall activity is highest during daytime (Stoddart 1969, Airolidi 1979).

In coastal northern Norway, the eagle owl is sympatric with another avian apex predator, the white-tailed eagle *Haliaeetus albicilla*. Here, these two species are competitors, both having seagulls, geese and ducks as part of their diets, although their main prey overlap to a lesser degree (voles for eagle owls, and fish for white-tailed eagles) (Cramp and Simmons 1985, Zawadzka 1999, Dahl 2015). Irrespective of the degree of dietary overlap and subsequent exploitation competition, interference competition can result in intraspecific killing (Linnell and Strand 2000). Mikkola (1976) reported cases of intraspecific killing in both directions between eagle owls and white-tailed eagles, and we have recorded several cases of eagle owl fledglings killed by white-tailed eagles in our study area (Wabakken and Dahl unpubl.). Interference competition can also result in spatial and temporal segregation (Sergio et al. 2007, May et al. 2008). White-tailed eagles are generally strongly diurnal (Cramp and Simmons 1985, Krone et al. 2009). Hence, in areas/periods with dark nights, eagle owls and white-tailed eagles are temporally segregated, which may reduce the potential for aggression. It is not known what continuous midsummer daylight does to the circadian rhythms, and hence to the degree of temporal overlap between these two species.

During periods of continuous midsummer daylight in coastal northern Norway, we assessed four hypotheses (H1-4) regarding the activity of eagle owls (hereafter termed owls), their main prey the water vole (hereafter termed voles) and their competitor the white-tailed eagle (hereafter termed eagles). Within this context, we use the terms 'night-time' and 'nocturnal activity' about the 12 h approximately centred on the solar midnight, starting at 7 pm and ending at 7 am (see Study area), and for the 12 h centred around the solar noon we use the terms 'daytime' and 'diurnal activity'. During constant daylight, the benefit of maintaining a cyclic circadian activity pattern may be minimal. The study species may therefore show less pronounced differences between daytime and night-time activity in order to maximize foraging activity at the time of year when they are raising young (H1). However, reducing the difference between daytime and night-time activity would increase the temporal overlap between owls and eagles. Alternatively, to avoid increasing the potential for interference competition, the owls and eagles may retain their usual nocturnal and diurnal activity patterns, maintaining temporal segregation (H2). Eagle owls expose themselves visually at their hunting posts (Penteriani et al. 2008, Campioni et al. 2010), and acoustically during vocal territorial displays (Delgado and Penteriani 2007, Campioni et al. 2010). In order to minimize exposure, the owls may reduce vocal activity when visually exposed, and use less conspicuous call sites during their vocal displays (H3). Interference competition may result in habitat mediated avoidance (Sergio et al. 2007). Because open water is prime foraging habitat for white-tailed eagles (Zawadzka 1999, Salo et al. 2008), the owls may avoid the eagles spatially by staying farther away from larger open water areas (H4).

## Methods

### Study area

The study area represents the north-westernmost edge of the range of nesting eagle owls in Eurasia, i.e. the north-western edge of the Sleneset archipelago (66°21'N, 12°35'E), 21 km from the mainland of the Helgeland coast in northern Norway. Located only 17 km south of the Arctic Circle, the sun does not go below the horizon during a four-week period every summer (21 June  $\pm$  14 d). Before and after this period, the midnight light intensity remains high for additional  $\pm$  1–2 weeks, when the sun is only slightly below the horizon. In summer, the solar midnight, i.e. when the sun is at its lowest, is at 01:12 am local time. The climate is relatively mild, with temperatures above 0°C most days in winter. The archipelago covers a total land area of 30.2 km<sup>2</sup>, distributed on 1544 rocks and islets (< 1 ha) and 294 islands (> 1 ha). Fresh water ponds are found on many of the islands. The terrain is flat, at low altitude (mainly < 10 m a.s.l.), yet, the vegetation shares several similarities to alpine areas on the mainland. The land is mostly treeless (96.7%) covered with bare rock, bogs, short grasses and other short-growing vegetation on a thin layer of soil.

The Sleneset archipelago represents a rather unique system for studying interspecific interactions between an avian predator, its main prey and its competitor during constant daylight: in this coastal environment, the eagle owl and the white-tailed eagle are the only owl and raptor species that are common and breed regularly, and both species are resident throughout the year. In addition, a pair of golden eagles *Aquila chrysaetos* occasionally nests potentially within reach of the study area, but are rarely observed. The water vole is the only wild mammalian herbivore, and the eagle owl is its major predator (Frafjord 2003). The archipelago is one of the few places in northern Europe with absence of the alien American mink *Mustela vison*, which elsewhere may greatly reduce water vole populations (Barreto et al. 1998, Rushton et al. 2000). As a result, the owls have almost exclusive access to the voles, and the density of breeding eagle owl pairs may be among the highest worldwide (> 8 pairs/10 km<sup>2</sup> land area; Wabakken et al. unpubl.).

The community of large to medium-sized birds is dominated by geese, and includes grey lag geese *Anser anser*, ducks, cormorants, skuas *Stercorarius parasiticus*, gulls, terns, alcids, oystercatchers *Haematopus ostralegus*, plovers, sandpipers, and a few terrestrial birds like willow grouse *Lagopus lagopus*, hooded crows *Corvus corone*, and two thrush species. Several of the birds mentioned are prey both to the owls and the eagles. However, in two multi-year studies, voles were found to be the major food source for nesting eagle owls in the study area, in frequency as well as biomass (Bichsel 2012, Dahl 2015).

The piscivorous Eurasian otter *Lutra lutra* is the only mammalian carnivore in the study area, both common and

widely distributed on the archipelago. In addition, domestic sheep *Ovis aries* are found grazing throughout the year on some of the islands. Among the approx. 350–400 human residents, the great majority (> 98%) are concentrated on one central island.

The fieldwork was conducted in the north-westernmost part of the archipelago on two neighbouring, treeless islands, Burøya (0.272 km<sup>2</sup>) and Oddøya (0.300 km<sup>2</sup>), only separated by a 10 m sound. To the west, marine environment and open water dominated, while the proportion of nearby land areas, i.e. the density of islands, was higher to the east. From both islands, owls from four known breeding localities could be observed within less than 1 km, one to the west and three to the east of both islands. Adult owls from three of the localities were seen and heard regularly, whereas territorial birds at the fourth locality were observed somewhat less frequently.

### Data collection

The data collection was non-invasive as it was based exclusively on intensive visual and acoustic observations, and involved no marking or trapping of animals. We counted eagle owls and water voles that could be observed from two 500 m transect lines, on the two islands Burøya and Oddøya during June and July of 2005 through 2011. In 2005, we walked each transect line in one direction every three hours, four days on Burøya and three days on Oddøya. In 2006 through 2011, one day per year we walked each transect line in both directions every two hours, with the time between the start of the initial walk and the return walk ranging from 17 to 48 min (mean = 28 min, SD = 5 min). Consequently, in 2005 the transect lines were walked in one direction eight times per island per day (Table 1) and in 2006–2011, the 500 m transect lines were walked in both directions 12 times per island per day, (Table 1). The data collection on the two islands was staggered so that one of the two transects was walked every 1.5 h (2005) or every one hour (2006–2011). When the transect lines were walked in both directions (2006–2011), the difference between the number of voles observed on the initial walk (n = 25) and the return walk (n = 21) was not statistically significant (Wilcoxon test:  $W = 10286.5$ ,  $p = 0.85$ ). Furthermore, there was no significant correlation between the time difference between the onset of the initial walk and the return, and the number of voles observed on the return walk (Spearman rank correlation,  $r_s = -0.02$ ,  $p = 0.69$ ). We therefore consider it reasonable to assume that disturbance from the initial walk did not affect the number of vole observations on the return walk.

In addition to the transect lines, eagle owls and white-tailed eagles were counted, spatial distribution (west or east of the transect line) noted and their behaviour observed during a five-minute period, 200 m from the end point of each of the two transect lines. These point counts were done on every round-trip during one 24-h period each year on each of the two islands, i.e. 8 (2005) and 12 (2006–2011) times per island per year (Table 1).

Table 1. Summary of count data collected during seven field seasons. Eagle owls and water voles were observed along 500 m transect lines on the two islands Burøya (B) and Oddøya (O). In addition, eagle owls and white-tailed eagles were observed during five-minute periods 200 m from the end points of each transect line (point counts).

	2005		2006		2007		2008		2009		2010		2011		Tot.
	B	O	B	O	B	O	B	O	B	O	B	O	B	O	
No. field days	4	3	1	1	1	1	1	1	1	1	1	1	1	1	10
Transect walks*	32	24	12	12	12	12	12	12	12	12	12	12	12	12	200
Point counts	8	8	12	12	12	12	12	12	12	12	12	12	12	12	160
Owl count	2	3	4	2	3	7	0	5	7	4	0	0	3	6	46
Vole count	38	32	10	9	3	2	3	3	4	9	0	1	0	2	116
Eagle count	0	1	0	3	1	2	3	0	11	7	11	0	7	6	52

\*In 2005 the transect lines were walked in one direction only. In 2006–2011 the transects were walked in both directions.

In the open landscape of our study area, owls and eagles are easily observed when looking for prey from an elevated perch such as a rock or a power pole (Cramp and Simmons 1985, Penteriani et al. 2008, Campioni et al. 2010), and eagle owls can be detected acoustically while displaying territorial calls (Delgado and Penteriani 2007, Campioni et al. 2010). The owls and eagles in our study were observed in flight, or sitting scanning their surroundings from the ground or a perch within sight from the transect line or observation point. In addition, eagle owls were often detected acoustically. The voles were mostly observed when crossing the transect line where they were not concealed by the low vegetation.

During fieldwork on the two islands, eagle owls from 3–4 territorial pairs could be observed, and a maximum of 5 adults were observed simultaneously. All field observations were conducted by the same person (P. Wabakken), avoiding the effect of inter-observer variability.

## Analyses

For each species, we pooled the count data from observation bouts including one one-way walk (2005) or roundtrip (2006–2011) along a transect line, and when applicable, one 5-min period at the observation point on the same island, all happening within a one-hour period. This gave a data set consisting of count data for the three study species from 200 observation bouts (Table 1). All vole observations were treated as independent observations. Because of our non-intrusive method in which the animals were not individually marked, we may occasionally have observed the same individual more than once during an observation bout. However, this should not result in a significant bias in our data, as the data sampling was balanced over the 24-h period. In cases in which the same owl was observed more than once during the same observation bout (e.g. when perching on the same post when walking the transect in both directions, or both at the transect and during the point observation), only the first observation was included.

In order to examine circadian activity rhythms, we ran generalized linear mixed models (GLMM) with the count data for each species separately using the ‘glmmTMB’ package in R (Magnusson et al. 2016, Brooks et al. 2017). Number

of individuals counted during one observation bout was the response variable, and was assumed to reflect the activity level of the species. Time of day was fitted as a numerical, circular fixed effects variable according to Pewsey et al. (2013), using  $\cos(\pi/12 \times t) + \sin(\pi/12 \times t)$ . Year was included as a random factor in all the models to account for between-year population variations. We ran the models with Poisson response distributions and used the R package ‘sjstats’ (Lüdtke 2017) to test for overdispersion and zero-inflation. In cases of overdispersion we re-ran the model with a negative binomial response distribution, and in cases of zero-inflation we added a single, constant zero-inflation parameter (zero-inflated poisson or zero-inflate negative binomial models). Using the Akaike information criterion corrected for small sample sizes (AICc), the models were compared to a null model for the same species including only the random factor, representing the null hypothesis that the activity was independent of the time of day.

We evaluated the temporal overlap between owl and vole activity and between owl and eagle activity using the methods developed by Ridout and Linkie (2009) using the R package ‘overlap’ (Meredith and Ridout 2014, 2017). We first plotted kernel density curves for the circadian activity of each species, with a smoothing parameter of 0.8. We then estimated overlap coefficients  $\Delta$ , which represents the proportion of overlap between two density curves, ranging from 0 (no overlap) to 1 (complete overlap). We used the  $\hat{\Delta}_1$  estimator recommended for small samples (Ridout and Linkie 2009). We calculated 95% confidence intervals for the estimated overlap coefficients from 10 000 bootstrap samples from the kernel density distributions.

We assessed whether there was a time lag between eagle owl territorial calling activity and visual exposure during hunting. We performed Spearman rank correlations for the acoustic observations of calling owls versus the visual observations with time lags from –12 to +12 h. Finally, we used chi square tests to determine whether the observations of the three species were distributed differently in space on the west side versus the east side of the transect lines, i.e. open water vs land dominated areas. All analyses were performed in the software RStudio 0.99.902 running R 3.3.0 (R Development Core Team).

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.11g3s9t>> (Eriksen and Wabakken 2018).

## Results

### Circadian activity patterns

During the 200 observation bouts, we counted owls a total of 46 times (mean = 0.23, range = 0–5), voles 116 times (mean = 0.58, range = 0–5) and eagles 52 times (mean = 0.32, range = 0–2 per observation bout). Plotting the means and 95% confidence intervals for the owl, vole and eagle counts against time of day indicates a clearly nocturnal activity pattern for eagle owls (i.e. highest activity during the 12 h centred on the solar midnight, Fig. 1a). The two other species remained active throughout the 24-h period, but with an increase in water vole activity during daytime (i.e. the 12 hours centred on the solar noon) (Fig. 1b and c).

When modelling the eagle owl counts, including time of day as a fixed effect improved the fit substantially compared to the null model, reducing AICc by 36.3 (Table 2A). We used a Poisson distribution and no zero-inflation parameter (dispersion ratio = 1.04, Pearson's  $X^2 = 204.61$ ,  $p = 0.32$ , predicted/observed zero-counts 164/168 = 0.98). The model suggests a clearly nocturnal activity pattern with an activity peak during the hours around midnight, and consistently low activity during daytime (Fig. 1a).

For the vole counts, including time of day as a fixed effects variable improved the fit compared to the null model, reducing AICc by 5.0 (Table 2B). We used a Poisson distribution and no zero-inflation parameter (dispersion ratio = 1.14, Pearson's  $X^2 = 224.33$ ,  $p = 0.08$ , predicted/observed zero counts 125/131 = 0.95). The model suggests an increase in activity during daytime hours (Fig. 1b).

For the eagle counts, including time of day did not improve the fit relative to the null model, but increased AICc by 4.2 (Table 2C). We used a Poisson distribution and a single, constant zero-inflation parameter due to overfitting of zero-counts (dispersion ratio = 0.63, Pearson's  $X^2 = 97.90$ ,  $p = 0.99$ , predicted/observed zero counts 118/110 = 1.07),

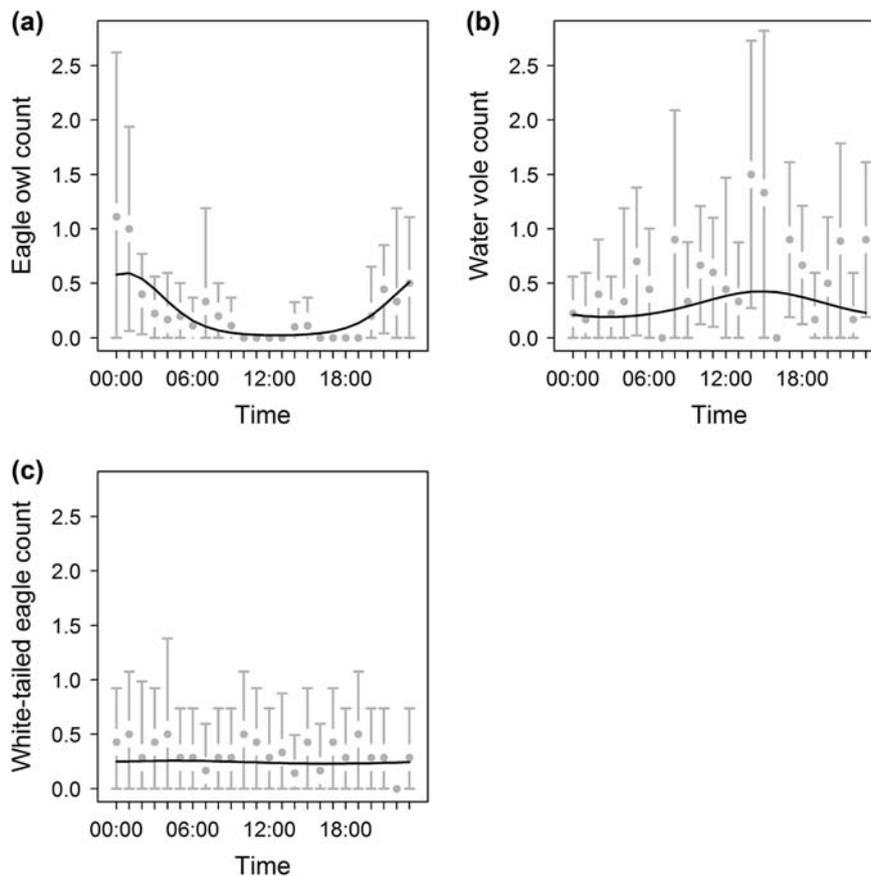


Figure 1. Diel activity of eagle owls (a), water voles (b) and white-tailed eagles (c) at 24 h of daylight. Activity was measured as the number of individuals observed during observation bouts including 500 m transect lines (eagle owls and water voles) and five-minute point counts 200 m from the end point of the transect lines (eagle owls and white-tailed eagles). Grey dots represent means and error bars represent 95% confidence intervals. Black lines are prediction curves from GLMMs regressing individual counts against time of day as a circular, continuous fixed effects variable (Table 2).

Table 2. Summary of generalized linear mixed models regressing counts of eagle owls (A), water voles (B) and white-tailed eagles (C) against time of day as a circular fixed effects variable. Year was included as a random effect in all models. The eagle owl model and the vole model were improvements of their respective null models (lowering AICc by 36.3 and 5.0 respectively), and they both had Poisson response distributions and no zero-inflation parameter. The white-tailed eagle model was not an improvement of the null model (increasing AICc by 4.2), and had a Poisson response distribution and a single, constant zero-inflation parameter.

Predictor	Coeff.	SE	Z	p
<b>(A) Eagle owls</b>				
Intercept	-2.14	0.36	-5.94	< 0.0001
$\text{Cos}(\pi/12 \times \text{Time})$	1.60	0.31	5.16	< 0.0001
$\text{Sin}(\pi/12 \times \text{Time})$	0.29	0.24	1.19	0.23
<b>(B) Water voles</b>				
Intercept	-1.25	0.46	-3.02	0.003
$\text{Cos}(\pi/12 \times \text{Time})$	-0.30	0.13	-2.23	0.026
$\text{Sin}(\pi/12 \times \text{Time})$	-0.27	0.13	-2.02	0.044
<b>(C) White-tailed eagles</b>				
Intercept	-1.41	0.34	-4.15	< 0.0001
$\text{Cos}(\pi/12 \times \text{Time})$	0.02	0.20	0.10	0.92
$\text{Sin}(\pi/12 \times \text{Time})$	0.05	0.20	0.27	0.79

The model suggests that eagle activity was independent of the time of day (Fig. 1c).

The estimated overlap between diel activity of owls and voles was  $\hat{\Delta}_1 = 0.52$  (95% CI = 0.40–0.63, Fig. 2a), and for owls and eagles it was  $\hat{\Delta}_1 = 0.58$  (95% CI = 0.44–0.72, Fig. 2b).

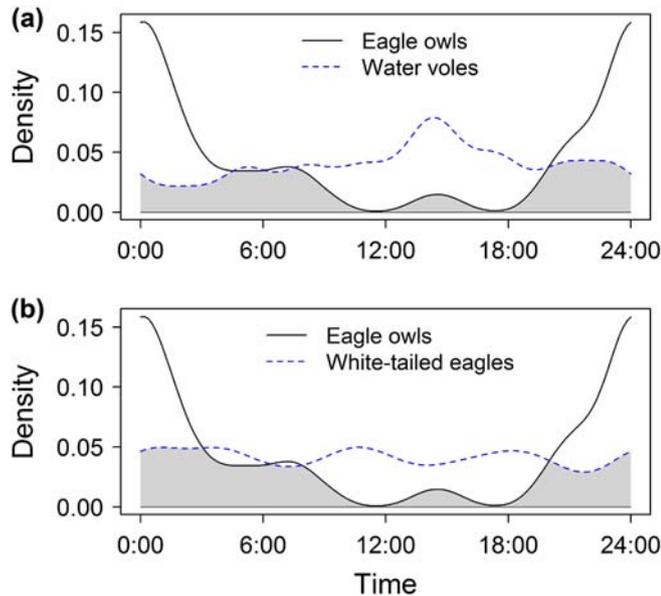


Figure 2. Fitted kernel density curves for eagle owl and water vole activity (a) and eagle owl and white-tailed eagle activity (b), using a smoothing parameter of 0.8. The overlap coefficient equals the area below both curves (grey).

## Eagle owl exposure and vocal activity

Only 14% of calling eagle owls were also detected visually (9 out of 22 acoustic observations, Fig. 3). The correlation between acoustic and visual observations of eagle owls peaked at a time lag of three hours (calling preceding visual exposure, Fig. 4). However, the positive correlation was statistically significant at time lags of zero to six hours. Seventeen out of 22 acoustic observations (77%) happened between 20:00 and 01:00 (i.e. before sun at the lowest), and the remaining five observations (23%) of calling eagle owls happened between 01:00 and 03:00 (Fig. 3).

## Spatial distribution

Chi square tests showed that eagle owls were observed more often east of the transect lines ( $\chi^2 = 2.89$ ,  $df = 1$ ,  $p < 0.0001$ ), whereas white-tailed eagles were observed more often west of the lines ( $\chi^2 = 1.84$ ,  $df = 1$ ,  $p = 0.028$ ). Water voles were observed on both sides with similar frequency ( $\chi^2 = 0.16$ ,  $df = 1$ ,  $p = 0.69$ ).

## Discussion

### Circadian activity patterns and temporal overlap

In areas/periods with dark nights, eagle owls are nocturnal and crepuscular hunters (Cramp and Simmons 1985, Penteriani et al. 2000). We found that eagle owls were clearly nocturnal also during 24-h midsummer daylight, with the highest activity occurring when the sun was at its lowest around midnight, and with minimal activity in the middle of the day (Fig. 1a). Elsewhere, in areas/periods with dark nights, the water vole is the one of our three study species with the least pronounced difference between daytime and night-time activity, showing both nocturnal and diurnal activity bouts, but with a marked activity maximum during daytime (Stoddart 1969, Erkinaro 1973a, b, Airolidi 1979). Erkinaro (1973b) found that the activity of captive water voles was a function of light intensity, reaching a maximum at 2.6–3.5 lux ( $4.81e^{-2}$ – $6.48e^{-2}$   $\mu\text{Einsteins}$ ). We did not measure light intensity directly, but during summer at the Arctic Circle, the light would be closer to the optimal  $\sim 3$  lux around midnight when the sun was near the horizon, presumably increasing the advantage of night-time activity. Nevertheless, our findings suggest that the voles had higher activity during daytime (Fig. 1b), similar to areas/periods with dark nights. The eagles on the other hand did expand their activity into the night, showing a fairly constant activity level throughout the 24-h cycle (Fig. 1c), in clear contrast to the strictly diurnal activity reported elsewhere for this species (Cramp and Simmons 1985, Krone et al. 2009). Hence, the white-tailed eagle is the only species for which we found support for the hypothesis of less pronounced differences between daytime and night-time activity (H1).

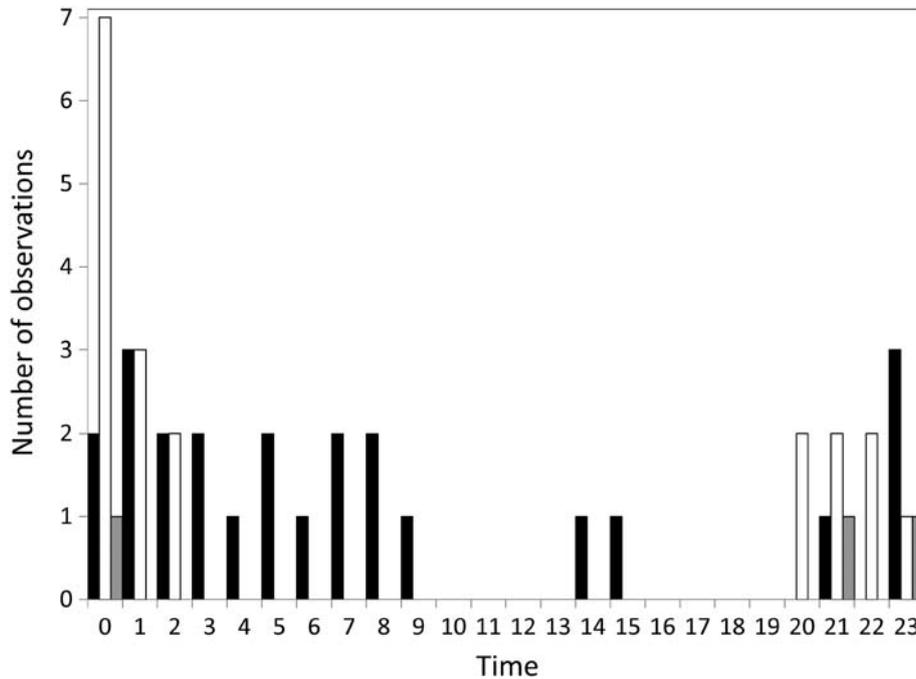


Figure 3. Eagle owls detected only visually (black bars), only acoustically (white bars), or both visually and acoustically (grey bars) at different times of day.

The hypothesis that owls and eagles would retain their usual nocturnal and diurnal activity patterns to keep interference competition at a minimum (H2) only found support in our owl data. In areas/periods with dark nights, the temporal

overlap between the nocturnal eagle owls and the diurnal white-tailed eagles will be quite low. By increasing nighttime activity, the white-tailed eagles in our study increased the temporal overlap with eagle owls to an estimated 0.58.

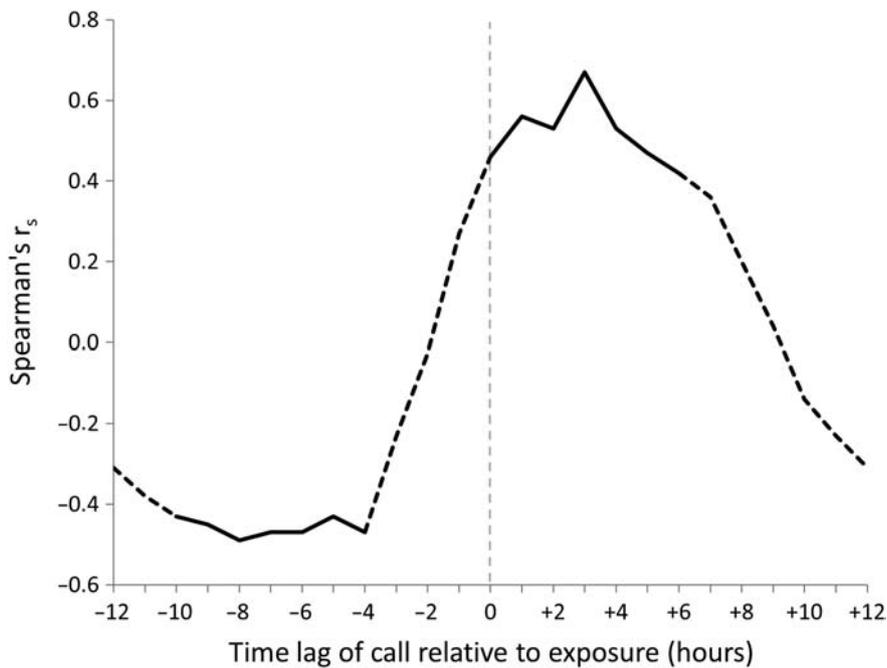


Figure 4. Spearman's rank correlation coefficients of acoustic observations of calling eagle owls vs visual observations of eagle owls at different time lags. At positive time lags, calling preceded visual exposure. Solid line represents a statistically significant correlation at the indicated time lag.

If the owls had increased their daytime activity as proposed in H1, the temporal overlap between the two species would have increased even further. Temporal segregation to avoid interference competition is therefore a possible interpretation of why the owls retained their nocturnal activity pattern. The observation that the eagles changed their circadian rhythms in a way that increased the temporal overlap, whereas the owls did not, may reflect an asymmetry between the two competitors, and may indicate that eagle owls are facing a higher risk of interspecific aggression and hence a higher cost of temporal overlap with the white-tailed eagle.

There are alternative interpretations other than interference competition that are consistent with the observed activity patterns. Light intensity varies with the angle of incidence, and even during the arctic summer the light is dimmer when the sun is closer to the horizon. The solar midnight may therefore offer the best hunting conditions for eagle owls during 24-h midsummer daylight. Note however that more than half of the eagle owl observations during the three darkest hours (0, 1 and 2 am) were acoustic observations of calling owls rather than visual observations of hunting owls, whereas the visual observations, mostly of hunting owls, extended later into the morning (Fig. 3). The eyes of eagle owls have features of both nocturnal and diurnal birds, with retinas showing high sensitivity to low light levels as well as features mediating vision at higher light intensity (Alix et al. 2017). That is, even though eagle owls may hunt more efficiently in the dark, they are also capable of hunting during daylight, and will have to do so when the night does not have enough dark hours. For the otherwise diurnal white-tailed eagles, the light may have been sufficient for foraging throughout most of the 24-h period.

Rather than resulting from optimal adaptations to 24-h daylight, the observed circadian rhythms may reflect differences in the plasticity of the internal biological clocks of the three species. There is evidence that the circadian rhythms of eagle owls (Cramp and Simmons 1985), water voles (Airoldi 1979) and white-tailed eagles (Krone et al. 2009) all vary with season and latitude. Nonetheless, the circadian rhythms of eagle owls and water voles may still not be flexible enough to follow the extreme variation in the light-dark cycle at such high latitudes, i.e. from 24-h darkness in winter to 24-h daylight in summer. The degree of flexibility in circadian rhythms can also present challenges in other circumstances in which light is no longer a reliable cue for important changes in the environment, e.g. in the cases of rapid climate change, or light pollution in urban areas (Kronfeld-Schor et al. 2017).

We collected activity data only during the weeks around the summer solstice, and did not have data for comparison from the same area during times of year when the night would have a varying number of dark hours. Hence, when our results are interpreted as the animals changing or retaining their usual activity patterns, it is based on the assumption that the circadian rhythms during dark-night periods in our study area do not differ substantially from those reported in the literature. In order to confirm this assumption, intrusive

methods such as trapping would have been necessary, as our method of visual field observations would not be feasible in the dark. Our activity models indicate circadian rhythms that are clearly similar to those reported elsewhere for owls, and clearly different for eagles, leaving room for moderate geographic variation without changing our conclusions. Also our water vole data are consistent with the small differences between daytime and night-time activity reported elsewhere. However, our data and modelling approach were unsuitable for detecting a finer-scale polyphasic pattern. Hence, we do not know whether the fine-scale activity rhythms of voles in this study differed from elsewhere, and whether such differences would be due to geographic variations or to the constant daylight.

A consequence of collecting data from unmarked individuals is pseudoreplication. Our owl observations include four known breeding localities. The low daytime activity level of the owls showed little dispersion around the means, and hence a nocturnal activity pattern is a reasonable conclusion. Our method did not allow us to identify individual voles, or to assign eagles to different breeding localities. In the case of the voles, it is unlikely that the same individuals survived to be observed for more than one field season, which somewhat reduces the problem of pseudoreplication in this species.

### Vocal activity, exposure and owl-eagle interactions

Elsewhere, eagle owls often select highly visual call posts in order to enhance signal transmission (Delgado and Penteriani 2007, Campioni et al. 2010). In contrast, when owls were detected acoustically in our study, we could rarely see them, even though exposed posts were available and used at other times (Fig. 3), and even though the calls revealed their approximate position, facilitating visual detection if the owls were not concealed. This is consistent with the hypothesis that the owls in our study area reduced their vocal activity when visually exposed, and used less conspicuous call sites during their vocal displays in order to minimize exposure to eagles (H3). In our study area, the open, treeless landscape would give eagle owls limited cover in the case of a sudden eagle attack. However, the owls had the option of making their vocal displays from depressions in the terrain or concealed by shrubs on the ground, rather than calling from the top of power poles or exposed rocks.

Previous studies on eagle owl vocal behaviour were conducted in sparse woodland providing cover, and had dark hours during which the owls could call with low risk of aggression by diurnal raptors (Penteriani et al. 2005, Delgado and Penteriani 2007). In the current study, the presence of eagles that were active throughout the 24-h cycle, combined with the openness of the landscape and the continuous midsummer daylight, may have made it too risky to be exposed during territorial displays. Moreover, the need for long distance call transmissions may have been reduced in our study area because of the open landscape and the high density of eagle owl territories. The study areas of Delgado

and Penteriani (2007) and Campioni et al. (2010) also had high densities of eagle owls, sometimes with only 250 and 500 m between neighbouring males, yet the males always used conspicuous calling posts (V. Penteriani pers. comm.), possibly because they did not face the threat of interspecific aggression. The need to be concealed in the presence of potentially aggressive competitors finds support in an experiment by Lourenco et al. (2011b), and the risk of interspecific killing has been found to constrain calling activity of smaller owl species (Lourenco et al. 2013). Furthermore, the owls in our study may have had to trade-off between calling and foraging during the few hours around the solar midnight when slightly dimmer light reduced the risk of detection during territorial displays as well as providing better hunting conditions (Fig. 3).

During the years of our study, four territorial eagle owl pairs were resident within 1 km of the two transect lines. It is therefore likely that the majority of eagle owl observations were of adult breeders, which elsewhere have been found to call from more visible posts than non-territorial floaters (Campioni et al. 2010). Eagle owl vocal behaviour is associated with territorial disputes and courtship behaviour (Penteriani 2002), and the vocal activity peaks during the pre-laying period (Delgado and Penteriani 2007). Our data were collected in June and July, when the owls in the area already had chicks that were starting to move away from the nests (Frafjord 2003). Hence, the majority of acoustic observations in this study were probably of territorial calls rather than calls intended for courtship. Both sexes were calling regularly, distinguished by high and low pitch and a few times by visual observation. The use of inconspicuous calling posts suggests a strong trade-off between the need to defend the territory and to avoid giving up their position to eagles that might pose a threat to the caller itself or to nearby chicks.

In accordance with the hypothesis of habitat mediated avoidance (H4), the owls were observed largely east of the transect lines where there was a higher density of islands, whereas the eagles were observed largely west of the transect lines where there was more open water. Water voles were observed at similar frequencies on both sides of the transect lines. However, the difference in spatial distribution of owls and eagles may still reflect prey distribution as the higher density of islands to the east would provide more habitat for catching voles, whereas the open water to the west would provide better foraging opportunities for the eagles (Zawadzka 1999). Nevertheless, the finding suggests a spatial segregation between the two avian apex predators, which may be due to a combination of habitat mediated avoidance and differences in main prey type and hunting behaviour.

We found that the peak in eagle owl vocal activity preceded the visual observations by up to five hours, with the strongest correlations found at a time lag of one to three hours (Fig. 4). That is, the majority of observations of calling eagle owls happened in the evening, before the peak in visual observations of hunting owls. Also previous studies have reported a period in the evening in which eagle owls engage

in territorial display before they start foraging (Penteriani 2002, Delgado and Penteriani 2007). This is reminiscent of the dawn chorus of diurnal birds and consistent with a hypothesis of an equivalent dusk chorus in nocturnal birds (Hardouin et al. 2008). Singing before the onset of foraging, at dawn for diurnal birds and at dusk for nocturnal birds, is believed to be relatively costly and therefore ensure signal reliability (Hardouin et al. 2008). In a high-density eagle owl population, such as our study area, defending the territory is probably of critical importance, despite the trade-off with exposure to interspecific aggression.

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## References

- Airoldi, J. P. 1979. The activity rhythm of *Arvicola terrestris scherman* Shaw. – *Mammalia* 43: 25–52.
- Alix, B., Segovia, Y. and Garcia, M. 2017. The structure of the retina of the Eurasian eagle-owl and its relation to lifestyle. – *Avian Biol. Res.* 10: 36–44.
- Barreto, G. R., Rushton, S. P., Strachan, R. and Macdonald, D. W. 1998. The role of habitat and mink predation in determining the status and distribution of water voles in England. – *Anim. Conserv.* 1: 129–137.
- Bichsel, M. 2012. Diet of an avian top-predator: analyzing eagle owl pellets from nests on a north-Norwegian archipelago. – Hedmark Univ. College, Norway.
- Blumstein, D. T. 2008. The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling. – In: Wolff, J. O. and Sherman, P. W. (eds), *Rodent societies: an ecological and evolutionary perspective*. Univ. of Chicago Press, p. 610.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. and Bolker, B. M. 2017. Modeling zero-inflated count data with glmmTMB. – bioRxiv: 132753.
- Campioni, L., Delgado, M. D. M. and Penteriani, V. 2010. Social status influences microhabitat selection: breeder and floater eagle owls *Bubo bubo* use different post sites. – *Ibis* 152: 569–579.
- Cramp, S. and Simmons, K. E. L. (eds) 1985. *Handbook of the birds of Europe, the Middle East and north Africa: the birds of the Western Palearctic*. – Oxford Univ. Press.
- Daan, S. and Aschoff, J. 1975. Circadian rhythms of locomotor activity in captive birds and mammals: their variation with season and latitude. – *Oecologia* 18: 269–316.

- Dahl, E. R. 2015. Eagle owl *Bubo bubo* in coastal northern Norway – diet during breeding seasons 1995–2014. – Dept for forestry and wildlife management. Hedmark Univ. of Applied Sciences.
- Delgado, M. M. and Penteriani, V. 2007. Vocal behaviour and neighbour spatial arrangement during vocal displays in eagle owls (*Bubo bubo*). – *J. Zool.* 271: 3–10.
- Erkinaro, E. 1973a. Short-term rhythm of loco motor activity within the 24 hour period in the Norwegian lemming *Lemmus-lemmus* and water vole *Arvicola terrestris*. – *Aquilo Ser. Zool.* 14: 46–58.
- Erkinaro, E. 1973b. Activity optimum in *Microtus agrestis*, *Arvicola terrestris* and *Apodemus flavicollis* Rodentia dependent on the intensity of illumination. – *Aquilo Ser. Zool.* 14: 89–92.
- Eriksen, A. and Wabakken, P. 2018. Data from: Activity patterns at the Arctic Circle: nocturnal eagle owls and interspecific interactions during continuous midsummer daylight. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.11g3s9t>>.
- Frafjord, K. 2003. Do eagle owls select larger water voles? – *Fauna Norv.* 23: 42–47.
- Gerber, B. D., Karpanty, S. M. and Randrianantenaina, J. 2012. Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. – *J. Mammal.* 93: 667–676.
- Halle, S. 2000. Ecological relevance of daily activity patterns. – In: Halle, S. and Stenseth, N. C. (eds), *Activity patterns in small mammals: an ecological approach*. Springer, pp. 67–90.
- Hardouin, L. A., Robert, D. and Bretagnolle, V. 2008. A dusk chorus effect in a nocturnal bird: support for mate and rival assessment functions. – *Behav. Ecol. Sociobiol.* 62: 1909–1918.
- Jenny, D. and Zuberbühler, K. 2005. Hunting behaviour in west African forest leopards. – *Afr. J. Ecol.* 43: 197–200.
- Krone, O., Berger, A. and Schulte, R. 2009. Recording movement and activity pattern of a white-tailed sea eagle (*Haliaeetus albicilla*) by a GPS datalogger. – *J. Ornithol.* 150: 273–280.
- Kronfeld-Schor, N., Visser, M. E., Salis, L. and van Gils, J. A. 2017. Chronobiology of interspecific interactions in a changing world. – *Phil. Trans. R. Soc. B* 372: 13.
- Linnell, J. D. and Strand, O. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. – *Divers. Distrib.* 6: 169–176.
- Lourenco, R., Santos, S. M., Rabaca, J. E. and Penteriani, V. 2011a. Superpredation patterns in four large European raptors. – *Popul. Ecol.* 53: 175–185.
- Lourenco, R., Penteriani, V., Delgado, M. D., Marchi-Bartolozzi, M. and Rabaca, J. E. 2011b. Kill before being killed: an experimental approach supports the predator-removal hypothesis as a determinant of intraguild predation in top predators. – *Behav. Ecol. Sociobiol.* 65: 1709–1714.
- Lourenco, R., Goytre, F., Delgado, M. D., Thornton, M., Rabaca, J. E. and Penteriani, V. 2013. Tawny owl vocal activity is constrained by predation risk. – *J. Avian Biol.* 44: 461–468.
- Lüdecke, D. 2017. sjStats: statistical functions for regression models. – R package ver. 0.13.0.
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B. and Brooks, M. 2016. glmmTMB: generalized linear mixed models using template model builder. – R package ver. 0.0.2.
- May, R., van Dijk, J., Wabakken, P., Swenson, J. E., Linnell, J. D. C., Zimmermann, B., Odden, J., Pedersen, H. C., Andersen, R. and Landa, A. 2008. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. – *J. Appl. Ecol.* 45: 1382–1391.
- Meredith, M. and Ridout, M. 2014. overlap: estimates of coefficient of overlapping for animal activity patterns. – R package ver. 0.2.4.
- Meredith, M. and Ridout, M. 2017. Overview of the overlap package. – <<https://cran.r-project.org/web/packages/overlap/vignettes/overlap.pdf>>.
- Mikkola, H. 1976. Owls killing and killed by other raptors in Europe. – *Br. Birds* 69: 144–154.
- Nelson, B. V. and Vance, R. R. 1979. Diel foraging patterns of the sea-urchin *Centrostephanus coronatus* as a predator avoidance strategy. – *Mar. Biol.* 51: 251–258.
- Nouvellet, P., Rasmussen, G. S. A., Macdonald, D. W. and Courchamp, F. 2012. Noisy clocks and silent sunrises: measurement methods of daily activity pattern. – *J. Zool.* 286: 179–184.
- Penido, G., Astete, S., Jacomo, A. T. A., Sollmann, R., Torres, N., Silveira, L. and Arinho, J. M. 2017. Mesocarnivore activity patterns in the semiarid Caatinga: limited by the harsh environment or affected by interspecific interactions? – *J. Mammal.* 98: 1732–1740.
- Penteriani, V. 2002. Variation in the function of eagle owl vocal behaviour: territorial defence and intra-pair communication? – *Ethol. Ecol. Evol.* 14: 275–281.
- Penteriani, V., Gallardo, M. and Cazassus, H. 2000. Diurnal vocal activity of young eagle owls and its implications in detecting occupied nests. – *J. Raptor Res.* 34: 232–235.
- Penteriani, V., Delgado, M. M., Maggio, C., Aradis, A. and Sergio, F. 2005. Development of chicks and predispersal behaviour of young in the eagle owl *Bubo bubo*. – *Ibis* 147: 155–168.
- Penteriani, V., Delgado, M. D. M., Bartolommei, P., Maggio, C., Alonso-Alvarez, C. and Holloway, G. J. 2008. Owls and rabbits: predation against substandard individuals of an easy prey. – *J. Avian Biol.* 39: 215–221.
- Penteriani, V., Kuparinen, A., Delgado, M. D., Palomares, F., López-Bao, J. V., Fedriani, J. M., Calzada, J., Moreno, S., Villafuente, R., Campioni, L. and Lourenco, R. 2013. Responses of a top and a meso predator and their prey to moon phases. – *Oecologia* 173: 753–766.
- Pewsey, A., Neuhauser, M. and Ruxton, G. D. 2013. Circular statistics in R. – Oxford Univ. Press.
- Reierth, E. and Stokkan, K. A. 1998. Activity rhythm in High Arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). – *Can. J. Zool.* 76: 2031–2039.
- Ridout, M. S. and Linkie, M. 2009. Estimating overlap of daily activity patterns from camera trap data. – *J. Agric. Biol. Environ. Stat.* 14: 322–337.
- Ruby, N. F., Joshi, N. and Heller, H. C. 2002. Constant darkness restores entrainment to phase-delayed Siberian hamsters. – *Am. J. Physiol.* 283: R1314–R1320.
- Rushton, S., Barreto, G., Cormack, R., Macdonald, D. and Fuller, R. 2000. Modelling the effects of mink and habitat fragmentation on the water vole. – *J. Appl. Ecol.* 37: 475–490.
- Salo, P., Nordstrom, M., Thomson, R. L. and Korpimäki, E. 2008. Risk induced by a native top predator reduces alien mink movements. – *J. Anim. Ecol.* 77: 1092–1098.
- Sergio, F., Marchesi, L., Pedrini, P. and Penteriani, V. 2007. Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? – *Anim. Behav.* 74: 1607–1616.
- Speakman, J. R., Rydell, J., Webb, P. I., Hayes, J. P., Hays, G. C., Hulbert, I. A. R. and McDevitt, R. M. 2000. Activity patterns

- of insectivorous bats and birds in northern Scandinavia (69 degrees N), during continuous midsummer daylight. – *Oikos* 88: 75–86.
- Stoddart, D. M. 1969. Daily activity cycle of water vole (*Arvicola terrestris*). – *J. Zool.* 159: 538–540.
- Street, L. E., Shaver, G. R., Rastetter, E. B., van Wijk, M. T., Kaye, B. A. and Williams, M. 2012. Incident radiation and the allocation of nitrogen within Arctic plant canopies: implications for predicting gross primary productivity. – *Global Change Biol.* 18: 2838–2852.
- Zawadzka, D. 1999. Feeding habits of the black kite *Milvus migrans*, red kite *Milvus milvus*, white-tailed eagle *Haliaeetus albicilla* and lesser spotted eagle *Aquila pomarina* in Wigry National Park (NE Poland). – *Acta Ornithol.* 34: 65–75.