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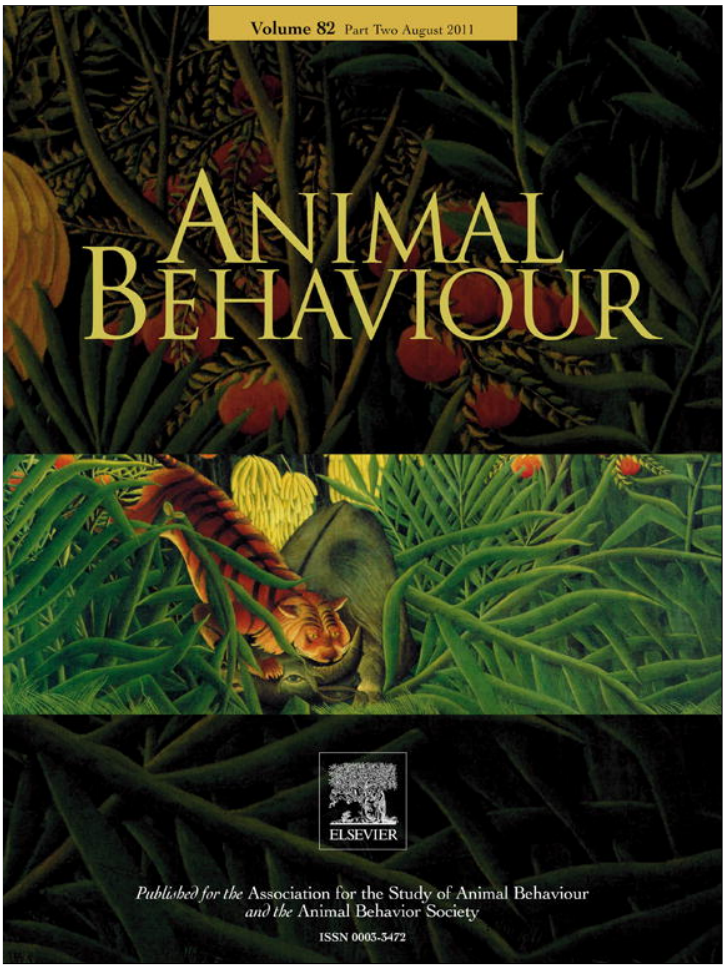

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Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases

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The effects of moon phases on predator–prey relationships have so far been mainly investigated from the prey's perspective. The response of a predator to moon phases may represent a complex trade-off between overcoming the antipredator strategies of its prey and balancing other needs/constraints (e.g. individual status and condition). We explored the year-round effects of the lunar cycle on radiotagged breeders and dispersers of an avian predator, the eagle owl, *Bubo bubo*, from the perspective of movement patterns, foraging effort and display intensity. In general, the movements of breeders suggested an increase in activity around the time of the full moon. This may be related to an increase in both the time needed to detect prey (on brighter nights prey are more concealed and wary) and the time the predator devotes to visual displays (the full moon increases the conspicuousness of signalling). However, hunting activity also peaked during dark nights, when prey might be harder to see. In contrast, the behaviour of dispersing owls was not affected by lunar cycles. Natal dispersal involves potentially dangerous crossings of unknown landscapes (which probably requires similar effort throughout the year), and because of the absence of reproductive constraints should not require greater activity when food profitability is low. The status of individuals may thus play a crucial role in cost–benefit considerations and behavioural decisions, by directly affecting the time and effort individuals need to allocate to various activities related to their most immediate needs (e.g. breeding successfully versus overcoming dispersal costs).
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Moonlight influences the behaviour of a number of prey and predator species, and markedly influences predator–prey relationships among both invertebrates (e.g. Skutelsky 1996; Tigar & Osborne 1999) and vertebrates (e.g. Daly et al. 1992; Brown & Kotler 2004, Kotler et al. 2010). Under bright moonlight, prey species are generally less active, more vigilant and feed in safer habitats because of an increased risk of predation, as at this time they are more obvious to their predators (lunar phobia: e.g. Vasquez 1994; Brown & Kotler 2004; Griffin et al. 2005). As a consequence, predators are expected to be more active around the time of the full moon because of two opposing factors (but see Sábato et al. 2006): (1) they must search intensively for prey that is concealed and attentive, because on bright moonlit nights prey species shift to more apprehensive foraging strategies (Kotler et al. 2010) and/or are less active (Clarke 1983; Sábato et al. 2006; Berger-Tal et al. 2010) and (2) they benefit from higher light levels when seeking prey (Clarke 1983; Kotler et al. 1988), as predators are most lethal during moonlit hours of the night (Kotler et al. 2002).

Despite long-term interest in the influence of lunar phases on prey behaviour and antipredator strategies in mammals (e.g. seals versus sharks: Trillmich & Mohren 1981; deer mice and gerbils versus owls: Clarke 1983; Kotler et al. 1991; Schmidt 2006; Berger-Tal et al. 2010; bats versus owls: Law 1997; elk, *Alces alces*, versus wolves, *Canis lupus*: Creel et al. 2008; red fox, *Vulpes vulpes*, versus striped hyaenas, *Hyaena hyaena*: Mukherjee et al. 2009) and birds (e.g. auklets versus gulls: Nelson 1989; desert rodents versus owls: Price et al. 1984; petrels versus skuas: Mougeot & Bretagnolle 2000), less information is available on the response of predators to moonlight (but see Grassman et al. 2005; Di Bitetti et al. 2006; Sábato et al. 2006; Mukherjee et al. 2009). Study of the effects of moonlight on the behaviour of predators is important mainly

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because predator behaviour is not primarily driven by the ultimate risk of predation (especially in the case of top predators, which do not have intraguild predators; Lourenço et al. 2011); in addition, this topic has received little attention in behavioural ecology research. From this perspective the response of a predator to moon phases may represent a complex trade-off between countering the antipredator strategies of its main prey(s) and (2) finding a balance among the interactions of several needs/constraints associated with its status (breeder versus disperser) and internal state (i.e. health), the composition and structure of its home range habitat, and differing periods in its biological cycle (breeding versus nonbreeding periods).

A long-term study of the breeding and dispersal sectors of an eagle owl, *Bubo bubo*, population in southern Spain has provided detailed and diverse information on radiotagged individuals, offering an opportunity to assess the year-round effects of lunar cycles on this predator. In this study we analysed individual responses to moon phases with respect to three main types of behaviour: (1) movement patterns (for both breeders and dispersers); (2) foraging effort required (calculated as the time between the beginning of a hunting event and the capture of a prey; for breeders only); and (3) intensity of breeder vocal/visual displays (dispersers do not perform any display).

Our main hypothesis was that behavioural patterns fluctuate during the cycles of the moon as a result of the balance between changing hunting conditions and those aspects of the biological cycle most closely related to lunar brightness (e.g. the need for greater foraging efficiency during the nestling and fledging periods, and to be conspicuous for territorial/sexual signalling), which are mediated by internal (i.e. physiological conditions) and external (i.e. landscape, trophic resources) factors. Although we did not measure the behaviour of the main prey of eagle owls in the study area (rabbits, *Oryctolagus cuniculus*, and rats, *Rattus* spp.; see Resource abundance), we are confident that a pattern of increased activity of this predator around the time of the full moon should correspond to (1) reduced prey activity (in all lagomorphs and rodents studied to date this response to moonlight has been observed; Lockard & Owings 1974; Clarke 1983; Sábato et al. 2006) and (2) increased difficulty of prey detection because of cover-seeking behaviour (lagomorphs and rodents prefer covered to open habitats during the full moon; Clarke 1983; Wolfe & Tan Summerlin 1989; Gilbert & Boutin 1991; Daly et al. 1992; Leaver & Daly 2003). It is known that rabbits are significantly more active during the new moon period than during the full moon (Kolb 1992; Twigg et al. 1998). However, we also expected an increase in hunting activity around the time of the new moon, when darkness may make prey location and pursuit difficult (Clarke 1983; Kotler et al. 1988, 1991; Longland & Price 1991). Additionally, we expected that breeders and dispersers would show different behavioural responses to the moon phases because of diverse constraints acting upon them. Whereas the focus of breeders is mainly related to territorial/sexual displays and reproductive tasks, dispersers face the many uncertainties of dispersal and, more frequently than breeders, they need to move across unknown areas prior to settlement in more-or-less fixed locations (Delgado et al. 2010; Penteriani et al. 2011).

METHODS

Data Collection from Radiotagged Breeders and Dispersers

During the period 2003–2010 we studied the movement behaviour and rhythms of activity of 31 breeders and 40 dispersing juveniles. The breeders (21 males, 10 females) and dispersers (28 males, 12 females) were from 29 nest sites in Sierra Morena (southwestern Spain; for more details see Penteriani et al. 2007). Each individual was fitted with a 30 g harness-mounted backpack (Biotrack, Wareham BH20 5AJ, Dorset, U.K.) containing a mercury posture sensor, which enabled us to discriminate hunting behaviour from other activities (see below) through changes in the radio signal from the transmitter (for more details see Delgado & Penteriani 2008 and Penteriani et al. 2008). The weight of the transmitter was less than 3% of the weight of the smallest adult male (1550 g; mean ± SD = 1667 ± 104.8 g), and 3.5% of the smallest fledgling weight (850 g; mean ± SD = 1267 ± 226.4 g) at the time of tagging. We manipulated and marked owls under Junta de Andalucía–Consejería de Medio Ambiente authorizations No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02.

Breeding males were captured by simulating a territorial intrusion using a taxidermic mount and playback of a male call. A net behind the mount caught responding individuals. The capture and manipulation of breeding owls posed little risk to the birds because we immediately removed them from the net, and they remained motionless when manipulated. Females were trapped with a bownet placed in the nest when nestlings were 20–35 days old; at this age they can thermoregulate, and night temperatures were always warm (about 20 °C). Nestlings were put in a box with a metal grid to make them visible to their parents, who were caught on return to the nest. After each bownet trapping session (which lasted from sunset to sunrise) we fed the nestlings and released them in the nest. We never carried out trapping on more than 3 nights at the same nest per breeding season. For trapped breeders we measured the body mass (to the nearest 10 g, using 1 kg Pesola scales) and wing length to calculate the body condition index, and took blood samples from adults (2 ml, taken from the brachial vein) to obtain haematocrit values (see Internal state of individuals). The blood samples were stored in tubes with heparin at 4 °C for transport to the laboratory, where they were centrifuged for 10 min at 4000 rpm to separate the plasma, which was stored at −78 °C. During 8 years of continuous radiotracking of more than 150 eagle owls (both breeders and dispersers) we never observed any adverse effects of the backpacks on the birds or their breeding performance. The backpacks were not removed after the study because it was impossible to trap tagged individuals again.

The juveniles were aged following Penteriani et al. (2005), and sexed by molecular procedures using DNA extracted from blood samples (2 ml) collected from the brachial vein of each bird when it was still a nestling (ca. 30–35 days old).

Tagged individuals were tracked continuously on a nightly basis ($N = 459$ nights, for a total of 5343 h of continuous radiotracking) from 1 h before sunset to 1 h after sunrise (mean duration of tracking sessions ± SD = 11.3 ± 1.9 h). Each night the location ($N_{total} = 8494$) of each individual was recorded each time a change in its posture or position was detected by the posture mercury sensor (mean number of locations per radiotracking session ± SD = 17.6 ± 4.9). Thus, the number of locations recorded effectively represented the movement of an individual during the night. During the 8-year study period, individuals were tracked on a rotational basis throughout the year, providing a homogeneous distribution of radiotracking nights per lunar phase (Fig. 1).

Locations were determined by triangulation using a three-element hand-held Yagi-antenna connected to an ICOM (IC-R20) portable receiver (www.icom.co.jp). Based on the error in radiotracking localization (mean accuracy ± SE = 83.5 ± 49.5 m) and to ensure independence among locations, 150 m was set as the minimum threshold distance necessary to distinguish locations while tracking at night. To avoid unnecessary disturbance during continuous tracking we attempted to maintain a distance at least 100–300 m from the focal individual, although directly following individuals did not appear to affect their behaviour (i.e. the owls

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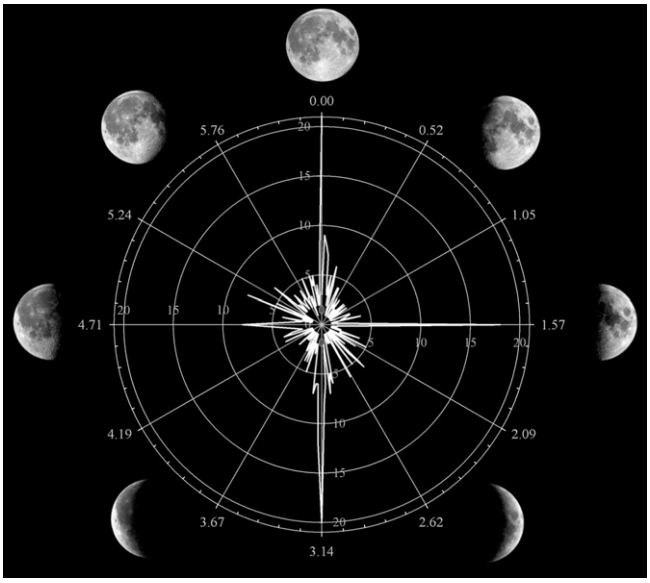

Figure 1. Distribution of the 459 radiotracking nights (2003–2010) per lunar phase for 31 eagle owl breeders (21 males, 10 females) and 40 dispersing juveniles (28 males, 12 females). Moon phases were converted to the fraction of moon disk illuminated, and expressed as radians (θ): one lunar cycle corresponds to a gradual increase from 0 to 2π radians (e.g. 0 and 2π radians correspond to the full moon and π radians to the new moon).

appeared to ignore the observer when the latter accidentally approached closer to the bird; V. Penteriani & M. M. Delgado, unpublished data).

General Movement Patterns and Rhythms of Activity

Owl movement patterns and activity were calculated per night and at the spatial scale of the home range and core area(s), for both breeder home ranges and disperser settlement areas. We first estimated the home range size using fixed-kernel methods (Worton 1989) with a least-squares cross-validation (LSCV) process to determine the optimal value of the smoothing parameter for a given kernel and sample size. To establish home range boundaries we used density isopleth values of 90% (Seaman et al. 1999). We characterized the internal structure of home ranges by estimating the core area(s) of each home range, defined by the 50% density isopleths. As it was not always possible to distinguish the core nest area from the core hunting area(s), in this study core areas represent both nesting and hunting areas.

Movement behaviour at the spatial scale of the home range has been described by four variables (Delgado et al. 2010): (1) total distance, corresponding to the sum of the distance between successive steps on the same nightly path; (2) step length, which is the distance between successive locations; (3) time step, which is the time elapsed between successive moves; (4) speed, which is determined by dividing the step distance by the time interval between successive locations. As rhythms of activity, we used the total number of movements per night (i.e. movement rates). As night length varies throughout the year, we standardized movement rates by dividing them by the total time that the owl was active each night.

Two types of behaviour were recorded within the core areas. (1) Core area activity was the time an owl spent inside the home range core area(s). This is a measure of time devoted to major activities including breeder territorial displays, as well as hunting and feeding of both breeders and dispersers. Feeding behaviour included nestling/fledgling feeding (if the focal owl was a breeder) and female feeding (if the focal owl was a breeding male during incubation and nestling periods). (2) We also recorded the number of movements within the core area(s).

Assessing Prey Capture by Breeders

The difficulties faced by breeders in catching rabbits under various moon phases were assessed following Penteriani et al. (2008), based on a subsample of 13 individuals (11 males and two females; $N_{\text{nights}} = 98$). We were able to discriminate hunting behaviour from other activities (e.g. vocal displays, feeding young, roosting) when the following three conditions were met. First, when the tag pulse increased in frequency and its volume changed we assumed that the owl had shifted from a vertical and fixed position (i.e. a perched individual) to a horizontal and dynamic position (i.e. a flying individual). The change in volume was because of the variation in the distance between the owl and the car antenna, as a consequence of the bird's movement. Second, we assumed that the owl had started to hunt when it ceased sunset vocal activity (during which it made short and rapid movements between the call perches surrounding the nest; Delgado & Penteriani 2007) and undertook either a long flight to the hunting area or a short flight, but roosted for a long time (i.e. an ambushing individual). Third, we assumed that the owl had hunted successfully and was eating the prey when the frequency of the tag pulse increased and decreased rhythmically but the volume remained unchanged (i.e. a perched individual), and the owl was not calling (because vocal displays generate similar patterns in frequency pulse). This discrimination of hunting activity was supported by direct observations of radiotagged individuals hunting at sunset and sunrise, or on full moon nights (M. M. Delgado & V. Penteriani, unpublished data). The foraging effort of the owls was calculated as the amount of time between the start of one hunting event and the capture of a prey (as indicated by the second condition used to discriminate hunting behaviour). If hunting conditions are favourable, owls should rapidly capture their prey after hunting begins, and spend a larger proportion of the night motionless or in activities other than hunting. If owls easily catch their prey they will not need to hunt for long periods, as would occur if there were repeated unsuccessful attacks or it was necessary to explore several different areas per night before locating a prey.

Intensity of Breeders' Call Displays

We previously showed that lunar brightness increases the frequency of breeder call displays because moonlight enhances the conspicuousness of the white badge on the throat, which is a visual signal associated with vocalization (Penteriani et al. 2010). To take this additional effect on the time budget of individuals into account, we included in the present analyses a subsample of radiotagged owls ($N_{\text{individuals}} = 21$; 13 males and eight females; $N_{\text{nights}} = 174$) for which we recorded the number of call bout series (a proxy for call activity under the various moon phases). A series of vocal bouts is defined as a series of single 'oohu' calls, and we defined the end of a series as the last call heard at least 60 s before the next call (Delgado & Penteriani 2007). Because the vocalization peaks of eagle owls at sunset and sunrise may be influenced more by twilight (Delgado & Penteriani 2007; Penteriani & Delgado 2009) than by lunar phase, we excluded crepuscular call displays (i.e. those during the first hour after sunset and the first hour before sunrise) from our analysis.

Moon Phases

The daily moon phase at the geographical location of the study area was obtained from the Naval Oceanography Portal

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(http://www.usno.navy.mil/USNO/astronomical-applications/data-services/rs-one-day-world) and expressed in terms of the fraction of moon disk illuminated and whether the moon was waxing or waning. Following the periodic regression approach suggested by deBruyn & Meeuwig (2001) and applied elsewhere (e.g. Kuparinen et al. 2010), the fraction of moon disk illuminated was converted into radians (θ), with one lunar cycle corresponding to a gradual change from 0 to 2π radians (0 and 2π radians correspond to the full moon, and π radians corresponds to the new moon). Cos(θ), sin(θ), cos(2θ) and sin(2θ) transformations were included in the statistical model as explanatory variables, to investigate possible lunar effects on eagle owl behaviour throughout the lunar cycle (see deBruyn & Meeuwig 2001 for details). We were confident that the effect of lunar light was not altered by cloud cover because of the long-term nature of the study and consequent large number of nights of radiotracking, and because we always avoided cloudy nights owing to the risk that rain could alter owl behaviour.

Individual Status

Breeders and dispersers occur in the same population, but the differences in status entail different constraints (Campioni et al. 2010; Penteriani et al. 2011). Therefore, to accommodate this additional potential source of variation in individual behaviour we took into account three explanatory variables specifically related to the status of breeders and dispersers: (1) the different phases of the biological cycle (for breeders only: 1 = prelaying, 2 = incubation, 3 = nestling and 4 = postfledging); (2) days spent in dispersal (for dispersers only); and (3) the phase of dispersal (for dispersers only: 1 = wandering, 2 = stop; Delgado et al. 2010). Because of the increasing experience of juveniles during natal dispersal (Delgado et al. 2009), and behavioural shifts during the different stages of dispersal (Delgado & Penteriani 2008), both variables (2) and (3) have the potential to affect individual responses to moon phases.

Internal State of Individuals

To account for the health state of individuals we measured two physiological/morphological indexes for breeders (at the moment of trapping) and dispersers (when they were 35 days old): (1) the body condition index and (2) the haematocrit value. These have previously been found to affect the behaviour of individuals, with higher values of both reflecting individuals of better quality (for more information see Delgado et al. 2010).

External Cues Acting on Individuals

To test for the possible effect of habitat heterogeneity on individual behaviour we analysed the landscape structure and the composition of habitats to which the owls were exposed during nightly tracking sessions. We evaluated both landscape structure and composition using ArcMap of ARCGIS version 9.0 (Esri, Redlands, CA, U.S.A.), and reclassified the map into three main land cover elements: forest, scrubland and cultivated areas. We then calculated the proportion of each habitat type within the area traversed by individuals on each night. The calculated areas (in raster format; cell size: 0.5×0.5 km) were used as a basic input data layer for measuring landscape metrics. We used the raster version of FRAGSTATS 3.3 (McGarigal et al. 2002) to calculate the edge density and Shannon's diversity index.

Resource Abundance

We considered the main features of the diet and prey abundance as explanatory variables, because they are potentially additive factors affecting individual behaviour. In particular, as previous diet analyses have shown that rabbits and rats are the main prey of our study population (R. Lourenço, M. M. Delgado & V. Penteriani, unpublished data), we considered three parameters in our study: (1) the relative rabbit abundance in the breeder home ranges and disperser settlement areas (see below), and the biomass of (2) rabbits and (3) rats in the diet of the breeders. The diet of eagle owls was determined by analysing prey remains and pellets collected from 2003 to 2008 during visits to nests, and roosting and feeding perches in the breeding territories of tagged breeders. We identified prey species using bone identification keys and comparison with a reference collection (Laboratory of Archaeosciences, IGESPAR, Lisbon, Portugal), and from these data determined the minimum number of prey individuals involved. Biomass percentages were calculated using the mean weight value obtained from previous studies, or bone measurements to estimate the weight of each individual (see Lourenço 2006 for more details). In 2009, a census from the beginning of March to the beginning of May was used to estimate the relative rabbit abundance at 26 nesting sites and 17 disperser settlement areas, using rabbit faecal pellet counts (latrine counts; Palomares 2001a, b). To obtain comparable indexes of prey abundance (i.e. number of latrines per km of transect), we drew a circular plot around each nest (or the central point of the settlement areas for dispersers), such that the area was equal to the mean eagle owl home range size in our study population, calculated using the minimum convex polygon method. Inside these plots we walked transects of 2.2 km length, and recorded the number of latrines ($N_{total} = 3440$ latrines) within 4 m on either side of each transect. Rabbit density over the years can be considered relatively stable in our study area because of continual management and frequent releases (V. Penteriani & M. Delgado, unpublished data).

Statistical Analyses

Breeders and dispersers were analysed separately because several variables (individual condition, phases of dispersal and resource abundance) were specific or available for just one status, and covariate effects were likely to differ between breeders and dispersers. To test the effects of moon phase, health state of individuals, external factors, status and resource availability on movement patterns, foraging effort and vocal displays, we modelled these behaviours using multilevel models. Total distance, speed, movement rate and foraging effort were modelled with linear mixed-effect models, and time step and numbers of call bout series were modelled with generalized linear mixed-effects models assuming Poisson error structure. To ensure normality, total distance, speed and foraging effort were log transformed. Additive main effects of the variables whose effects on movement were to be tested were considered as explanatory variables. Because we had repeated measures for the same owls over different years, we considered individual nested in year as a random effect. As suggested by Crawley (2007), model simplification was performed by backward selection of variables from the full model, and models were compared using likelihood ratio tests until a minimal adequate model was obtained. For the 'different phases of the biological cycle 'factor, model reduction was performed by joining factor levels closest to each other, after which nested models were compared similarly as explained above. For each analysis we used slightly different subsamples of the data (detailed in Tables 1, 2), representing those individuals for which it was possible to collect the specific information sought. Residuals of the final models

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Table 1
Linear mixed model fitted by maximum likelihood showing the effect of the moon on movement patterns and foraging effort of eagle owl breeders

	Estimate	SE	*df*	*t*	*P*
log (Total distance)*					
Intercept (Periods 1, 3†)	9.32	0.18	218	51.77	<0.0001
Sex	−0.21	0.08	39	−2.58	0.014
Period 2	0.23	0.09	218	2.63	0.009
Period 4	−0.23	0.06	218	−4.00	<0.0001
Age	−0.00	0.00	218	−2.74	0.007
Edge density	−0.00	0.00	218	−2.13	0.034
Shannon diversity index	0.19	0.09	218	2.03	0.044
% Shrubs	−0.38	0.13	218	−3.00	0.003
Moon phase: cos(θ)	0.08	0.03	218	2.32	0.021
log (Speed)‡					
Intercept (Periods 1, 3, 4†)	2.80	0.13	5368	21.74	<0.0001
Period 2	0.17	0.06	5368	2.68	<0.01
Age	−0.0001	0.00	5368	−2.29	0.022
Moon phase: cos(θ)	0.06	0.02	5368	2.42	0.015
Movement rate§					
Intercept (Periods 1, 2†)	0.02	0.001	195	16.73	<0.0001
Sex	−0.006	0.001	35	−4.64	<0.0001
Periods 3, 4	0.002	0.00	195	2.64	0.009
% Forest	0.015	0.004	195	3.55	<0.001
Rabbit biomass in the diet	−0.000	0.000	195	−3.78	<0.001
Rat biomass in the diet	0.000	0.000	195	4.02	0.0001
Moon phase: cos(θ)	0.001	0.000	195	2.38	0.018
Foraging effort**					
Intercept	4.21	0.08	77	51.51	<0.0001
Moon phase: cos(2θ)	0.20	0.10	77	2.06	0.043

* Sum of the distance between successive steps of the same nightly path ($N = 309$).
† Factor levels were included in the model simplification process.
‡ Step distance divided by the time interval between successive locations ($N = 5431$).
§ Total number of movements divided by the length of the night ($N = 297$).
** Amount of time between the beginning of a hunting session and the capture of a prey ($N = 98$).

were explored for normality, homogeneity (except in the case of the generalized linear model) and independence assumptions. All statistical analyses were performed in R 2.10.1 statistical software (R Development Core Team 2009) with nlme (Pinheiro et al. 2009), lme4 (Bates & Maechler 2009) and MASS (Venables & Ripley 2002) packages. Statistical significance was set at $\alpha < 0.05$.

Table 2
Generalized linear mixed model fitted by the Laplace approximation showing the effect of the moon on time elapsed between successive moves (time steps) and vocal displays of eagle owl breeders

	Estimate	SE	*Z*	*P*
Time step*				
Intercept (Period 1†)	−3.62	0.028	131.85	<0.0001
Period 2	−0.09	0.009	−9.69	<0.0001
Period 3	−0.15	0.009	−15.76	<0.0001
Period 4	−0.11	0.006	−19.28	<0.0001
Moon phase: cos(θ)	−0.06	0.003	−18.21	<0.0001
Moon phase: sin(2θ)	−0.01	0.004	−3.03	0.003
Numbers of call bout series‡				
Intercept	0.53	0.26	2.01	<0.01
Sex	−2.09	0.55	−3.81	<0.01
Moon phase: cos(θ)	0.63	0.08	7.64	<0.01
Moon phase: sin(θ)	0.22	0.10	2.16	<0.01

* $N = 5702$.
† Different phases of the biological cycle: 1 = prelaying, 2 = incubation, 3 = nestling, 4 = postfledging.
‡ $N = 174$.

RESULTS

Moon Phase Affects Breeders but not Dispersers

An effect of the lunar cycle was only detected for breeders, while the behaviour of dispersing owls was never affected (in all model reduction steps $P > 0.5$ for lunar effects). For breeders the total distance moved, time steps, speed and total number of movements per night were influenced by the lunar cycle (Tables 1, 2, see Supplementary Material). Together these results suggested a higher movement activity around the time of the full moon than around new moon (Tables 1, 2, Fig. 2, see Supplementary Material): (1) the total distance moved during the night was greatest at the time of the full moon and least at the time of the new moon; (2) the total number of movements per night increased at the time of the full moon and decreased at the time of the new moon; (3) the proxy for flight speed increased at the time of the full moon and was least at the time of the new moon; and (4) the time between movement steps was low at the time of the full moon and increased at the time of the new moon (i.e. the resting time between movements was longer at the time of the new moon).

The reasons for the highest activity on the brightest moonlit night may be related to an increase in the time needed to find prey (Tables 1, 2, Fig. 3a, see Supplementary Material) and the time devoted to vocal displays at the full moon phase (Tables 1, 2, Fig. 3b, see Supplementary Material). These activities are not mutually exclusive, as breeders both have to contend with less active/more concealed prey and ensure greater conspicuousness of their visual displays in moonlight. The additional increase in activity because of moonlight territorial/sexual displays may have concealed a peak in hunting activity during dark nights in the general patterns of movement (when activity peaks were only present at the time of the full moon; Fig. 2).

Additional Effects

In addition to the lunar effect, several other variables influenced the behavioural patterns of breeders (Tables 1, 2, see Supplementary Material). The various phases of the biological cycle always entered in the whole set of movement models, probably highlighting constraints related to the diverse tasks of breeders during the year. The age of breeders seemed to influence both total distances moved during the night and movement speed, that is, younger individuals moved longer distances and faster. The total distance moved during the night was less for females (which probably reflects the time they spend in the proximity of both the nest and young) and was (1) negatively influenced by the landscape structure and composition, expressed as the edge density and the percentage of shrubs (i.e. when owls moved mainly in patches with denser vegetation and frequent ecotones, their nightly total distance was shorter) and (2) positively influenced by landscape heterogeneity. Movement rates were (1) sex dependent, with males moving more than females, as the former are responsible for most territorial displays and provide food to both females and nestlings for most of the breeding season; (2) affected by landscape composition (i.e. denser habitats such as forests increase movement rates); and (3) positively affected by the percentage of rat biomass (and negatively affected by the percentage of rabbit biomass) in the diet, because owls living in home ranges with low availability of rabbits had to rely on smaller prey (including rats), and consequently needed to hunt more to obtain comparable energy to those owls catching rabbits. The effect of sex on the intensity of call displays is attributable to the fact that these were mainly performed by males (Delgado & Penteriani 2007).

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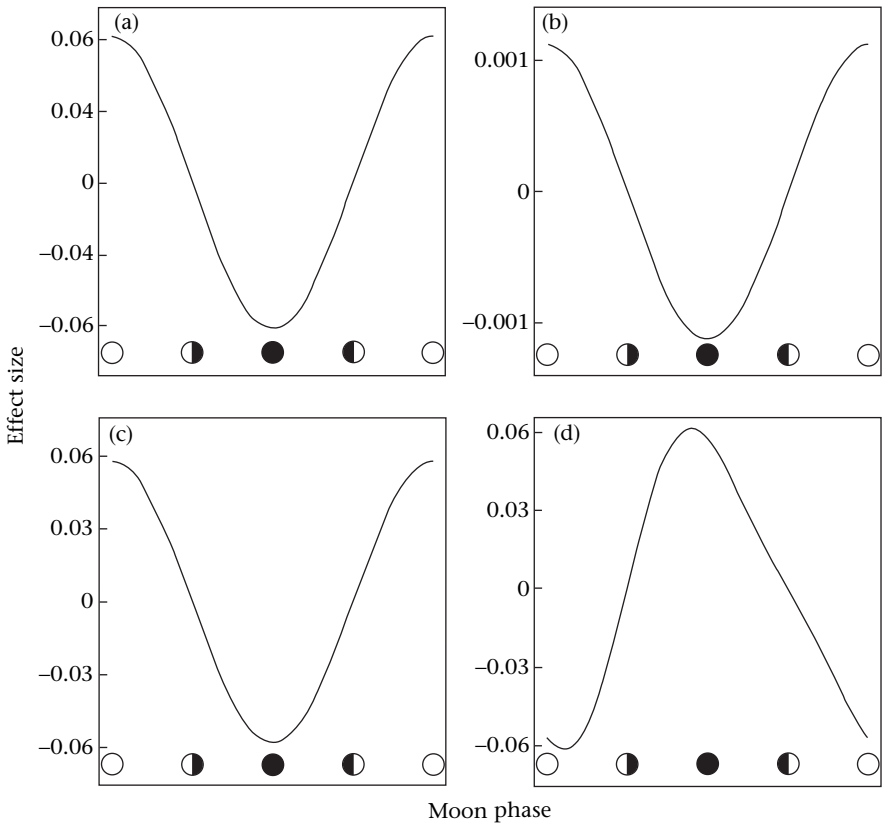

Figure 2. Moon phase effect on (a) log-transformed total distance, (b) movement rates, (c) log-transformed speed and (d) time steps, as estimated by the linear and generalized linear mixed-effect models (Tables 1, 2).

Because the absence of a moon effect on disperser behaviours meant that we were not interested in this group in the specific context of the present study, and because most of the effects of additional covariates on disperser behaviours have been investigated in our previous studies (e.g. Delgado et al. 2009, 2010; Penteriani & Delgado 2011, unpublished data), the effects of those covariates not directly related to the moon phases are not presented here.

DISCUSSION

The general pattern of high activity of breeding eagle owls during moonlit nights could represent a cost/benefit trade-off between preying on less active/more concealed prey and taking advantage of the easier visual location of prey (illumination may enhance the efficiency of visually orienting nocturnal predators; Clarke 1983; Kotler et al. 1988, 1991; Longland & Price 1991). That is, while the potential for owls to detect prey might increase with increasing light, so does the effort involved in encountering active prey under these conditions (e.g. Daly et al. 1992). Consequently, the observed movement patterns could be interpreted as an increase in search effort to maintain a constant food intake, independent of the moon phase (and thus prey availability). The effect of dense patches of cover (shrubs) on movement may be related to the more difficult hunting conditions during the full moon, when prey associates with shrub to avoid predators (Clarke 1983; Travers et al. 1988; Longland & Price 1991; Kotler et al. 1991): the owls moved shorter distances during the night when hunting in dense patches of vegetation, probably because of the difficulty in detecting prey. This general scenario is consistent with the specific analysis of owl foraging efforts, which highlighted the increased difficulty owls encountered in locating and/or catching prey during bright moonlit nights. Nightly catching effort also increased during dark nights, as previously observed for owls under experimental conditions (Kotler et al. 2002). Thus, the chance of encountering active prey increases with decreasing light (Lockard & Owings 1974; Clarke 1983; Sábato et al. 2006), but the ability of owls to detect prey visually might decrease. The finding of reduced hunting efficiency of eagle owls at the time of the new moon is first evidence of the constraints of extreme darkness on the foraging effort of nocturnal predators under natural conditions.

Nestling/fledgling feeding (and female feeding during incubation) should prevent breeders, males in particular, from reducing their activity to save energy during periods of low prey availability, as may occur for nonbreeding individuals, including dispersers. Although optimal foragers should concentrate their foraging activity during periods when the benefits of foraging exceed the costs, breeders cannot always afford to wait for the most favourable hunting conditions. In fact, patterns of lower activity at the time of the full moon, as a direct consequence of reduced prey availability, have been noted in other predators not constrained by reproductive tasks (Lang et al. 2006; Sábato et al. 2006).

Dispersers did not show any behavioural response to the changing lunar cycle, suggesting that constraints on their 'lifestyle' are probably unrelated to lunar phases. Natal dispersal is a complex process characterized by potentially frequent, dangerous crossings of unknown landscapes, and probably requires similar effort at any time of the year. In addition, the absence of constraints associated with reproduction should not result in an increase in activity when food profitability is low. The individual's status may thus play a crucial role in cost–benefit considerations and behavioural decisions (Campioni et al. 2010), by directly affecting the time and

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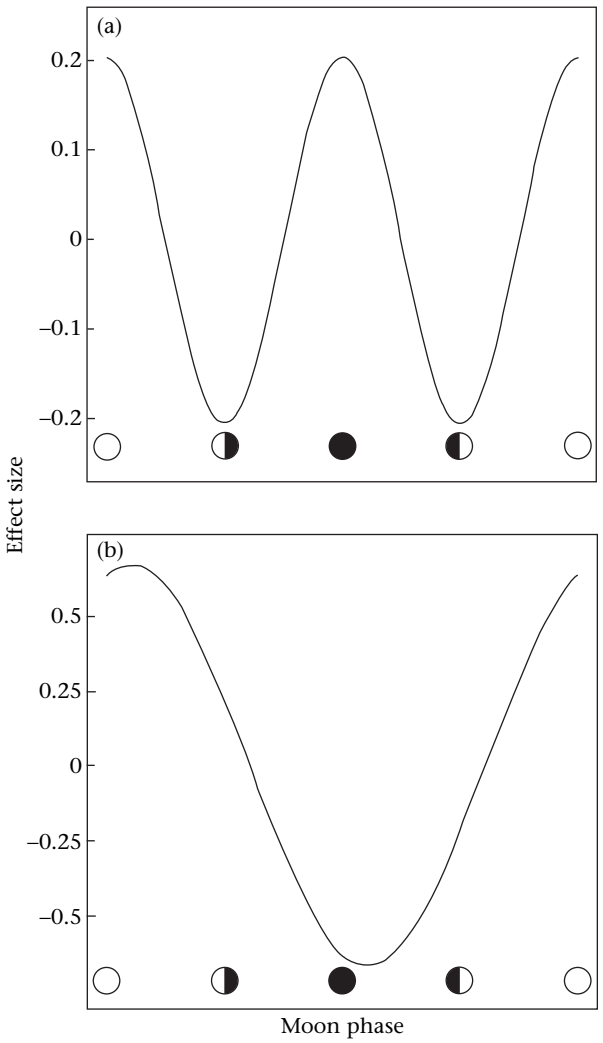

Figure 3. Time budget allocation at various moon phases. (a) Time spent successfully hunting a prey (a proxy of hunting conditions/prey availability). (b) Call activity. See text for further details.

effort individuals allocate to activities related to their most immediate needs (e.g. defending a territory and breeding successfully versus overcoming the multiple costs of dispersal).

We have previously used the brightness of the white tails of predated rabbits as an index of condition, and shown that eagle owls apparently prey more on substandard individuals (Penteriani et al. 2008). We hypothesized that such a preference could be in part explained by easier detection of unhealthy prey individuals using the brightness of the tail as a visual cue. Empirical studies have shown that visual signals may inform the predator of the health state of prey, and consequently their potential to elude predators. In the light of our new findings on eagle owl activity under various lunar phases, another (not mutually exclusive) explanation for biased predation on substandard prey can be hypothesized. The value of food will be higher to a hungry or unhealthy individual than to an individual that has large reserves of energy, or is in a good physical state, that is, hungry individuals should be willing to trade greater mortality risks for additional energy gain (Brown 1992). Because poor body condition may increase the rate of risk-prone prey behaviour (e.g. compensatory foraging) and alter normal behaviour (Murray 2002 and references therein; Wirsing et al. 2002), the greater number of substandard prey in the diet could also be the result of predation events at the time of the full moon. For prey individuals in a healthy state the costs incurred by temporary inactivity, such as reduced foraging, would be exceeded by the benefit of avoiding owl predation, but this would not apply to those individuals in poor health. Therefore, the presence of more substandard rabbits in the diet may be the consequence of more unhealthy individuals always being available (i.e. under all moonlight conditions), whereas healthy prey individuals are principally available (or more easily located and hunted) on dark nights. Evidently, as previously suggested, moon brightness might also increase the conspicuousness of the rabbit's visual signal, making the difference between dull versus bright tails more evident.

It has been recently discovered that eagle owls use visual signalling for intraspecific communication (Penteriani et al. 2007; Penteriani & Delgado 2009), and that such visual displays are strongly related to specific moon phases. Silent nights are more frequently associated with dark nights than bright ones, as owls take advantage of lunar light to increase the effectiveness of their visual communication (Penteriani et al. 2010). Because vocal displays also involve frequent and rapid movements from one call post to another (Delgado & Penteriani 2007; Campioni et al. 2010), some of the important activity at the time of the full moon is also due to the more frequent vocalizations of breeding individuals during moonlit nights.

The moon phases, as a direct indicator of lunar brightness, have an important effect on predator behaviour in more than the context of prey–predator relationships. Behavioural shifts at the time of the full moon are also status dependent, the rank of individuals being a major constraint acting differently within the same species. From this perspective, moonlight has the ability to modify the intensity of interactions among specific classes of conspecifics via territorial/sexual displays, altering patterns of time budget allocations. Because lunar brightness might also bias predation rates on substandard prey, it has the potential to modify the phenotypic structure (high- versus low-quality phenotypes) of prey populations under high predation pressure.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2011.05.027.

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