

Bright moonlight triggers natal dispersal departures

Vincenzo Penteriani, María del Mar Delgado, Anna Kuparinen, Pertti Saurola, Jari Valkama, Eino Salo, Jere Toivola, Adrian Aebischer, et al.

Behavioral Ecology and Sociobiology

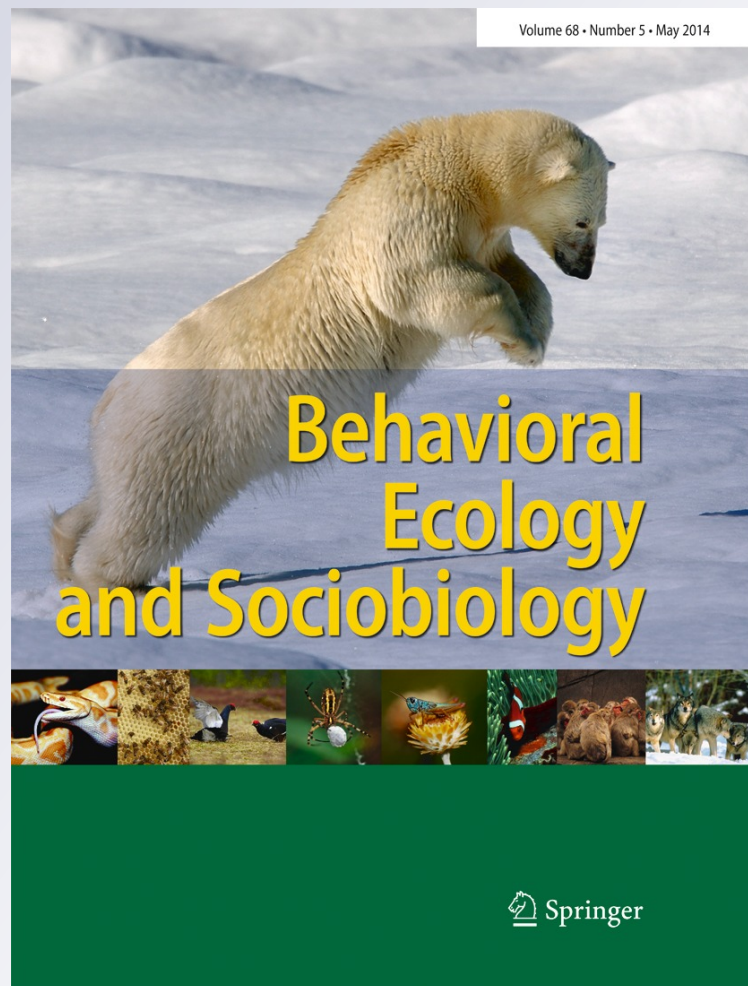
ISSN 0340-5443

Volume 68

Number 5

Behav Ecol Sociobiol (2014) 68:743-747

DOI 10.1007/s00265-014-1687-x



Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Bright moonlight triggers natal dispersal departures

Vincenzo Penteriani · María del Mar Delgado · Anna Kuparinen · Pertti Saurola · Jari Valkama · Eino Salo · Jere Toivola · Adrian Aebischer · Raphaël Arlettaz

Received: 20 April 2013 / Revised: 21 January 2014 / Accepted: 22 January 2014 / Published online: 7 February 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Upon leaving their natal area, dispersers are confronted with unknown terrains. Species-specific perceptual ranges (i.e. the maximum distance from which an individual can perceive landscape features) play a crucial role in spatial movement decisions during such wanderings. In nocturnal animals that rely on vision, perceptual range is dramatically enhanced during moonlight, compared to moonless conditions. This increase of the perceptual range is an overlooked element that may be responsible for the successful crossing of unfamiliar areas during dispersal. The information gathered from 143 radio-tagged eagle owl *Bubo bubo* juveniles in Spain, Finland and Switzerland shows that, although the decision to initiate dispersal is mainly an endogenous phenomenon determined by the attainment of a given age (~6 months), dispersers leave their birthplace primarily under the best light

conditions at night, i.e. when most of the lunar disc is illuminated. This sheds new light into the mechanisms that may trigger dispersal from parental territory.

Keywords Dispersal age · Lunar cycle · Moon phase · Perceptual range · Timing of dispersal · Visual cues · *Bubo bubo*

Introduction

The start of natal dispersal represents a risky stage in the life of animals, which entails multiple costs (Bonte et al. 2012). Consequently, when the time comes to leave

Communicated by E. Korpimäki

Electronic supplementary material The online version of this article (doi:10.1007/s00265-014-1687-x) contains supplementary material, which is available to authorized users.

V. Penteriani (✉)
Department of Conservation Biology, Estación Biológica de Doñana,
C.S.I.C., c/ Americo Vespucio s/n, 41092 Seville, Spain
e-mail: penteriani@ebd.csic.es

M. del Mar Delgado
Metapopulation Research Group, Department of Biosciences,
University of Helsinki, 00014 Helsinki, Finland

A. Kuparinen
Department of Environmental Sciences, University of Helsinki,
00014 Helsinki, Finland

A. Kuparinen
Department of Biosciences, University of Helsinki,
00014 Helsinki, Finland

V. Penteriani · P. Saurola · J. Valkama
Finnish Museum of Natural History, Zoology Unit, University of
Helsinki, 00014 Helsinki, Finland

E. Salo
Paloniityntie 90, Forssa, Finland

J. Toivola
Taailantie 74, Tarttila, Finland

A. Aebischer · R. Arlettaz
Division of Conservation Biology,
Institute of Ecology and Evolution,
University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

V. Penteriani
Research Unit of Biodiversity (UMIB, UO-CSIC-PA),
Oviedo University - Campus Mieres, 33600 Mieres, Spain

the birthplace, individuals are expected to start their dispersal under the best conditions.

Visual cues are crucial for animals moving at night; for instance, many migratory birds refer to moonlight position to establish and maintain orientation during their nocturnal journey (Martin 1990). The lunar cycle (full moon to full moon, 29.5 days) determines important environmental changes that influence and can be perceived by animals. Night-time light levels are far from uniform: around full moon, the increased light levels at night may determine the occurrence of occasional nocturnal activities (like night foraging and migration) in otherwise strictly diurnal birds (Pienkowski 1982; Martin 1990; Bulyuk et al. 2009). Nocturnal birds also benefit from the additional light provided by a completely, or nearly, full moon (Martin 1990; Brigham and Barclay 1992): night-time movements and feeding appear to be enhanced by moonlight, independent of the visual sensitivity of owls and other nocturnal birds. Thus, although there are certainly many more favourable conditions than those provided by moonlight, the lunar light has the potential to represent an important factor affecting nocturnal movement across unknown landscapes.

The perceptual range of animals, i.e. the maximum distance from which an individual can perceive landscape features and elements, plays an important role in spatial processes (Zollner and Lima 1997). The perceptual range affects movement strategies and behaviours during dispersal, as well as the probability of successfully reaching suitable habitats (Lima and Zollner 1996; Zollner and Lima 1999a, b). For nocturnal species, the perceptual range is strongly affected by the ambient light (Zollner and Lima 1997; Zollner and Lima 1999a, b): their perceptual abilities increase as ambient illumination increases, even though they have considerable visual acuity (Zollner and Lima 1999a, b). It remains poorly understood to which extent moonlight phases may interfere with spatial movement decision such as natal dispersal in nocturnal species.

Here, we show that a nocturnal avian predator, the eagle owl *Bubo bubo*, starts dispersal primarily when juveniles are ~6 months old and the ambient light is the most favourable for perceiving and exploring unfamiliar lands. This phenomenon occurs within its whole distribution range, as demonstrated here by eagle owl natal dispersal in three geographically and ecologically diverse European areas spread over a wide latitudinal gradient.

Study area and methods

Data collection

From 2003 to 2012, we marked 95 juveniles (from 23 nests) in Spain with conventional units (Biotrack; <http://www.biotrack.co.uk>; for details on study area and radiotracking procedure,

see Delgado et al. 2010; Penteriani and Delgado 2011) and 24 juveniles (from 18 nests) in Finland with satellites units (Microwave Telemetry; <http://www.microwavetelemetry.com>). Twenty-four juveniles (from 17 nests) were marked in Switzerland (for details on the study area and radiotracking procedure, see Aebischer et al. 2010; Schaub et al. 2010) with: (1) 30 g battery-powered satellite transmitters supplied by North Star (<http://www.northstarst.com>) and (2) 15 g VHF tags (Holohil; <http://www.holohil.com>). The weight of the transmitters was between the 3 and the 3.5 % of the weight of the smallest individual at the time of tagging (Spain—850 g, mean±SD=1267±226.4 g; Finland—1,370 g, mean±SD=1861.2±283.8 g; Switzerland—1,000 g, mean±SD=1506±260.9 g; see also Penteriani et al. 2011). Signals from the satellite transmitters were recorded by the ARGOS satellite system (www.cls.fr). To make comparable the data acquired by different radiotracking equipments and methods, for each individual we estimated the start of dispersal in the same way (Delgado and Penteriani 2008): we defined dispersal as starting when the distance of each location from the nest became larger than the global mean distance travelled to the nest, that is, when the distance of each location from the nest started progressively increasing rather than fluctuating around a low value. Owls were sexed by molecular procedures using DNA extracted from blood samples (Delgado et al. 2010).

Moon phases

Over the study years, daily variations of the moon phases were obtained from the Naval Oceanography Portal (http://aa.usno.navy.mil/data/docs/RS_OneYear.php) and expressed in terms of the fraction of moon disc illuminated and whether the moon was waxing or waning. Following the periodic regression approach suggested by de Bruyn and Meeuwig (2001) and applied elsewhere (e.g. Kuparinen et al. 2010; Penteriani et al. 2011, 2013), the fraction of moon disc 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). $\cos(\theta)$, $\sin(\theta)$, $\cos(2\theta)$ and $\sin(2\theta)$ 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 and Meeuwig (2001) for details). Given that the probability to have a cloudy night is equally distributed over the study period and, consequently, among all moon phases, we considered such variation to lead to additional noise, which is likely to weaken the signal strength in our results rather than to create systematic biases (Penteriani et al. 2013).

Statistical analyses

To test the effects of moon phase, age (days after hatching) and sex of individuals, as well as the interactions between age and the different moon phases on the decision to start dispersal (as Julian date), we used linear mixed-effects models. We first selected the optimal structure of the random component, which was the one containing three levels of random effects, represented by birthplace nested in country nested in year (ESM 1). The response variables were scaled, i.e. normalised to zero mean and unit variance. 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 (Crawley 2007). An ANOVA test compared age of dispersal among the three countries. All statistical analyses were performed in R 2.10.1 statistical software (R Development Core Team 2009), nlme (Pinheiro et al. 2009) package.

Results

Mean age of dispersal (\pm SD) was 163.6 ± 20.1 days (range=116–222 days), not differing significantly ($F_{2,140}=2.40$, $P=0.10$) between Spain (mean= 166.8 ± 20.1 days, range=128–222 days), Finland (mean= 150.0 ± 18.6 days, range=116–185 days), and Switzerland (mean= 164.1 ± 16.6 days, range=140–209 days).

The linear mixed-effects model (Table 1 and ESM 1) demonstrated that the decision to start dispersal was influenced by: (1) age of individuals, i.e. dispersal mainly started when juveniles were ~6 months old; (2) sex, with males (age of dispersal= 161.3 ± 22.1 days, range=116–222 days) showing more variation in their departure age than females (age of dispersal= 166.6 ± 16.9 days, range=127–206 days); (3) the moon phase, with dispersal departures mostly occurring during a full moon (Fig. 1); and (4) the interaction between age and moon phase: the moonlight effect was the highest when owls dispersed at the average dispersal age of this species.

Table 1 The linear mixed-effects model showing the effect of moon phase, age and sex of individuals on the decision to start dispersal

	Value	SE	df	t	P
Intercept	264.63	8.28	65	31.96	<0.001
Age	20.65	0.99	62	20.79	<0.001
Sex2	-2.05	0.81	62	-2.54	0.014
I(cos(rad))	-2.23	1.23	62	-1.81	0.074
Age: I(cos(rad))	-3.01	1.13	62	-2.66	0.010

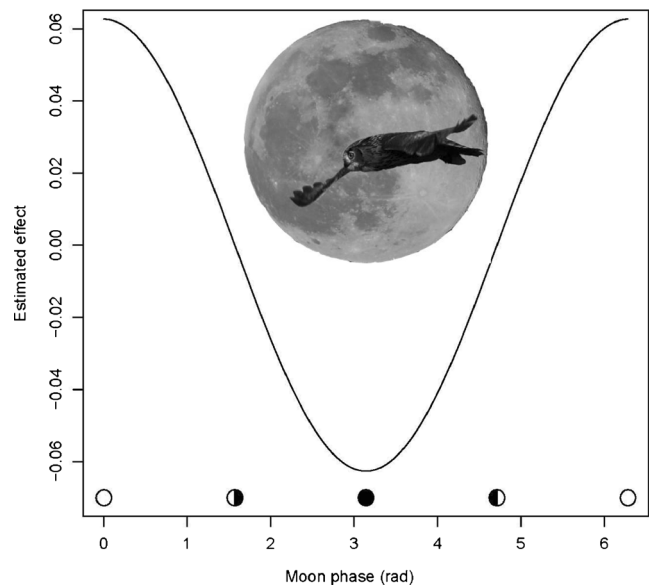


Fig. 1 Dispersal departures of eagle owls at various moon phases. When individuals reach their dispersal age (see Results), they mainly leave the natal area during bright nights

Discussion

Dispersal age appears to be a constant trait of eagle owl life history: most departures occurred in a relatively narrow time window, despite the diverse ecological conditions and wide latitudinal gradient in this study (from Mediterranean to boreal habitats). Yet, most juveniles approaching dispersal age preferred to initiate dispersal when most of the lunar disc was illuminated. However, when individuals are not able to disperse within that favourable temporal window, they cannot pay much attention to the environmental conditions under which to initiate dispersal. Despite the importance of age-specific dispersal, this latter has been ignored in most of the evolutionary theory of dispersal (Johst and Brandl 2000). In an evolutionary context, the evolution of age-specific dispersal strategies may be due to an increase in the efficiency of dispersal at certain age classes (Johst and Brandl 2000). Actually, within the life cycle, timing of dispersal may influence the evolution of dispersal strategies and can be important in predicting the favoured dispersal strategies (Johst and Brandl 1997). One common advantage driving all juveniles of a same species to disperse as soon as they are ready (i.e. at the same age) is the increased access to higher quality breeding sites: the rapid acquisition of an area where to settle is likely to be especially important in resident, territorial birds, principally if residence is determined by order of arrival (Ellsworth and Belthoff 1999). Though the proximate factors that stimulate juveniles to initiate dispersal are not well understood, either exogenous or endogenous factors may influence the timing of dispersal (Belthoff and Dufty 1998). Several behaviours have been suggested to appear as the

post-fledging period progresses, e.g. parental aggression towards young (Bunn et al. 1982; Wiggett and Boag 1993), aggression of young toward each other (De Laet 1985; Strickland 1991) and decreasing food availability within the natal area (Veltman 1989; Kenward et al. 1993). Despite evidence that exogenous factors may drive dispersal, in some birds neither diminishing food supplies nor parental aggression elicited dispersal, dispersal being mostly initiated by endogenous mechanisms (Nilsson 1990; Belthoff and Dufty 1998). For example, body condition or social status have been considered to play a role in triggering dispersal (Nilsson and Smith 1985; Ellsworth and Belthoff 1999). In two owl species, the western *Otus kennicottii* and the eastern *Otus asio* screech owls, the action of a specific hormone, the adrenal glucocorticoid corticosterone, seems to be responsible of increasing activity levels and changes in body condition (see also Silverin 1997; Wingfield and Ramenofsky 1997), which ultimately trigger juvenile dispersal (Ritchison et al. 1992; Belthoff and Dufty 1995, 1998). That is, exogenous stimuli related to the termination of parental feeding, increased aggression among siblings or other factors may not be required for dispersal departure to start, a hypothesis which is supported by the evidence that eagle owls under different exogenous stimuli started dispersal at the same age. However, the interaction between endogenous and external stimuli at the origin of dispersal initiation demonstrates that the dispersal of eagle owls provides a good example of an ecological process modulated by the combination of internal and environmentally determined behaviours, which have evolved to fit within the natural geophysical periods (Brown 1972).

Because light and dark cycles have existed throughout evolutionary time, many organisms have evolved behaviours that are cued by moon cycles. Indeed, this is not the first time that animal movements have shown an association with moon phases. Increased lunar illumination can increase: (a) swimming depth of pelagic sharks and seals in response to changes in the vertical distribution of their prey related to the aforementioned illumination (e.g. Trillmich and Mohren 1981; Saunders et al. 2011); (b) fish migrations given that they may utilise moonlight to navigate and relocate themselves more easily (e.g. Leatherland et al. 1992; Hasegawa 2012); (c) dispersal and migration movements in some insects and crustaceans, which may use the moon for vision, orientation and navigation (e.g. Danthanarayana 1986; Scapini et al. 1997); (d) perceptual abilities of dispersing rodents (Zollner and Lima 1999a, b); (e) locomotor activity in owl monkeys of the genus *Aotus* (Fernández-Duque et al. 2010); and (f) nocturnal bird migrations (e.g. Richardson 1978; James et al. 2000). In the case of eagle owls, we consider plausible the possibility that starting dispersal during the brightest nights increases the perceptual range of dispersers (Zollner and Lima 1997), helping inexperienced juveniles deal with unfamiliar habitats and find prey. Actually, the potential for owls to detect

prey increases with increasing light levels (e.g. Clarke 1983; Kotler et al. 1991), which could be crucial for juvenile survival in the days immediately following departure from the natal area. Furthermore, moonlight intensity (due to moon phases) and the time during which the moon is visible in the night sky are correlated (i.e. the nights are brighter for longer), which might represent an additional advantage for individuals to disperse during full moon. Lunar light can thus be considered both an environmental condition that is as important as diurnal light and a resource, similar to time, space and temperature (Gerrish et al. 2009).

Finally, it is well known that predator-prey interactions are subject to monthly changes owing to the lunar cycle, with predators adjusting their activity rhythms and strategies in response to the increased concealment of prey during the brightest nights (Mukherjee et al. 2009; Kotler et al. 2010; Penteriani et al. 2011). In view of the current results, the lunar cycle might also have the potential to influence predator-prey relationships on a seasonal basis. If, as we may expect, other nocturnal predators also take advantage of the lunar light to start dispersal (Zollner and Lima 1997), we might observe an increased number of predators (adults + dispersers) actively moving around the full moon phase after reproductions. This phenomenon could in turn increase overall predation risk and pressure, exerting a temporally short but profound influence on predator-prey dynamics.

Acknowledgments A special thanks to an anonymous referee and Hannu Pietiäinen, who helped us to improve the manuscript, and Heikki Lokki and Jyrki Savolainen who helped during fieldwork. The Spanish Ministry of Economy and Competitiveness (CGL2012–33240, FEDER co-financing), Junta de Andalucía (Excellence Project, RNM-5090), and Swiss MAVA Foundation funded this study. MD and AK received postdoctoral grants (nos 140367 and 132828) from the Academy of Finland.

Ethical standards We manipulated and marked owls under: (1) Spanish Junta de Andalucía-Consejería de Medio Ambiente authorizations no. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02; (2) Finnish regional Centres for Economic Development, Transport and Environment; and (3) Swiss Federal Office for the Environment.

References

- Aebischer A, Nyffeler P, Arlettaz R (2010) Wide-range dispersal in juvenile Eagle Owls (*Bubo bubo*) across the European Alps calls for transnational conservation programmes. *J Ornithol* 151:1–9
- Belthoff JR, Dufty AM Jr (1995) Locomotor activity levels and the dispersal of western screech-owls, *Otus kennicottii*. *Anim Behav* 50:558–561
- Belthoff JR, Dufty AM Jr (1998) Corticosterone, body condition and locomotor activity: a model for dispersal in screech-owls. *Anim Behav* 55:405–415
- Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado MM et al (2012) Costs of dispersal. *Biol Rev* 87:290–312

- Brigham RM, Barclay RMR (1992) Lunar influence on foraging and nesting activity of common whippoorwills (*Phalaenoptilus nuttallii*). *Auk* 109:315–320
- Brown FA (1972) Clocks timing biological rhythms. *Am Sci* 60:756–766
- Bulyuk VN, Mukhin A, Kishkinev D, Kosarev V (2009) To what extent do environmental factors affect the long-distance nocturnal post-fledging movements of the Reed Warbler? *J Ornithol* 150:339–350
- Bunn DS, Warburton AB, Wilson RDS (1982) The barn owl. Buteo Books, Vermillion
- Clarke JA (1983) Moonlight's influence on predator-prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behav Ecol Sociobiol* 13:205–209
- Crawley MJ (2007) *The R book*. Wiley, Chichester
- Danthanarayana W (1986) Lunar periodicity of insect flight and migration. In: Danthanarayana W (ed) *Insect flight: dispersal and migration*. Springer, Berlin, pp 88–119
- de Bruyn AMH, Meeuwig JJ (2001) Detecting lunar cycles in marine ecology: periodic regression versus categorical ANOVA. *Mar Ecol Prog Ser* 214:307–310
- de Laet JV (1985) Dominance and aggression in juvenile great tits, *Parus major major* L. in relation to dispersal. In: Sibly RM, Smith RH (eds) *Behavioral ecology: ecological consequences of adaptive behavior*. Blackwell, Oxford, pp 375–380
- Delgado MM, Penteriani V (2008) Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. *Am Nat* 172:475–485
- Delgado MM, Penteriani V, Revilla E, Nams VO (2010) The effect of phenotypic traits and external cues on natal dispersal movements. *J Anim Ecol* 79:620–632
- Ellsworth EA, Belthoff JR (1999) Effects of social status on the dispersal behaviour of juvenile western screech-owls. *Anim Behav* 57:883–892
- Fernandez-Duque E, de la Iglesia H, Erkert HG (2010) Moonstruck primates: owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS ONE* 5:e12572
- Gerrish GA, Morin JG, Rivers TJ, Patrawala Z (2009) Darkness as an ecological resource: the role of light in partitioning the nocturnal niche. *Oecologia* 160:525–536
- Hasegawa EI (2012) Chum salmon *Oncorhynchus keta* respond to moonlight during homeward migrations. *J Fish Biol* 81:632–641
- James D, Jarry G, Erard C (2000) Influence of the moon on the nocturnal postnuptial migration of the skylark *Alauda arvensis* L. in France. *CR Acad Sci III Vie* 323:215–224
- Johst K, Brandl R (1997) Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. *Proc R Soc Lond B* 264:23–30
- Johst K, Brandl R (2000) Evolution of age specific dispersal: a general discussion from the standpoint of the invasion fitness concept. *Web Ecol* 1:82–85
- Kenward RE, Marcström V, Karlbom M (1993) Post-nesting behaviour in goshawks, *Accipiter gentilis*: I. The causes of dispersal. *Anim Behav* 46:365–370
- Kotler BP, Brown JS, Hasson O (1991) Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260
- Kotler BP, Brown J, Mukherjee S, Berger-Tal O, Bouskila A (2010) Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proc R Soc Lond B* 277:1469–1474
- Kuparinen A, Klefoth T, Arlinghaus R (2010) Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*). *Fish Res* 105:111–117
- Leatherland JF, Farbridge KJ, Boujard T (1992) Lunar and semi-lunar rhythms in fishes. In: Ali MA (ed) *Rhythms in fishes*. Plenum Press, New York, pp 83–107
- Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends Ecol Evol* 11:131–135
- Martin G (1990) *Birds by night*. Poyser, London
- Mukherjee S, Zelcer M, Kotler BP (2009) Patch use in time and space for a meso-predator in a risky world. *Oecologia* 159:661–668
- Nilsson J-A (1990) Family flock break-up: spontaneous dispersal or parental aggression? *Anim Behav* 40:1001–1003
- Nilsson J-A, Smith HG (1985) Early fledgling mortality and the timing of juvenile dispersal in the marsh tit *Parus palustris*. *Ornis Scand* 16:293–298
- Penteriani V, Delgado MM (2011) Birthplace-dependent dispersal: are directions of natal dispersal determined a priori? *Ecography* 34:729–737
- Penteriani V, Kuparinen A, Delgado MM, Lourenco R, Campioni L (2011) Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. *Anim Behav* 82:413–420
- Penteriani V, Kuparinen A, Delgado MM, Palomares F, López-Bao JV et al (2013) Responses of a top and a meso predator and their prey to moon phases. *Oecologia* 173:753–766
- Pienkowski MW (1982) Diet and energy-intake of grey and ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *J Zool* 197:511–549
- Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Core team (2009) nlme: linear and nonlinear mixed effects models. R package version 3.1-96, <http://cran.r-project.org/web/packages/nlme/nlme.pdf>
- R Development Core Team (2009) 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>
- Richardson WJ (1978) Timing and amount of bird migration in relation to weather—review. *Oikos* 30:224–272
- Ritchison G, Belthoff JR, Sparks EJ (1992) Dispersal restlessness: evidence for innate dispersal by juvenile eastern screech-owls? *Anim Behav* 43:57–65
- Saunders RA, Royer F, Clarke MW (2011) Winter migration and diving behaviour of porbeagle shark, *Lamna nasus*, in the Northeast Atlantic. *ICES J Mar Sci* 68:166–174
- Scapini F, Audoglio M, Chelazzi L, Colombini I, Fallaci M (1997) Astronomical, landscape and climatic factors influencing oriented movements of *Talitrus saltator* in nature. *Mar Biol* 128:63–72
- Schaub M, Aebischer A, Gimenez O, Berger S, Arlettaz R (2010) Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Conserv Biol* 143:1911–1918
- Silverin B (1997) The stress response and autumn dispersal in willow tits. *Anim Behav* 53:451–459
- Strickland D (1991) Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. *Can J Zool* 69:2935–2945
- Trillmich F, Mohren W (1981) Effects of the lunar cycle on the galapagos fur-seal, *Arctocephalus galapagoensis*. *Oecologia* 48:85–92
- Veltman CJ (1989) Effects of experimental food addition on post-natal dispersal, polygyny, and reproductive success in pair-defended territories of the Australian magpie (*Gymnorhina tibicen*). *Ardea* 77:211–216
- Wiggett DR, Boag DA (1993) The proximate causes of male-biased natal emigration in Columbian ground squirrels. *Can J Zool* 71:204–218
- Wingfield JC, Ramenofsky M (1997) Corticosterone and facultative dispersal in response to unpredictable events. *Ardea* 85:155–166
- Zollner PA, Lima SL (1997) Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* 80:51–60
- Zollner PA, Lima SL (1999a) Illumination and the perception of remote habitat patches by white-footed mice. *Anim Behav* 58:489–500
- Zollner PA, Lima SL (1999b) Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030