Breeders and nonterritorial individuals of a long-lived species,the eagle owl *Bubo bubo*: differences in space use and movement patterns

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REPRODUCTORES Y DISPERSANTES DE UNA ESPECIE DE LARGA VIDA, EL BÚHO REAL (*BUBO BUBO*): DIFERENCIAS EN EL USO DEL ESPACIO Y PATRONES DE MOVIMIENTO DE DOS FACETAS DE UNA MISMA POBLACIÓN

BREEDERS AND NONTERRITORIAL INDIVIDUALS OF A LONG-LIVED SPECIES, THE EAGLE OWL *BUBO BUBO*: DIFFERENCES IN SPACE USE AND MOVEMENT PATTERNS

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A mia nonna,
mia madre e
mia sorella

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ABSTRACT

Many animal species live in societies in which nearby conspecifics are vital elements of their social environment, with the nature and quality of their behavioral interactions determining the type of social organization. As a group, birds show a wide range of social organizations where, in some cases, social status gives priority of access to resources, ultimately affecting individual fitness. For example, in territorial species where at least two social groups –breeders and non-territorial floaters – are recognized, territorial ownership can lead to holders behaving differently compared to the floating counterpart of the population. For this reason, social structure is often considered a key determinant of population biology, influencing fitness, gene flow, and spatial pattern and scale. Nonetheless, nonsocial factors (e.g., environmental condition, food supply) can also affect behavioral interactions, individual relationships, and, ultimately, social organization. In the present thesis, we studied the behavioral differences between individuals of different social status; we focused in particular on the analysis of habitat selection, space use behavior and movement patterns of breeders and nonterritorial eagle owls (*Bubo bubo*).

The focal radio-tracking of breeders and nonterriotrial floaters during 8 years demonstrated that owls perform different behavioral strategies in relation to different life cycle stages, social status and the behavioral trait under study. These observations emphasize the existence of more structured inter-individual relationships than expected. Moreover, previous investigations of social interactions (vocal and visual communication) support the importance of territoriality and social dominance on owls' behavioral decisions. Our results indicate a scenario in which both social and nonsocial factors seem to affect the behavioral mechanisms that regulate habitat selection, space use and movement behavior in different ecological contexts. In contrast to our initial predictions, trophic resource abundance in our study area does not correlate directly with owls' space use behavior. However, the large abundance of the staple prey across this area, due primarily to management and release of rabbits (the study area serving as game reserve), might actually favor a high density of conspecifics over a reduced area (40 breeding pairs/100 km^2) by relaxing environmental constrictions like resource competition (e.g. food). In line with this prediction, we show that territory holders (Chapter 5) occupy reduced home ranges of high quality for reproduction. Surprisingly, the home range size (mean HR size ~ 220 ha) appears to be a direct consequence of landscape structure rather than prey abundance available across the study area. Across the mosaic of territories settled by owls, females - the sex that experiences less social constriction - are those which exhibit wider home ranges that overlap to a greater extent with those of their neighbors. Nevertheless, within the boundaries of their home ranges, adults' behavioral decisions were significantly affected by nonsocial factors such as the biological needs and individual identity. Similarly, external cues like the lunar cycle (Chapter 3), act to regulate the time and effort that owls allocated to social (communication) or physiological (feeding) activities.

A key finding demonstrated here is that nonterritorial floaters show a tremendous capacity to adapt their behaviour to their immediate needs and social and physical surroundings. As with other territorial species, floating owls show cryptic behaviour, living in a parallel "underworld" where individuals make decisions while considering social constraints (Chapter 1-2), acquired experience (Chapter 4) and landscape features. At the end of their natal dispersal, the most likely fate for our floaters was to settle close to the natal population while awaiting circumstances that would offer greater reproductive opportunities. In conclusion, the study of the relationships between animals and their environment is a field where ecology and behavior are tightly intertwined. In my opinion, and as stressed in the present study, social organization is a key determinant of population biology with important implications on spatial processes.

INTRODUCCIÓN

Organización social, sistemas territoriales y estatus sociales

Gran parte de las especies animales viven en una sociedad. Sociedad cuya organización (término análogo a sistema o estructura) puede venir fuertemente determinada por el comportamiento, por ser éste responsable en gran medida de las interacciones entre los individuos. De hecho, son las *interacciones* las que representan el nivel basal de cualquier organización social, mientras que las características de las mismas (es decir, naturaleza, calidad y patrones) son las que caracteriza una *relación.* El conjunto de las relaciones interindividuales, su naturaleza, calidad y patrón son los elementos que componen una estructura social (Hinde 1976, BOX 1a). En este sentido, las organizaciones sociales pueden ser definidas como la síntesis de las interacciones interindividuales (Whitehead 2008).

En general, las aproximaciones que se han utilizado para el estudio de las organizaciones sociales pueden englobarse en dos categorías (Whitehead 2008): (a) etológica, enfocada en comprender la organización de patrones de interacciones entre individuos y su variación en el tiempo; y (b) ecología de comportamiento (sub-disciplina de la biología evolutiva darwiniana) centrada mayormente en las consecuencias - a nivel de éxito reproductor y supervivencia - de diferentes patrones de comportamiento. Tanto una escuela como la otra, y con el transcurso de los años, han observado que, en una gran variedad de vertebrados sociales y especies de insectos, diferentes organizaciones sociales pueden variar no sólo entre especies, si no también dentro de la misma especie o incluso en la misma población. De hecho, en una población pueden existir marcadas variaciones en la composición de grupos de individuos o en la repartición de las tareas reproductoras entre miembros del mismo grupo (p. ej. diferentes números de reinas reproductoras en distintas colonias de hormigas, Ross and Keller 1995). Esta variación, ha sido el punto de partida para abrir un largo debate acerca de cuestiones con fuertes implicaciones ecológicas: ¿Cuáles son las causas que promueven la variación en los sistemas sociales (factores ecológicos extrínsecos y factores sociales intrínsecos)?

En cuanto a los diferentes factores que pueden promover tal variación, merece la pena señalar en primer lugar que, si bien la organización social es el resultado de las interacciones entre individuos, estas interacciones pueden estar asimismo afectadas por la misma estructura social (Hinde 1976). Sin embargo, no hay que olvidar que existen otros factores no sociales que pueden afectar la estructura social a diferentes niveles, entre lo que podríamos mencionar la abundancia de recursos tróficos. De hecho, muy a menudo, el grado de asociación entre individuos depende de características espaciales como la distribución de los recursos (Pusey and Packer 1997; Johnson et al. 2002). De la misma forma, diferencias en las características morfológicas (Krause et al. 2005) y en el comportamiento individual (Viscido, Parrish and Grünbaum 2004) pueden a su vez determinar la tipología y la estructura de relaciones inter-individuales, así como la formación y la composición de grupos de individuos.

La presencia de posibles heterogeneidades tanto espaciales como inter-individuales hace que en presencia de recursos limitados (como por ejemplo alimento, parejas o sitios de reproducción) la competencia por ellos conlleve a la formación de jerarquías de dominancia. En este contexto jerárquico el estatus social es clave en la regulación del acceso a los recursos, afectando la eficiencia biológica tanto de los individuos dominantes como de los subordinados. Estos sistemas sociales pueden regular el número de individuos en función de la disponibilidad de los recursos o de cualquier otro requerimiento que se encuentre en cantidad limitada o variable para la especie (Newton 1998).

Los sistemas territoriales son la manifestación más evidente de dominancia (BOX 1b; Newton 1998). En dichas especies se pueden claramente diferenciar dos grupos sociales: (a) los reproductores, aquellos individuos que poseen y defienden un territorio; y (b) los individuos no territoriales, con un estilo de vida exploratorio (Brown 1969, Smith 1978).

BOX 1.

(a) Definiciones de organización social y términos relacionados

Organización social	"Patrón de interacciones entre individuos, una descripción de los comportamientos" (Rowell 1972, 1979) "Unión de nichos sociales que se solapan" (Flack et al. 2006)
Estructura social	"Patrón de interacciones sociales y resultantes relaciones entre miembros de una sociedad (Keppeler and van Schaik 2002)
Sistema social	"Conjunto de animales conspecíficos que interactúan regularmente y más entre sí que con miembros de otras sociedades" (Keppeler and van Schaik 2002)
Tipos de interacciones	*Agonística*: interacción asociada con conflictos entre individuos *Cooperativa*: tipo de interacción entre individuos que trae beneficio mutuo *Reciproca*: interacción en la que un individuo da más a aquellos individuos de los que recibe más (Hemelrijk 1990) *Simétrica*: si el individuo A interacciona con el individuo B, entonces B interacciona con A (ejemplos: apareamiento, intercambio de vocalizaciones) *Asimétrica*: si el individuo A interacciona significativamente más con el individuo B más de cuanto B interacciona con A (ejemplos: intromisión, amamantar)

Relaciones	*Enlace*: sugiere algo más que una atracción mutua, generalmente implica interacciones de larga duración
	Reciproca: un individuo da más a aquellos individuos de los que recibe más (Hemelrijk 1990)
	Dependencia es una relación asimétrica, donde el individuo A depende del individuo B para necesidades básicas, normalmente alimento, o protección desde los depredadores
	Dominancia: atributo que caracteriza el patrón de interacciones agonísticas repetidas entre dos individuos, con un constante resultado a favor de uno de los individuos (Drews 1993)
	Parentela: relaciones de sangre entre individuos: padre-hijo, hermano-hermano
Elementos que caracterizan la estructura social	*Grupos*: un conjunto de animales en mutua relación (independiente de la escala temporal de análisis)
	Jerarquías de dominancia: un descriptor de dinámicas sociales; se describe utilizando medidas de interacciones asimétricas, por ejemplo el ganador de interacciones agonísticas, la prioridad de acceso a los recursos
	Rol: el papel de un especifico individuo que actúa en un contexto social. Los roles son fundamentales en las sociedades de insectos sociales
	Unidades sociales: conjunto de individuos en asociación mutua (casi) permanente
	Nivel, orden, rango: posición relativa de un individuo en una sociedad

(b) Definición de territorialidad y términos relacionados

Territorialidad	La territorialidad se manifiesta cuando los individuos muestran un comportamiento agresivo orientado en el espacio, es decir una defensa agresiva de un espacio que proporciona recursos limitados (Burt 1943; Brown and Orians 1970, Adams 2001)
Territorio	Área caracterizada por (i) su estabilidad en el tiempo y en espacio, (ii) ser activamente defendido por los individuos que en él habitan, y (iii) un uso exclusivo por parte de su posesor (Brown and Orians 1970)
Dominio vital	Es la manifestación en el espacio del comportamiento que los animales desempeñan para vivir el día a día y reproducirse (Burt 1943). El dominio vital es el resultado de procesos dinámicos y, por tanto, fluctuante en el tiempo y en el espacio. Los dominios vitales pueden presentar una estructura multimodal interna (Börger et al. 2008)
Centros de actividad	Definidas como zonas internas del domino vital más frecuentadas por los individuos con diferentes fines. Incluyendo áreas de forrajeo, sitios de reproducción, estas áreas se caracterizan por presentar una variación, en el tiempo y en el espacio (Samuel et al. 1985).
Uso del hábitat	Generalmente se refiere a la forma en que un individuo o una especie elige los recursos del hábitat o condiciones ambientales para cumplir con las necesidades de su historia de vida. Por lo tanto puede ser descrito directamente a partir de observaciones de cómo el animal interactúa con las características del hábitat, o se puede inferir desde la asociación entre las características del hábitat y la presencia de los individuos o de la especie bajo estudio (Gaillard et al. 2010).

Preferencia de hábitat	se define como la probabilidad de un recurso o de un hábitat de ser seleccionado por un animal cuando se le ofrecen opciones alternativas en condiciones igualadas (Johnson 1980)
Dispersión natal	Movimiento pasivo o activo desde el área natal hasta la futura área de reproducción. La dispersión puede verse como un proceso multifacético, incluyendo tres fases secuenciales llamada inicio, transición/búsqueda y parada/asentamiento. La dispersión puede ocurrir en cualquier etapa de la vida de un animal, a diferentes escalas espaciales y a través de ambientes con distinta heterogeneidad (Clobert et al. 2009).
Dispersión de los reproductores	se define como el movimiento entre sucesivos sitios de reproducción o grupos sociales (Greenwood & Harvey 1982, Clobert et al. 2001)

El pertenecer a una u otra clase social va a determinar cuando los individuos tendrán acceso a los recursos, pudiendo consecuentemente afectar su supervivencia y éxito reproductor a lo largo de la vida (Hansen & Closs, 2009), y como consecuencia, la dinámica, estabilidad y viabilidad de una población.

El comportamiento territorial puede manifestarse con distintos niveles de tolerancia, desde individuos que defienden activamente áreas de uso completamente exclusivo hasta individuos que toleran un alto grado de solapamiento con otros conspecíficos, siendo posible todos aquellos niveles intermedios entre estos dos extremos. Pese a la motivación que puede llevar a una especie a evolucionar un comportamiento territorial, el compromiso entre los costes y beneficios asociados a la defensa de determinados recursos tiene que estar necesariamente sesgado hacia los últimos (Brown 1969). Importante es también resaltar el hecho de que, además de presentar una variabilidad en el espacio, la territorialidad puede presentar una variabilidad temporal, es decir que según las exigencias de cada especie, la defensa y el uso exclusivo de los recursos puede variar en el tiempo.

Miembros de los sistemas territoriales son también los individuos no territoriales, comúnmente conocidos como individuos flotantes. Esta porción de los sistemas territoriales se caracteriza por estar formada por aquellos individuos que, aún siendo sexualmente maduros, se encuentran a la espera para entrar a formar parte de la porción reproductora hasta el momento en el que un sitio de reproducción y una pareja estén disponibles (Penteriani et al. 2005a, 2006a, b, 2008, 2011). Los individuos flotantes pueden encontrarse en la fase de dispersión (Penteriani and Delgado 2009a), siendo la madurez sexual la característica fundamental que los diferencia del concepto de dispersante (Penteriani et al. 2011). Dado que el estudio de los individuos flotantes ha sido y es actualmente abordado bajo diferentes enfoques ecológicos, desde estudios de dinámica de poblaciones hasta análisis de dispersión natal, su definición se encuentra sujeta a una cierta ambigüedad.

El estatus social de los individuos puede verse reflejado en algunas características físicas de los individuos, como en el fenotipo, variaciones en el tamaño corporal, diferencias en los patrones de plumaje en el caso de las aves y en la condición física. Sin embargo, el rango social puede a su vez reflejarse en otros rasgos asociados a aspectos eco-etológicos, como la adquisición de recursos (Fero and Moore 2008), patrones de inmigración (Höner et al. 2010), e interacciones con conspecíficos (Smith 1978, King 1980, Robitaille and Prescott 1983, Rohner 1997, Gese & Ruff 1998, King and Allainé 2002, McGowan et al. 2006, Fero et al. 2007, Herberholz et al. 2007). Si bien la bibliografía acerca del comportamiento de los reproductores es amplia (Hojesjo et al. 2007, Afonso et al. 2008, Kinahan and Pillay 2008), los individuos no territoriales han sido sujetos a un menor número de estudios, probablemente debido a que en general manifiestan un comportamiento más críptico y, por tanto, son más difícil de detectar (Rohner 1997). Es por ello que este sector de las poblaciones animales es aún hoy en día sorprendentemente inexplorado, dado su importancia en la dinámica, estructura y viabilidad de las poblaciones (Penteriani et al. 2006, 2011).

La organización social juega un papel clave en la biología de las poblaciones, afectando la eficiencia ecológica de los individuos, el flujo génico, y el patrón de distribución de los individuos en el espacio (Wilson 1975). Sin embargo, hasta los años ochenta no se reconoció la porción de los flotantes como elemento fundamental en la regulación de la estructura de las poblaciones, afectando la distribución espacio-temporal y la estabilidad de las mismas. Fue en aquella década cuando se comenzó a considerar la importancia de los individuos no reproductores como elementos amortiguadores para disminuir el riesgo de extinción de las poblaciones animales (Jamieson and Zwickel 1983, Kokko and Sutherland 1998). Por último, y desde una perspectiva ecológica más aplicada, la estructura social puede también tener importantes implicaciones en el manejo y conservación de las poblaciones. Entender las relaciones sociales entre conspecíficos puede indudablemente ayudarnos a comprender las relaciones espaciales (por ejemplo, la distribución) de los individuos y, por tanto, representa una herramienta esencial para el manejo y conservación de las especies (Sutherland 1998). En este contexto, la falta de informaciones sobre la porción flotantes de las poblaciones puede desembocar en conclusiones erróneas acerca de la salud y persistencia de éstas y, como consecuencia, llevarnos a tomar decisiones inadecuadas (Penteriani et al. 2011).

Una especie territorial de larga vida como modelo biológico

El Búho real (*Bubo bubo*) se caracteriza por ser una especie (*i*) principalmente monógama y (*ii*) territorial, pudiéndose encontrar sus poblaciones formadas por (*iii*) adultos reproductores y flotantes. Por lo tanto, esta especie es ideal para profundizar en el estudio de numerosos aspectos acerca de las estrategias de comportamiento empleadas por parte de cada grupo social a la hora de integrarse en su entorno físico. Además y debido a las frecuentes interacciones sociales que caracterizan esta especie

(Delgado & Penteriani, 2007, Penteriani and Delgado 2009), representa un modelo biológico adecuado para analizar las relaciones intraespecíficas bajo diferentes constricciones impuestas por el contexto social. Asimismo, como predador y debido a su historia de vida y a su elevada fidelidad a los sitios de cría, el búho real es una especie que permite explorar a una larga escala temporal la relación de los individuos con el medio que los rodea, así como su efecto sobre las comunidades de presas y otras especies de predadores (Sergio et al. 2003, Lourenço et al. 2011).

OBJETIVOS Y ESTRUCTURA DE LA TESIS

El objetivo principal de esta tesis es estudiar las diferencias en el comportamiento de individuos con diferente estatus social, centrándonos en el análisis de (a) la selección de hábitat, (b) del uso del espacio, y (c) de los patrones de movimiento (BOX 1b).

Puesto que estos aspectos del comportamiento de los individuos están fuertemente relacionados con una componente espacial y temporal, el estudio de la selección de hábitat, del uso del espacio y de los patrones de movimiento se abordó a diferentes escalas. Por un lado, en cuanto a la escala temporal consideramos: (a) una macroescala temporal, en la que pretendíamos comparar patrones de comportamiento en distintas *fases del ciclo de vida* de los individuos (reproductores *vs*. flotantes); (b) una *escala anual*, con el objetivo de poder encontrar y estudiar una potencial heterogeneidad a nivel del individuo; y por ultimo (c) una *escala estacional* para analizar patrones relacionados a las distintas tareas asociada a la etapa reproductora (defensa del territorio, copula, cría de los pollos, volantones). Por otro lado, pero de forma simultánea, empleamos también múltiples escalas espaciales: (a) una *escala* a nivel del *dominio vital*, con la intención de realizar estudios comparativos del comportamientos de conspecíficos dentro de un mismo grupo social, (b) una *escala a nivel de centros de actividad*, para estudiar aspectos comportamentales importantes como comparar la selección de hábitat y los patrones de movimiento dentro de las áreas de caza, y (a) una microescala (a nivel de *sitio de cría y posaderos*) para analizar el uso de diferentes elementos/características del hábitat por parte de individuos flotantes y reproductores.

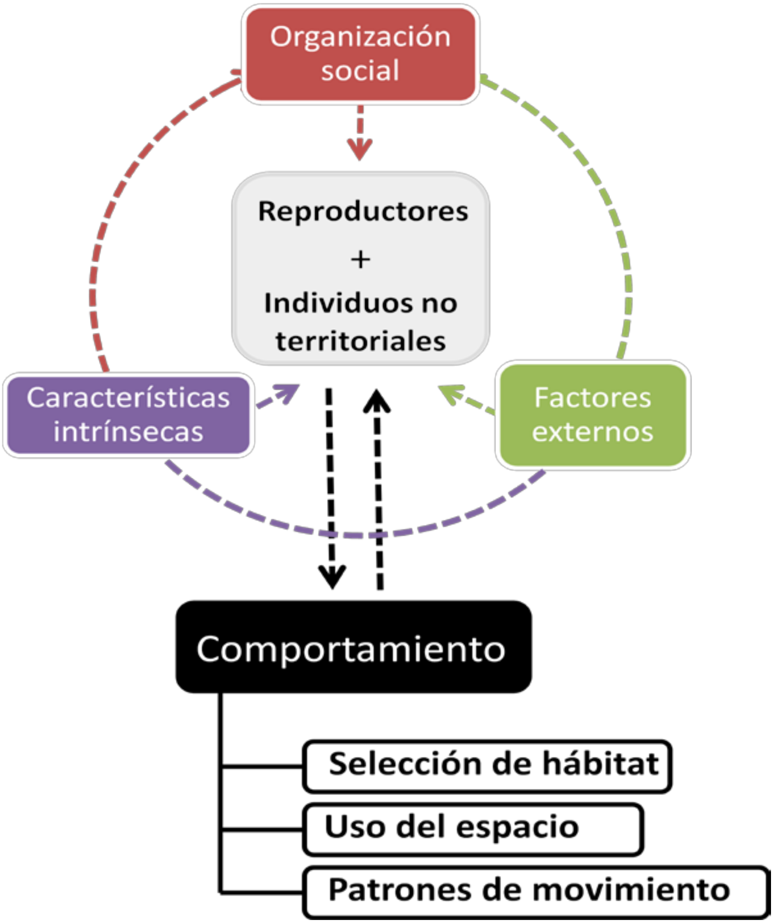

Figura 1. Esquema del contexto ecológico en el que podrían actuar individuos reproductores y non territoriales en especies territoriales, y que podrían regula su comportamiento de selección de hábitat/uso del espacio/movimientos, compuesto por tres componentes básicas: (a) un componente social (caja roja) que representa las relaciones que se establecen entre conspecíficos (dominancia vs. subordinación); (b) un componente (caja morada) relacionado con los factores internos del individuo (es decir, tamaño, sexo, condición fisiología, habilidades cognitivas) que pueden afecta la forma de explotar y explorar el entorno externo; y por ultimo (c) un componente que comprende el conjunto de factores externos, tanto biótico como abióticos (caja verde), que afectan las decisiones individuales relacionadas al uso del espacio.

Siguiendo el esquema presentado en la Fig. 1 abordamos el estudio del comportamiento de individuos reproductores y no territoriales de búho real cubriendo los siguientes objetivos específicos.

En primer lugar (**Capítulo 1**) exploramos el efecto del estatus social en la selección del hábitat, a una escala espacial pequeña. En particular, analizamos algunas características físicas tales como la dominancia y la visibilidad de los posaderos seleccionados por los dos grupos sociales y según el sexo de los individuos. Ampliando nuestra escala espacial de análisis (**Capítulo 2**), nos centramos en el estudio del uso de hábitat a nivel de estructura forestal de las parcelas en el entorno próximo al nido para los individuos reproductores y los comparamos con la estructura en torno a los posaderos diurnos utilizados por los individuos flotantes. En el **Capítulo 3**, abordamos el estudio del posible efecto de factores externos, y en particular de la luna (como aproximación de la luminosidad ambiental), en el comportamiento de individuos de distintos estatus sociales.

Un elemento que puede determinar una diferencia entre la forma de explorar y explotar un aérea por parte de un reproductor o de un joven en dispersión es el grado de familiaridad con el entorno exterior. En el **Capítulo 4**, nuestra atención fue dirigida hacia el estudio del efecto de la familiaridad con el entorno físico en los patrones de movimiento, en la selección de los posaderos y en las aéreas de caza en función del estatus social. Por último (**Capítulo 5**) analizamos el "*comportamiento de uso del dominio vital*" de los individuos reproductores en función de factores externos (composición y heterogeneidad del hábitat, y disponibilidad de recursos tróficos) y características intrínsecas de los individuos (sexo, condición física). Por *comportamiento de uso del espacio* entendemos el uso del espacio, los patrones de movimientos y los ritmos de actividad, que fueron analizados a escala temporal estacional y general, así como a escala espacial de dominio vital y centro de actividad (BOX 1b).

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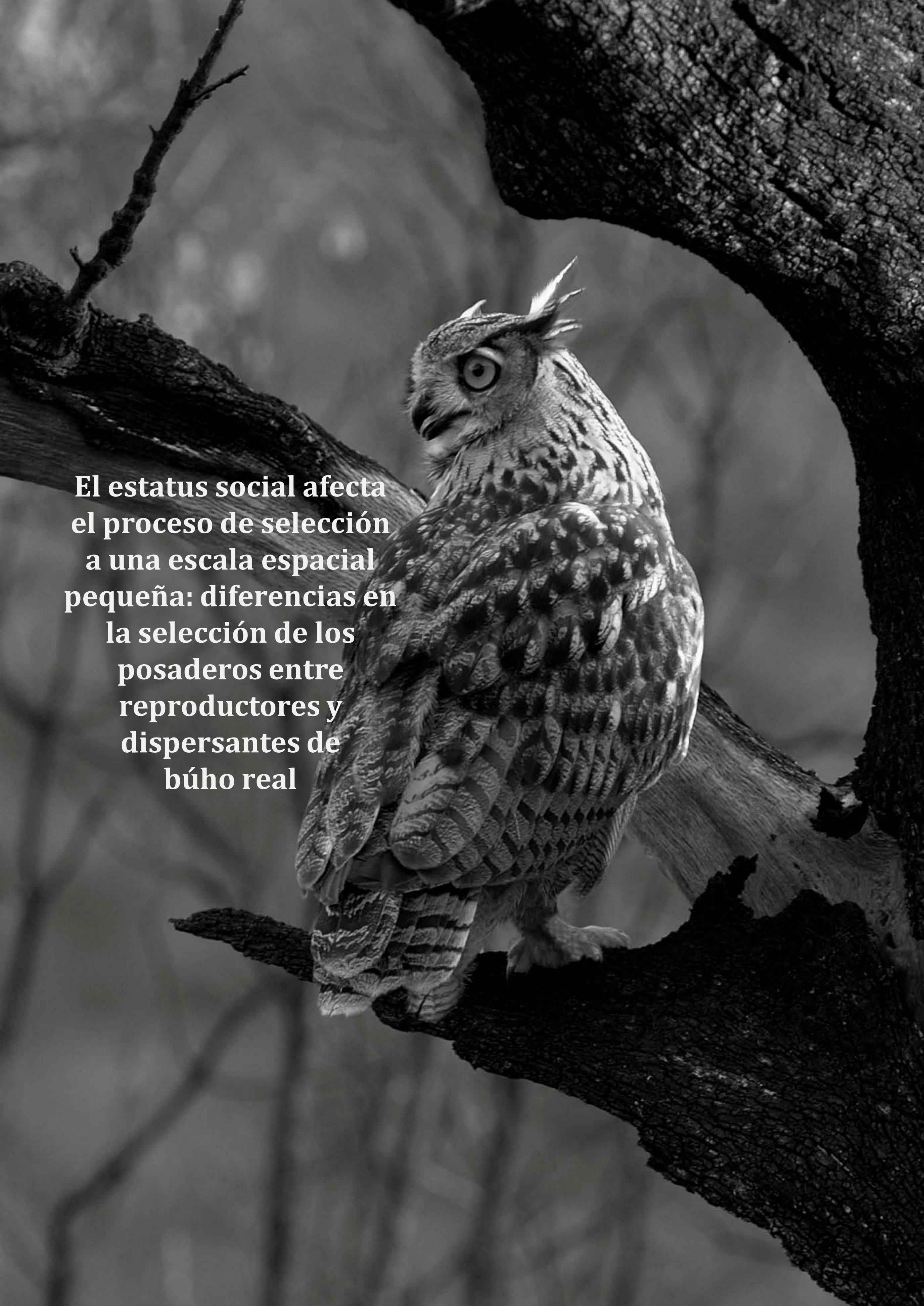
CAPÍTULO 1

Social status influences microhabitat selection: breeder and floater Eagle Owls *Bubo bubo* use different post sites

Campioni L, Delgado MM and Penteriani V (2010) *IBIS*, 152: 569–579

El estatus social afecta el proceso de selección a una escala espacial pequeña: diferencias en la selección de los posaderos entre reproductores y dispersantes de búho real



RESUMEN

El estatus social de los individuos puede reflejarse en muchos aspectos de su comportamiento y de su ecología, incluyendo el uso del hábitat y las interacciones inter-específicas. En las especies territoriales se pueden diferenciar dos grupos sociales — los reproductores y los dispersantes — caracterizados por tener diferentes tareas y, por tanto, diferentes comportamientos. Por ejemplo, mientras los individuos territoriales tienen que invertir parte de su tiempo en la defensa de su área de reproducción y en tareas reproductivas, los individuos dispersantes tienen una vida más transitoria, no mostrando comportamientos territoriales, ni siquiera en la última fase de la dispersión, cuando pueden encontrar un área en la que asentarse de manera estable. En aquellas especies cuyas interacciones sociales se basan en señales visuales y vocales, la elección y el uso de lugares específicos para el envío y la recepción de señales es crucial en la vida de un animal. En este trabajo se analizó la selección de posaderos de individuos reproductores y dispersantes de búho real *Bubo bubo* durante su actividad nocturna. Los resultados mostraron la existencia de dos comportamientos diferentes, fuertemente ligados al estatus social de los individuos. Mientras que los reproductores seleccionan posaderos más visibles, probablemente para expresar su condición de dominancia en su territorio de forma efectiva, los dispersantes seleccionan posaderos menos visibles y menos dominante. Esta selección de posaderos por parte de los dispersantes va en línea a una vida más reservada, en la que divagan desapercibidos entre territorios ocupados. Esta vida secreta ayuda a reducir los riesgos asociados a posibles agresiones intraespecíficas. Estas agresiones son, además, menos frecuentes cuando el dispersante es hembra, lo que podría explicar el hecho de que observásemos más intrusiones de hembras dispersantes en territorios de reproductores.

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ABSTRACT

Social status can be reflected in many aspects of an individual's behaviour and ecology, including habitat use and conspecific interactions. In territorial species where at least two social groups – breeding birds and non-territorial floaters – are recognized, the diverse tasks associated with territorial ownership can lead territory holders to behave differently from the non-territorial part of the population. Territory holders defend their breeding area and reproduce, whereas floating individuals are dispersing and lead a more transient life, during which they do not show any territorial behaviour even when settling in a more or less fixed area (known as the stop phase). As social interactions are based on visual and vocal cues, the use of specific sites for sending and / or receiving signals can be a crucial choice in an animal's life. By analysing the post-site selection of Eagle Owl *Bubo bubo* breeders and floaters during their nocturnal activity, we found that: (1) territory holders selected more visible and dominant posts than non-territorial floaters; (2) the choice of posts made by floating individuals did not differ between the wandering and stop phases of dispersal; and (3) floating females intruded more frequently than floating males within a breeder's home-range. These findings highlight the fact that two social strategies are possible within the same species, depending on an individual's social status and its related tasks. Breeders could take advantage of visible locations to declare their status as territory holders, whereas floaters could benefit from a more secretive life to wander unnoticed among occupied territories. This secretive life would help floaters to reduce the risks associated with conspecific aggression. Finally, the greater occurrence of floating females within breeders' home-ranges can be explained by the fact that female incursions in a breeder's home-range are less risky than male intrusions.

Keywords: conspecific interactions, dispersal, post-site selection, territorial intrusions, territory holders.

From a behavioural perspective, social status is assumed to lead to variation in animal behaviour (Smith 1978, King 1980, Rohner 1997, King and Allainé 2002, McGowan et al. 2006, Fero et al. 2007, Hojesjo et al. 2007). Specifically, in territorial species where at least two social groups –breeders and non-territorial floaters – are recognized, territorial ownership can lead to holders behaving differently from the floating counterpart of the population (Jamieson and Zwickel 1983, Arcese 1987, Zach and Stutchbury 1992, Rohner 1997, Stamps and Krishnan 1998). Additionally, social status can be reflected in many aspects of an individual's behaviour and ecology, including habitat use, interactions with conspecifics or willingness to take risks (Robitaille and Prescott 1983, Gese and Ruff 1998, Fero et al. 2007, Herberholz et al. 2007). Several behavioural traits have been described in detail for territorial individuals of many species (Hojesjo et al. 2007, Afonso et al. 2008, Kinahan and Pillay 2008), whereas behaviours of the less detectable and frequently overlooked floating contingent of animal populations remain largely unexplored (Penteriani and Delgado 2009a). In birds, for instance, there are few studies that have been able to record and quantify floaters' behaviour (Smith 1978, Stutchbury and Robertson 1987, Stutchbury 1991, Rohner 1997). Moreover, studies including both floaters and breeders have mainly focused on investigating mechanisms of territory acquisition or understanding fundamental ecological dynamics at the population level (e.g. Hamilton and May 1977, Johnson and Gaines 1990, Whitlock 2001, Penteriani et al. 2005a,b, 2006, 2008a,b). However, and perhaps due to the difficulties related to data collection on floaters, differences in behavioural strategies due to their different social status still need to be understood in greater depth. Knowledge of the behavioural tactics and role of floaters in a population is essential to the understanding of the evolution of animal behaviour under the social constraints determined by differences in social status.

The social context of territorial breeders is generally characterized by long-lasting stable interactions (e.g. territorial displays) among territorial neighbours. Floaters are mainly dispersing individuals that lead a more wandering life and do not show any territorial behaviour even when settling in a more or less fixed area (e.g.

Rohner 1997). Indeed, during their more nomadic life, non-breeders encounter new social and physical environments that may affect their behaviour at different spatial and temporal scales during the different phases of dispersal (Smith 1978, Foster 1987, Arcese 1989, Stutchbury 1991, Tobler and Smith 2004, Aragón et al. 2006, Delgado and Penteriani 2008, Delgado et al. 2009). Nevertheless, peculiar social interactions also exist among breeders and floaters, mainly when both these portions of a population share the same space at the same time. Evidence exists that floaters are like a 'shadow population', living close to territory holders or sharing portions of their home-ranges with them (Jamieson and Zwickel 1983, Arcese 1987, Walls and Kenward 1995, 1998, Rohner 1997). When floaters are close to or within the territory of a breeder, they can be very secretive because holders are typically aggressive towards floaters (Arcese 1987). The sites used by birds for specific activities represent focal points, both within home-ranges and in the routine movements of breeders and floaters, and could potentially represent a key element of individual behavioural strategies, especially when individuals with different social status move within the same areas.

Territory holders and non-territorial floaters of Eagle Owls *Bubo bubo* share (to some extent) the same areas. Both social groups present similarities in the use of habitat-elements, i.e. they both use distinct post sites to perform routine activities. For instance, being 'sit and wait' predators, owls use perch-sites during nocturnal hunting sessions where they can spend several hours (Penteriani et al. 2008c). Breeding owls select precise plucking and defecation sites within their nesting sites (Penteriani and Delgado 2009b,c), territory holders repeatedly use call-posts during vocal and visual communication (Delgado and Penteriani 2007, Penteriani et al. 2007a,b) and breeders and floaters tend to be faithful to the same diurnal roosting sites when ending their nocturnal activities (Delgado et al. 2009). This evidence allows us to hypothesize that, depending on their different social status and the diverse tasks associated with it, the tradeoff between costs and benefits that influence behavioural decisions of individuals of different social classes may produce divergent behavioural strategies. The strategy of breeders is primarily aimed at maintaining the holding of resources and mates. The floaters' strategy is principally aimed at searching for an empty breeding site while reducing the risks associated with conspecific aggression due to visible intrusions. In species such as raptors, contests between conspecifics can end up in wasteful and potentially injurious fights. As a result, we should expect that internal (i.e. social status) and external (i.e. environmental features such as social context) factors might interact in a divergent way when determining the behavioural choices of these two distinct social statuses.

Very few studies have attempted to determine the potential effect of social status on the behavioural process of habitat selection (but see Brown and Long 2007). This information is even scarcer when considering species that not only show elusive behaviour due to their status of floaters but also because of their nocturnal activity. Here, we analysed the post-site selection of both breeder and floater Eagle Owls. Floating Eagle Owls go through a multiphase natal dispersal process characterized by an intense exploratory stage (the wandering phase) followed by the establishment of one or more temporary settlement areas (the stop phase; Delgado and Penteriani 2008). During such phases, floating individuals may live very close to the breeding portion of the population and share large portions of their home-ranges with breeders (Rohner 1997). Moreover, in the stop phase, floaters can show well-defined home-ranges quite similar to those of territory holders (Delgado et al. 2009). In contrast to territorial conspecifics, they behave as elusive individuals that do not declare their presence. In fact, they have never been observed displaying territorial behaviours in any areas of their range (Delgado 2008, Delgado et al. 2009). Breeders maintain their territory year-round and over several years, having well-defined home-ranges with internal core areas (e.g. nest territory, hunting areas) of intense use (Delgado and Penteriani 2007). As previously stated, owls show a clear preference for exposed locations during many intra-specific communication activities. Therefore, we specifically focus on several features characterizing the dominance and the visibility of post sites to determine the degree of selection performed by individuals of each social status.

If post-site selection constitutes a relevant aspect of social status-dependent strategies, three predictions can be made. First, we expect that territory holders and non-territorial floaters will select post sites with different visibility. Given the behavioural dependency of territorial individuals on vocal and visual communication, we expect a disproportionate selection of dominantly located posts by breeders relative to non-breeding individuals. Secondly, due to their lack of territorial behaviour and their main need to remain hidden from breeders during dispersal, we can consequently expect that floaters will always select post sites with similar characteristics of visibility, independent of their phase of dispersal. In fact, male territory holders are very aggressive, mainly towards male intruders, and such attacks frequently end with the death of one of the opponents (see also Penteriani et al. 2007a for more details on intra- and inter-sexual contests). For this reason, our final expectation was that floating females will be found more frequently in a breeder's home-range than will floating males.

METHODS

Study area and data collection

The study site was a hilly area of the Sierra Norte of Seville (Sierra Morena massif) located in southwestern Spain (for more details, see Penteriani et al. 2005c).

To compare perching behaviours of breeders and floaters, we used information from 39 radiotagged individuals: two females and 13 males from 15 different breeding sites, and 24 floaters (nine females and 15 males). Juveniles were radiotagged at the nest when they were approximately 35 days old, 5–10 days prior to the onset of fledging. Breeding Owls were captured by simulating a territorial intrusion with a combination of a taxidermic mount of an Eagle Owl and a net (Penteriani et al. 2007a). Owlets were aged following Penteriani et al. (2005c) and were sexed by molecular procedures using DNA extracted from blood (Griffiths et al. 1998). Both adults and young were fitted with a teflon ribbon backpack harness that carried a 30-g radio-transmitter (Biotrack Ltd, Wareham, Dorset, UK), with a mercury posture sensor that allowed us to discriminate perching behaviour from periods of activity (e.g. vocal display, hunting or flying) by changes in the radio signal of the transmitters. When the tag pulse increased its frequency and its volume changed, we assumed that the Owl was shifting from a vertical and fixed position (i.e. perched individual) to a horizontal and dynamic position (i.e. flying individual). The change in volume was due to the variation of the distance between the individual and the car antenna because of the individual's movement (Penteriani et al. 2008c). Furthermore, vocal and hunting activities, while perching (i.e. at constant pulse volume), produced iterative changes of the tag pulse due to repeated movements of the Owl's body, which allowed us to discriminate Owl behaviour while perching (Penteriani et al. 2008c). As the young were still growing, the backpacks were adjusted so that the teflon ribbon could expand (Delgado and Penteriani 2007). The manipulation was always safe: after 7 years of continuous radiotracking of both breeders and floaters, we never recorded a potential adverse effect of backpacks on birds or breeding performance (Delgado and Penteriani unpubl. data). The backpacks were not removed after the study due to the difficulty in retrapping the same individual (Penteriani and Delgado unpubl. data). Owls were trapped and marked under the Junta de Andalucía – Consejería de Medio Ambiente permit nos. SCFFSAFR/GGGRS-260/02 and SCFFS-AFR/CMMRS-1904/02. Locations of radio-marked animals were determined by triangulations using three-element hand-held Yagi antennas (Biotrack) with Stabo (XR-100) portable ICOM receivers (IC-R20). We performed continuous radiotracking year-round following a single Owl during the whole night from 1 h before sunset to 1 h after sunrise. Juveniles were followed from the beginning of natal dispersal (end of August in our study area, Delgado and Penteriani 2008) until either death of the animal or failure of the battery transmitter (~1.5 to ~2.5 years); this is across both the wandering and the stop phases.

Triangulations were generally done at a low range of distances (100–300 m), with an accuracy of mean ± se = 83.5 ± 49.5 m (Penteriani and Delgado 2008). Such a value was calculated when, after a triangulation, we needed to locate the individual exactly to manipulate it during field experiments (e.g. Penteriani et al. 2007b) or to record the cause of mortality if it died.

To determine the beginning and the end of the different phases (i.e. start, wandering and stop phases) of dispersal, we recorded the position of each juvenile weekly, typically when Owls were at their diurnal roost sites. For each individual, we plotted the distances between its natal nest and diurnal roost site for each weekly location and an individual's mean distances of all weekly locations and the natal nest during the entire dispersal period. We considered dispersal to have started when individuals left their parents' home-range (i.e. at the end of August at a mean (± sd) age of 170 ± 20.51 days; range: 131–232 days), which we estimated as the point when the distance of each weekly location from the nest becomes larger than the individual's mean distance during the dispersal period (Delgado and Penteriani 2008). After leaving the natal territories, dispersal distances progressively increased. Finally, when Owls reached the stop phase of dispersal, dispersal distances levelled off. We considered that Owls had settled in a stable settlement area when the distances between successive weekly locations became smaller than the average distance of previous weekly movements calculated for each dispersing Owl separately (for more details see Delgado and Penteriani 2008). The transition from the wandering to the stop phase typically occurred in mid March of the following year at a mean (± sd) age of 395 ± 109.86 days (range: 181–640 days). Therefore, the wandering phase encompasses the movements between the start of dispersal and the final settlement in a more or less stable area.

Post sites were selected from data collected during 226 nights of radiotracking (132 for breeders and 94 for floaters). To ensure independence between points, for each individual: (1) the whole set of points was placed on a map by GIS software (ArcVIEW 3.2) and a distance of 150 m between locations was set as the minimum threshold to consider two fixes as two distinct perch sites; (2) in several cases (i.e. sunset, sunrise, moonlight), it was possible to make visual contact with the perched individual and, consequently, to confirm the radiotracking localization; and, when possible, (3) faeces, plucked prey, Owl feathers and/or pellets were used to confirm the exact location of perching posts.

Post-site characteristics

To analyse the degree of prominence of Owls' posts, we calculated two indices. First, the dominance index was used, which quantifies the domination of a focal point with regard to the surroundings. This index is calculated as the average difference of altitude between the elevation of the post-site location and the elevations at the end of three lines of 100 m that, starting from the post site, progress in the direction of the main valley, at 45 and at 90° (Gainzarain et al. 2000, Delgado and Penteriani 2007). Secondly, the visibility index of the post sites was calculated with regard to the surroundings, i.e. the number of contour lines covered by the diameter of a circle around the post site with a radius of 100 m. The diameter was drawn perpendicular to the general slope of the contour lines surrounding the post site. High values of these two indices indicate increasing dominance and visibility (Gainzarain et al. 2000).

Floater's post-site locations within breeder's home-ranges

As additional information on the relationships between breeders and floaters, we explored the frequencies of male and female floater post sites within the 15 breeder home-ranges. We considered the frequencies of floater roosts inside vs. floater roosts outside breeders' home-ranges (calculated by minimum convex polygon, MCP; Hayne 1949) as an indirect measure of the number of intrusions of each sex in the breeder's home-ranges.

Statistical analysis

We performed five separate generalized linear mixed models (GLMMs, McCullagh and Nelder 1989) using SAS macro program GLIMMIX (version 8.2; SAS Institute 2001), which iterates procedure MIXED (PROC MIXED in SAS software). Degrees of freedom have been computed by using the containment method, i.e. the PROC MIXED default method when one or more random statements are used to specify the variance–covariance structure. The use of the containment method is justified because the design of our matrix is balanced and our random statement has been written so that the relationship between fixed and random effects is clear. We modeled the response variables, dominance index and visibility index, using a Poisson distribution (or a negative binomial distribution when Poisson was not appropriate) with a log link function always including individual identity as a random effect. The dominance index was transformed by adding 30 (the largest negative value) to each value, enabling us to model it with a Poisson distribution. We assessed whether the selection of post sites characterized by different degree of dominance (first model) and visibility (second model) were influenced by social status (1 = breeder; 0 = floater). To avoid the possibility that our results could be biased because floaters select less dominant and visible points as they may occur in areas with less irregular topography (i.e. the selection of posts is the by-product of the general areas where they live), we repeated these two models selecting only those post sites that were located in the areas in which the home-ranges of breeders and floaters overlapped (i.e. the habitat structure was equal for both social groups). The third and fourth models assessed the effect of the dispersal stage (indexed as 1 for wandering and 0 for stop phases) as a categorical (explanatory) variable on the floater post-site selection, again with dominance and visibility indices as the response variables. In all these models, we initially considered sex as a further potential factor affecting the selection of post sites. As its effect was never significant (always $P > 0.10$), we removed this factor from the models. Finally, to assess whether the presence of floaters' post sites inside breeders' home-ranges was associated with the sex of floating Owls, we modelled the location of the post site (indexed as 1 for a post inside and 0 for a post outside an adult's home-range) against the sex of the floater, in this case using a binomial error distribution. The significance of all explanatory variables (and their interaction) was tested in turn in the models (stepwise forward procedure), retaining only those that contributed significantly to the change in deviance. Statistical significance was accepted at $P \leq 0.05$.

RESULTS

Breeders and floaters use different post sites

A total number of 679 post sites of 15 breeders (n = 225 post sites) and 24 floaters (n = 454 post sites) were identified. Posts differed significantly between the two social statuses on the basis of the dominance ($F_{1,643} = 5.73$, $P = 0.017$; Fig. 1a) and visibility indices ($F_{1,643} = 20.92$, $P < 0.0001$; Fig. 1b). That is, breeders (visibility range: 0–10, median = 3; dominance index range: 30–90, median = 38) preferred dominant posts, whereas floaters mainly selected hidden locations (see Fig. 2 for an example of the three-dimensional spatial distribution of post sites). This happened also when considering only those floater posts (n = 245 post sites) that overlapped with the breeder's home ranges, i.e. when taking into account the potential effect of the habitat structure (dominance index: $F_{1,432} = 4.76$, $P = 0.03$; visibility index: $F_{1,432} = 9.34$, $P = 0.0024$; Fig. 3).

Phases of dispersal do not affect floater selection of posts

When comparing the visual characteristics of 171 posts used during the wandering phase with the features of 199 post locations during the stop phase of 19 floaters that shifted between these phases (a subsample of the whole set of floaters), there was no significant difference in post-site selection (all $P > 0.1$; Fig. 1).

Floating females intrude more frequently than males in breeders' home-ranges

The mean home-range size (MCP 100%) of floating females (mean $A_f = 769 \pm 187$ ha; n = 9) was smaller than the mean home-range of floating males (mean $A_m = 1053 \pm 402$ ha; n = 15). Nevertheless, floating males intruded less frequently than floating females into the breeders' home-ranges: posts of floating females (n = 172) were more frequently (70.3%) located inside a breeder's home-range than outside ($F_{1,430}$ = 5.64, P = 0.018). Conversely, floating males' post sites (n = 284) were less commonly located inside (43%) a breeder's home-range. Because the home-ranges of floating females is smaller than for floating males, we can exclude the possibility that the recorded differences in locations of male and female floaters inside breeders' home-ranges are dependent on the sex-biased size of the floaters' home-ranges.

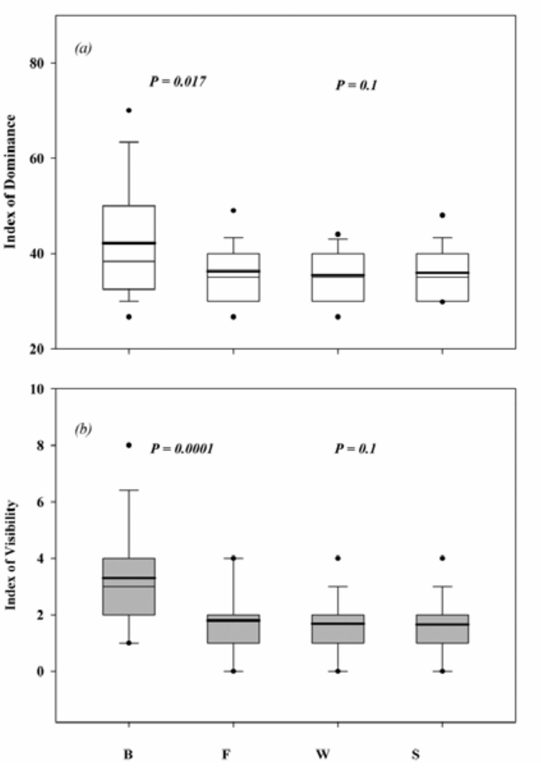

Figure 1. Full dataset box plots of: (a) the degree of dominance of breeders' (B) vs. floaters' (F) post sites, as well as floaters' during the wandering (W) vs. stop (S) phases of dispersal; and (b) the degree of visibility of breeders' (B) vs. floaters' (F) post sites and floaters' post sites during the wandering (W) vs. stop (S) phases of dispersal. For each box plot the total data range, the 25 and 75% quartiles (box), the mean (bold line) and the median (thin line) are presented. P-values (from GLIMMIX procedure) show the levels of significance of both degree of dominance and visibility for the comparisons between breeders vs. floaters and wandering vs. stop.

DISCUSSION

Our results highlight how a spatial characteristic of animal habitats, hunting post sites, was selected differently by individuals of the same species depending on their territorial status. Breeders and floaters selected post sites with distinctly different visibility, with the most visible locations occupied by breeders. This implies that individuals of different social status may employ different behavioural strategies, which may produce divergent patterns of habitat use and selection. While breeders can take advantage of visible locations to declare their status as territory owners, floaters can take advantage of secrecy to wander unnoticed among territorial conspecifics during the whole natal dispersal period.

The importance of post sites in territorial behaviour, and their influence on life-history traits, has previously been demonstrated for true shrikes (Laniidae; Yosef 1993, Safriel 1995). Moreover, characteristics such as the height or dominance of post sites have been investigated in relation to vocalizations of breeding individuals (e.g. Marten and Marler 1977, Simpson 1985, Møller 1988, Mathevon and Aubin 1997, Beck and George 2000, Penteriani 2002, Delgado and Penteriani 2007, Naguib et al. 2008) or to hunting efficiency (Fitzpatrick 1980, Tye 1989, Sonerud 1992, Yosef 1993), providing some evidence for how adaptive behaviour can maximize the transmission of vocal signals and hunting success, respectively (Yosef 1993, 2004). In fact, we cannot ignore the fact that dominance and visibility of post sites can have a relevant function in hunting strategy as well. Being ambush predators, owls can obtain considerable advantages by perching on dominant locations. In fact, it has been shown that for many predator species, such as Hawk Owl *Surnia ulula*, Common Buzzard *Buteo buteo*, Rough-legged Buzzard *Buteo lagopus* and Common Kestrel *Falco tinnunculus* (Sonerud 1980, 1992), there exists a positive correlation between perching height and the size of the area that can be searched from a post site. From this perspective, post-site selection could have a function not only in the intra-specific communication but also in the hunting strategy. However, and depending on their main activity (vocalizations vs. hunting), Owl behaviour and localization within dominant posts can be different even when using the same post site (V. Penteriani and M.M. Delgado unpubl. data): call displays are generally performed from the top of dominant posts (e.g. the pinnacle of a tree canopy), whereas hunting prospection is more frequently done from a more concealed position (e.g. within the tree canopy) and silently.

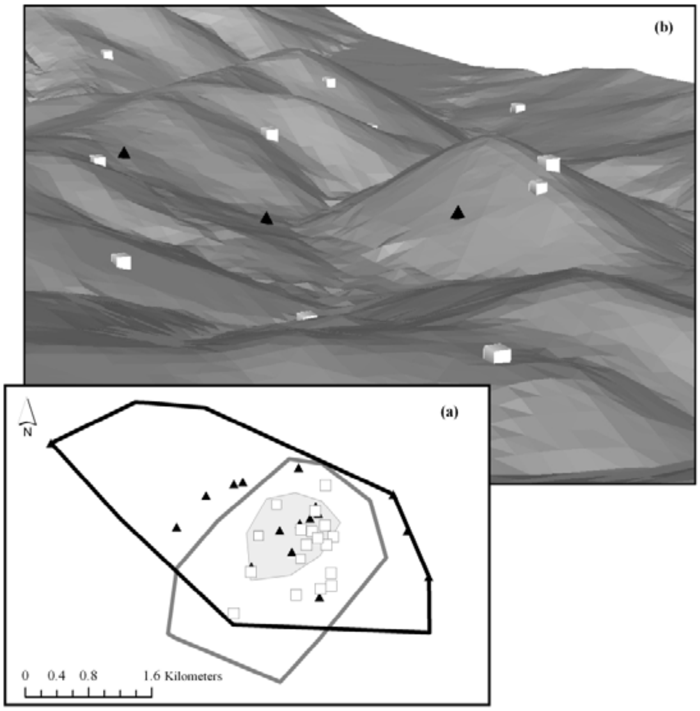

Figure 2. (a) Spatial distribution of Eagle Owl post sites (◤ = floater, □ = breeder) where the home-ranges (MCP 100%) of both social statuses; one breeding male (grey polygon, period: 2004–2005) and one floating male (in the wandering phase, period: 2005–2006; black polygon) occurred alongside one another. (b) Enlarged three-dimensional image of a small home-range's section [grey polygon in (a)] shared by the same two individuals, with post-site spatial distributions represented. The territory holder (□) preferentially selected the more dominant and visible locations, whereas the floater (◤) perched on more hidden posts.

To our knowledge, no attention has been paid to how the ‘visibility’ of perching locations relates to the social status of the chooser. Among social species, indirect warning signs used to inform about the occupancy of a territory are, in general, widespread (e.g. scent and faeces marking; Kappeler 1990, Katti 2001, Gese 2001). Such marking behaviours rely strictly on the use of strategic points, i.e. vantage points, visible locations or locations of easy access, where the marks are displayed. A similar behaviour has previously been observed in Eagle Owls during the breeding season, when Owls used either faeces or prey’s feathers to mark focal locations of their home-ranges (Penteriani and Delgado 2009c).

Territorial status incurs a cost to keep the possession of such resources, and breeding Owls are compelled to perform territorial defence and sexual displays to preserve their territory and mate. Under such a scenario, being in a dominant location facilitates both visual and vocal communication with conspecifics by informing the social environment of one’s presence. Moreover, in species characterized by aggressive territorial behaviours and weapons, several benefits can be gained by a territory holder selecting dominant and visually connected posts. Holders might avoid being involved in dangerous aggressive encounters with occasional intruders crossing their territorial boundaries because the latter are aware of their presence from afar. This might represent both a safe strategy and a way to reduce wasting time and energy in dangerous contests, which can then be invested in other activities. When floating Owls are crossing and/or sharing the areas occupied by territory holders, breeders’ visibility may also be acting, at least partially, as a signal received by several floating individuals. From the top of their dominant posts, territory holders might be acting as continuous signallers during the entire time spent perching (not only when actively performing vocal/visual displays). The high visibility achieved by such positions may expand the propagation distance of the signal and, as a consequence, increase the number of individuals able to receive the signal. This especially could be true when large numbers of floaters occupy a given area. In the case of the Great Horned Owls *Bubo virginianus*, for example, they may represent up to 40–50% of the whole population (Rohner 1996).

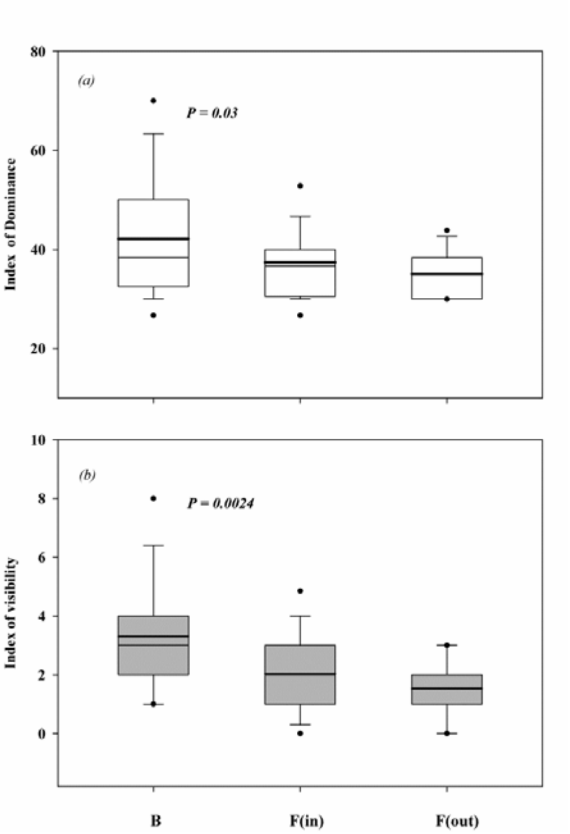

Figure 3. Box plot of (a) the degree of dominance and (b) the degree of visibility of post sites selected by breeders (B), by floaters inside (F in) and floaters outside (F out) the home-ranges of breeders. For each box plot the total data range, the 25 and 75% quartiles (box), the mean (bold line) and the median (thin line) are presented. P-values (from the GLIMMIX procedure) show the levels of significance of both degree of dominance and visibility for the comparisons among breeders and floaters inside and outside the breeders' home-ranges.

As floaters in breeding territories are unwanted individuals, they can be considered silent bystanders gathering information on the features of the social environment of the areas they cross during dispersal. Hence, we can hypothesize that the floaters in such a network might be able to obtain useful information just by attending to breeders' communication networks as eavesdroppers (Peake and McGregor 2005), while avoiding risky contests with holders.

For dispersing floaters that do not need to defend a territory, and whose principal need is the avoidance of aggressive encounters with conspecifics, 'visibility' can result in an increase of fatal aggressive encounters by territorial conspecifics. As Owls may cross several breeding areas of conspecifics during the different phases of dispersal, as well as settle within one of them, it might be advantageous for them to go unnoticed when gathering social and spatial information, while avoiding risky circumstances. The use of less visible post sites by floaters can be explained, at least partially, by the complex array of behavioural patterns that territorial Owls can exhibit, such as site-specific aggressiveness or the ability to discriminate neighbours from intruders (Penteriani et al. 2007a). Moreover, we can hypothesize that the voluntary selection of less dominant and concealed posts may also represent a way to communicate no intention of intrusion if discovered by a territorial individual. Thus, the selection of concealed posts might help floaters reduce the risk of conspecific aggression associated with dispersion. The secretive behaviour of floaters therefore allows them to overlap broadly with defended territories (Rohner 1996). As reported by Rohner (1997), floaters may settle in the interstices between different breeding territories and stay unobtrusively within the home-range of territory holders. However, this secretive behaviour of avoiding less dominant post sites does not imply that these are less efficient hunting posts and that floaters pay a cost. In fact, although both are dominant, optimal hunting and communication post sites differ in their dominance range: a tree or a cliff located on the lowest part of a valley does not represent a dominant point within the neighbours' network (i.e. it is not useful for territoriality), but it is a sufficiently high point to survey a hunting area and detect prey. Additionally, the different frequencies of occurrence of post sites of male vs. female floating Owls within breeders' home-ranges could be considered a consequence of the different intra- and intersexual aggressive behaviours shown by the study species. As shown in Penteriani et al. (2007a), when the territorial intruder is a female, both male and female holders respond weakly or do not react at all. In such a scenario, floating females may be performing less risky intrusions than floating males if perceived by territory holders. Finally, because polygamy can occur in Eagle Owls (Dalbeck et al. 1998, Penteriani and Delgado unpubl. data), a floating female entering a holder's territory might also represent to a male the possibility of occasionally reproducing with two females.

To conclude, the ultimate patterns encountered for breeder and floater Owls, as well as for male and female floaters, highlight that the social components that characterize the status of individuals cannot be neglected, as they can affect the individual behaviour and, consequently, produce divergent patterns of habitat selection.

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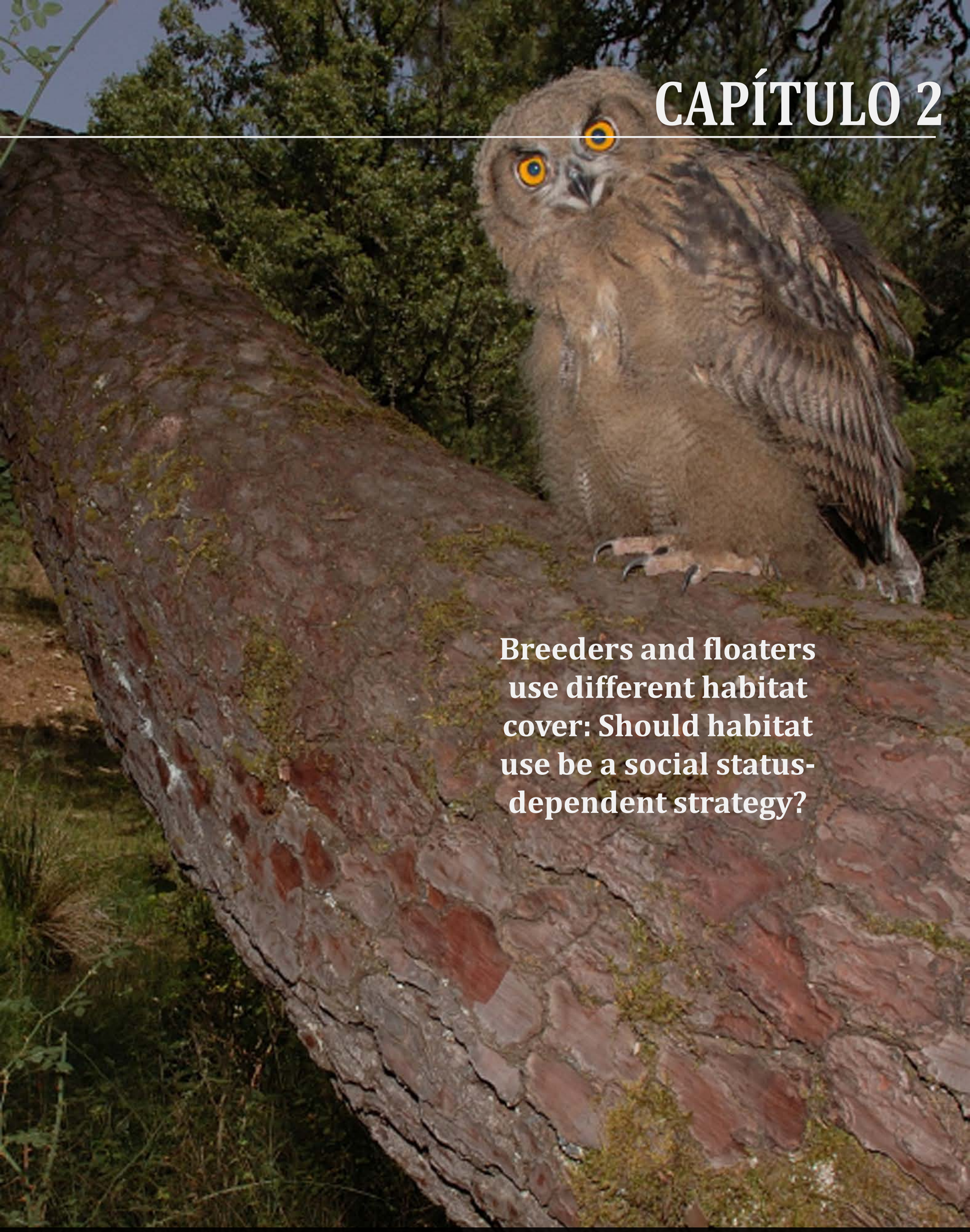
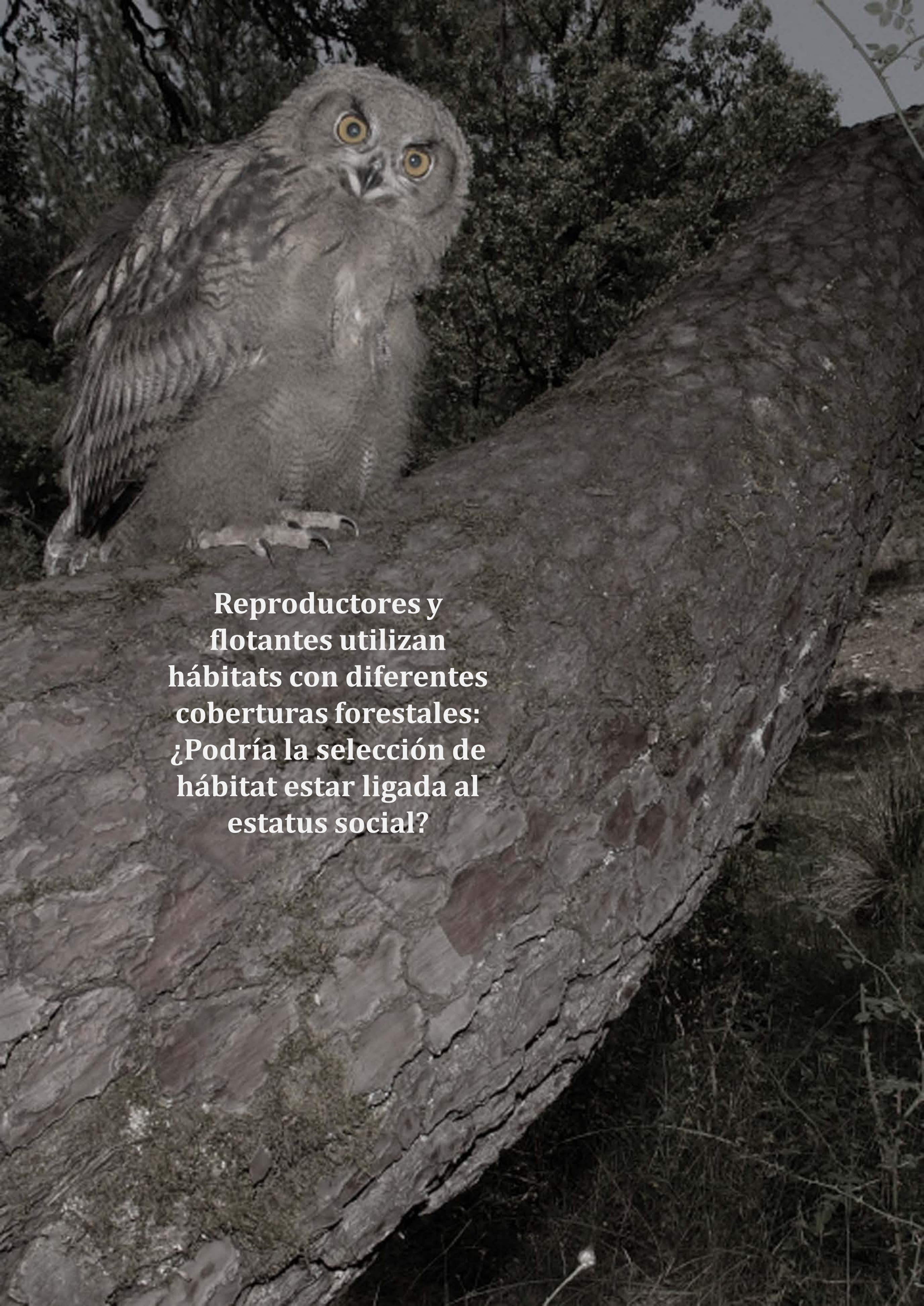
CAPÍTULO 2



Breeders and floaters use different habitat cover: Should habitat use be a social status-dependent strategy?

Campioni L, Lourenço R, Delgado MM and Penteriani V (second review)
Journal of Ornithology



Reproductores y flotantes utilizan hábitats con diferentes coberturas forestales: ¿Podría la selección de hábitat estar ligada al estatus social?

RESUMEN

Para comprender el uso del hábitat en especies territoriales, es importante considerar las tareas específicas y las constricciones asociadas a las diferentes etapas y/o estatus social del ciclo de vida de un individuo (por ejemplo; individuos territoriales vs. flotantes). Sin embargo, en estudios de preferencia, selección y uso del hábitat, raramente se ha tenido en cuenta el estatus social de un individuo. En el presente estudio, nos centramos en analizar diferencias entre las características del hábitat en los alrededores de los nidos de reproductores de Búho real *Bubo bubo* y las características de los lugares que los individuos flotantes utilizan como posaderos diurnos. Siendo la selección de los nidos y los posaderos un proceso importante con efectos en la eficiencia ecológica de un individuo (es decir, del suceso reproductor y de la supervivencia), esperamos que la preferencia para estos lugares refleje los diferentes compromisos entre costes/beneficios asociados con el estado de reproductor y flotante. Analizando la estructura de las parcelas forestales y las características del paisaje a los alrededores de los nidos y de los posaderos observamos que (1) reproductores y flotantes seleccionan parcelas de bosque con distintas estructura vertical. En comparación con los flotantes, los individuos reproductores nidificaron principalmente en parcelas más maduras, caracterizadas por tener arboles de mayor altura; sin embargo, (2) los reproductores y dispersantes no tuvieron ninguna preferencia de hábitat específica a escala de paisaje. Nuestros resultados apoyan una divergencia en el uso del hábitat en función del estatus social de los individuos, reflejo de que las diferentes tareas y constricciones sociales pueden determinar dos estrategias diferentes en el uso del hábitat.

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ABSTRACT

In order to understand habitat requirements in territorial species it is important to take into account the specific tasks and constraints associated with the different stages and social status of an individual life cycle (e.g. territorial breeder or nonterritorial floater). However, social status has rarely been taken into account in studies on habitat preference, selection and use. In the present study, we compare habitat characteristics nearby nesting sites of Eagle Owl Bubo bubo breeders with those of diurnal roosting places chosen by floating owls. Being both nesting and roosting sites important components of the individual fitness (e.g. mating success vs. survival) we expected that the use of those locations would reflect the different cost-benefit trade-offs related to the status of breeder and floater respectively. By analysing the structure of the forest stands and the landscape features surrounding both places at two spatial scales, we found that: (1) breeders and the floaters used forest stands with a different vertical structure. Compared with the floaters, the breeders used more mature stands characterised by higher trees; (2) as expected, breeders and floaters did not show any specific habitat use at landscape scale. Our results showed a clear discrepancy in habitat use according to social classes, suggesting social tasks/constraints (successful reproduction vs. overcoming dispersal costs) as potential determinants of two divergent strategies in habitat use.

Keywords: habitat use, social status, floaters, Eagle Owl, *Bubo bubo,* trade-off

The habitat requirements shown during an animal's lifetime is the likelihood that the animal will select a given item if offered alternative choices on an equal basis (Beyer et al. 2010). Habitat selection involves different aspects of the individual life history and has strong implications for individual fitness (e.g. survival, fecundity, and mating success; Millon et al. 2010; Morosinotto et al. 2010). The overall decision process implies a balance of costs and benefits from the earliest actions of an individual as an inexperienced juvenile to the subsequent actions of the individual as an experienced adult. Frequently, individuals or species have been associated with specific habitat types, e.g., under the assumption that they should occupy the same habitats over their whole lifetime (Dale and Christiansen 2010). However, there is evidence of a degree of individual flexibility in habitat preferences, use and selection over the different stages of the individual life cycle (Kozakiewicz 1995; Law and Dickman 1998; Terborgh 1989). For example, shifts in habitat preference, selection and use have been observed among fledglings as well as dispersing and breeding birds (e.g. Campioni et al. 2010; Dale and Christiansen 2010; Delgado et al. 2010; Ferrer and Harte 1997; King et al. 2006).

The habitat needs of territorial breeders has been extensively quantified for many species, whereas the current lack of understanding of the behavioural strategies of the floating individuals of a population during natal dispersal still represents an information need in population ecology (Penteriani et al. 2011). Very few studies have been able to address habitat use in terms of cost-benefit considerations and behavioural tactics related to the social status of individuals, e.g., the hypothesis that the individual's needs during its lifespan can vary with its social status (e.g., Brown and Long 2007; Campioni et al. 2010; Penteriani et al. 2011). A territorial breeder, which settles in a more established social context principally involving interactions with stable neighbours, needs to accomplish specific duties primarily related to its territory ownership and diverse reproductive tasks. In contrast, most floaters are dispersing individuals leading a transient life. Although they may settle in a more or less fixed area, they do not show any territorial behaviour (e.g. Delgado et al. 2009a; Rohner 1997; Penteriani and Delgado in press).

Consequently, the major threats faced by non-breeding individuals are imposed by dangerous travel through unknown landscapes and by frequent encounters with changing social contexts, which can drive floaters' behavioural decisions at different temporal and spatial scales (Arcese 1989, Smith 1978; Delgado and Penteriani 2008; Delgado et al. 2009a; Penteriani and Delgado 2011; Stutchbury 1991; Tobler and Smith 2004). Hence, the discrepancies among the specific tasks and constraints associated with each social status (reproducing successfully vs. overcoming dispersal costs) can potentially determine divergent habitat use strategies. In particular, because the characteristics of the nesting site are an important component of the breeder’s fitness and the choice of diurnal roosting places during dispersal may affect floater survival, we may expect that the use of these locations would reflect the different cost-benefit trade-offs related to the social status of different individuals.

To compare possible status-dependent differences in habitat use between floaters and breeders, we took advantage of an unusual opportunity furnished by the recent process of colonisation by a top predator, the Eagle Owl (*Bubo bubo*), in the Doñana National Park (henceforth Doñana), Andalusia, southern Spain (more details in Lourenço et al. 2011; Penteriani et al. 2008a). In this area, the nesting places and diurnal roosts of breeders and the diurnal roosting places of floaters are always located in forested patches, i.e., a similar type of cover that may potentially show different age structures and different degrees of extension for the two social classes. Thus, we focus here on the individual habitat use based on the following: (1) the structure of the forest stands and (2) the landscape features surrounding both places where (i) breeders reproduce and roost and (ii) floaters roost. While the adults may ‘prefer’ a particular habitat or forest structure and select for it, it doesn't really follow that juveniles or floaters are preferentially selecting the remaining habitat. The habitat used by the juveniles may principally be the use of what is left to them given that the paired adults have selected the optimal hunting and nesting habitat. For this reason, in the context of this work, we preferred to adopt the more neutral term ‘habitat use’ rather than ‘preference’ when referring to the juveniles. Our main expectation is that habitat use will show differences related to the different tasks/constraints peculiar to each social group. In particular, we expect that: (1) the structure of the forest stands used by breeding individuals primarily reflects the need of the breeders to fly easily within the breeding stand during the entire reproductive period, when they must care for nestlings (e.g., when the breeders are carrying a prey item to the nest) and must subsequently care for fledglings during the post-fledging dependence period, i.e., breeders prefer mature forest stands characterised by old, high and widely spaced trees and (2) the floaters' stand use primarily reflect the cost of dispersing to new environments, e.g., the need to avoid encounters with territory holders and potential predators, as well as reduce physical aggression/mobbing from other raptor species (Lourenço et al. 2011). Thus, the stand use of floaters might be directed towards denser and more closely spaced stands of forest than the stand preference of breeders. The forest patches used by the floaters should provide safer conditions than more open areas. Additionally, because of the above-cited needs and constraints acting at the scale of the entire stand, we expect (3) no differences at the broader spatial scale of the landscape surrounding the nests and roosts, although previous research in Doñana has revealed crucial elements of habitat heterogeneity within this study area: (i) Doñana scrublands are the preferred habitat type frequented by the European Rabbit *Oryctolagus cuniculus* (Fernandez et al. 2005; Palomares et al. 2001), the eagle owl's main prey and (ii) marshlands are among the most productive areas of Doñana and offer the greatest prey richness (Ferrer and Bisson 2003; Sergio et al. 2005).

MATERIALS AND METHODS

Study area

This study was conducted in an 870 km^2 area in southwestern Spain. Most of the area is included in the Doñana National and Natural Parks (Fig. 1), a natural area bounded by the Atlantic Ocean on the west, by the Guadalquivir River to the east, and by crops extending several kilometres to the north towards the Sierra Morena Mountains. This area is flat and generally near sea level, with a maximum elevation of 106 m (for additional details, see Fernandez et al. 2003). Three ecosystem types are predominant: fixed dunes, mobile dunes and marshes. The vegetation in the fixed dunes consists of autochthonous Mediterranean scrubland in a mixture of different stages of degradation (Castroviejo 1993). Many areas are dominated by plantations of pines (*Pinus pinea*), with variable understory vegetation. The scrubland is dominated by *Halimium halimifolium* and *Ulex* spp. or *Erica* spp. heaths depending on the depth of the water. More mature scrubland areas with *Pistacia lentiscus* and *Myrtus communis* are found primarily in the north. A number of other areas have been transformed by *Eucalyptus camaldulensis* plantations introduced during the first half of the 20th century.

Data collection

From 2005 through 2008, we followed the process of colonisation of Doñana by eagle owls. The first breeding of this species in this area was recorded in 1999 (Penteriani et al. 2008b). Every year, we systematically surveyed the study area and conducted a census of the newly settled population using a combination of different methods including: (a) passive auditory surveys at sunrise and sunset from October through February, when the vocal activity of adults was most intense; (b) visiting forest and open patches to detect nests, pellets, and feeding perches; and (c) passive auditory surveys of calling young, conducted from the stage at which the chicks were approximately 100 days old until they began to disperse (August–September in our study area). We located 15 breeding sites and 4 areas potentially suited for reproduction and widely spaced among these sites, with a mean nearest-neighbour distance of approximately 3.9 ± 0.4 km (Penteriani et al. 2008). In Doñana, the eagle owl used to nest in free or deserted nest structures previously built on trees by storks, heron and other raptor species. During the 3 years of the study, we were able to tag and then radiotrack 5 breeding adults (2006: n = 1; 2007: n = 3; 2008: n = 1) and 32 juveniles (2006: n = 9; 2007: n = 15; 2008: n = 8) from 11 nests. The owlets were tagged at the nest when they were approximately 35 days old, 5–10 days prior to the onset of fledging. They were aged following Penteriani et al. (2004) and were sexed by molecular procedures using DNA extracted from blood (Griffiths et al. 1998). They were fitted with a Teflon ribbon backpack harness that carried a 30g radio transmitter (Biotrack Ltd., Wareham, Dorset, UK) with a mercury posture sensor. Because the young were still growing, the backpacks were adjusted so that the Teflon ribbon could expand (Delgado and Penteriani 2007). The manipulation was always safe: after 7 years of continuous radiotracking of both breeders and floaters, we never recorded a potential adverse effect of backpacks on the birds or on breeding performance (Delgado and Penteriani unpubl. data). The backpacks were not removed after the study due to the difficulty of retrapping the same individual (Penteriani and Delgado unpubl. data). The locations of the radio-marked adults and juveniles were recorded with a triangulation method with an accuracy of 83.5 ± 49.5 m (mean ± SE) (Penteriani and Delgado 2008) using three-element hand-held Yagi antennas (Biotrack) with Stabo (XR-100) portable ICOM receivers (IC-R20). The accuracy value was calculated when, after a triangulation, we needed to locate the individual exactly to manipulate it during field experiments (e.g. Penteriani et al. 2007) or to record the cause of mortality if it died. The juveniles were located weekly during the daytime (when the owls were at their diurnal roost sites, Delgado et al. 2009a) from the beginning of natal dispersal (~170 days old, for details on the calculation of the beginning of dispersal see Delgado and Penteriani 2008) until either the death of the individual or the failure of the battery transmitter (~1.5 years to ~2.5 years).

Habitat structure at the stand level

We characterised the structure of the forest stand within a 50 m (surface = 0.39 ha) diameter plot around (*i*) the nest tree (*n* = 15 nesting sites) and (*ii*) the floaters' weekly locations (*n* = 17 roosting locations of different dispersers, i.e., a random selection from a total of 75 floaters' roosts, performed to avoid pseudoreplication and spatial autocorrelation problems). We were confident that a 50 m diameter plot allowed depicting the stand structure mainly because: 1) of the homogeneity of the artificial Doñana forest stands; and 2) the small surface of some forest patches occupied by the species for both breeding and roosting. Measurements were made using four transects per plot. Each transect formed 90° angles with the two adjacent transects. The transects were placed with one end at the centre of the plot and were arranged so that one transect extended towards each of the four cardinal points (N, S, E, W). Based on the line intercept method (Bonham 1989), three parameters were measured on the trees intercepted by the transect paths: (1) tree height (m); (2) diameter at breast height [√plot area/3.14]; and (3) tree density (trees number/m^2).

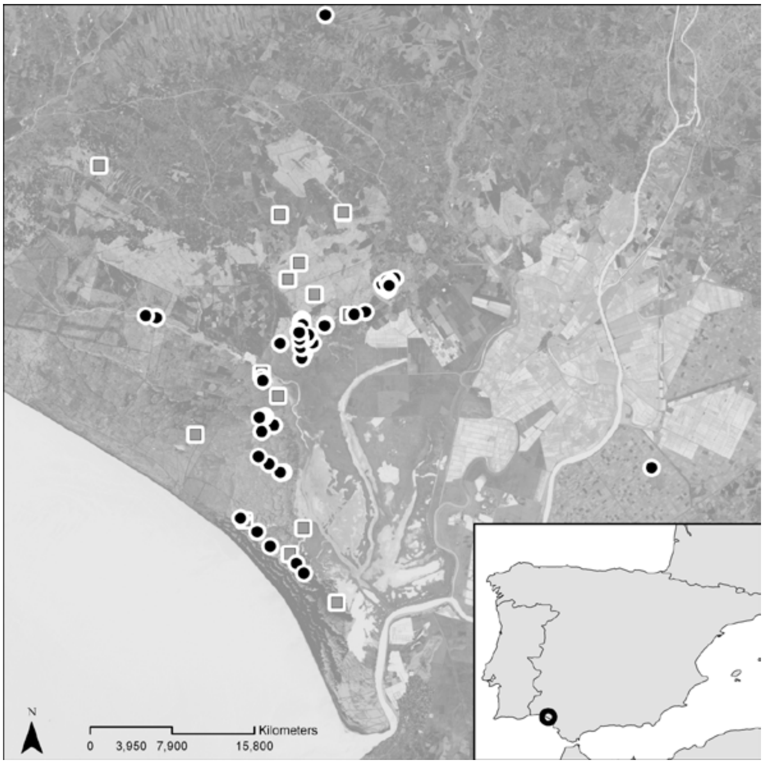

Figure 1. Distribution of the 15 nesting sites (grey squares) and 75 floater's roosting sites (black circles) of the eagle owl in the Doñana National and Natural Parks.

Moreover, we calculated the aerial flight space inside the stand for each plot, i.e., the free volume inside the forested stand available and necessary for owl flights near the nest and the roost locations, as in Penteriani and Faivre (1997). The aerial flight space was represented by a square-based parallelepiped whose major sides were defined by the heights of the tree trunks measured from the ground to the lowest limb and whose basal sides were defined by the distances between the trunks. Finally, we calculated the canopy cover (i.e., the percentage of sky obstructed by vegetation above the centre of the plot) from black-and-white photographs (18 mm, f/3.5 lens) of the canopy cover with a 50 x 50 grid of pixels arranged in a square that was the same size as the photograph (Penteriani and Delgado 2009a; Penteriani and Faivre 1997).

Habitat structure and composition at the landscape level

We characterised the landscape structure and composition within a circular plot with a radius of 1900 m. These plots were centred on the nesting and roosting sites. The area of the plot corresponds to the mean home range size (MCP 95%) calculated employing radiotracking data on 4 of the 5 tagged breeders within Doñana. The landscape characteristics were measured by constructing the intersection of a digital layer including those circular plots with a map of landcover elements (scale 1:25.000, Junta de Andalucia, Consejerìa de Medio Ambiente, 2003). The landscape composition was classified according to the following 7 categories: tall scrub, low scrub, pasture, woodland, marshes, sand dune and crops. In addition, we characterised landscape structures by calculating: (a) the number of patches; (b) the Shannon index of habitat diversity; (c) the edge density as a proxy of habitat heterogeneity (Anderson et al. 2005); and (d) for each nest tree and roost site, the distance (m) to the nearest marshland. In our study area, the proximity of marshes is associated with an increase in the richness of rabbits (Fernández et al. 2003; Palomares et al. 2001), the main prey of eagle owls (Penteriani et al. 2008a, b). The GIS application ArcView 3.2 and its extension Patch Analyst (Elkie et al. 1999) were used for the analyses of landscape characteristics.

Data analysis

We applied two General Linear Models (GLMs) with a distribution belonging to the binomial family. The dependent variable was social status (breeder = 1, floater = 0). In the first model, we analysed habitat preference at the forest stand level. The previously detailed descriptors of the stand structure represented the explanatory variables (Table 1). In the second model, we investigated habitat preference at the landscape level, employing habitat composition and structure as the explanatory variables (Table 1). To reduce collinearity and the number of explanatory variables, pairs of strongly inter-correlated variables ($r > 0.6$) were considered to be estimates of a single underlying factor. Only one of the two variables, usually the one perceived as more important by the study organism, was retained for analysis. Before performing any analysis, we tested for spatial autocorrelation among the locations of the breeders and floaters. For this purpose, we used a Moran's I test (Cliff and Ord 1981) under randomisation conditions at both the stand and the landscape level. No patterns of spatial autocorrelation were present in our data (stand: Moran's I statistic standard deviate = -0.0735, P value = 0.53; landscape: Moran's I statistic standard deviate = 0.2429, P value = 0.40). As suggested by Zuur et al. (2008), model simplification was performed by backward selection of variables from the full model. To find the minimal adequate model, models were compared using the Likelihood Ratio Test (LRT) approach employing the anova command in the R environment (R Development Core Team 2009). Logistic regressions were performed with the glm function in the R "stats" package. The percentage of deviance explained was calculated as follows: deviance (null model) - deviance (selected model)/deviance (null model) x 100. The means ± SD and the 95% CI are given in addition to these values. Statistical significance was set at $\alpha < 0.05$.

Table 1 Characterisation of the forest stand and landscape of breeder's nesting places and floater's roosting places of eagle owls employed in the GLM analyses.

	Individual status			
Variable	Breeder		Floater	
Stand plot level	mean ± SD	range	mean ± SD	range
Tree height (m)*	16.35 ± 3.5	11.88-21.24	9.70 ± 2.09	5.84-13.12
Diameter at breast height (m)	0.52 ± 0.2	0.25-0.87	0.40 ± 0.15	0.22-0.77
Density	0.02 ± 0.02	0.0001-0.06	0.03 ± 0.02	0.01-0.08
Canopy cover (%)	47.9 ± 23.3	11.8-96.6	65.1 ± 32.7	17.7-99.7
Flight space (m^3)	1745.0 ± 1553.2	106.8-5888.0	1099 ± 2061	150.2-8677
Landscape plot level				
Dense scrub (%)	24.1 ± 16.7	1.4-56.5	33.7 ± 12.4	12.8-59.6
Disperse scrub (%)	3.7 ± 3.6	0.01-9.8	2.7 ± 2.6	0.03-8.71
Pasture (%)	6.1 ± 12.0	0.1-44.0	10.5 ± 10.5	0.4-26.9
Woodland (%)	40.5 ± 24.6	2.7-73.2	30.9 ± 20.2	0.3-61.6
Marshes (%)	11.6 ± 17.2	0.01-52.7	4.9 ± 6.3	0.05-21.2
Sand dune (%)	6.2 ± 10.2	0.01-24.3	2.7 ± 7.9	0.01-26.8
Crops (%)	9.4 ± 15.4	0.01-48.0	7.8 ± 14.6	0.01-40.6
Edge density (m/ha)	61.0 ± 32.2	18.9-113.4	52.9 ± 31.1	20.1-101.7
Shannon index of diversity	0.7 ± 0.3	0.2-1.2	0.7 ± 0.3	0.2-1.3
Distance to marshes (m)	1028.0 ± 916.0	37.6-3637.0	908.4 ± 698.9	0.01-2384

* P = 0.007 in the GLM analysis

RESULTS AND DISCUSSION

The forest stand structure was analysed for a total of 32 locations (15 nesting places and 17 roosting places of floaters). The breeders and the floaters preferred forest stands with a different vertical structure. Compared with the floaters, the breeders preferred more mature stands characterised by higher trees (GLM tree mean height estimate ± SEM: 0.455 ± 0.168; *P* = 0.007; 95% CI: 0.186 - 0.865; % deviance explained = 33; Table 1 and Fig. 2). Although all the other parameters we took into account at the stand level did not showed any significant difference between breeders and floaters, we consider important to highlight that all of the stand measurements depicted a more mature and open stand structure for breeders (Table 1).

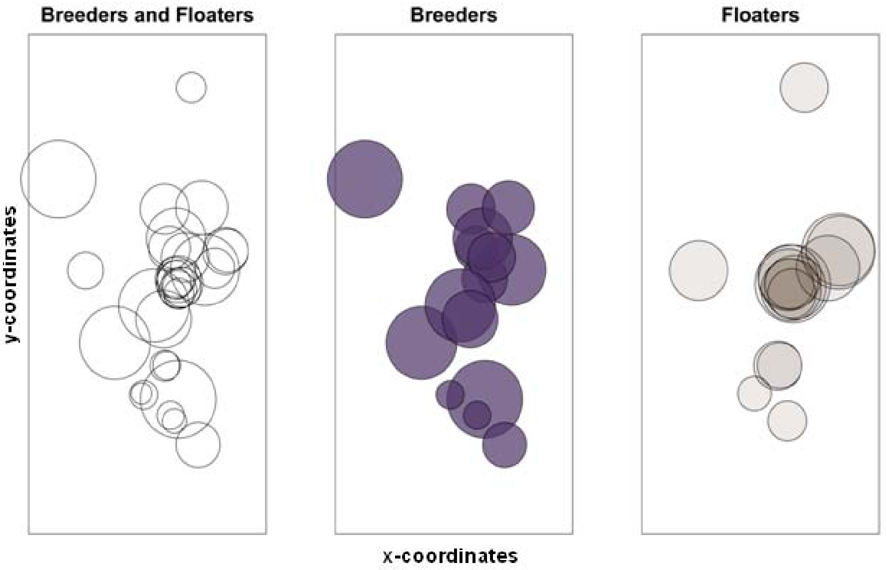

Figure 2. Point pattern representation of the original nest and roost locations preferred by breeders and floaters eagle owls at forest stand level. Bubble size represents the vertical structure and it is proportional to the mean tree height characterising breeding territories and roosting areas. Bubble size is automatically drawn taking into account the range of values of tree height (min-max values). Bubble centre is the X and Y coordinates in UTM system of each location. Panel (a) includes breeders and floaters locations; (b) shows breeders only and (c) shows floaters' locations.

At the landscape level (after accounting for outliers), we identified a total of 31 plots (n = 14 for breeders and n = 17 for floaters). Breeders and floaters did not show any specific habitat use at the level of the landscape surrounding their nesting and roosting places ($P > 0.1$ in all cases, Table 1).

Our findings mainly suggest that: (1) individuals of the same population but differing in social status can show different habitat use; and (2) the structure of the forested patches could have played a more important role than vegetation type (as also highlighted by Dale and Christiansen 2010) in determining the recorded patterns of habitat use.

The different patterns of habitat use of breeders vs. floaters (see also Campioni et al. 2010) may be explained by the tasks and constraints associated with these differences in status. For reproduction occurring within forested stands, the different activities that breeders perform in the area surrounding the nest specifically require easy access to the nest. This access is provided by the more open structure offered by the oldest stands: the preference for mature trees as breeding stand has been recorded in many other raptor species like, for example, the goshawk (*Accipiter gentilis*; Penteriani 2002) and the white-tailed eagle (*Haliaeetus albicilla*; Radović and Mikuska 2009).

In contrast, non-territorial floaters are free from these temporal and spatial constraints. They depend primarily on foraging, frequently in unfamiliar areas, and on conspecific avoidance. The high costs associated with diurnal activity are shown by the highly cryptic behaviour of the eagle owl and of many owl species during the day and by the aggressive reactions of other birds of prey towards the owls (Lourenço et al. 2011; Sunde et al. 2003). The choice of a safe area for diurnal inactivity (when owls are particularly vulnerable to predation or harassment by mobbers) can represent an adaptive strategy to overcome the costs of dispersal (Stamp 2005). This phenomenon may be even more apparent if owls and diurnal raptors can overlap in space and time. Such overlap occurs in our study area, where the high densities of diurnal raptors increase the risk of diurnal raptor attacks on roosting eagle owls (Lourenço et al. 2011). Indeed, it has been shown that the ways in which animals are distributed relative to conspecifics (and in our case relative to heterospecifics) often represent a trade-off between the costs and benefit of proximity, e.g., predator attraction vs. the dilution effect (Fero and Moore 2008).

We can expect the strategy of the territorial breeder to be directed to maximise individual benefits by selecting suitable breeding conditions that provide long-term individual benefits and increase fitness. In contrast, the strategy of the non-territorial floater appears to minimise the short-term negative effects of natal dispersal through behavioural mechanisms, such as specific cover use. Finally, we cannot discard the possibility that the behavioural strategies of floaters can be actuated through habitat-mediated avoidance or temporal segregation mechanisms (e.g. Sergio et al. 2007). As an ultimate consequence, habitat use patterns may then involve the interaction of multiple social, behavioural and ecological determinants with direct ecological and evolutionary consequences for population dynamics and colonisation (Clobert et al. 2001, 2009).

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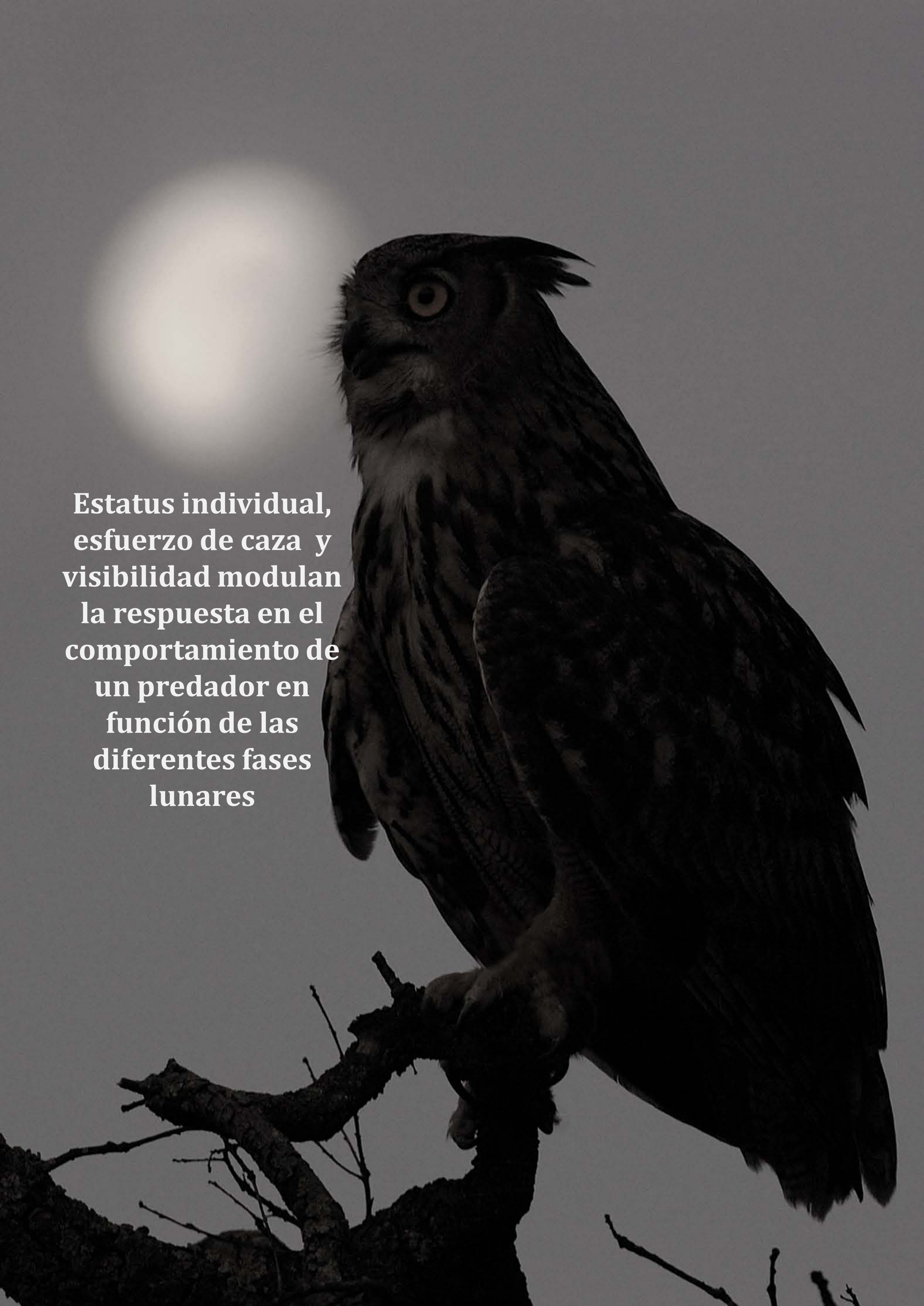
CAPÍTULO 3

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

Penteriani V, Kuparinen A, Delgado MM, Lourenço R, **Campioni L** (2011) *Animal Behaviour* , 82: 413-420

Estatus individual, esfuerzo de caza y visibilidad modulan la respuesta en el comportamiento de un predador en función de las diferentes fases lunares



RESUMEN

El efecto de las fases lunares sobre las relaciones predador-presa ha sido casi siempre hasta hora analizado desde el punto de vista de la presa. El comportamiento de un predador en las diferentes fases lunares es el resultado del compromiso entre varios factores, como la respuesta a las diferentes estrategias anti-predadoras de sus presas y las necesidades y constricciones del ciclo biológico. En este trabajo se exploró el efecto del ciclo lunar en reproductores y dispersantes de búho real *Bubo bubo* en los patrones de movimiento, el esfuerzo de caza y la intensidad de la comunicación (vocal y visual) intraespecífica. En general, observamos que el movimiento de los reproductores incrementaba alrededor de la luna llena, probablemente debido a la mayor dificultad de encontrar una presa (en condiciones de mayor luminosidad las presas suelen refugiarse) y al mayor tiempo dedicado a las exhibiciones visuales (la luna llena aumenta la visibilidad de señales visuales). Sin embargo, en las noches de luna nueva, cuando las presas son más difíciles de detectar, los búhos presentaron un pico en su actividad de caza.

Por otra parte, el comportamiento de los búhos durante la fase de dispersión no pareció verse afectado por el ciclo lunar. Durante la dispersión natal, los individuos se enfrentan a potenciales riesgos asociados con la travesía de aéreas desconocidas (que probablemente requieren un esfuerzo similar a lo largo de todo el año), y al mismo tiempo no presentan ningunas constricciones relacionadas a la reproducción, por eso es esperable que su actividad de movimiento no se vea afectada ni siquiera en situaciones de baja rentabilidad de las presas. En este contexto, pudimos ver como el estado social de un individuo puede jugar un papel importante en las consideraciones costes-beneficios y en las decisiones comportamentales, determinando directamente el tiempo y el esfuerzo dedicado a cada actividad relacionadas a necesidades inminentes (por ejemplo, llevar a cabo la reproducción vs. superar los riesgos asociados a la dispersión natal).

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ABSTRACT

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).

Keywords: animal movement, *Bubo bubo*, eagle owl, foraging effort, individual status, lunar brightness, moon phase, natal dispersal, predator-prey relationship, visual/vocal display.

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 and Osborne 1999) and vertebrates (e.g. Daly et al. 1992; Brown and 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 and 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 and 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 and 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 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 and 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 and Tan Summerlin 1989; Gilbert and Boutin 1991; Daly et al.

1992; Leaver and 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 and 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 and 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 AndalucíaConsejería 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) from1 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 appeared to ignore the observer when the latter accidentally approached closer to the bird; V. Penteriani and 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.

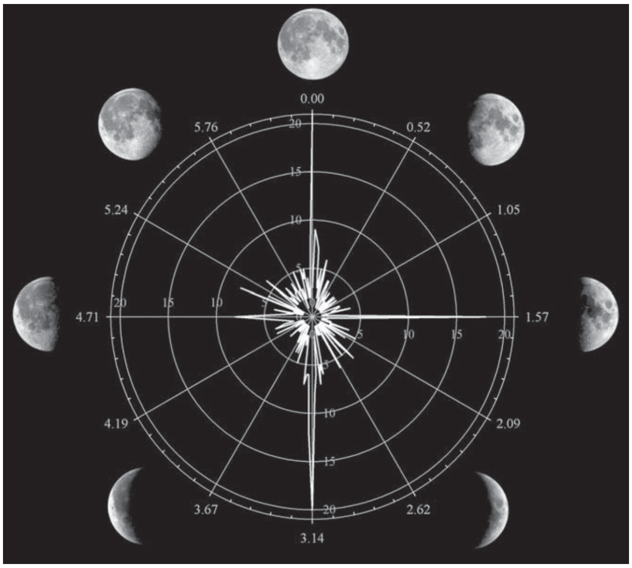

Figure 1. Distribution of the 459 radiotracking nights (2003-2010) per lunar phase for 31 eagle owl breeders (21 males, 10 females) and 40 dispersing juveniles (28 males, 12 females). Moon phases were converted to the fraction of moon disk illuminated, and expressed as radians (θ): one lunar cycle corresponds 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).

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; $N_{nights\ =}$ 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 and 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 and 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 ($N_{individuals} = 21$; 13 males and eight females; $N_{nights} = 174$) 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 and Penteriani 2007). Because the vocalization peaks of eagle owls at sunset and sunrise may be influenced more by twilight (Delgado and Penteriani 2007; Penteriani and 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 (http://www.usno.navy.mil/USNO/astronomical-applications/dataservices/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 and 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 and 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 = pre-laying, 2 = incubation, 3 = nestling and 4 = post-fledging); (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 and 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 x 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 and 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 Archaeo sciences, 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 2 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 and 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 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 and Maechler 2009) and MASS (Venables and Ripley 2002) packages. Statistical significance was set at $\alpha < 0.05$.

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

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* Sum of the distance between successive steps of the same nightly path (N = 309).

‡ 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).

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).

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.

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 and Penteriani 2007).

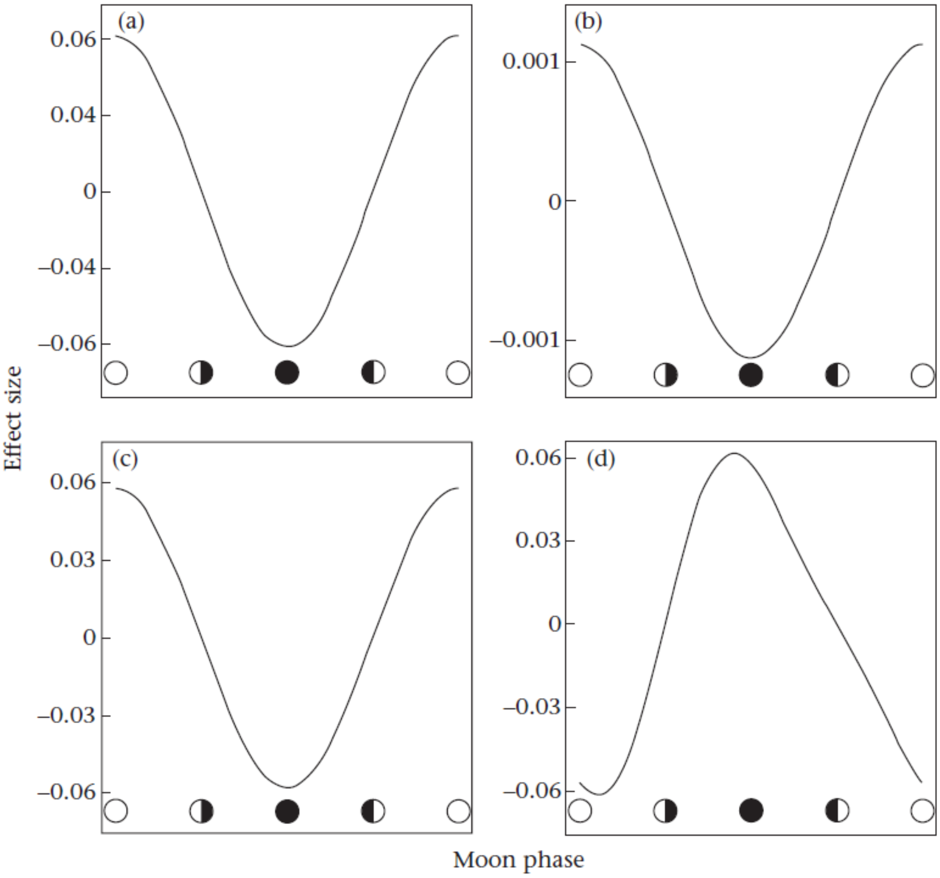

Figure 2. Moon phase effect on (a) log-transformed total distance, (b) movement rates, (c) log-transformed speed and (d) time steps, as estimated by the linear and generalized linear mixed-effect models (Tables 1, 2).

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 and 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 and 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 and 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 and 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 costbenefit considerations and behavioural decisions (Campioni et al. 2010), by directly affecting the time and 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.

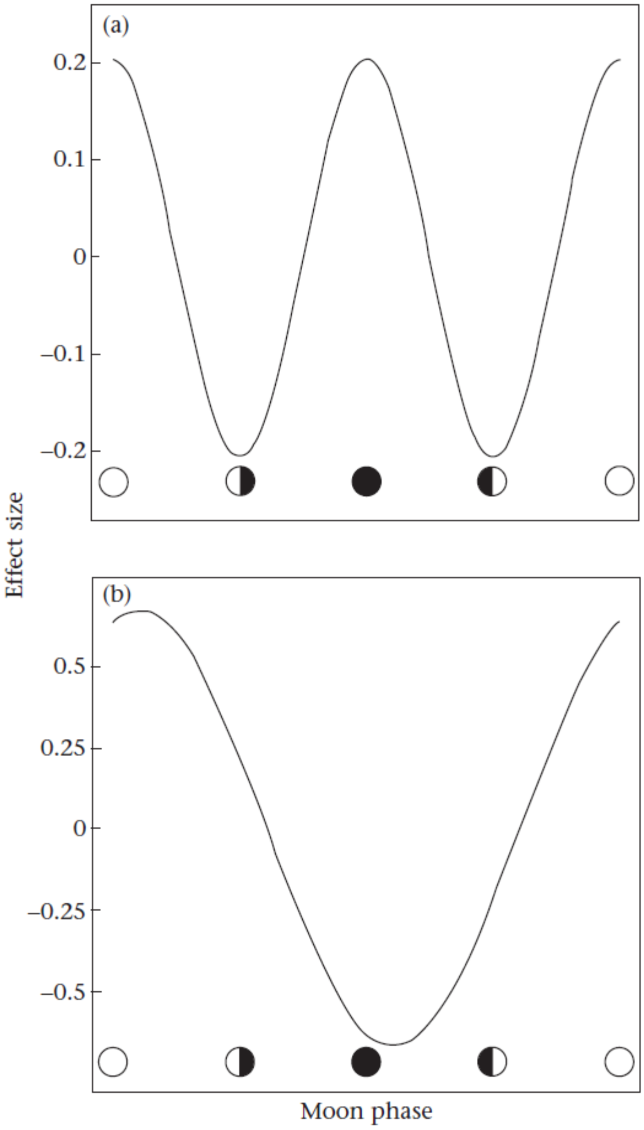

Figure 3. Time budget allocation at various moon phases. (a) Time spent successfully hunting a prey (a proxy of hunting conditions/prey availability). (b) Call activity. See text for further details.

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 intra-specific communication (Penteriani et al. 2007; Penteriani and 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 and 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 preypredator 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.

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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CAPÍTULO 4

Changes of movement patterns from early dispersal to settlement

Delgado MM, Penteriani V, Nams VO and **Campioni L** (2009) *Behavioral Ecology and Sociobiology*, 64: 35–43

Niveles de familiaridad durante la dispersión

RESUMEN

Los movimientos y el aprendizaje espacial son dos procesos entrelazados entre ellos. Los cambios en el comportamiento de movimiento de un animal pueden influenciar el aprendizaje del entorno espacial. Del mismo modo, la información espacial juega un papel crucial en muchas decisiones relacionadas con los movimientos de los animales. Una forma muy útil de explorar las interacciones entre las decisiones relacionadas con los movimientos y el aprendizaje del entorno espacial es a través de la comparación del comportamiento de los individuos durante las diferentes fases de la dispersión natal (es decir, cuando los individuos se mueven en hábitats desconocidos) con las decisiones y movimientos de los reproductores (que utilizan dominios vitales fijos y conocidos por los individuos). Es decir, comparando el comportamiento de individuos que continuamente tienen que recoger nueva información vs. individuos que presentan un conocimiento completo de su entorno. En este capítulo analizamos los patrones de movimiento de individuos de búho real *Bubo bubo* en tres grupos sociales distintos (a) dispersantes en la fase de búsqueda (que exploran ambientes desconocidos), (b) dispersantes en la fase de asentamiento (establecidos temporalmente en áreas de asentamiento), y (c) adultos reproductores con un área de campeo bien definida. Los resultados mostraron que: (1) los dispersantes en la fase de búsqueda se mueven más rápido que los búhos establecidos temporalmente en las aéreas de asentamiento, recorriendo mayores distancias con trayectorias más rectas y movimientos más largos; (2) cuando los dispersantes están asentado en un área más estable, presentan un comportamiento de movimiento más similar a los adultos territoriales. Pudimos de esta forma comprobar cómo los individuos mostraron una transición que puede verse reflejada en sus patrones de movimientos, desde una estrategia más exploratoria, cuando los animales posen escasa información del entorno físico, hasta una más óptima para explotar aquellas áreas que son familiares para los individuos.

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ABSTRACT

Moving and spatial learning are two intertwined processes: (a) changes in movement behavior determine the learning of the spatial environment, and (b) information plays a crucial role in several animal decision-making processes like movement decisions. A useful way to explore the interactions between movement decisions and learning of the spatial environment is by comparing individual behaviors during the different phases of natal dispersal (when individuals move across more or less unknown habitats) with movements and choices of breeders (who repeatedly move within fixed home ranges), that is, by comparing behaviors between individuals who are still acquiring information vs. individuals with a more complete knowledge of their surroundings. When analyzing movement patterns of eagle owls, *Bubo bubo*, belonging to three status classes (floaters wandering across unknown environments, floaters already settled in temporary settlement areas, and territory owners with a well-established home range), we found that: (1) wandering individuals move faster than when established in a more stable or fixed settlement area, traveling larger and straighter paths with longer move steps; and (2) when floaters settle in a permanent area, then they show movement behavior similar to territory owners. Thus, movement patterns show a transition from exploratory strategies, when animals have incomplete environmental information, to a more familiar way to exploit their activity areas as they get to know the environment better.

Keywords: *Bubo bubo,* familiarity, floater, learning, movement behavior, natal dispersal

Animal movement is an essential mechanism underlying many ecological processes at individual (e.g., home ranging, site fidelity, foraging), population (e.g., metapopulation connections and persistence, invasion spreading), community (e.g., assemblages, species coexistence), and ecosystem levels (Nathan 2008; Revilla and Wiegand 2008; Fryxell et al. 2008). The implications of movement behavior on several evolutionary and ecological processes have been recently emphasized (Dingemanse et al. 2003; Davis and Stamps 2004; Hansson et al. 2004; Haughland and Larsen 2004; Nathan 2008; Schick et al. 2008). In particular, spatial memory and learning allow animals to move through their landscape as efficiently as possible (Saarenmaa et al. 1988; Vuilleumier and Perrin 2006). However, there is still a lack of knowledge on the characteristics of the process by which individuals learn and acquire experience to move within and through environments (e.g., Dukas 2004).

Cognitive abilities and learning affect behavior and choices related to habitat selection, mate choice, foraging, social interactions, and space use (Dukas 2004; Dall et al. 2005). Until now, most of the models that have been used to explore some aspects of spatial learning have assumed that individuals are “omniscient”, i.e., that they have complete information on the quality of all patches in the habitat. However, it is unlikely that individuals could always have an *a priori* information on the surroundings (e.g., Vos et al. 1998 and references therein; Stamps and Krishnan 1999): individuals need time to acquire knowledge about the surroundings in which they move and, consequently, adopt some site-specific mechanisms or rules which allow them to exploit habitat patches optimally (Stamps 1995; Thield and Hoffmeister 2004; Dall et al. 2005).

Moving and learning are intertwined processes: (a) changes in movement behavior during the different phases of the biological cycle or a switch in an individual status (floater vs. breeder) allow the individuals to better learn about and/or differently perceive their environment, and (b) information plays a crucial role in several animal decision-making processes, like movement decisions during natal dispersal, a crucial phase of animal life. Individuals actively sampling novel and temporary patches should show different movement behaviors from when they settle in a stable area. Indeed, natal dispersal presents a unique opportunity to explore interactions among animal movements and learning because of the specific stages that individuals go through (Stamps 2001; Andreassen et al. 2002; Clobert et al. 2004; Bowler and Benton 2005; Heinz and Strand 2006; Baguette and Van Dyck 2007; Delgado and Penteriani 2008), shifting from a wandering to a more stable phase characterized by a settlement in quite fixed areas of activity. Moreover, natal dispersal involves considerable time spent alone traveling across unknown areas, and therefore, the costs of dispersal can be significant because of both mortality risks and missed reproductive opportunities (e.g., Waser et al. 1994; Alberts and Altmann 1995). But the costs of uncertainty during dispersal may be reduced by becoming familiar with the environment. Thus, the comparison of movement behaviors of floaters throughout the dispersal process vs. movements of territory owners within their well-established home ranges presents a unique opportunity to evaluate the effects of local familiarity on animal movement decisions.

The eagle owl *Bubo bubo* has a multiphase dispersal process (Delgado and Penteriani 2008). At the beginning, during the wandering phase (i.e., the exploratory stage of natal dispersal), individuals survey different unknown areas for a variable time period. Once they find a suitable temporary settlement area, they enter the stop phase of dispersal (Delgado and Penteriani 2008). Such settlement areas represent those zones occupied during the longest time period of the whole dispersal, sometimes until floaters become territory owners and start breeding. At this stage, due to the amount of time they spend in the settlement area, individuals become more familiar with their environment and learn what significant habitat features are in the area, where these are, and how to move to exploit them (Stamps and Krishnan 1999).

By using data from a 4-year radiotracking study on the movement behavior of eagle owls, we tested the following main hypothesis: throughout natal dispersal, the shift from a more wandering and explorative stage to a quite stable settlement stage will increase local familiarity due to increasing spatial learning. As a consequence, we may expect a progressive change in movement patterns: since they become more familiar with their surroundings, owls in their settlement phase (i.e., when they reach the stop phase) should show movement patterns more similar to territory owners than to wandering floaters at the beginning of dispersal. We expect the following: (a) Since animals with a preferred (i.e., learned) diurnal roost site are expected to frequently return to it after their activity period, floating owls in settlement areas and territory owners will show shorter distances between the first and the last location recorded in the same night; (b) Since wandering individuals are continuously exploring novel areas and sampling different patches, they will not show movements within well-defined foraging areas. However, if owls have learned the spatial distribution of resources within their home range once they have settled in an area, they may tend to concentrate their foraging efforts in specific restricted areas; (c) Because individuals dispersing through new habitats vs. individuals moving within their own home range use different spatial domains, the structure of individual movement paths will change. (d) Finally, because dispersal costs are high and floaters only hope is to locate a patch as quickly as possible, wandering owls traveling through unknown environments will travel faster and straighter than individuals moving in a familiar habitat.

MATERIALS AND METHODS

Data collection

We radiotagged 40 juveniles (born in 12 breeding sites) and nine territory owners in the 2003–2006 period in the Sierra Morena massif (south-western Spain; for more information see Penteriani et al. 2007). Marked individuals were equipped with a Teflon ribbon backpack harness that carried a 30-g radio-transmitter (Biotrack Ltd, Wareham BH20 5AJ, Dorset, UK; www.biotrack.co.uk). Each transmitter package and harness weighed less than 3% of the total body mass (as recommended by the US Geological Survey Bird Banding Laboratory), with a mercury posture sensor that allowed us to discriminate rhythms of activity by changes in the radio signal. Juveniles were radiotagged when they were approximately 35 days old. Because they were still growing, backpacks were adjusted so that the Teflon ribbon could expand. After 4 years of continuous radiotracking, we never recorded a possible adverse effect that could be directly attributed to backpacks on birds (Delgado and Penteriani, unpublished data). Owlets were aged following Penteriani et al. (2005) and sexed (n_{males} = 26; n_{females} = 14) by molecular procedures using DNA extracted from blood (Griffiths et al. 1998).

We followed both territory owners and juveniles ($n_{\text{wandering phase}}$=32 individuals—19 males and 13 females; $n_{\text{stop phase}}$ = 25 individuals—18 males and seven females) individually in continuous radiotracking sessions (n = 285 entire nights—119 for adults and 166 for dispersing during a total time of 1,214 and 1,840 h, respectively). A continuous radiotracking session means following a focal individual during the whole night (i.e., from 1 h before sunset to 1 h after sunrise; mean duration of a radiotracking session ± SD = 10.56 ± 0.08 h) and recording a new location (n = 4,758 recorded locations; mean total number of locations per individual ± SD = 97 ± 92) each time that we detected a change in individual position (mean number of locations per radiotracking session ± SD = 18 ± 4). Thus, the number of locations recorded is a measure of the amount of movement during the night. The mean time between owl movements was 32.7 ± 30.8 min, not being significantly different between categories ($F_{2,\ 4,185}$ = 1.7, p = 0.1). We note that: (a) the high variation in the mean number of locations per individual is mainly due to the different activity patterns of each individual; and (b) the low mean number of locations per radiotracking session is due to the large amount of time that the species spend roosting (Penteriani et al. 2008). Individual movements were detected by a fixed antenna located on the roof of a car. Locations were done using triangulation with three-element hand-held Yagi antenna connected to ICOM (IC-R20) portable receivers. To avoid unnecessary disturbance during continuous tracking, we attempted to maintain a distance of at least 100–300 m from the focal animal. In general, the tracking did not seem to affect owl behavior, which appeared to ignore the observer (Delgado and Penteriani, unpublished).

Data analysis

Defining dispersal phases

To determine the different phases (i.e., *start*, *wandering*, and *stop* phases) of dispersal, we recorded the position of each juvenile weekly, typically when owls were at their diurnal roost sites. For each individual, we plotted both the beeline distance between its natal nest for each weekly location and the individual average of beeline distances between the whole set of locations and the nest (the latter representing the individual global mean distance) covered for each individual during the dispersal period. When juveniles left the nest, they still remained in their parental home range for a while. We considered dispersal to have started when individuals left their parent's home range, which we estimated when the distance of each weekly location from the nest becomes larger than the global mean distance traveled by each animal during the dispersal period (Delgado and Penteriani 2008). After leaving the natal territories, dispersal distances progressively increased. Finally, when owls reached the stop phase of dispersal, dispersal distances leveled off. We considered that owls settled in a stable settlement area when the distances between successive weekly locations became smaller than the average distance of previous moves traveled by each dispersing owl (for more details, see Delgado and Penteriani 2008). The wandering phase encompasses the movements between the start of dispersal and the final settlement in a stable area.

Once dispersing owls settled in a stable settlement area, we never observed a shift again to the wandering phase. However, we could not have detected such behavior if some individuals shifted to the wandering phase after their third year because the battery life was ~2.5 years. Although such a behavioral shift has been recorded in some other species (e.g., Ferrer 1993a, b), some dead individuals were found more than 4 years after the battery failed (Delgado and Penteriani, unpublished results) in the same settlement area where they were located the last time. To better understand individual behavior across the whole natal dispersal, we are now marking "older" dispersing owls directly in their settlement areas (Penteriani and Delgado, unpublished results).

Owl status, movements, and spatial learning

To find out how movements at each floater stage differed from the breeding stage, we compared three different aspects: roost sites, foraging areas, and spatial domains.

Roost sites To analyze if animals frequently return to a given roost site, we calculated the distance between the first and the last owl location recorded on the same night, i.e., before the start and after the end of the nightly activities).

Foraging areas Firstly, we calculated the activity areas for both dispersing and breeding individuals. For each individual night, activity area was estimated using the 95% kernel of all night locations (fixed-kernel method, Worton 1989), and core area estimated using the 50% kernel. We used the fixed kernel least squares cross-validation estimate because it is best at defining interior contours (Seaman et al. 1999; Blundell et al. 2001). Secondly, we used this information to: (a) identify foraging areas: by recording hunting events (see Penteriani et al. (2008) for more details), we were able to discriminate foraging areas from other areas of intensive use (e.g., refuges); and (b) calculate their extensions relating to the 95% area of floaters' vital ranges and breeders' home ranges.

Spatial domains Animals often react differently to their environment at different spatial scales (these areas of spatial scales are called spatial domains); we used fractal analysis to determine these spatial domains (as in Nams and Bourgeois 2004). To test for changes in movement paths (following Nams 2005), we measured: (1) path tortuosity (*D*) of each nightly movement path as a function of spatial scale. Fractal *D* measures movement path tortuosity, where $D = 1$ indicates a perfectly straight line, and $D = 2$ suggests approximately Brownian (plane-filling) movement. To look for variation in *D* with changes in the spatial scales, we determined the value of *D* for a series of small ranges of divider size ranging from 20 to 1,000 using Vfractal estimator (Fractal 4.0 software; see Nams 2005 for a detailed explanation of the procedure). Window sizes at each spatial scale were chosen with a minimum value of midpoint/1.35 and a maximum value of midpoint ×1.35. This window size definition gave symmetrical, fixed width windows on the log-transformed spatial-scale axis (Nams 2005). A discontinuity in fractal *D* vs. scale relationship indicates a change in path structure from one spatial domain to another; (2) the movement path heterogeneity by dividing the path into segments and estimating the variance in tortuosities among segments. The resulting plots of divider size vs. *D* were used to describe the pattern of scale variance. The specific pattern of scale variance may provide information on the spatial scales at which the animal views the landscape (Nams 2005). A sharp drop in the variance of tortuosity also indicates a change in path structure from one domain to another; and (3) the correlation in tortuosity between pairs of adjacent segments of the total path, as a function of segment length. If the segments are much smaller than patch sizes, then their correlation would be positive because both path segments would be either inside or outside of a patch. For segments that are the size of patches, one would be in a patch (and therefore tortuous), while the adjacent would be outside (and therefore straight), and thus, their correlation would be negative.

Finally, when segments are large enough to cover several patches, then their correlation would be zero. Thus, when there is a zero correlation at all scales, this means no patch use, while a positive correlation of tortuosities dropping to a negative correlation indicated a patch use. In such a case, patch size may be estimated as the spatial scale at which the correlation declines below zero (Nams 2005). Finally, in order to characterize owls' motor skills (i.e., how individuals exploit the elements inside the space in which they move), we estimated various movement path statistics. First, we estimated path tortuosity, by the overall fractal dimension (*D*). This was done using the same range of spatial scales for all individuals (from 20 to 160 m), with the upper limit set at less than half the lengths of the longest path, and the lower limit the minimum distance between locations (Halley et al. 2004). Using the same range of scales allowed us to compare fractal *D* among paths even though *D* varied with scale (Turchin 1996; Nams and Bourgeois 2004). *D* was computed using the fractal mean estimator with the program Fractal (Nams 1996, 2006a), and fractal *D* was normalized by log ($D-1$). Finally, we estimated the overall traveling speed, mean step lengths, and the total length of nightly movement paths. Both the overall speed and the total path length were based on the gross distance traveled.

Statistical analyses

Because repeated measures were made for each owlet, we considered individuals as sampling units (SUBJECT Statement in PROX MIXED) and used a repeated measurements mixed model (PROX MIXED in SAS software; SAS Institute 2001), including sex as a random factor. Moreover, since we radiotagged many owls per nest, we also tested the possible effect of nest as an additional random effect (Littell et al. 1996). But the effect of sex and nest was never significant (always $p > 0.10$), and they were therefore removed from the models. We used a restricted maximum likelihood method to estimate all the unknown variance–covariance parameters (Jennrich and Schluchter 1986) and selected autoregressive (AR1) as the covariance structure that best fitted the Akaike Information Criterion (AIC). The variance structure with the lowest AIC value is deemed the best one. Finally, statistical significance was considered to be $\alpha < 0.05$.

RESULTS

Most juveniles started their dispersal at the end of August (mean age at the beginning of dispersal (± SD) = 170 ± 20.51 days old, range = 131–232 days old). Although there was a high degree of individual variation, 30% of eagle owls found a stable settlement area (i.e., shifted from the wandering to the stop phase of dispersal) in the middle of March (mean dispersal age of the stop phase (± SD) = 395 ± 109.86 days old, range = 181–640 days old). The time between when a disperser finds a settlement area and becomes a breeder is very unpredictable in this species. We observed some dispersing owls that accidentally crossed an empty territory or that arrived close to an available mate halfway during the wandering route, settled and became breeders, when they were only 1 year old. On the other hand, and more commonly, other dispersers that encountered a stable settlement area and decided to settle remained there for several years without breeding.

Floaters during the wandering phase traveled significantly further (net distances) during the night than both floaters during the stop phase and territory owners ($F_{2,\ 3}$ = 14.99, $p < 0.0001$; Table 1). As expected, individuals already established in a stable area (floaters in their settlement areas or territory owners) come back to a given roost site or area more frequently than did owls during the wandering phase, i.e., they traveled shorter (net distances) during the night. On the contrary to what was hypothesized for foraging areas, we did not detect any significant differences in the relative size of the foraging areas ($F_{2,\ 3}$ = 2.06, p = 0.13) among the different life stages. However, the relative size of foraging areas gradually decreased (Table 1) from territory owners to the wandering phase of dispersal. The floaters in the stop phase showed an intermediate behavior between wandering and territorial owls.

Table 1. Estimates of focal movement parameters for both type of floaters ($n_{wandering\ phase} = 32$; $n_{stop\ phase} = 25$) and territory owners ($n = 9$)

	Juveniles(wandering phase; mean ± SE)	Juveniles (stop phase; mean ± SE)	Territory owners (mean ± SE)
Roost site (m)	1,396.54 ± 174.67	725.25 ± 67.21	762.86 ± 77.12
Foraging areas (%)	0.12 ± 0.009	0.10 ± 0.007	0.09 ± 0.007
Speed (m/h)	874.98 ± 54.26	801.06 ± 35.82	641.75 ±37.07
Fractal D	1.06±0.005	1.08±0.005	1.09±0.006
Path length (m)	9,958.56±614.63	9,248.99±395.25	6,676.09±359.73
Step length (m)	608.16±21.78	546.70±32.94	456.68±23.42

Roost site distance between the first and last owl locations of the night, *foraging area* proportion of the total home range

There was a gradual change in response to spatial scale across the two phases of dispersal (Fig. 1). During the wandering phase of dispersal, owls moved with homogeneous movement paths, as shown by the continuous change in fractal D and the variance of fractal *D* with spatial scale and the non-positive values of correlation (Fig. 1). On the other hand, territory owners showed the most heterogeneous paths, with strong responses at different spatial scales (Fig. 1). This was shown by the drop in fractal *D* and variance at ~350 m and the crossing of the y-axis from positive to negative values by the correlation at ~300 m. These indicate two potential domains of scale for territory owners, suggesting that their movement paths differed qualitatively at scales of below 300 m and above 350 m. At scales below 300 m, the shape of the fractal *D* curve is similar to that of a correlated random walk, but at scales above 350 m, the shape is more similar to a directed walk (Nams 2006b); thus, perhaps, the owls traveled with more directed movement at larger scales. The owls in the stop phase showed intermediate responses to the wandering and territorial owls.

Almost all variables describing motor skills experienced a gradual but significant transition from the beginning of dispersal to the acquisition of a territory. Wandering individuals with an incomplete information of the environment traveled faster ($F_{2,\ 3}$ = 5.73, p = 0.0048; Table 1) with longer step lengths ($F_{2,\ 3}$ = 7.90, p = 0.0005; Table 1) and had the longest ($F_{2,\ 3}$ = 12.09, p = 0.0001; Table 1) and straightest trajectories ($F_{2,\ 3}$ = 6.51, $p < 0.0021$; Table 1). On the contrary, territory owners moved slower, with shorter and more tortuous movement paths. Floaters in the stop phase clearly represented a transition stage between wandering owls and territory owners, characterized by high traveling speed but quite shorter and more tortuous movement trajectories than floaters during the transition phase (Table 1).

DISCUSSION

Animals living in a changing world have to continuously reduce uncertainty by gathering information (Dall and Johnstone 2002). Our findings suggest that movement behavior experienced a transition from wandering exploratory strategies to a more specific use of spatial resources, when it is supposed that individuals increase the value of familiar space.

At the beginning of dispersal, when individuals frequently travel across unfamiliar (and sometimes unfavorable) areas, they have less time to become familiar with their surroundings. Uncertainty regarding location of conspecifics, predators, and resources may pose significant problems (Stamps 1995; Stamps and Krishnan 1999; Dall et al. 2005). But the costs of uncertainty during dispersal may be reduced by becoming familiar with the spatial and social environment, e.g., searching actively for temporary, stable settlement areas. This phenomenon is evidenced by the observed changes in movement patterns shown by dispersing owls when they reach a settlement area. At that moment, although floaters never show territorial displays (Delgado and Penteriani, unpublished results), they do have a well-defined home range, as has been reported for the floaters of some bird species (e.g., Smith 1978;

Arcese 1989; Zack and Stutchbury 1992). However, our results highlight that the home range of floating birds is not a characteristic of the floating population from their beginning (i.e., when individuals start natal dispersal), but a consequence of the time they have spent as dispersing individuals.

The benefits of local familiarity have been generally linked with the increase in foraging efficiency, breeding performance, and survival (Pärt 1995). By learning the physical and social structures of their environment, floaters can remember the location and qualities of the resources they learn about (e.g., roost sites and foraging areas), attend to conflicting needs and sensory inputs, engage in social interaction, and balance all of these considerations. Even though we did not detect any significant differences in the relative size of the foraging areas among the different life stages, preferred foraging areas within the home ranges used by floaters during both the wandering and the stop phases of dispersal seemed to be less restricted than for territory owners. This could be interpreted as the result of individual adjustment responses of foraging behavior to local habitat structure (Fortin 2002). Since the vital ranges of floating owls are not defended (the floater social status does not include territorial disputes), a non-breeder has a higher mobility within its range, allowing it to displace among different hunting areas more easily than a breeder. Constrictions such as complex social organization and territoriality among neighbors could oblige territory owners to respect the limit of their hunting areas to avoid the high cost of intrusions in neighboring territories and consequent territorial contests.

We consider it important to underline here that the concepts of territory and home range involve pivotal differences that explain some of our results. Home ranges refer to areas: (a) over which an animal travels in its day-today activities to join the most focal elements for their survival; (b) which, due to the scattered distribution of resources, also include large portions of landscape that individuals are just passing through; and, consequently, (c) that are too large to be efficiently protected from intrusions (e.g., eagle owls are territorial only in a restricted portion of the home range; Delgado and Penteriani 2007).

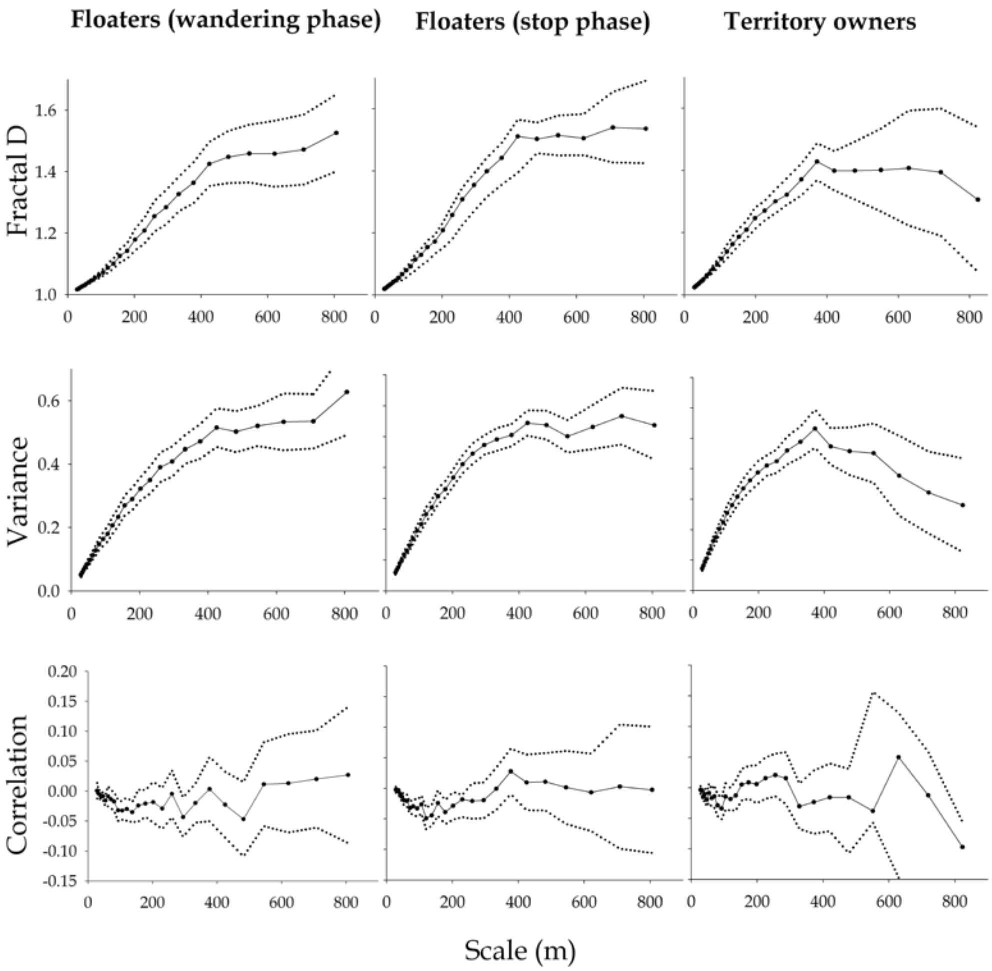

Figure 1. Movement patterns of floating owls (during the wandering and the stop phases of natal dispersal) and territory owners, as represented by three statistics estimated at different spatial scales (more detailed information in the text): a fractal *D*, as a measure of path tortuosity; b variance, an index of variance in tortuosity among path segments; and c correlation, which measures correlation in fractal D between adjacent path segments. Dispersing owls showed homogeneous movement paths (i.e., defining a unique domain of scale), while territory owners showed two domains of scale (i.e., they were traveling with heterogeneous paths): below 300 m and above 350 m. Dotted lines represent 95% confidence intervals.

On the other hand, territory refers to an exclusive portion of the whole home range that is defended to exclude other conspecifics (Maher and Lott 1995) and, consequently, does not overlap with the home range of neighboring residents. These differences between home ranges and territories explain some of the different behaviors we observed. To improve the efficacy of territory acquisition and defense, territory owners exhibit a complex array of behavioral patterns, such as site-specific aggressiveness, the ability to discriminate neighbors from intruders, and contests involving complicated exchanges of communication signals (for more information, see also Penteriani et al. 2007). Floaters, who do not show such behavioral displays because they do not actively defend an exclusive area, can benefit from living in a restricted area through gaining knowledge of the habitat and establishing dominance relations with other floaters and territory owners (Smith 1978; Stutchbury 1991; Bruinzeel and van de Pol 2004).

The needs for territorial tasks (as well as reproductive ones) of territory owners could contribute to the slower movements of territory owners in comparison to floaters during dispersal. For example, territory owners spend large amounts of time calling on posts located close to the core areas of their home range, both for territorial demarcation and mate–mate communication (Delgado and Penteriani 2007). This means long pauses of territory owners on strategic posts, which are not included in the time budget of floaters that mainly roost, hunt, and survey new areas (Delgado and Penteriani, unpublished data).

Differences in the speed of movement may also have generated the detected differences in the patterns of patch use between dispersers and territory owners, which in turn may also be reflecting differences in individual perceptive resolutions (With 1994). Animal perceptive resolution, which may integrate sensory perceptive abilities, physical constraints, and behavioral preference, is inversely related with the rate of movement. The ability of animals to perceive habitat heterogeneity at small scales decreases as speed increase, whereas the spatial extent at which they operate increases (Kolasa and Rollo 1991). Because floaters moved faster than territory owners, floaters perceive environmental patterns at a larger spatial scale, and as a consequence, dispersing owls show a large and unique domain of scale. On the other hand, territory owners can operate at different and well-defined domains of scale, each one reflecting different aspects of their biology (e.g., foraging behavior, crossing home range, and reproduction).

Animal movement behavior can be classified into random and systematic strategies (Fortin 2002). In systematic movement strategies (such as the ones shown by owners and well-settled floaters), which only work when some a priori relevant information is available, the rules to optimally cover a given area are based on quite fixed and controlled plans. By contrast, in a random strategy (such as the one shown by wandering floaters), animals must attempt to move in order to optimize their chances of locating resources (i.e., food, mates, shelter, breeding habitats), the search rules rely on stochastic processes. Although it is not possible to completely neglect the existence of chance in nature, sensorial or cognitive improvements could override the need of random search in nature by, e.g., creating more and better sensory cues, improving high-level environmental information processing mechanisms, and synchronizing spatial variations of the abundances of resources.

Dispersal costs are many and might include the risk of starvation and other mortality (see Stamps et al. 2005 and reference therein). In general, animals dispersing through an inhospitable and unknown habitat should follow straighter paths, to better avoid redundant searches and to locate a patch as quickly as possible (Zollner and Lima 1999). Wiens et al. (1995) found that darkling beetles (*Eleodes obsoleta*) move in straighter paths through highrisk areas than they do through low-risk ones. A variety of other organisms (Crist and MacMahon 1991; Madison 1997) follow straighter paths when displacing long distances through unknown habitats. When habitat features are known, as is the case for floaters during the stop phase and territory owners, individuals should be able to efficiently regulate their movements (Klaassen et al. 2006): owls in the stop phase adjusted the length and the tortuosity of their movements, showing movement patterns more similar to territory owners than wandering floaters.

To conclude, while spatial familiarity is undoubtedly one of the multiple key factors in determining movement patterns, the patterns that we recorded can be also considered to be the result of diverse individual needs associated with different social status. That is, two non-mutually exclusive elements affect movement behavior: learning of the spatial environment that individuals move across and social status of the individuals (e.g., wandering floaters vs. breeders).

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CAPÍTULO 5

Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species

Campioni L, Delgado MM, Lourenço R, Bastianelli G, Fernández N and Penteriani V (second review) *OECOLOGIA*

Variación individual y espacio-temporal del comportamiento de uso del dominio vital en una especie territorial de larga vida

RESUMEN

A pesar de que los estudios sobre el comportamiento relacionado con el uso del dominio vital de los animales hayan evolucionado exponencialmente en el campo teórico, analítico y tecnológico, la identificación de los factores responsables de dicho comportamiento sigue siendo todavía un campo de investigación con muchos desafíos y con preguntas sin contestar. Sin embargo, muy recientemente se ha creado un marco conceptual integrado para el estudio del comportamiento de uso del dominio vital de los animales, que considera este comportamiento como el resultado del efecto simultáneo de procesos temporales, espaciales e individuales con potenciales consecuencias a nivel de población. Utilizando un aproximación integral, estudiamos el efecto de factores externos e internos en la variación del comportamiento del uso del dominio vital de 34 reproductores de búhos real *Bubo bubo*. El comportamiento del uso del dominio vital se estudió a través de un análisis complementario del uso del espacio, patrones de movimiento y ritmos de actividad a distintas escalas espaciales y temporales. El efecto de las diferentes fases del ciclo biológico fue significativamente evidente en los patrones de movimiento, siendo los machos los individuos que se movían con mayores distancias durante los períodos de incubación y de pollo nidícola. Tanto los factores externos (es decir, la estructura y composición del hábitat) como los internos (es decir, el sexo y el estado de salud) juegan un papel importante en el comportamiento del uso del dominio vital. Ampliando la escala temporal, encontramos que el tamaño del dominio vital y de las aéreas de mayor actividad estaban negativamente correlacionadas con la heterogeneidad del paisaje. Además, los reproductores machos mostraron (a) un dominio vital y áreas de mayor actividad de tamaños más pequeños, (b) una estructura más compleja del interior del dominio vital y (c) una tasa de movimientos más elevada. Asimismo, individuos en mejor condición física presentaban una estructura más simple del interior del dominio vital. Por último, los efectos inter- e intra-individulales contribuyeron a explicar el comportamiento del uso del espacio y los patrones de movimiento durante el ciclo biológico. En un ambiente estable y homogéneo como el que hemos analizado, las diferencias de comportamiento entre individuos puede hacerse más evidente, representando uno de los factores cruciales en el patrón de comportamiento de los individuos de una misma población.

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ABSTRACT

Despite the fact that investigations of home range behaviour have exponentially evolved on theoretical, analytical and technological grounds, the factors that shape animal home range behaviour still represent an unsolved question and a challenging field of research. However, home range studies have recently begun to be approached under a new integrated conceptual framework, considering home range behaviour as the result of the simultaneous influences of temporal, spatial and individual-level processes, with potential consequences at the population level. Following an integrated approach, we studied the influence of both external and internal factors on variations in the home range behaviour of 34 radiotagged eagle owl (*Bubo bubo*) breeders. Home range behaviour was characterised through complementary analysis of space use, movement patterns and rhythms of activity at multiple spatio-temporal scales. The effects of the different phases of the biological cycle became considerably evident at the level of movement patterns, with males travelling longer distances than females during incubation and nestling periods. Both external (i.e., habitat structure and composition) and internal (i.e., sex and health state) factors explained a substantial amount of the variation in home range behaviour. At the broader temporal scale, home range and core area size were negatively correlated with landscape heterogeneity. Breeding males showed (a) smaller home range and core area sizes, (b) more complex home range internal structure and (c) higher rates of movement. The better the physiological condition of the individuals was, the simpler the internal home range structure. Finally, inter- and intra-individual effects contributed to shaping space use and movement patterns during the biological cycle. Because of the plurality of behavioural and ecological processes simultaneously involved in home range behaviour, we claim that an integrative approach is required for adequate investigation of its temporal and spatial variation.

Keywords: spatial ecology, animal movement, behavioural consistency, *Bubo bubo*, homogeneous environment.

From early observations regarding the fundamental characteristics of animal movement within a limited space ("…most animals and plants keep to their proper home" Darwin 1861) to the advent of sophisticated telemetry technology, such as GPS devices (Cagnacci et al. 2010), for tracking animal movements in challenging environments and conditions, the study of home range behaviour has exponentially evolved on theoretical, analytical and technological grounds, which have now diverged into separate lines of research (Börger et al. 2008; Kie et al. 2010; Smouse et al. 2010). However, the factors that shape animal home range behaviour (i.e., restricted movements in finite areas) still represent an unsolved question and a challenging field of research (Hays 2008). Home range behaviour is comprised of complex and dynamic patterns of space use resulting from routine activities associated with basic aspects of species life-histories (Börger et al. 2006). While the intrinsic complexity of home range behaviour and its consequential spatial expression (i.e., home range patterns) could be the result of potential influences of both internal (e.g., body condition, reproductive status) and external (e.g., landscape structure and composition, food availability) factors, the dynamic nature of home range behaviour may be the consequence of temporal changes of internal and external factors during an individual's lifetime (Börger et al. 2008). Specifically, changes in the internal state of individuals may determine the specific time allocated to different behaviours (e.g., food acquisition, predator avoidance and landscape exploration), thus affecting the properties of the resultant home range patterns. Accordingly, the time allocated to different behaviours may have relevant consequences at both the individual and population levels through modulating survival, reproduction and, as an end result, population dynamics (Morales et al. 2010).

Recently, home range behaviour has begun to be approached from a new perspective intended to redirect previous disconnected areas of knowledge to an integrated conceptual framework that recognises home range behaviour as the result of the simultaneous influences of temporal, spatial and individual-level processes

(Börger et al. 2006; Börger et al. 2008; Horne et al. 2008; Indermaur et al. 2009; van Beest et al. 2011). This integrative approach is particularly needed when considering that different home range patterns can emerge from multiple spatio-temporal scales (e.g., McLoughlin and Ferguson 2000; Anderson et al. 2005; van Beest et al. 2011). Following this integrated approach, we investigated here the influence of both external and internal factors on the variations of home range behaviour in a long-lived, territorial (i.e., the same home range is expected to be occupied over many years) nocturnal raptor, the eagle owl (*Bubo bubo*), during different phases of its biological cycle and at different spatial scales. We expected to detect the concurrent action of three main factors. Firstly, the effect of the individual changing needs during different periods of the year. Because each period of the biological cycle entails specific tasks (e.g., territorial and sexual displays, feeding of young), the home range behaviour is expected to change over the year. Secondly, the physical characteristics of the nest site surroundings. Because the structure and composition of the home range environment and the availability of the main trophic resources have been shown to represent some of the key factors determining differences in owner's behaviours (Saïd et al. 2009; Rivrud et al. 2010), it is also to be expected that individuals inhabiting areas characterised by different environmental conditions should show different behaviours and home range structures. Finally, the characteristics of the home range owners. If variations in home range behaviours are not only based on external factors but also on the intrinsic characteristics of the breeders (i.e., their sex and physiological condition), then we should expect that behaviours and home range features will also be influenced by individual heterogeneity. Shifting from a more general to a species-specific perspective, we may also expect that (a) males should present higher activity rates than females because they perform most of the territorial displays and that the home ranges and core areas of males should increase during the incubation and nestling periods, when males have to find food for both females and chicks, and successively decrease during the post-fledging dependence period, when breeders frequently follow fledglings during their relatively short displacements around the nest (Delgado et al. 2009); (b) habitat heterogeneity and high food availability should decrease both home range sizes and daily movements; and (c) because of their extremely territorial behaviour, males should exhibit smaller home ranges than females, as females are allowed to intrude into the territories of neighbouring pairs with less conflict (Penteriani et al. 2007a).

MATERIALS AND METHODS

Data collection

This study was conducted in a hilly area of the Sierra Norte of Seville (Sierra Morena massif) located in south-western Spain. From 2004 to 2010, 34 breeding individuals (24 males and 10 females) from 24 nests were radiotracked. Each individual was fitted with a 30-g radio-transmitter using a Teflon ribbon backpack harness (Biotrack Ltd, Wareham BH20 5AJ, Dorset, UK; www.biotrack.co.uk). The mass of the backpack was less than 3% of the mass of the smallest adult male (1550 g) in our population (mean ± SE = 1667 ± 105 g). The transmitters included a mercury posture sensor that allowed us to record individual activity (roosting vs. movement) through changes in the frequency of the signal (Penteriani et al. 2008). We trapped breeding individuals using two methods: (a) simulating an intrusion with a taxidermic mount and playback of a male call (see Penteriani et al. 2010 for more details), during which a net behind the mount caught responding individuals that only included males because this is the sex that generally engages in aggressive interactions towards intruders (Penteriani et al. 2007a); and (b) using a bow-net (Northwoods Limited, Inc., Rainier, Washington) placed in the nest when nestlings were 20–35 d old (i.e., when they were already able to thermoregulate). Specifically, nestlings were moved to a box with a metal grid, making them visible to their parents, which were caught when they returned to the nest. After each bow-net trapping session (which lasted from sunset to sunrise), we fed the nestlings and released them into the nest. The individual manipulation was always safe: during 7 years of trapping and continuous radiotracking of breeders (and >100 dispersing individuals), we never recorded a potential adverse effect of the backpacks on bird survival or on breeding performance.

We followed territory holders individually throughout the night (from 1 hour before sunset to 1 hour after sunrise; total time duration = 3333 hours) during 296 continuous radiotracking sessions (mean number of radiotracking session per owl ± SD = 10 ± 6). We recorded a new location (total number of locations = 5298) each time we detected a change in the position of the focal individual (for more detail on movement detections, see Penteriani et al. 2008; mean number of locations per radiotracking session ± SD = 17.2 ± 5.2). Therefore, the number of recorded locations represented the effective number of movements for an individual during each night. The continuous radiotracking sessions (mean time duration of a radiotracking session ± SD = 11.3 ± 1.8 hr) were performed year-round in an attempt to obtain an homogenous dataset over the different phases of the owl's biological cycle until either the individual died or the battery of the transmitter ran out (lifespan of transmitters from ~1.5 to ~2.5 years). The locations of radiotagged individuals were determined by triangulations using three-element hand-held Yagi antennae (Biotrack) with Stabo (XR-100) portable ICOM receivers (IC-R20). Triangulations were generally performed within a small range of distances of the focal owl (100–300 m), with an accuracy of 83.5 ± 49.5 m (mean ± SE) (Penteriani and Delgado 2008a). This value was estimated in cases when, after a fix, we needed to locate an individual to manipulate it during field experiments (Penteriani et al. 2007b) or to record the cause of mortality when the individual died. The tracking did not appear to affect the behaviour of the owls, which generally appeared to ignore the observer (Delgado et al. 2009a).

Characterising home range behaviour

Space use

Space use was studied at two different temporal scales. First, the seasonal scale relies on the biological cycle of the species, i.e., the pre-laying (September to mid-January, period 1), incubation (mid-January to mid-March, period 2), nestling (mid-March to early April, period 3) and fledgling/post-fledging dependence (F/PFD) (early-April to August, period 4; see: Delgado and Penteriani 2007) periods. Second, the overall scale encompassed the entire period during which we were able to follow an individual (mean number of months during which each radiotagged owl was followed ± SD = 15 ± 8; range = 5-33). That is, this scale is not linked to the biological cycle and it has been only used to describe general patterns (i.e. global home range and core area sizes, core area-nest distance).

Working at two different spatial scales (home range and core area), we quantified the space use of tagged individuals using 4 descriptors. We first estimated (1) home range size through fixed-kernel methods (Worton 1989) using the Animal Movement Extension for ArcView 3.2 (Hooge and Eichenlaub 2000). We calculated the 50% and 90% fixed kernels using the least squares cross validation (LSCV) procedure (Silverman 1986) to determine the optimal value of the smoothing parameter for a given kernel and sample size (Seaman et al. 1999). The LSCV process generates the best value of the smoothing parameter for multimodal data with respect to the other methods (Silverman 1986; Worton 1989; Seaman and Powell 1996). We chose the 50% kernel to represent the core areas after a detailed exploratory analysis because it allows (i) including a sufficient number of locations and (ii) comparisons with similar studies. To establish home range boundaries, we preferred to use density isopleth values of 90% because this value fitted better with our data, giving more accurate estimates when analysing more than 30 relocations. In fact, when visually exploring both 90 and 95% isopleths, the density isopleth values of 95% over-estimated the areas crossed by tagged individuals. We used all data available for each individual, focusing more on the biological process that shaped home range internal structure (De Solla et al. 1999) than on obtaining statistical independence of the relocations. This was possible because we followed each focal owl during the entire period of its nocturnal activity, thus recording its entire set of movements. Finally, because individual variation in the number of relocations may potentially contribute to variability in estimates of space use (Kernohan et al. 2001), we regressed the number of relocations with home range size, but no relationships were found ($r^2 = 0.008$; $F_{1,25} = 0.19$; $P = 0.67$).

Second, with the aim of characterising the internal structure of each home range, we estimated (2) the size of core area(s), i.e., the areas most frequently used within the home range. Because it was not always possible to distinguish between the core area of the nest and the core area(s) where individuals repeatedly hunted every night, in the present study, core area(s) represented both nesting and hunting areas. Again, when regressing the number of relocations with core area size, we did not find any relationship ($r^2 = 0.008$; $F_{1,25} = 0.81$; $P = 0.38$). We also estimated (3) the number of core areas per home range as a measure of the amount of most frequently visited sites; and (4) the distance between the exact location of the nest and the geometrical centre of each core area.

Movement patterns

Individual nightly movement behaviour was characterised by five variables: (1) total distance, as the sum of the distance between successive steps of the nightly displacements; (2) step length, as the distance between successive locations; (3) speed, as the step length divided by the time interval between successive locations; (4) turning angle between successive movements; and (5) time step, as the time elapsed between successive moves. The movement variables were analysed at two different spatial scales, home range and core area, and two temporal scales, overall and seasonal.

Rhythms of activity

The nocturnal activity of tagged owls was estimated using two indices: (1) core area activity, i.e., the % of time an owl spent inside the core area(s); and (2) individual movement rates, calculated as the movement frequencies (i) per night and (ii) within the core areas. Core area activity is a measure of the time devoted to main activities, such as hunting, feeding (including nestling/fledgling feeding and female feeding during breeding if the focal owl was a male) and territorial defence. Because night lengths vary year round, we standardised the core area activities and movement rates per night by dividing them by the total time the owl was active each night; movement rates within core areas were standardised to account for the total amount of movements performed by the focal owl per night.

Laying dates and breeding success

During the entire study period, for each of the 24 nests where we trapped breeders, we recorded (1) the egg laying date and (2) the number of fledglings. Egg laying dates were determined by estimating the age of nestlings following Penteriani et al. (2005) and assuming 33 days of incubation. Both the egg laying date and number of fledglings were used as response variables to detect potential effects of home range behaviour and internal and external factors on breeding phenology and success.

Individual characteristics and internal state

We correlated space use, movement patterns, rhythms of activity and breeding success with three characteristics of an individual: (1) sex, determined by molecular procedures using DNA extracted from blood (Griffiths et al. 1998); (2) age, estimated based on the moult pattern of the feathers (Martínez et al. 2002); and (3) haematocrit (HT), as an indicator of physiological condition. HT has been widely used as an indicator of nutritional status because nutritional deficiencies result in anaemia due to shortages in essential amino acids (e.g., Costa and Macedo 2006). To obtain HT values, blood samples were collected and stored in tubes with heparin at 4° C until arrival at the laboratory, where they where centrifuged for 10 min at 4000 rpm.

External factors

To determine the possible influence of external factors on home range behaviour and breeding success, we estimated three variables (detailed in the following Eagle owl diet and rabbit census and Landscape characteristics of home ranges and core areas): (1) as diet analyses showed that the rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) is the main prey of our eagle owl population (mean biomass percentage of rabbit in the diet = 62.0 ± 19.1%, range = 16-94%) and given the distribution overlap of both species (Delibes-Mateos et al. 2007), we considered rabbit abundance within the home ranges of tagged individuals as an indicator of habitat quality (González et al. 2008); (2) the contribution of rabbits (% of biomass) to the diet of breeders; and (3) landscape characteristics of home ranges and core areas.

Eagle owl diet and rabbit census

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 24 nest sites. Following Lourenço (2006), we identified 4203 prey items using identification keys for bones and feathers and comparisons with a reference collection (Laboratory of Archaeo-sciences, IGESPAR, Portugal), followed by determining the minimum number of individuals. When possible, prey items were identified to the species taxonomic level. We calculated the biomass percentage for each prey species using its mean weight value from bibliographic references or bone measurements to estimate the weight of each individual (Cramp and Simmons 1977–1994; Donázar and Ceballos 1989; MacDonald and Barret 1993).

The relative rabbit abundance was estimated in the 24 breeding areas using rabbit faecal pellet counts (i.e., latrine counts). Latrine counts have been previously used as an index to estimate rabbit abundance (Palma, Beja and Rodrigues 1999) and are a good indirect estimator of rabbit abundance in large-scale studies (Palomares 2001a, b; Fernández 2005). The census was conducted in 2009 from the beginning of March to the beginning of May. This period corresponds to the nestling and F/PFD phases of eagle owls, when it is expected that parents exhibit the highest hunting effort. To obtain comparable indices of prey abundance (IKA) for each territory and around each nest, we drew a circular plot with an area equal to the mean eagle owl home range size in our study population, which was calculated using the Minimum Convex Polygon method (MPC, Hayne 1949). Inside these plots, we walked 2.2-km-long transect lines, recording the number of latrines found on both sides of each transect within a 4 m width. Latrine counts were always performed by the same observers (walking at the speed of 1 kmh^{-1}), and the IKA was expressed as the number of latrines per km of transect; the total length of transects walked was 150 km, in which we counted 3440 latrines (mean ± SE: 20.6 ± 12.4 km-1, range: 7.7- 46.0 km^{-1}). Rabbit density over the years can be considered relatively stable in our study area: rabbit management and frequent releases inside our study area have created extremely favourable and steady trophic conditions (Penteriani and Delgado, unpublished data).

Landscape characteristics of home ranges and core areas

We measured landscape characteristics by intersecting a digital layer representing the boundaries of the owl's home ranges and core areas with a map of landcover elements (scale 1:25.000, Junta de Andalucia, Consejería de Medio Ambiente, 2003). Landscape composition was analysed at the two spatial scales previously used in the analyses of home range behaviour. Following Aebischer et al. (1993), with the aim of selecting only those habitat types that were most relevant for eagle owls, we (a) first performed a compositional analysis to test owl habitat selection and then (b) classified the landscape at the two different spatial scales. At the fine-grained spatial scale of analysis (i.e., the core area), landscape composition was represented by 10 landcover types: urban areas, water bodies, forests, dense scrublands with trees, sparse scrub with trees, herbaceous vegetation with trees, scrublands, low vegetation, woody crops and herbaceous. For the coarse-grained scale (i.e., the home range), landscape composition was simplified into 6 categories: urban /crops areas, water bodies, dense vegetation (forest and dense scrubs with trees), sparse scrub with trees, herbaceous areas with and without trees, and scrublands. These habitat types were then employed to model the variation in individual home range behaviour. Additionally, we used edge density (i.e., the total length of the patch edge per unit area within each landscape; Elkie et al. 1999) as a proxy for the effect of habitat heterogeneity (Donovan et al. 1995; Kie et al. 2002; Anderson et al. 2005). The GIS application ArcView 3.2 and its extension Patch Analyst (Elkie et al. 1999) were used for the analyses of landscape characteristics.

Data analysis

We constructed a set of a priori competing models starting from the simplest null model (intercept only model) to a full model that included all of the explanatory variables (see Tables S1-S4 in Online Resource for fitted variables).

First, we conducted a graphical analysis for the entire set of explanatory variables and checked for correlations (Spearman's rank correlation) among predictors, excluding variables with $r_s \geq 0.6$. For each analysis, we used different subsamples, represented by those owls for which it was possible to obtain the required information. Thus, in each analysis, the type and number of explanatory variables were selected on the basis of their biological relevance, our interest and sample sizes. Because we had repeated measures for the same individual within and between years, we included individual identity (ID), together with nest site nested in year as first-, second- and third-level random effects, respectively. Following Pinheiro and Bates (2004), the significance values of random effects were estimated using the Akaike information criterion (AIC). When random factors did not improve the model's likelihood value, we built a less complex model class. The models were checked for unequal variance structures of the within-group errors by investigating relevant model diagnostic plots (plots of residuals vs. fitted values for the relevant model and variable; Pinheiro and Bates 2004) and by comparing models with and without different variance functions using the AIC. If selected, following Pinheiro et al. (2009), we implemented variance functions in the models. We also checked for any remaining dependencies among the within-group errors after the fixed and random effects were fitted. If present, these were modelled using correlation structures. The spatial autocorrelation between home ranges and core areas was corrected using the mean coordinates of each home range and core area, while movement variables were corrected using the spatial coordinates of each fix (UTM coordinates). In all cases, different correlation structures were specified, and if necessary, the most appropriate was selected by comparing the AIC values of the fitted models (see Pinheiro and Bates 2004). Detection of the most parsimonious hypothesis was based on (a) model selection procedures using the AIC, which allows the comparing of multiple working hypotheses and weighting their level of support in the data; or (b) a second order AIC derivation, the AICc, which is appropriate when the ratio of the sample size to the number of parameters is less than 40 (Burnham and Anderson 2002). Two AIC statistics were also calculated for each model: ΔAIC and AICw, which indicate the probability that the model selected is the best among the different candidates. Values of $\Delta AIC \leq 2$ were used as the criterion for selecting the best models, i.e., those with substantial support from the data (Burnham and Anderson 2002). For simple linear models (LMs), we also reported r^2 values. For models including random terms, we presented (a) the intraclass correlation coefficient (hereafter ICC, see Zuur et al. 2009), which is a measure of the correlation between observations from the same group (i.e., owl ID) and is expressed as ICC = $d^2/d^2 + \sigma^2$, where d^2 is the covariance between any two observations for the same individual and its variance is $d^2 + \sigma^2$; and (b) a generalised R^2 for random effect, which provides information about the amount of variation in the data explained by the random effect (i.e., between-individual variation). This parameter was calculated as the squared correlation between the fitted values of the model and the observed values in the data (Zheng and Agresti 2000). Sex was a relevant factor in almost all analyses, but the small sample size of some subsamples did not allow the testing for interactions; therefore, we divided the database into two different subsets: one for males and one for females. Because females rest motionless in the nest during most of the incubation period, no data were available to make inter-gender comparisons in this period. Values are given as the mean ± SD and range. All analyses were performed using the R software package (R Development Core Team 2009). The following specific R functions were performed: (i) adehabitat 1·8·3, for compositional analysis (Calenge 2006); (ii) nlme 3.1-92 (Pinheiro et al. 2009), for linear multilevel mixed-effects models (LMMs), as described by Pinheiro and Bates (2004); and (iii) the lme4 0.999375-28 package for GLMM (Bates and Sarkal 2007) and multcomp (Hothorn et al. 2009) for multiple comparisons.

Post-hoc test for seasonal effects

To obtain additional insights regarding seasonal variations in the owls' space use, movement patterns and rhythms of activity, we used Simultaneous Tests for General Linear Hypotheses, in which multiple comparisons of means were performed using the Tukey Contrasts method (Hothorn et al. 2009). This type of post-hoc test allows for the detecting of differences among all factor levels: in our case, there were four factor levels corresponding to the different phases of the eagle owl biological cycle. Differences among levels were considered significant at $P < 0.05$.

Characterising home range behaviour

Space use

Depending on the nature of the response variables and the presence or absence of random effects, we fitted a suite of different models: (a) LMs, for log-transformed home range size, core area size and core area-nest distance at the overall timescale; (b) LMMs, for the same log-transformed response variables cited above (but at the seasonal timescale), including individual identity (i.e., owl ID) as a random effect; and (c) general linear models (GLMs) for the number of core areas at the overall and seasonal timescales. Because the number of core areas could be 1 or >1, this response variable was modelled using a binomial distribution (0 = >1 core area; 1 = 1 core area).

Movement patterns

Some variables describing movement patterns (total distance, step length, time step and speed) were log+1-transformed and modelled using LMMs at both the home range and core area spatial scales. We always included individual identity as a random effect at the home range spatial scale when fitting the LMMs. Additionally, temporal autocorrelation (using the corExp function in the R library nlme) was included when fitting the step length and speed models, while a variance structure (using the varPower function with the year as a covariate) was used to model the time step. Turning angles were simplified into an index of 1 for positive and 0 for negative angle cosine values (forward and backward movements, respectively) and modelled using a GLM with a binomial distribution. At the core area spatial scale, the entire models included individual identity as a random effect, and the time step and speed models also included year, as a second-level random effects. A temporal autocorrelation (using the corExp function) was fitted to improve the step length, time step and speed models. Finally, at this spatial scale, turning angle was modelled using a GLMM.

Rhythms of activity

While at the core area spatial scale, core area activity was log+1 transformed and modelled together with movement rate using LMs; at the home range scale, movement rate was log+1-transformed and modelled using an LMM, in which year was specified as a random effect.

Laying dates and breeding success

For laying date, we fitted a LMM that included individual identity and nest site as first- and second-level nested random effects. Similarly, the mean number of fledglings was modelled using LM (see Table S4 in Online Resource).

RESULTS

Characterising home range behaviour

Space use

The home ranges of females were larger and showed higher inter-individual variation than the home ranges of males (Table 1); the size of core areas for females was also larger than for males, although the variation in core area size was consistently similar between sexes (Table 1). The size variations of home range and core areas at the overall timescale (Table 1 and Fig. 1) were explained by two models that included the same factors, i.e. edge density (home range model estimates ± SE = -0.006 ± 0.003; core area = -0.007 ± 0.002) and sex (home range model estimates ± SE = -0.596 ± 0.299; core area = -0.333 ± 0.373); a second competing model for core area only included edge density as the unique explanatory variable (Table S1 in Online Resource; Fig. 2). That is, an increase in the amount of edge density, which is a proxy of habitat heterogeneity, at both spatial scales resulted in a decrease of the home range and core area sizes (Table S1 in Online Resource).

With respect to home range and core area size variations at the seasonal timescale (Table S1 in Online Resource), no single model was strongly supported as approximating home range and core area variations (Table 1 and Fig. 3). Additionally, an ICC value (for the owl ID random term) of 0.63 supported this consistency in home range size during each period of the biological cycle. Although in the core area analysis, the model that included sex as a predictor ranked as the second best model, the set of the most supported models included the null model, and thus, it was not possible to distinguish the most plausible model. In summary, our seasonal analyses did not find relevant differences in home range behaviour between sexes or among the four periods of the owl biological cycle. This result was confirmed by post hoc analysis (always $P > 0.05$). Conversely, we observed high between-individual variation in home range size, as shown by the R^2 value for the random term of 0.71 (Table S1 in Online Resource).

When analysing the internal structure of the home ranges at the overall timescale (Table S1 in Online Resource), we first found that the better the physiological condition of the individuals was (i.e., the higher the HT values; 50.28 ± 1.52 %), the simpler the internal structure of their home range, i.e., closer to the nest (model estimate ± SE = -0.053 ± 0.018) and a smaller number of core areas (model estimate ± SE = 0.207 ± 0.111). Additionally, males exhibited a slightly greater number of core areas than females (Table 1); the core areas of males were located at greater distances from the nest than those of females (Table 1).

Regarding our analysis of the internal structure of the home ranges at the seasonal scale (Table S1 in Online Resource), the owls did not show any variation in the internal structure of their home ranges among different phases (Table 1). Finally, none of the models was supported regarding core area-nest distances at the seasonal timescale (Table 1 and Table S1 in Online Resource).

Movement patterns

At the home range spatial scale, the period of the biological cycle affected both total distance (intercept + period1 model estimate ± SE = 8.757 ± 0.060; period2 = 0.228 ± 0.078; period3 = 0.134 ± 0.099; period4 = -0.121 ± 0.060) and step length (intercept + period1 model estimate ± SE = 5.661 ± 0.050; period2 = 0.191 ± 0.048; period3 = 0.086 ± 0.064; period4 = 0.016 ± 0.039; Table 1, Table S2 in Online Resource and Fig. 2). Again, as was found for home range and core area size variations at the seasonal timescale, the between-individual variation (R^2 = 0.25) and consistency (ICC = 0.21) regarding total distance were considerable. Individuals travelled longer distances during incubation and nestling periods than during pre-laying and F/PFD periods (Table 1). Differences in speed could not be discerned because the intercept only model was included as the best supported model. Finally, the best models for turning angle and time step (Table 1) included the combination of two vegetation types (turning angle: dense vegetation model estimate ± SE = 0.004 ± 0.001; sparse scrub:

0.004 ± 0.002) and age (model estimate ± SE = 0.082 ± 0.021), respectively (Table 1 and Table S2 in Online Resource).

At the finer core area spatial scale, speed and turning angle were not related to any of the considered external or internal factors (Table 1). Similarly, despite the fact that step length and time step were sex-dependent, with females travelling in shorter steps at longer time intervals than males (Table 1 and Table S2), the null models always ranked as the most parsimonious for all analyses. Moreover, we observed high intra-individual consistency in speed (ICC values for owl ID = 0.94) and step length (ICC = 0.35), with a moderate percentage of variance ($R^2 = 0.21$) explained by owl ID for step length (Table S2 in Online Resource). Post hoc analysis, at both the home range and core area spatial scales, showed that males and females presented similar movement behaviour at the seasonal scale ($P > 0.05$ for all periods).

Rhythms of activity

The activity patterns of eagle owls (n = 11 males, n = 6 females; number of radiotracking nights = 259) were quite constant year round and did not show any clear differences between periods. Movement rate at the home range spatial scale (0.0276 ± 0.0004 number of movements night length^{-1}, n = 256) was not influenced by any external factor. However, we found differences between sexes, with males (model estimate ± SE = 0.005 ± 0.001) moving at higher rates than females (model estimate ± SE = 0.023 ± 0.001; Table 1 and Table S3 in Online Resource, Fig. 2). At the core area spatial scale, the models that included edge density were always the best supported for explaining variation in the owls' movement (edge density model estimate ± SE = -0.0005 ± 0.0003) and activity rates (edge density model estimate ± SE = -0.0004 ± 0.0002; Table S3 in Online Resource), with individuals showing higher movement and activity rates when the density of edges decreased.

Table1.

Scale		Space use				Rhythms of Activity		
		Home range	*Core area*			*Home range*	*Core area*	
		Home range size (ha)	*Core area size* (ha)	*Core area number*	*Nest-core area distance* (m)	*Movement rate*^{a}	*Movement rate*^{b}	*Activity*^{c}
Overall								
	Male	187.1 ± 28.8	34.1± 6.8	1.5± 0.2	486 ± 64.4	0.028 ± 0.001	0.27 ± 0.01	0.38 ± 0.02
		283.7-548.4	4.4-104.4	1-3	76-869	0.011-0.042	0-1	0-1
		20	19	19	19	216	176	220
	Female	309.7 ± 85.4	56.3 ± 18.5	1.2 ± 0.2	287 ± 99.6	0.025 ± 0.001	0.35 ± 0.05	0.35 ± 0.05
		121.3-695.0	12.3-123.4	1-3	140-731	0.014-10.042	0-1	0-1
		7	7	7	6	40	29	40
	All	218.9 ± 30.8	40.1 ± 6.9	1.4 ± 0.1	438.2 ± 55.5	0.028 ± 0.0004	0.29 ± 0.01	0.37 ± 0.02
		283.7-695.0	4.4-123.4	1-3	76-869	0.011-0.047	0-1	0-1
		27	26	26	25	256	205	260
Seasonal								
Pre-laying	All	149.0 ± 17.7	26.8 ± 3.9	1.6 ± 0.2	485.7 ± 80.7	0.026 ± 0.001	0.28 ± 0.03	0.42 ± 0.03
		23.1-324.1	3.6-589.7	1-3	137-1504	0.013-0.046	0-1	0-1
		21	21	21	21	81	68	75
Incubation	male	156.7 ± 25.3	32.7 ± 6.4	1.3 ± 0.2	522.1 ± 132.4	0.028 ± 0.001	0.30 ± 0.03	0.45 ± 0.04
		28.4-340.1	41.0-760.3	1-3	48-1720	0.018-0.044	0-1	0-1
		15	14	16	15	44	37	41
Nestling	All	136.3 ± 23.3	21.6 ± 5.3	1.9 ± 0.4	509.9 ± 109.6	0.029 ± 0.001	0.30 ± 0.06	0.44 ± 0.07
		57.9-225.0	53.290-462.6	1-3	201-967	0.017-10.047	0-1	0-1
		8	8	8	8	21	15	17
F/PFD	All	218.0 ± 5.4	36.3 ± 6.3	1.6 ± 0.2	504.4 ± 68.7	0.028 ± 0.001	0.30 ± 0.02	0.39 ± 0.03
		39.4-570-0	52.2-940.2	1-3	80-1140	0.011-0.047	0-1	0-1
		20	20	22	20	114	85	103

Scale		Movement patterns								
		Home range scale					*core area scale*			
		total distance (m)	*step length* (m)	*speed* (m/min)	*time step* (min)	*cos (turning angle)*	*step length* (m)	*speed* (m/min)	*time step* (min)	*cos (turning angle)*
Overall										
	Male	6881 ± 203.3	414.5 ± 5.6	32.3± 1.1	33.5 ± 0.51	0.03± 0.01	244.1 ± 7.2	18.5 ± 1.4	33.3 ± 1.3	0.02 ± 0.02
		1543-16190	3.2-2844	0.001-1199	1-217	-1-1	4-2096	0.001-403.8	1-195	-1-1
		231	4062	4067	4066	4068	823	800	797	760
	Female	6713 ± 489.8	437.8 ± 15.3	36.8 ± 3.7	36.8 ± 1.38	0.03 ± 0.03	220.1 ± 16.5	21.7 ± 4.3	42.1 ± 2.4	0.01 ± 0.05
		1152-14350	14.1-2843	0.07-1254	1-213	-1-1	14-2075	0.07-397.9	1-195	-1-1
		46	705	690	689	689	184	175	181	177
	All	6322 ± 187.4	418.0 ± 5.2	33.0 ± 1.1	34.0 ± 0.5	0.03± 0.01	224.5 ± 6.64	19.0 ± 1.4	34.9 ± 1.1	0.02 ± 0.02
		1701-16190	3.2-28440	0.001-1254.0	1-217	-1-1	4-2096	0.001-403.8	1-195	-1-1
		277	4767	4757	4756	4757	1007	975	978	973
Seasonal										
Pre-laying	All	6912 ± 320.4	396.2 ± 8.1	31.9 ± 1.71	36.35 ± 0.89	0.03 ± 0.01	231.0 ± 10.7	21.8 ± 2.8	36.7 ± 2.0	0.01 ± 0.04
		1701-16190	3.2-2317.0	0.001-1254	1-213	-1-1	4-1628	0.001-403.8	1-178	-1-1
		88	1632	1632	1651	1631	355	349	350	331
Incubation	male	8573 ± 514.5	469.0 ± 13.4	31.6 ± 1.79	33.82 ± 1.12	0.03 ± 0.02	246.2 ± 18.1	16.1 ± 1.9	35.6 ± 2.6	0.07 ± 0.05
		2983-15680	6.6-2844.0	0.001-845.6	1-213	-1-1	4-2096	0.07-201.4	1-195	-1-1
		43	865	864	866	868	185	179	181	179
Nestling	All	7077± 489.7	402.7 ± 15.9	21.9 ± 1.41	33.17 ± 1.37	0.04 ± 0.03	241.1 ± 23.5	20.2 ± 6.0	32.2 ± 2.7	0.04 ± 0.07
		3637-13500	4.5-2310.0	0.001-605.2	1-157	-1-1	4-1174	0.11-397.9	1-103	-1-1
		23	408	405	391	409	88	84	84	79
F/PFD	All	6168 ± 275.2	416.7 ± 8.8	31.9 ± 1.54	32.87 ± 0.74	0.03 ± 0.01	204.0 ± 10.1	17.6 ± 2.0	33.5 ± 1.6	0.01 ± 0.04
		1792-15310	5.8-2843.0	0.001-1249	1-217	-1-1	6-2075	0.07-363	1-195	-1-1
		123	1862	1844	1848	1849	379	363	363	348

Laying dates and breeding success

Laying dates ranged from 24-Dec to 08-Apr, while the mean number of fledgling chicks was 2.18 ± 1.03 (range: 1-4 chicks). Although none of the factors considered seem to affect owl laying dates (Table S4 in Online Resource), variation in the number of fledglings was better explained by two univariate competing models (Table S4 in Online Resource): the pairs successfully rearing the highest number of fledglings were those (1) with widest core areas and (2) that consumed the highest % of rabbits.

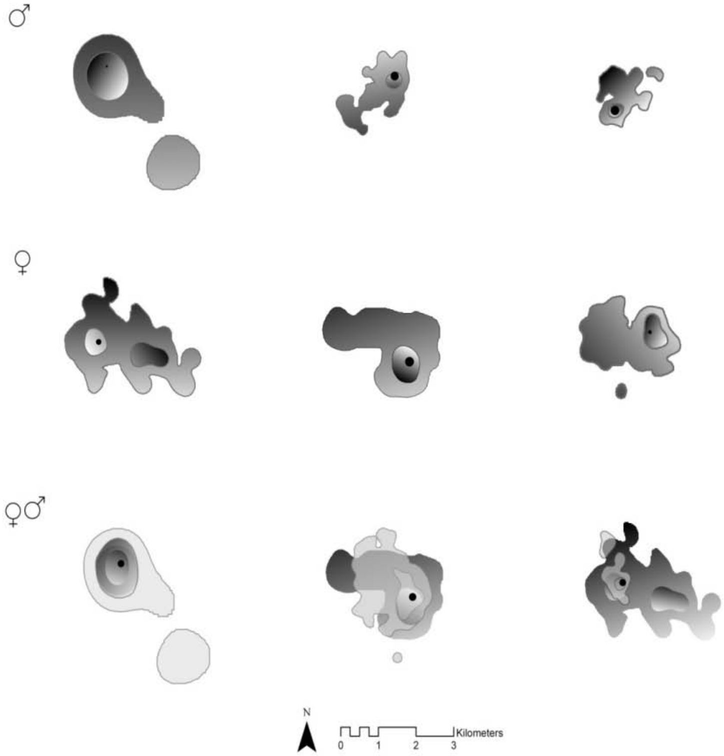

Figure 1. Examples of several eagle owl (*Bubo bubo*) home range and core area size variations among males, females and both mates from the same pair, at the overall time scale (see the main text for more details). From left to right are showed maximum, mean and minimum home range and core area(s) size found among tagged owls. When presenting home range variations between mates from the same pair, dark grey and bright grey represent males and females, respectively.

DISCUSSION

Our long-term radiotracking study of many individuals followed continuously throughout the year, support the importance of considering a combination of different spatio-temporal scales and individual-level processes when studying home range behaviour. We showed that (*i*) external and internal determinants may simultaneously affect the home range behaviour of owners and that (*ii*) their relative effects differ among different spatio-temporal scales. Our most important results indicated that (a) the effect of the different phases of the biological cycle became evident at the level of movement patterns; (b) both external (i.e., habitat structure and composition) and internal (i.e., sex and health state) factors explained a substantial amount of the observed home range behaviour in terms of space use, movement patterns and rhythms of activity; and (c) among individual heterogeneity and within-individual consistency in behaviours played important roles in shaping home range characteristics.

With respect to temporal implications of the observed home range behaviour, as expected, the owls showed seasonal variations in their movement patterns at the home range scale. Males travelled longer distances during the incubation and nestling periods, probably because they play a key role during the beginning of the breeding period, as they are responsible for female feeding and breeding territory defence (Penteriani and Delgado 2008). These two activities may require males to continuously move back and forth from and to the nest site, crossing extensive portions of their home range and core area(s) to (a) prevent intruders from approaching their breeding areas; (b) perform territorial displays (eagle owl territorial displays do not end after the egg-laying period; Delgado and Penteriani 2007); and (c) search for food. It is well known that reproduction is energetically expensive for both mates, but from a movement perspective, males have to sustain more continuous activities, travel over longer distances and undergo higher rates of movement. Additionally, most likely due to offspring-parent interactions throughout the F/PFD period, both males and females exhibited decreased displacements during this phase of the breeding cycle. From fledging, when sibling movement skills are still limited, to the post-fledging dependence period, when the distances travelled by juveniles from the nest increase, the explorations of the natal area by young birds are mainly limited to near the nest (Delgado et al. 2009). At this stage, because siblings are still under the nearly continuous control of their parents (females at least, Delgado et al. 2009), they might be forced to move shorter distances than in other periods.

Despite these temporal variations in movement patterns, eagle owl home range behaviour as a whole did not vary across the biological cycle, suggesting extremely stable home ranges. Constant and well-established home ranges may be the result of systematic movement strategies (Fortin 2002), such as those shown by the owners of a breeding site (Delgado et al. 2009), that work when *a priori* information is available and allow optimal coverage of a given area based on relatively fixed and controlled plans. In fact, sedentary species are expected to exhibit strong interactions between individual behaviours and their spatial context (Börger et al. 2006). However, although we did not take into account the possible effect of conspecific density in the present study, the extremely high density of breeders in our study area, combined with the high territoriality of males (Penteriani et al. 2008), could have strongly limited conspicuous home range expansions/contractions. Each eagle owl home range seems to have a well-determined location and size throughout the year. Under this framework, considerable alterations of home range boundaries among periods are not allowed, whereas within-boundary movements (e.g., total distance and step length) were somewhat variable over the temporal scale examined in this study.

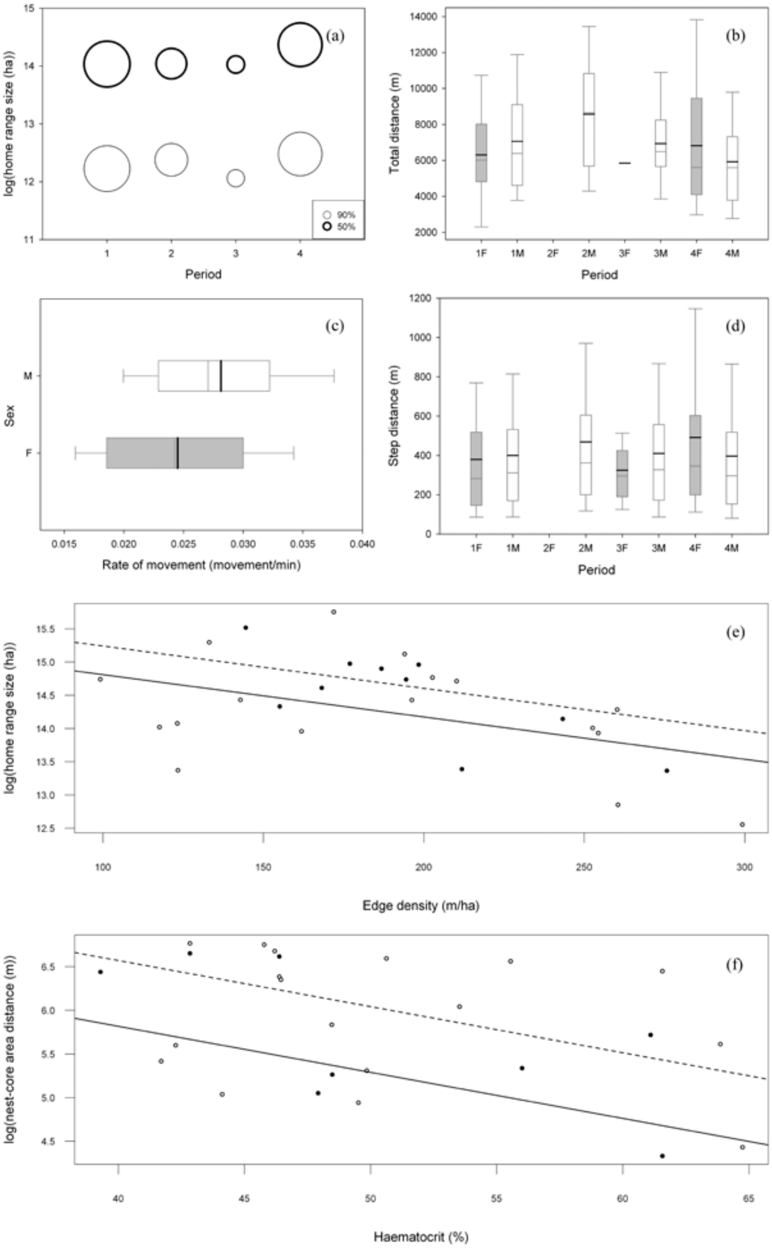

Figure 2. Main patterns of eagle owl (*Bubo bubo*) space use, movements and rhythms of activity in relation to internal and external factors. (a) Size variation of home range and core area (ha) per period (sexes are grouped together). Bubble dimensions are proportional to the different sample sizes. (b) Box plot of the total distances (m) moved by males (white) and females (grey) during different periods of the biological cycle: pre-laying (1), incubation (2), nesting (3), and fledging/post-fledging dependence (4) periods. For each box plot the 25% and 75% quartiles, the mean (bold line) and the median (thin line)

are presented. (c) Box plot of movement rate [number of movements min-1)] by males (white) and females (grey) at the overall time scales (see the main text for more details). For each box plot the 25% and 75% quartiles, the mean (bold line) and the median (thin line) are presented. (d) Box plot of step length (m) moved by males (white) and females (grey) during the different periods of the biological cycle: pre-laying (1), incubation (2), nesting (3) and fledging/post-fledging dependence (4) periods. For each box plot the 25% and 75% quartiles, the mean (bold line) and the median (thin line) are presented. (e) Plot of log-transformed home range size (ha) in relation to edge density (m ha-1) at the overall time scale for males (open circle) and females (filled circles). Lines represent the predicted effect for males (continuous line) and females (dashed line) separately. (f) Plot of log-transformed core area-nest distance (m) in relation to haematocrit value (%) at the core area and overall spatio-temporal scale (see the main text for more details) for males (open circle) and females (filled circles). Lines represent the predicted effect for males (continuous line) and females (dashed line) separately.

Home ranges may represent an invisible link between the movements of individuals and the distribution of the resources necessary to survive and reproduce (Börger et al. 2008). Hence, if such resources are heterogeneously distributed among different habitat types, or if their occurrence is influenced by landscape structure, then landscape properties can affect habitat selection and use, which in turn, can modify home range spatial patterns (Pasinelli 2000; Indermaur et al. 2009). Our findings indicate that most of the variation in home range and core area size is principally determined by edge density, which is a proxy of landscape heterogeneity and fragmentation. As previously observed (e.g., Kie et al. 2002; Saïd and Servanty 2005), the dimensions of home ranges may be negatively correlated with the density of edges; i.e., most complex landscape matrices determine smaller home ranges. Higher densities of edges have the potential to aggregate different patch types in a reduced space (Tufto et al. 1996; Revilla et al. 2004), consequently determining a more clustered distribution of basic resources. As an end result, such crowded resources can reduce individual rates of movement and, thus, home range sizes.

Additionally, edge density has been considered to be a good predictor of the distribution of areas suitable for the reproduction of another Mediterranean rabbit-specialist species, the Iberian lynx (*Lynx pardinus*), as increased edge density favours rabbit abundance (Fernández et al. 2003). Specifically, the structure of edges between shrubs and open areas allows rabbits to optimise their spatial behaviour and to easily access feeding and refuge patches (Lombardi et al. 2003; Lombardi et al. 2007). Because of the dependence of rabbits on this combination of edges, shrubs and open patches, it is not surprising that we also found a correlation between certain components of eagle owl movement patterns (i.e., turning angle) and rhythms of activity (i.e., movement rates) with landscape structure and composition. Thus, as predicted, the spatial heterogeneity of nesting site surroundings can affect the characteristics of a home range, which reveals individual decisions at this spatial scale (Hinsley et al. 1995; Knick and Rotenberry 1995). In fact, both the quality and the structure of habitats may engender diverse costs and benefits and, consequently, cause conspicuous behavioural differences (Diffendorfer, Gaines and Holt 1995), with landscapes being frequently highlighted as major factors driving animal movement patterns (e.g., Nathan et al. 2008; Delgado et al. 2010).

Given the general importance attributed to prey availability and distribution in shaping the behaviours of predators (e.g., Marquis and Newton 1981; Selås and Rafoss 1999; Fernández et al. 2009), we expected that owl home range behaviour would also be highly responsive to rabbit abundance, with the owls varying their space use behaviour according to prey density. In contrast to our expectations, rabbit availability did not appear to affect home range behaviour at any spatio-temporal scale. The absence of a *prey abundance effect* on eagle owl home range behaviour could be due to the fact that preys do not generally represent a limiting factor in our population: our rabbit latrine count indicated high availability and abundance of rabbits inside the owl home range boundaries. For example, rabbit densities (1.0 - 4.6 individuals/ha) lower than those recorded in our study area have been suggested to be suitable to support successful reproduction of Iberian lynxes, which do not alter their space use behaviour at this threshold of density (Palomares et al. 2001). Although heterogeneous patterns of prey spatial distributions are common in most natural scenarios (Bell 1991), rabbit management and frequent releases inside our study area could have created extremely favourable and steady trophic conditions. This peculiar abundance of a homogeneously distributed prey may also be reflected in the persistence of an extremely saturated eagle owl population, with a breeding density reaching approximately 40 breeding territories per 100 km^2 with a mean NND of approx. 1 km (mean ± SD: 982 ± 491 m, range: 250 - 2729 m; Mora et al. 2010). Under these circumstances, we can hypothesise that (a) prey density has reached a threshold that exceeds the eagle owls' *pro capita* needs everywhere in our study area, including during the most constraining periods (i.e., feeding of large broods) and, because of this peculiar ecological scenario, (b) individuals do not need to alter their behaviour to confront seasonal environmental heterogeneity (e.g., Ferguson et al. 1999) or prey fluctuations (Delibes-Mateos et al. 2008).

Figure 3. Examples of eagle owl (*Bubo bubo*) home range overlaps and size variations among males (dark grey), females (bright grey) and both mates from the same breeding pair during different periods of the biological cycle. Pre-laying period: filled surface; incubation period: dashed line; nestling period: dotted line; fledging/post-fledging dependence period: solid line.

However, we should note that although food appears to be abundant and homogeneously distributed throughout the entire study area, our results also confirmed one of the anticipated patterns, i.e., that individual variation in reproduction may be related to the intrinsic properties of home ranges, such as resource (i.e., prey) abundance. In fact, higher fecundities were associated with higher rabbit abundance in the eagle owl diet. This result means that under a scenario in which prey abundance is high in every nesting site and breeding pairs may reproduce successfully every year, certain home ranges particularly rich in rabbits allow the extremely high fecundity rates (i.e., 3-4 fledglings per nest per year) that eagle owls mainly exhibit when their range of distribution overlaps with that of rabbits (Delibes and Hiraldo 1981).

If our results have drawn attention to the occurrence of multi-level factors and processes affecting home range behaviour, one of our most important and probably unexpected results was the detection of a scenario that is profoundly dominated by the *individual* and its intrinsic characteristics (as revealed by the ICC and R^2 values for owl ID random terms). Across the different spatial and temporal components of our study, we detected both inter-individual variations in home range behaviour (to a relatively variable degree, depending on the specific variable we were analysing) and intra-individual consistency in the way the owls behaved over the study period: both inter- and intra-individual effects largely contributed to shaping (a) home range and core area sizes and (b) movement patterns during different periods of the biological cycle. These findings are in agreement with those of recent studies that assessed intraspecific variations in home range behaviour (Saïd et al. 2009; Börger et al. 2006; van Beest et al. 2010), in which a considerable portion of the home range variance was partly ascribed to differences among individuals; i.e., every individual is a unique entity as a result of its own experience across the different life stages, as a nestling, fledgling, dispersing and floating juvenile as well as a more or less experienced breeder. Each individual is the result of a series of complex, reciprocal interactions between factors that can occur throughout an individual's lifetime and are responsible for the emergence of different personalities (Sasha, Houston and McNamara 2004; Stamps and Groothuis 2010). Thus, it makes sense to assume that heterogeneity in home range behaviours, which at the individual-level, could be consistent over time (i.e., year-round) and may be not fully captured by certain fundamental biological traits (e.g., sex, age or physiological condition), could be partly explained by different personality types within the same population (Both et al. 2005). Although different home range behaviours may also be a consequence of changing environmental conditions and habitat heterogeneity (e.g., Fraser et al. 2001; Delgado and Penteriani 2008; Stamps and Groothuis 2010), when local conditions and resources are stable over time and homogeneously distributed in space, individual personalities may become more evident and may thus be one of the most crucial factors in determining the behavioural patterns of a population.

Despite this strong individual *signature* regarding home range behaviour, sex and health state represented two additional factors that contributed to shaping home range behaviour, which was in agreement with our predictions. First, sex-dependent tasks have the potential to affect movement decisions at both daily (e.g., rhythm of activities) and seasonal (e.g., movement patterns) temporal scales and, thus, contribute to differentiating the patterns of space use of males and females that we observed at the larger (overall) temporal scale. In addition, male home range behaviour may also reflect social constraints because of strong male territoriality (Penteriani et al. 2007a). For example, males exhibited smaller home ranges with a simpler internal structure in which core areas were smaller in size than was seen for females (which are allowed to intrude into the territories of neighbouring pairs with less conflict; Penteriani et al. 2007a). Because the home ranges of neighbouring owls in our population may overlap and are very close to each other (V. Penteriani, M.M.

Delgado and L. Campioni in preparation), the movements of males outside their own home range boundaries can lead to risky and dangerous encounters with other males, which can show extremely aggressive behaviour (Penteriani et al. 2007a). In contrast, the intrusion of a new female can represent the possibility of occasional bigamy (Dalbeck et al. 1998; V. Penteriani and M.M. Delgado unpublished data), and eagle owl females generally show low levels of aggression towards other females approaching their nesting site (Penteriani et al. 2007a). Finally, home range internal structure was related to differences in the state of individuals, with healthier owners being associated with a simpler internal home range structure. This relationship could suggest, for example, that the existence of fewer core areas and smaller distances between breeding and foraging sites may reduce movements and, consequently, minimise daily energetic expenditures allocated to unprofitable and costly activities (e.g., McNab 1963; Schoener 1968; Bell 1991).

Because of the plurality of behavioural and ecological processes simultaneously involved in the individual behavioural response to temporal and spatial variations of internal and external factors, home range behaviour remains one of the most appealing and challenging processes to study in the field of animal ecology. Our results provide strong empirical evidence of the crucial relevance of individual-level processes over time and space, suggesting that variation of space use patterns within the same population can be the *fingerprint* of individual- and site-specific behavioural and ecological dynamics taking place under unique local conditions. In a time associated with great environmental changes, in which the majority of attention is currently focused on the effects of habitat heterogeneity, alterations and/or fragmentation, we emphasised the importance to still address our interest on favourable and homogeneous environmental conditions. Stable environments may provide a fertile context in which to re-direct our interest toward exploring and analytically capturing intraspecific differences in behaviour, which up to date, remain difficult to recognise as personality types, even though inter-individual variation in behaviour is often distributed in a non-random manner, suggesting that it is likely to have consistent ecological and evolutionary consequences (Sasha et al. 2004).

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SÍNTESIS

Durante esta tesis he estudiado las diferencias en el comportamiento de individuos pertenecientes a distintos grupos sociales en una especie territorial y de larga vida, el búho real (*Bubo bubo*). Entre los numerosos rasgos de comportamiento que caracterizan a esta rapaz, me he centrado en aquellos estrechamente relacionados a la selección de hábitat, el uso del espacio y los movimientos, caracterizados todos ellos en ser un reflejo de la relación entre el entorno externo, el entono social y las características individuales. En general, y a través del seguimiento intensivo de los individuos reproductores y dispersantes llevado a cabo durante 8 años he podido demostrar la existencia de dos estrategias de comportamiento ligadas a las distintas etapas de vida y al estatus social. Este resultado enfatiza la existencia de importantes relaciones entre conspecíficos, que podrían estar más estructuradas de la que al principio de este estudio pensábamos.

Una primera evidencia de la importancia de la organización social en esta especie se intuyó ya hace unos años cuando con el estudio del uso de señales visuales (y vocales) por parte de los reproductores como medio de comunicación intra-específica, subrayaron el peso que las interacciones sociales, la territorialidad y la dominancia podrían tener en las decisiones comportamentales tomadas por los individuos. Sin embargo, hasta ahora y en esta especie, nadie había profundizado el efecto que el contexto social puede tener en algunos comportamientos de los individuos no territoriales una vez empezada su etapa de dispersión.

En su conjunto los resultados apuntan a la existencia de un escenario en el que los factores sociales parecen regular algunos de los mecanismos que guían el comportamiento de los individuos. Contrariamente a nuestras predicciones, la abundancia de los recursos tróficos en nuestra área de estudio no parece ser un factor determinante del *por qué* y *cómo* los individuos utilizan el espacio. La súper-abundancia de recursos en esta área, debida al constante manejo y suelta de conejos de campo (por ser nuestra área de estudio un área de caza menor), podría estar relajando las constricciones impuestas por el entorno externo (p. ej. competencia para los recursos tróficos) favoreciendo una elevada densidad de conspecíficos en un espacio muy reducido. En mi opinión, esto ha representado una ventaja en el marco de este estudio, ya que nos ha permitido estudiar la organización social en un ambiente muy saturado (40 parejas/100 km^2), en el que las interacciones sociales son muy frecuentes y donde la territorialidad sigue marcando el límite entre los recursos compartidos y aquellos de uso exclusivo.

En este escenario y según nuestras predicciones, los adultos territoriales (Capítulo 5) tienden a ocupar aéreas muy favorables para la reproducción, con al presentar una elevada densidad de presas. La alta densidad de individuos junto a la elevada densidad de recursos es probablemente la causa directa de que los individuos utilicen en general un espacio muy reducido (dominio vital medio ~ 300 ha). Frente al mosaico de territorios que nos hemos encontrado, las hembras - sexo caracterizado por sus menores restricciones sociales – han tendido a utilizar áreas más amplias y parcialmente compartidas con las de sus vecinos. Sin embargo, dentro del espacio denominado dominio vital, el comportamiento de los reproductores se ha visto sensiblemente afectado por factores no sociales como las necesidades biológicas y la identidad de los individuos mismos. De la misma forma, otros factores externos como el ciclo lunar (Capítulo 3) también modulan el tiempo y el esfuerzo que los reproductores dedican a actividades sociales (comunicarse) o necesidades fisiológicas (alimentarse).

Un resultado importante presentado en este trabajo es la gran capacidad que los individuos no territoriales tienen para adaptar su comportamiento a sus necesidades, según el entorno físico y social que les rodeas. Al igual que en otras especies territoriales, los flotantes de búho real también adoptan comportamientos crípticos, viviendo en un *submundo* paralelo al sector reproductor, en el que los individuos toman decisiones bajo normas impuestas por el contexto social (Capítulo 1-2), la experiencia adquirida (Capítulo 4) y según las características del entorno externo en el que se mueven. Al final del viaje que representa la dispersión natal, el destino más probables para los flotante de nuestra población parece ser el encontrar un área próximas a la población natal donde asentarse de forma estable, a la espera de un sitio y pareja donde y con quien reproducirse (Delgado et al 2010, Penteriani and Delgado en prensa). En conclusión, el estudio de las relaciones entre los animales y el entorno físico en el que se distribuyen y mueven es un ámbito que engloba ecología y comportamiento. En mi opinión, y tras este estudio, no podemos prescindir del contexto social si queremos entender procesos relacionados con la biología de las poblaciones, el flujo génico, la eficiencia ecológica o la distribución espacial de los individuos.

CONCLUSIONES

Los resultados obtenidos en la presente tesis apoyan que:

1. El estatus social es un factor importante en el estudio del comportamiento de especies territoriales, afectando procesos elementales como la selección de hábitat y los patrones de movimientos.

2. En función del estatus social, los individuos pueden mostrar diferentes comportamientos relacionados a procesos de selección de hábitat a una escala espacial pequeña. En particular, los individuos reproductores podrían estar seleccionando aquellos posaderos que por sus características parecen ser más óptimos para el envío y recepción de señales visuales y vocales – posaderos en general dominantes y visibles. Sin embargo los dispersantes, con un estilo de vida más transitorio y no territorial, seleccionan posaderos menos visibles y menos dominantes durante toda la fase de dispersión natal.

3. En cuanto a la selección de los sitios de nidificación en hábitat forestales, los reproductores suelen elegir parcelas de bosque maduras, con una estructura vertical que les podría estar facilitando tareas asociadas a la defensa del territorio y a la reproducción. Por el contrario, los dispersantes utilizan parcelas de bosque en general más jóvenes y más densas, características que posiblemente les ayuda a reducir los costes asociados durante la dispersión y que les podrían facilitar el llevar un estilo de vida más secreto.

4. Factores externos, como los cambios en las condiciones de luminosidad debidas al ciclo lunar, pueden regular el patrón temporal de actividad de depredadores nocturnos. Sin embargo, reproductores y dispersantes no se ven afectados de la misma forma. Durante las fases lunares, la actividad de los reproductores refleja el tiempo y el esfuerzo que los individuos dedican a varias actividades relacionadas con sus necesidades más inmediatas. Por ejemplo, los individuos incrementan la actividad de canto y de caza en las fases de luna llena cuando su luminosidad aumenta la visibilidad de señales visuales y cuando las presas se encuentran con mayores dificultades. Sin embargo, también en las noches de luna nueva los búhos presentan un pico en su actividad de caza ya que las presas son más difíciles de detectar. A diferencia de esto, el patrón de actividad de los dispersantes no parece estar afectado por el ciclo lunar.

5. La información espacial adquirida por los animales representa un elemento clave para una exploración y explotación eficiente de su entorno. De la misma forma, los patrones de movimiento pueden estar afectados por la familiaridad que los individuos tienen con su entorno. Aquellos individuos que durante su dispersión natal se encuentran prospectando nuevas áreas presentan movimientos exploratorios y diferentes a aquellos individuos que se asientan de forma estable, es decir, dispersantes en áreas temporales de asentamiento e individuos reproductores en sus territorios. Estos últimos, en general, presentan movimientos que reflejan una explotación de sus áreas.

6. El *comportamiento de uso del dominio vital* de los animales es el resultado de procesos dinámicos a diferentes niveles - espacio, tiempo e individuo – que originan diferencias en los patrones de movimiento, en el uso del espacio y en los ritmos de actividad. Estas diferencias en el comportamiento se encuentran además relacionadas con la estructura del hábitat, características internas de los individuos y por las distintas fases del ciclo biológico. Estos resultados soportan la necesidad de una aproximación integrada, que tenga en cuenta la pluralidad de los factores implicados en el *comportamiento de uso del dominio vital.*

7. La estructura social representa un elemento clave en la biología de las poblaciones animales, modulando procesos elementales del comportamiento espacial de los individuos. Por ello, subrayamos la necesidad de considerarla como una herramienta importante en el manejo y conservación de las poblaciones, cuya demografía, dinámica, estructura y persistencia depende en gran medida del comportamiento de los individuos.

APÉNDICE

Electronic Supplemental Material Table S1, S2, S3 and S4

Table 1

Summary of *a*) fitted parameters employed in model formulation to analyse space use behaviour of eagle owl at both spatial (home range and core area) and temporal (*overall* and *seasonal*) scale; *b)* selected models (ΔAIC ≤ 2) with the relative (β ± SE), number of estimated parameters (K), AIC AICc, ΔAICc, AICcw values, r^2, intraclass correlation coefficient (ICC) and R^2 for random effect (owl ID) are showed.

Temporal scale	**Dependent variable**	**Parameters**	**Set of models**	**Selected models**	**β ± SE**	**K**	**AICc**	**ΔAICc**	**AICc w**	**r^2**		**Ranking**
overall	Home range size[a]	IKA, sex, HT, edge density, dense vegetation, sparse scrabes + trees	12	intercept	15.956 ± 0.557							
				edge density	-0.006 ± 0.003	3	54.4	0	0.85	0.23		1
				sex[d]	-0.596 ± 0.299							
	Core area size[a]	IKA, sex, HT, edge density, sparse scrabs + trees	11	intercept	14.472 ± 0.520							
				edge density	-0.008 ± 0.002	2	61.1	0	0.61	0.37		1
				intercept	14.571 ± 0.535							
				edge density	-0.007 ± 0.002	3	62.8	1.7	0.26	0.36		2
				sex[d]	-0.330 ± 0.373							
	Core area-nest distance[a]	IKA, sex, HT, edge density, dense vegetation, sparse scrubs + trees	12	intercept	7.929 ± 0.896							
				HT	-0.053 ± 0.018	3	55.0	0	0.60	0.26		1
				sex[d]	0.753 ± 0.317							
	Core area number[c]	IKA, sex, HT, edge density, sparse scrubs + trees	11	intercept	-9.083 ± 5.256							
				HT	0.207 ± 0.111	2	29.1	0	0.43	.		1
				intercept	-8.530 ± 5.229							
				HT	0.216 ± 0.111	3	30.5	1.4	0.21	.		2
				sex[d]	-1.293 ± 1.296							
										ICC	**R^2**	
seasonal	Home range size[b]	IKA, sex, HT, age, PERIODs	9	intercept	14.136 ± 0.130	3	123.4	0	0.65	0.63	.	1
				intercept	14.413 ± 0.287	4	124.9	1.5	0.30	0.63	0.71	2
				sex[d]	-0.349 ± 0.322							
	Core area size[b]	IKA, sex, HT, age, PERIODs	9	intercept	12.324 ± 0.159	3	144.5	0	0.72	0.63	.	1
	Core area-nest distance[b]	IKA, sex, HT, age, PERIODs	9	intercept	5.979 ± 0.116	3	151.8	0	0.73	0.22	.	1
	Core area number[c]	IKA, sex, HT, age, PERIODs	9	intercept	-5.074 ± 2.112	2	87.4	0	0.52	.	.	1
				HT	0.105 ± 0.042							
				intercept	-4.146 ± 2.017							
				HT	0.122 ± 0.045	3	88.1	0.7	0.37	.	.	2
				sex[d]	-0.918 ± 0.763							

[a] = Linear Model

[b] = Linear Mixed-Effect Model

[c] = General Linear Model

[d] = Reference level female

ICC and R^2 = Calculated for random term (owl ID)

Set of models is the number of formulated models always including the only-intercept and the full models

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Table *S*2.

Summary of *a*) fitted parameters employed in model formulation to analyze movement behaviour of eagle owl at both spatial (home range and core area) and temporal (*overall* and *seasonal*) scale; *b)* selected models (ΔAIC ≤ 2) with the relative (β ± SE), number of estimated parameters (K), AIC, ΔAIC, AICw values, intraclass correlation coefficient (ICC) and R^2 for random effect (owl ID) are showed.

Spatial scale	Dependent Variable	Parameters	Set of models	Selected Models	β ± SE	K	AIC	ΔAIC	AIC w	ICC	R^2	Ranking
home range	Total distance[a]	IKA, sex, HT, edge density, dense vegetation sparse scrubs + trees, age, PERIODs	14	intercept PERIOD2[d] PERIOD3[d] PERIOD4[d]	8.757 ± 0.060 0.228 ± 0.078 0.134 ± 0.099 -0.121 ± 0.060	6	340.8	0.0	0.93	0.21	0.25	1
	Step length[a]	IKA, sex, HT, edge density, dense vegetation, sparse scrubs + trees, age, PERIODs	14	intercept	5.706 ± 0.044	4	12358	0.0	0.53	0.05		1
				intercept PERIOD2[d] PERIOD3[d] PERIOD4[d]	5.661 ± 0.050 0.191 ± 0.048 0.086 ± 0.064 0.016 ± 0.039	6	12359	1.0	0.33	0.05	0.05	2
	Speed[a]	IKA, sex, HT, edge density, dense vegetation, sparse scrubs + trees, age, PERIODs	14	intercept age	3.147 ± 0.144 -0.117 ± 0.039	5	14546	0.0	0.59	0.06	0.04	1
				intercept	2.794 ± 0.076	4	14547	1.0	0.30	0.04	.	2
	Turning angle[b]	IKA, sex, HT, edge density, dense vegetation, sparse scrubs + trees, age, PERIODs	14	intercept dense vegetation	-0.024 ± 0.050 0.004 ± 0.001	2	6534.5	0.0	0.37	.	.	1
				intercept sparce scrubs	-0.008 ± 0.050 0.004 ± 0.002	2	6535.7	1.20	0.20	.	.	2
	Time step[a]	IKA, sex, HT, edge density, dense vegetation, sparse scrubs + trees, age, PERIODs	14	intercept age	2.900 ± 0.078 0.082 ± 0.021	10	12749	0.0	0.77	0.02	0.02	1
core area	Step length[a]	IKA, sex, HT, edge density, sparse scrabs + trees, age, PERIODs	14	intercept	4.976 ± 0.091	6	2492	0.0	0.58	0.35	.	1
				intercept sex[e]	5.196 ± 0.177 -0.295 ± 0.201	7	2493	1.0	0.31	0.35	0.21	2
	Speed[a]	IKA, sex, HT, edge density, sparse scrubs + trees, age, PERIODs	14	intercept	2.308 ± 0.109	5	2704	0.0	0.73	0.94	.	1
	Turning angle[c]	IKA, sex, HT, edge density, sparse scrubs + trees, age, PERIODs	14	intercept	0.053 ± 0.065	1	1371	0.0	0.32	.	.	1
	Time step[a]	IKA, sex, HT, edge density, sparse scrubs + trees, age, PERIODs	14	intercept	3.181 ± 0.051	5	2690	0.0	0.76	0.06	.	1
				intercept sex[e]	3.352 ± 0.118 -0.206 ± 0.125	6	2692	2.0	0.25	0.06	0.10	2

[a] = Linear Mixed-Effect Model

[b] = General Linear Model

[c] = Generalized Linear Model

[d] = Reference level PERIOD1

[e] = Reference level female

ICC= Calculated for random term (owl ID)

Set of models is the number of formulated models always including the only-intercept and the full models

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Table S3.

Summary of *a*) fitted parameters employed in model formulation to analyse the activity rhythms of eagle owl at both spatial (home range and core area) and temporal (*overall* and *seasonal*) scale; *b)* selected models (ΔAIC ≤ 2) with the relative estimate (*β* ± SE), number of estimated parameters (K), AIC, AICc, ΔAIC, AICw values, r^2 and the intraclass correlation coefficient (ICC) are showed.

Spatial scale	**Dependent variable**	**Parameters**	**Set of models**	**Selected Models**	***β* ± SE**	**K**	**AIC**	**ΔAIC**	**AIC w**	**ICC**	**Ranking**
home range	Movement rate[a]	IKA, sex, HT, edge density, age, PERIODs	13	intercept sex[c]	0.023 ± 0.001 0.005 ± 0.001	4	1832.4	0	0.43	0.10	1
										r^2	
core area	Movement rate[b]	IKA, sex, HT, edge density age, PERIODs	13	intercept edge density	0.508 ± 0.067 -0.0005 ± 0.0003	2	56.0	0	0.38	0.1	1
	Core area activity[b]	IKA, sex, HT, edge density age, PERIODs	13	intercept edge density	0.3285 ± 0.0413 -0.0004 ± 0.0002	2	-194.6	0	0.45	0.2	1

[a] = Linear Mixed-Effect Models

[b] = Linear Models

[c] = Reference level: female

ICC = = Calculated for random term (year)

Set of models is the number of formulated models always including the only-intercept and the full models

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Table S4.

Summary of *a*) fitted parameters employed in model formulation to analyze the breeding phenology and performance of eagle owl (from 2004 to 2010); selected models (ΔAIC ≤ 2) with the relative estimate (*β* ± SE), number of estimated parameters (K), AIC, AICc, ΔAICc, AICcw values and r^2 are showed.

Dependent variable	Parameters	Set of models	Selected Models	*β* ± SE	AICc	ΔAICc	AICc w	ICC	Ranking
Laying date[a]	% rabbit biomass, mean core area size HT, mean core area-nest distance	9	intercept	5·064 ± 0·030	-21.6	0.001	0.95	0.05	1
								r^2	
Number of chicks[b]	% rabbit biomass, mean core area size mean core area-nest distance, mean movement rate	9	intercept mean core area size	2·09 ± 0·21 0·000001 ± 0·00000	39.7	0	0.27	0.15	1
			intercept % rabbit biomass	1·92 ± 3·05 0·00002 ± 0·00001	40.4	1	0.19	0.13	2

[a] = Linear Mixed-Effect Models

[b] = Linear Models

ICC = Calculated for random term (nest)

Set of models is the number of formulated models including always the only-intercept and the full models

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