1   Bright moonlight triggers natal dispersal departures

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29 ABSTRACT

30 Upon leaving their natal area, dispersers are confronted with unknown terrains. Species-specific

31 perceptual ranges (i.e., the maximum distance from which an individual can perceive landscape

32 features) play a crucial role in spatial movement decisions during such wanderings. In nocturnal

33 animals that rely on vision, perceptual range is dramatically enhanced during moonlight, compared

34 to moonless conditions. This increase of the perceptual range is an overlooked element that may be

35 responsible for the successful crossing of unfamiliar areas during dispersal. The information

36 gathered from 143 radio-tagged eagle owl *Bubo bubo* juveniles in Spain, Finland and Switzerland

37 shows that, although the decision to initiate dispersal is mainly an endogenous phenomenon

38 determined by the attainment of a given age (~6 months), dispersers leave their birthplace primarily

39 under the best light conditions at night, i.e. when most of the lunar disc is illuminated. This sheds

40 new light into the mechanisms that may trigger dispersal from parental territory.

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42 Keywords: dispersal age, lunar cycle, moon phase, perceptual range, timing of dispersal, visual cues,

43 *Bubo bubo*

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45 Word count: 3808

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 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 1999). For nocturnal species, the perceptual range is strongly affected by the ambient light (Zollner and Lima 1997; Zollner

69   and Lima 1999): their perceptual abilities increase as ambient illumination increases, even

70   though they have considerable visual acuity (Zollner and Lima 1999). It remains poorly

71   understood to which extent moonlight phases may interfere with spatial movement

72   decision such as natal dispersal in nocturnal species.

73   Here, we show that a nocturnal avian predator, the eagle owl *Bubo bubo*, starts

74   dispersal primarily when juveniles are ~6 months old and the ambient light is the most

75   favourable for perceiving and exploring unfamiliar lands. This phenomenon occurs within

76   its whole distribution range, as demonstrated here by eagle owl natal dispersal in three

77   geographically and ecologically diverse European areas spread over a wide latitudinal

78   gradient.

79

80   **STUDY AREA AND METHODS**

81   *Data collection*

82   From 2003 to 2012 we marked 95 juveniles (from 23 nests) in Spain with conventional

83   units (Biotrack, http://www.biotrack.co.uk; for details on study area and radiotracking

84   procedure see Delgado et al. 2010, Penteriani and Delgado 2011) and 24 juveniles (from

85   18 nests) in Finland with satellites units (Microwave

86   Telemetry, http://www.microwavetelemetry.com). 24 juveniles (from 17 nests) were

87   marked in Switzerland (for details on the study area and radiotracking procedure see

88   Aebischer et al. 2010, Schaub et al. 2010) with: (*i*) 30 g battery-powered satellite

89   transmitters supplied by North Star (http://www.northstarst.com); and (*ii*) 15 g VHF tags

90   (Holohil, http://www.holohil.com). The weight of the transmitters was between the 3 and

91   the 3.5 % of the weight of the smallest individual at the time of tagging (Spain: 850 g,

92   mean ± SD = 1267 ± 226.4 g; Finland: 1370 g, mean ± SD = 1861.2 ± 283.8 g;

93   Switzerland: 1000 g, mean ± SD = 1506 ± 260.9 g; see also Penteriani et al. 2011). Signals

94   from the satellite transmitters were recorded by the ARGOS satellite system (www.cls.fr).

95   To make comparable the data acquired by different radiotracking equipments and

96   methods, for each individual we estimated the start of dispersal in the same way (Delgado

97   and Penteriani 2008): we defined dispersal as starting when the distance of each location

98   from the nest became larger than the global mean distance travelled to the nest, that is,

99   when the distance of each location from the nest started progressively increasing rather than

100   fluctuating around a low value. Owls were sexed by molecular procedures using DNA

101   extracted from blood samples (Delgado et al. 2010).

102   *Moon phases*

103   Over the study years, daily variations of the moon phases were obtained from the Naval

104   Oceanography Portal (http://aa.usno.navy.mil/data/docs/RS_OneYear.php) and expressed

105   in terms of the fraction of moon disk illuminated and whether the moon was waxing or

106   waning. Following the periodic regression approach suggested by deBruyn and Meeuwig

107   (2001) and applied elsewhere (e.g. Kuparinen et al. 2010; Penteriani et al. 2011, 2013), the

108   fraction of moon disk illuminated was converted into radians (θ), with one lunar cycle

109   corresponding to a gradual change from 0 to 2π radians (0 and 2π radians correspond to

110   the full moon, and π radians corresponds to the new moon). $\cos(\theta)$, $\sin(\theta)$, $\cos(2\theta)$ and

111   $\sin(2\theta)$ transformations were included in the statistical model as explanatory variables, to

112   investigate possible lunar effects on eagle owl behaviour throughout the lunar cycle (see

113   deBruyn and Meeuwig 2001, for details). Given that the probability to have a cloudy night

114   is equally distributed over the study period and, consequently, among all moon phases, we

115 considered such variation to lead to additional noise, which is likely to weaken the signal

116 strength in our results rather than to create systematic biases (Penteriani et al. 2013).

117 *Statistical analyses*

118 To test the effects of moon phase, age (days after hatching) and sex of individuals, as well as

119 the interactions between age and the different moon phases on the decision to start

120 dispersal (as Julian date), we used linear mixed-effects models. We first selected the optimal

121 structure of the random component, which was the one containing three levels of random

122 effects, represented by birthplace nested in country nested in year (ESM1). The response

123 variables were scaled, i.e. normalised to zero mean and unit variance. Model simplification

124 was performed by backward selection of variables from the full model, and models were

125 compared using likelihood ratio tests until a minimal adequate model was obtained

126 (Crawley 2007). An ANOVA test compared age of dispersal among the three countries. All

127 statistical analyses were performed in R 2.10.1 statistical software (R Development Core

128 Team 2009), nlme (Pinheiro et al. 2009) package.

129

130 RESULTS

131 Mean age of dispersal (±SD) was 163.6 ± 20.1 days, (range = 116 – 222 days), not differing

132 significantly ($F_{2,140}$ = 2.40, P = 0.10) between Spain (mean = 166.8 ± 20.1 days, range =

133 128 – 222 days), Finland (mean = 150.0 ± 18.6 days, range = 116 – 185 days), and

134 Switzerland (mean = 164.1 ± 16.6 days, range = 140 – 209 days).

135 The linear mixed-effects model (Table 1 and ESM1) demonstrated that the

136 decision to start dispersal was influenced by: (*i*) age of individuals, i.e. dispersal mainly

137 started when juveniles were ~6 months old; (*ii*) sex, with males (age of dispersal = 161.3 ±

138 22.1 days, range = 116 – 222 days) showing more variation in their departure age than

139 females (age of dispersal = 166.6 ± 16.9 days, range = 127 – 206 days); (*iii*) the moon

140 phase, with dispersal departures mostly occurring during a full moon (Fig. 1); and (*iv*) the

141 interaction between age and moon phase: the moonlight effect was the highest when owls

142 dispersed at the average dispersal age of this species.

143

144 DISCUSSION

145 Dispersal age appears to be a constant trait of eagle owl life-history: most departures

146 occurred in a relatively narrow time window, despite the diverse ecological conditions and

147 wide latitudinal gradient in this study (from Mediterranean to boreal habitats). Yet, most

148 juveniles approaching dispersal age preferred to initiate dispersal when most of the lunar

149 disc was illuminated. However, when individuals are not able to disperse within that

150 favourable temporal window, they cannot pay much attention to the environmental

151 conditions under which to initiate dispersal. Despite the importance of age specific

152 dispersal, this latter has been ignored in most of the evolutionary theory of dispersal (Johst

153 and Brandl 2000). In an evolutionary context, the evolution of age specific dispersal

154 strategies may be due to an increase in the efficiency of dispersal at certain age classes (Johst

155 and Brandl 2000). Actually, within the life cycle, timing of dispersal may influence the

156 evolution of dispersal strategies and can be important in predicting the favoured dispersal

157 strategies (Johst and Brandl 1997). One common advantage driving all juveniles of a same

158 species to disperse as soon as they are ready (i.e., at the same age) is the increased access to

159 higher quality breeding sites: the rapid acquisition of an area where to settle is likely to be

160 especially important in resident, territorial birds, principally if residence is determined by

161   order of arrival (Ellsworth and Belthoff 1999). Though the proximate factors that stimulate

162   juveniles to initiate dispersal are not well understood, either exogenous or endogenous

163   factors may influence the timing of dispersal (Belthoff and Dufty 1998). Several behaviours

164   have been suggested to appear as the post-fledging period progresses, e.g. parental

165   aggression towards young (Bunn et al. 1982; Wiggett and Boag 1993), aggression of young

166   toward each other (De Laet 1985; Strickland 1991) and decreasing food availability within

167   the natal area (Veltman 1989; Kenward et al. 1993). Despite evidence that exogenous

168   factors may drive dispersal, in some birds neither diminishing food supplies nor parental

169   aggression elicited dispersal, dispersal being mostly initiated by endogenous mechanisms

170   (Nilsson 1990; Belthoff and Dufty 1998). For example, body condition or social status

171   have been considered to play a role in triggering dispersal (Nilsson and Smith 1985;

172   Ellsworth and Belthoff 1999). In two owl species, the western *Otus kennicottii* and the

173   eastern *Otus asio* screech-owls, the action of a specific hormone, the adrenal glucocorticoid

174   corticosterone, seems to be responsible of increasing activity levels and changes in body

175   condition (see also Silverin 1997; Wingfield and Ramenofsky 1997), which ultimately

176   trigger juvenile dispersal (Ritchison et al. 1992; Belthoff and Dufty 1995, 1998). That is,

177   exogenous stimuli related to the termination of parental feeding, increased aggression

178   among siblings or other factors may not be required for dispersal departure to start, a

179   hypothesis which is supported by the evidence that eagle owls under different exogenous

180   stimuli started dispersal at the same age. However, the interaction between endogenous and

181   external stimuli at the origin of dispersal initiation demonstrates that the dispersal of eagle

182   owls provides a good example of an ecological process modulated by the combination of

183   internal and environmentally determined behaviours, which have evolved to fit within the

184   natural geophysical periods (Brown 1972).

185   Because light and dark cycles have existed throughout evolutionary time, many

186   organisms have evolved behaviours that are cued by moon cycles. Indeed, this is not the

187   first time that animal movements have shown an association with moon phases. Increased

188   lunar illumination can increase: (a) swimming depth of pelagic sharks and seals in response

189   to changes in the vertical distribution of their prey related to the aforementioned

190   illumination (e.g. Trillmich and Mohren 1981; Saunders et al. 2011); (b) fish migrations

191   given that they may utilize moonlight to navigate and relocate themselves more easily (e.g.,

192   Leatherland 1992; Hasegawa 2012); (c) dispersal and migration movements in some insects

193   and crustaceans, which may use the moon for vision, orientation and navigation (e.g.

194   Danthanarayana 1986; Scapini et al. 1997); (d) perceptual abilities of dispersing rodents

195   (Zollner and Lima 1999); (e) locomotor activity in owl monkeys of the genus *Aotus*

196   (Fernández-Duque et al. 2010); and (f) nocturnal bird migrations (e.g., Richardson 1978;

197   James 2000). In the case of eagle owls, we consider plausible the possibility that starting

198   dispersal during the brightest nights increases the perceptual range of dispersers (Zollner

199   and Lima 1997), helping inexperienced juveniles deal with unfamiliar habitats and find

200   prey. Actually, the potential for owls to detect prey increases with increasing light levels

201   (e.g. Clarke 1983; Kotler et al. 1991), which could be crucial for juvenile survival in the

202   days immediately following departure from the natal area. Furthermore, moonlight

203   intensity (due to moon phases) and the time during which the moon is visible in the night

204   sky are correlated (i.e. the nights are brighter for longer), which might represent an

205   additional advantage for individuals to disperse during full moon. Lunar light can thus be

206   considered both an environmental condition that is as important as diurnal light and a

207   resource, similar to time, space and temperature (Gerrish et al. 2009).

208   Finally, it is well known that predator-prey interactions are subject to monthly

209   changes owing to the lunar cycle, with predators adjusting their activity rhythms and

210   strategies in response to the increased concealment of prey during the brightest nights

211   (Mukherjee et al. 2009; Kotler et al. 2010; Penteriani et al. 2011). In view of the current

212   results, the lunar cycle might also have the potential to influence predator-prey

213   relationships on a seasonal basis. If, as we may expect, other nocturnal predators also take

214   advantage of the lunar light to start dispersal (Zollner and Lima 1997), we might observe

215   an increased number of predators (adults + dispersers) actively moving around the full

216   moon phase after reproductions. This phenomenon could in turn increase overall predation

217   risk and pressure, exerting a temporally short but profound influence on predator-prey

218   dynamics.

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227   **Ethical standards**. We manipulated and marked owls under: (*i*) Spanish Junta de

228   Andalucía-Consejería de Medio Ambiente authorizations No. SCFFS-AFR/GGG RS-

229   260/02 and SCFFS-AFR/CMM RS-1904/02; (*ii*) Finnish regional Centres for Economic

230   Development, Transport and Environment; and (*iii*) Swiss Federal Office for the

231   Environment.

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351

352   TABLE 1 The linear mixed-effects model showing the effect of moon phase, age and sex of

353   individuals on the decision to start dispersal

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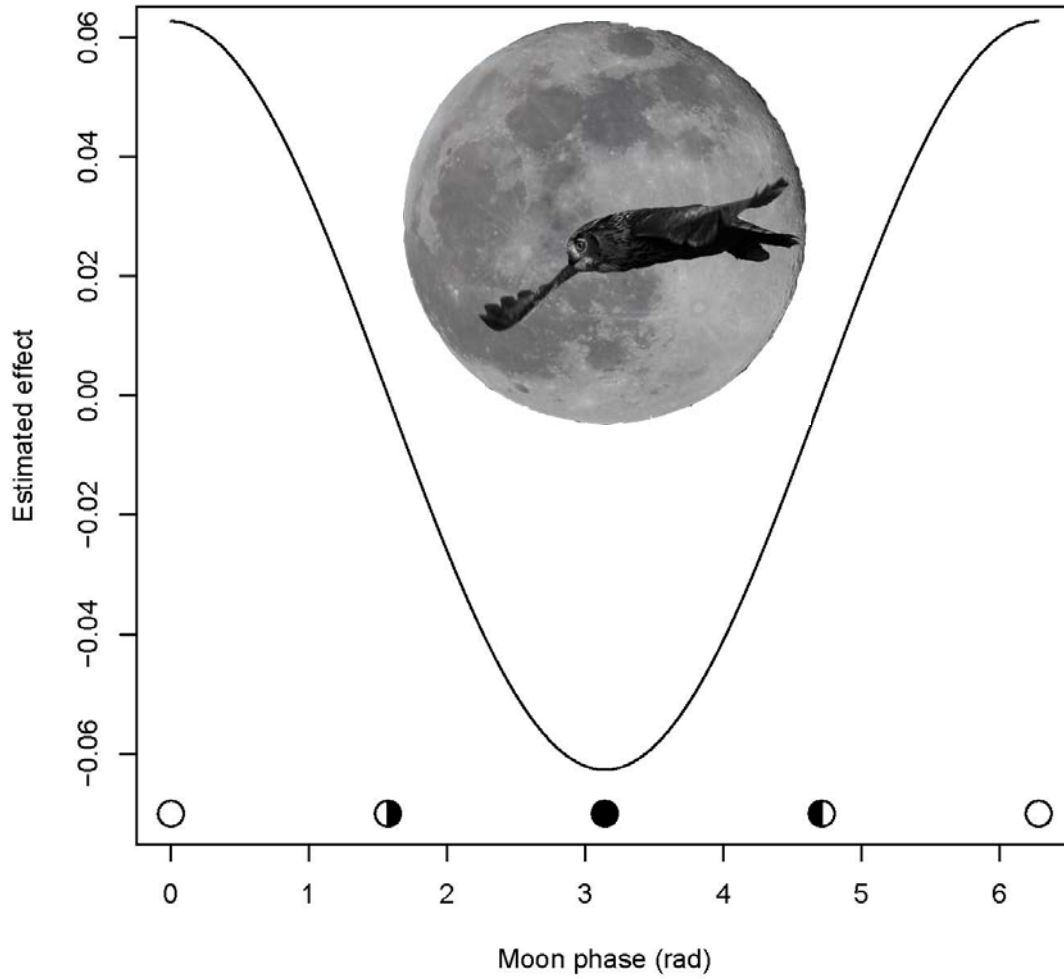|	Value	SE	df	t	P
355					
356 Intercept	264.63	8.28	65	31.96	<0.001
357 age	20.65	0.99	62	20.79	<0.001
358 sex2	-2.05	0.81	62	-2.54	0.014
359 I(cos(rad))	-2.23	1.23	62	-1. 81	0.074
360 age:I(cos(rad))	-3.01	1.13	62	-2.66	0.010

361   FIGURE LEGENDS

362   **Fig. 1** Dispersal departures of eagle owls at various moon phases. When individuals reach

363   their dispersal age (see Results), they mainly leave the natal area during bright nights

364

365   **Figure 1**

366