UNIVERSIDADE DE SANTIAGO DE COMPOSTELA

Tesis doctoral

Wolves in human-dominated landscapes of Northwestern Iberian Peninsula

Memoria presentada para optar al Grado de Doctor por:

Luis Llaneza Rodríguez

DEPARTAMENTO DE BIOLOXÍA CELULAR E ECOLOXÍA

Santiago de Compostela.Octubre de 2015


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D. José Vicente López-Bao y D. José Guitián Rivera, Doctores en Biología, respectivamente, director y tutor de la tesis doctoral titulada "Wolves in human-dominated landscapes of Northwestern Iberian Peninsula" presentada por D. Luis Llaneza Rodríguez

INFORMAN

Que la presente memoria, realizada en el Área de Ecología del departamento de Bioloxía Celular e Ecoloxía de la USC está concluida y reúne los requisitos para optar al grado de Doctor en Biología, por lo que autorizan su depósito y presentación al Tribunal Evaluador

Santiago de Compostela 5 de Octubre de 2015

Fdo: Dr. Jose V. López Bao

Director

Fdo: Dr. José Guitián Rivera

Tutor


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Los capítulos que componen la presente Memoria de Tesis Doctoral han sido y están siendo presentados a su publicación:

Capítulo 1.- "Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes". Publicado en 2012. *Diversity and Distributions*. 18:459–469.

Capítulo 2.- "Indirect effects of changes in environmental and agricultural policies on the diet of wolves". Publicado en 2015. *European Journal of Wildlife Research*, 61(6): 895-902.

Capítulo 3.- "Improving the interface between landscape planning and large carnivore conservation: accounting for fine-scale habitat selection patterns". Sometido a su publicación.

Capítulo 4.- "Resting in risky environments: the importance of cover for a large carnivore to cope with exposure risk in human-dominated landscapes". Sometido a su publicación.

Capítulo 5.- "Determinants of wolf home range size variation in human-dominated landscapes". Pendiente de someter a su publicación.


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A mis niños, Ana y Mario, y a mi compañera, Isabel.


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"Dous lobos grandísimos fórono acompañando. Iban sempre de par dil, ás duas maos. Cáseque parecían dous cás que foran co seu amo. Se il se paraba, tamén iles se paraban. Algunhas veces púñanselle diante."

Ánxel Fole, *Contos de lobos e utros relatos*.

AGRADECIMIENTOS

Llevo muchos años caminando tras el rastro del lobo. Arrancó en la Vega Baxo (Caso, Asturies) a finales del verano de 1985. Había visto gran cantidad de rastros en una collada. Madrugué y vi mis primeros lobos, 6 cachorros y una loba adulta. Han pasado ya 30 años y he visto muchos lobos. Esa afición se convirtió en profesión y ahora me enfrento a la defensa de mi Tesis Doctoral.

En los últimos 15 años una parte muy importante de mi trabajo profesional se desarrolló en Galicia. Comenzó con las estimas poblacionales realizadas en las cuatro provincias entre 1999 y 2003 por encargo de la Xunta de Galicia. Pedro Alonso, Francisco Alvares, Vicente Palacios, Andrés Ordiz, Pablo Sierra y Antonio Uzal fueron mis compañeros de trabajo durante esos años, ¡ magníficos loberos ! Conocimos intensamente Galicia y sus lobos. De esas prospecciones salió la información base que me ha permitido abordar el primero de los capítulos de esta tesis, ya convertido en un artículo publicado.

Gracias a las autorizaciones de la Consellería de Medio Ambiente de la Xunta de Galicia, comencé a acceder a los cadáveres de los lobos depositados en los Centros de Recuperación de Fauna Silvestre de la Xunta. Pasaron ya 14 años. Fueron muchos los lobos procesados. Luis Fidalgo, cuchillo afilado en mano, abrió conmigo numerosos cadáveres. También Emilio García, Vicente Palacios, Ana López-Beceiro y algunas personas más que ahora no recuerdo. Disculpad. Algunos Agentes de Medio Ambiente de la Xunta y empleados de los centros de recuperación curiosearon y ayudaron. ¡Gracias a todos por vuestra ayuda y colaboración! Toda la información se fue guardando pacientemente en bases de datos. Una parte de ella dio lugar al segundo capítulo, también ya artículo publicado.

Con mis compañeros de tajo, y amigos, Vicente Palacios, Emilio García, Víctor Sazatornil y Óscar Rivas, en 2006 iniciamos un periodo de trabajo que permitió generar ingentes cantidades de información sobre los lobos. Comenzamos a equipar lobos con collares GPS-GSM con el objetivo de evaluar los efectos de los parques eólicos sobre los lobos, por encargo de DESA y GAMESA y con la participación de la Consellería de Medio Ambiente de la Xunta de Galicia. Mi agradecimiento a Enrique Anchústegui y Aitxiber Céspedes, mis interlocutores de ambas empresas, y a los técnicos y responsables de la Consellería de Medio Ambiente de la Xunta de Galicia, Belén Bris, Susana Cuesta, Rogelio Fernández, Carmen

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El Dr. José Guitián ha sido mi tutor a lo largo de estos cinco años. Siempre, sabedor de mis ocupaciones profesionales y de mi carga de trabajo, me alentó a seguir, me reconfortaron sus ánimos, ¡*sempre adiante; sempre adiante*!, me decía. Revisó, anotó y aportó interesantes comentarios a los textos de esta tesis. Me facilitó viejos informes sobre los ungulados silvestres de Galicia para su consulta. Me ayudó con todo el papeleo de la tesis. Pepe, amigo, muchas gracias.

Bueno, Jose, no te creas que me he olvidado del director que guió esta tesis. Por supuesto que no. ¿Quién te diría que, cuando recalaste por Lugo a realizar prácticas de empresa con nosotros, allá por el 2004, creo, acabarías dirigiendo mi tesis doctoral? Dr. José Vicente López Bao has sido un verdadero DIRECTOR; llenaste cuartillas de rojo sobre blanco; discutimos todo; revisaste todo; me presionaste cuando me tenías que presionar; supiste entender los largos periodos de ausencia de trabajo en la tesis por mis ocupaciones profesionales; me animaste cuando necesitaba ánimos; cuando me hartaba del trabajo mecánico de generar datos, tus comentarios me relajaban; fuiste muy paciente conmigo. Al final, llegamos a la meta.

Isabel, tú has sido el pilar en el que me sostuve mientras me mantenía inestable en este largo trabajo. Cuando te propuse reducir mi jornada laboral durante algunos meses para dedicarme a la tesis, nada objetaste. Todas las tardes, y bastantes fines de semana, que dediqué a la tesis, y fueron muchas, muchísimas, te ocupaste de los niños. Saltaron chispas, a veces rayos, pero sin tu ayuda no habría llegado a la meta. Gracias a ti, esto está hecho.


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Índice:

RESUMEN

Esta Memoria de Tesis Doctoral se ha centrado en el estudio de la ecología de grandes carnívoros en paisajes dominados por el hombre. Para ello, se ha elegido como caso de estudio la persistencia del lobo *(Canis lupus)* en ambientes humanizados de Galicia, NW Península Ibérica. El contexto gallego es un buen ejemplo de un territorio humanizado con presencia y persistencia histórica de lobos, ocupando de manera constante la mayor parte del territorio gallego, al menos desde la segunda mitad del s. XIX. Así, la presente tesis se ha estructurado en cinco capítulos que abordan diferentes aspectos de la ecología de la especie en estos ambientes, tratando de aportar información sobre los mecanismos que explican la presencia y persistencia de los lobos en paisajes dominados por el hombre.

Comprender los factores ambientales y humanos que interactúan para permitir o limitar la persistencia de grandes carnívoros en paisajes dominados por el hombre es importante para su conservación efectiva, sobre todo ante el actual escenario de cambio global, donde las actividades humanas se han expandido notablemente y el tamaño de las áreas protegidas es, la mayor parte de las veces, demasiado pequeño como para mantener poblaciones viables de grandes carnívoros.

En el primer capítulo de esta tesis se han combinado datos sobre la distribución del lobo, obtenidos en varios seguimientos de la especie realizados entre 1999 y 2003 en Galicia, con factores ambientales y humanos para investigar la importancia relativa de tres grupos de predictores y sus interacciones: la disponibilidad de alimento, la presión humana (densidad de población, densidad de asentamientos y densidad de carreteras) y los atributos del paisaje (altitud, rugosidad y refugio), a fin de entender los factores que determinan la presencia del lobo en paisajes dominados por el hombre. Se usaron métodos de partición de la varianza y partición jerárquica a fin de identificar la importancia de los predictores de manera individual y sus efectos conjuntos, combinado con modelos lineares generalizados. A fin de considerar los efectos asociados a la autocorrelación espacial de las variables explicativas en nuestros análisis, se incluyó un polinomio espacial en todos los análisis.

Se encontró que el grupo de predictores relacionado con los atributos del paisaje (altitud, rugosidad y refugio) determinó de manera importante la presencia del lobo (16,4 %), seguido por la presión humana (11,17 %) y la disponibilidad de alimento (9,6 %). Los modelos finales para los tres bloques de predictores mostraron que i) respecto a la

disponibilidad de alimento, el modelo predice un incremento de la probabilidad de presencia del lobo a medida que se incrementa la densidad de caballos y ungulados silvestres; ii) respecto a la presión humana, el modelo predice que se incrementa la probabilidad de presencia de lobo a medida que decrece la densidad de edificios y carreteras; finalmente, iii) respecto a los atributos del paisaje se ha detectado un efecto positivo para todos los predictores (altitud, rugosidad y refugio).

Mediante el análisis de la partición de la varianza, se ha puesto de manifiesto que los tres componentes más importantes que determinan la presencia de lobos están relacionados con los atributos del paisaje: (i) el efecto conjunto de los tres grupos de predictores, (ii) el efecto combinado de los atributos del paisaje y la presión humana, y (iii) el efecto independiente de los atributos del paisaje. La altitud mostró la mayor contribución independiente a la hora de explicar la presencia de la especie en el área de estudio. Estos resultados evidencian la compleja interacción entre factores ambientales y humanos que determinan la presencia del lobo en paisajes dominados por el hombre. Las características del paisaje como la altitud, rugosidad y refugio, que permiten a los lobos pasar desapercibidos del hombre, juegan un papel clave en la presencia y persistencia de esta especie.

En el segundo capítulo de esta tesis, se han estudiado los efectos que cambios en las políticas sectoriales que implementan regulaciones sanitarias y ambientales pueden ocasionar a las especies y su coexistencia con el hombre. A pesar de que muchas veces las consecuencias para la conservación de la biodiversidad son evidentes de antemano o poco después de la aplicación de nuevas regulaciones, los conflictos potenciales entre políticas y conservación de la biodiversidad no siempre son fáciles de predecir. En el área de estudio donde se ha desarrollado esta tesis, los lobos se alimentan de fuentes de alimento de origen antrópico (depredación sobre el ganado, carroña, basura), que en ocasiones suponen la totalidad de la dieta para algunas manadas, lo que genera una situación de conflicto con el hombre, principalmente debido a la depredación del ganado. Sin embargo, la disponibilidad de alimento de origen antrópico es dependiente de múltiples políticas ambientales y sanitarias que pueden producir cambios en la dieta del lobo. Dependiendo del tipo y magnitud de dichos cambios es esperable que emerjan o se intensifiquen determinados conflictos entre el hombre y el lobo. En este capítulo se ilustra este hecho mostrando un cambio a largo plazo en la dieta de los lobos en el noroeste de la Península Ibérica, como resultado de cambios en las regulaciones sanitarias, ambientales y socioeconómicas ocurridos durante las últimas tres décadas.

Para estudiar los cambios en la dieta del lobo en las últimas décadas se han comparado dos periodos, 1970-1985 y 2002-2014. Utilizamos los datos publicados por Cuesta *et al*., (1991) referidos al análisis de 102 estómagos (1970-1985) procedentes del oeste de Galicia y los datos provenientes del análisis de contenidos estomacales de 93 lobos (2002-2014) recogidos en el mismo área de estudio descrito por Cuesta y colaboradores. La identificación de las presas se efectuó por el estudio cuticular de los pelos y restos óseos. Se comparó la frecuencia de aparición de los diferentes tipos de presa aplicando un test Chi-cuadrado. Se calculó el índice de diversidad trófica de Shanon "H" y el índice de Levins de amplitud de nicho "B". El test "Z" de análisis de las proporciones fue usado para comparar la importancia de las diferentes clases de alimento entre los dos periodos.

Nuestros resultados muestran como los lobos han persistido durante las últimas décadas aprovechando fuentes de alimento de origen antrópico, suponiendo éstos más del 94% de su dieta. Los lobos han pasado de una dieta que incluía, de manera notable, especies estabuladas en granjas (gallinas, conejos y cerdos, básicamente, y aprovechados en forma de carroña), basuras y carroña a una dieta menos diversa basada principalmente en el consumo de dos grandes ungulados domésticos, caballos y vacas. Se discuten las implicaciones potenciales que los cambios en los patrones alimenticios del lobo pudieran tener en el conflicto hombre-lobo. Se llama la atención sobre la urgente necesidad de integrar diferentes políticas sectoriales dentro de la conservación de la biodiversidad para lograr una anticipación efectiva de futuros dilemas de gestión y conservación.

En el tercer capítulo se ejemplifica, analizando los patrones de selección que los lobos hacen de sus áreas de cría, la necesidad de mejorar el interfaz entre la planificación del paisaje y la conservación de este gran carnívoro. En ambientes humanizados la recuperación de grandes carnívoros y su conservación, a menudo, está obstaculizada por las necesidades de espacio que presentan estas especies y por el uso que el hombre hace del paisaje. Dado que los espacios protegidos están aislados dentro de una matriz paisajística con usos múltiples y, por lo general, son demasiado pequeños para mantener poblaciones viables de estas especies, la conservación de los grandes carnívoros requiere una planificación del paisaje considerando una gran escala espacial. Esto implica focalizar esfuerzos de conservación sobre la matriz del paisaje, no solo mediante el incremento de la conectividad entre las áreas protegidas, sino fomentado la persistencia de estas especies en la matriz.

La mayoría de los factores críticos que determinan la persistencia de grandes carnívoros, relacionados con la disponibilidad de alimento y la supervivencia, interactúan de manera sinérgica en el espacio y en el tiempo durante el periodo de cría. En esta tesis se han

estudiado los factores que determinan la selección de los lugares de cría (homesites) por parte de los lobos en relación con la disponibilidad de alimento, la presión humana y la disponibilidad de refugio. Para ello, se usó la información de 33 lugares de cría localizados en el oeste de Galicia entre 2003 y 2011.

Los lugares de cría fueron identificados mediante tres procedimientos, i) aullidos simulados para estimular la respuesta de los cachorros (en 17 casos), ii) observaciones directas de cachorros en rendezvous sites (n = 12) y iii) datos de lobos equipados con collares GPS-GSM cuyas localizaciones han permitido identificar los lugares con presencia de cachorros (n = 4). A fin de analizar la selección del homesite, se compararon las características de los 33 homesites con 151 puntos aleatorios a dos escalas espaciales (1 km^2 y 9 km^2). Primeramente, se comprobó si la disponibilidad de alimento influye en la selección del lugar de cría, comparando la disponibilidad de alimento de origen antrópico de las áreas de cría a una escala espacial de 1 km^2 con los valores medios de 10 lugares elegidos al azar dentro del territorio de los lobos. A continuación, mediante la construcción de tres bloques de modelos lineales generalizados se evalúo el efecto de la presión humana, los atributos del paisaje y la combinación de ambos grupos de factores, sobre la selección de los lugares de cría. Además, se realizó un análisis de partición jerárquica sobre el mejor modelo que explicó la selección del lugar de cría a fin de identificar la contribución independiente y conjunta de cada variable.

La selección de los lugares de cría en ambientes humanizados no estuvo determinada por la disponibilidad de alimento en sus inmediaciones. Nuestros resultados muestran que los lobos localizan sus lugares de cría en zonas con una alta disponibilidad de refugio no fragmentado, baja accesibilidad humana y bajos niveles de actividad humana. Los predictores relacionados con la calidad del refugio (no fragmentación) mostraron la mayor proporción de contribución independiente a la hora de explicar los patrones de selección observados. Se ha constatado como la calidad del refugio prevalece sobre la cantidad de refugio a una escala espacial pequeña en comparación con el territorio de los lobos. En este sentido, la disponibilidad de parches de refugio de alta calidad, incluso a pequeñas escalas espaciales, podría compensar niveles moderados de actividad humana en el entorno próximo de los lugares de cría seleccionados por los lobos. Por otra parte, se observó que la intensidad de la selección cambia de acuerdo con el contexto en el entorno inmediato, lo que sugiere un proceso de selección jerárquica a pequeñas escalas espaciales. Se recomienda restringir temporalmente las actividades humanas en los lugares de cría y su entorno inmediato (1 km^2), así como mantener parches de refugio óptimos a la escala paisaje, para favorecer la presencia y persistencia del lobo en paisajes humanizados compatibilizando la conservación de esta especie con el uso del territorio por parte del hombre.

Siglos de persecución han influido en el comportamiento de los grandes carnívoros. Para aquellas poblaciones de grandes carnívoros que persisten en paisajes dominados por el hombre, la segregación espacial completa entre seres humanos y grandes carnívoros no es posible. Los grandes carnívoros están en contacto cercano con el hombre, incluso cuando éstos se encuentran descansando, momento en el que su vulnerabilidad aumenta de manera considerable. En este sentido, la selección de los lugares de descanso-refugio (encames) pasa por ser crucial para la persistencia de grandes carnívoros como el lobo. En el cuarto capítulo de esta tesis se estudió la selección de los lugares de descanso-refugio por parte de los lobos en paisajes humanizados de Galicia. Se establece como hipótesis de partida que la selección de los lugares de cría no estará solamente influenciada por las actividades humanas, sino también estará fuertemente determinada por una densa cobertura de la vegetación (refugio) que les permita descansar pasando desapercibidos al hombre. Se ha investigado la selección de los lugares de encame por parte de los lobos mediante el estudio del comportamiento espacial de 16 lobos equipados con collares GPS-GSM. Se ubicaron puntos de encame a través de la identificación de agrupaciones de localizaciones, seleccionando aquellas localizaciones sucesivas durante, al menos, un periodo de 6 h, con una distancia máxima entre las mismas de 30 metros. Una vez localizados los lugares de encame, se compararon sus características con alrededor de 35 puntos aleatorios dentro del territorio de cada lobo (determinado por el polígono mínimo convexo con el 100 % de las localizaciones). Cada punto, encames y puntos aleatorios, fue caracterizado para una serie de 10 variables relacionadas con la topografía, vegetación y actividades humanas y se evaluaron sus diferencias mediante el uso de modelos lineales generalizados mixtos. Considerando el modelo más parsimonioso, aplicamos el análisis de partición jerárquica de la varianza para identificar la contribución independiente y conjunta de cada predictor.

La mitad de los lugares de descanso-refugio se encontraron en bosques (50,8%), principalmente plantaciones forestales (41,7 % en pinares y 31,4 % en eucaliptales), seguido por matorrales (43,4%) y sólo el 5,8% se encontraron en tierras de cultivo. Los lobos seleccionaron sus lugares de descanso y refugio lejos de carreteras asfaltadas y de pistas con alta frecuencia de uso, así como de los asentamientos humanos. Además, seleccionaron de forma significativa áreas con una alta disponibilidad de cobertura vegetal (refugio). Todas las variables analizadas, salvo altitud y pendiente, difirieron significativamente entre los encames y los puntos aleatorios. La importancia del refugio en la selección de los lugares de descanso fue notable, siendo su contribución independiente más importante que la contribución de todas las variables agrupadas relacionadas con la presión humana (50.7% vs. 42.6%, respectivamente). La fuerte selección del refugio mostrada por los lobos en paisajes antropizados les permite refugiarse y descansar incluso relativamente cerca infraestructuras y asentamientos humanos (en ocasiones a menos de 200 m.). Se recomienda mantener zonas de refugio óptimas para el descanso-refugio de los lobos, lo que favorecería la persistencia de la especie en ambientes humanizados, además de su integración en la planificación del paisaje, lo que facilitaría la convivencia hombre-lobo.

A pesar de la constante influencia humana en los factores que modulan la ecología espacial de los grandes carnívoros, como puede ser la disponibilidad de alimento o la competencia intra-específica, la influencia de la actividad humana sobre determinados parámetros de la ecología espacial de estas especies, y en particular del lobo, permanece aún poco estudiado en determinados contextos. Por ejemplo, es esperable que en paisajes dominados por el hombre, la caza, las prácticas ganaderas, la antropización del paisaje derivada de las actividades humanas o la mortalidad causada por el hombre, influyan en la ecología espacial del lobo. Múltiples factores han sido correlacionados con las variaciones observadas en parámetros de la ecología espacial del lobo, pero apenas se han estudiado dichas relaciones en escenarios donde el ganado supone la fracción más importante de la dieta del lobo.

Por último, en el quinto capítulo de esta tesis, se han identificado los determinantes de la variación de tamaño del área de campeo del lobo en paisajes dominados por el hombre en el NW de España. Para ello se empleó la información espacial procedente de 29 lobos equipados con collares GPS-GSM (una media de 4.884 localizaciones por lobo). Para estimar la superficie de las áreas de campeo (HR) y las áreas de mayor uso (CA) se eligieron las isopletas que contienen el 90 % y 50 % de las localizaciones, respectivamente, tras aplicar el método de estimación Kernel. Para cada lobo adulto o subadulto se determinó su estatus social en base al análisis de su comportamiento espacial (distribución de localizaciones GPS) respecto a los lugares de cría de la manada. Lobos con localizaciones recurrentes en las áreas con presencia de cachorros fueron considerados como lobos integrados en una manada (n=19), mientras que 7 ejemplares fueron considerados como no integrantes de una manada (flotantes o dispersantes).

A fin de estudiar los parámetros que explican la variación de las áreas de campeo de los lobos, exploramos el efecto de los factores individuales (sexo y edad), sociales, ciclo de la especie (a dos niveles: periodo asociado al celo y periodo asociado a los partos y cría de los cachorros), y para los lobos integrados en una manada estudiamos el efecto de la configuración del paisaje, la disponibilidad de refugio y su fragmentación, y el nivel de antropización del territorio. Además, se comprobó el efecto de la disponibilidad del ganado sobre el tamaño de las áreas de campeo de los lobos, ya que la dieta de las manadas del área de estudio estuvo constituida básicamente por ganado - más del 85 % en todos los casos-. Por último, se analizó la influencia de la densidad de lobos sobre la variación del tamaño de las áreas de campeo. Utilizando modelos lineales generalizados, se evaluó la influencia del sexo, edad, estatus social, así como la interacción entre el sexo y edad en la variación de las áreas de campeo de los lobos. Empleando modelos lineales generales mixtos evaluamos el efecto del ciclo de la especie en la variación del HR conforme al sexo, edad y sus interacciones. Para los lobos integrados en manadas, se construyen modelos lineales generalizados para explicar el efecto de i) modelo nulo, ii) configuración paisajística, iii) cantidad y calidad del refugio, iv) presión humana (carreteras, pistas y asentamientos), v) disponibilidad de alimento, vi) importancia del ganado en la dieta del lobo y vii) densidad de lobos, sobre la variación del tamaño de los HR.

Los requerimientos espaciales de los lobos fueron similares con independencia de las clases de sexo y edad consideradas. Sin embargo, los integrantes adultos y subadultos de las manadas mostraron un tamaño medio anual del área de campeo cuatro veces más pequeño que los ejemplares adultos y subadultos no integrados en manadas. Para los lobos integrados en manadas observamos variaciones en el tamaño del HR en relación a la clase de edad y ciclo de la especie, siendo los HR más pequeños durante el periodo de cría de los cachorros. Se encontró además como la importancia del alimento de origen antrópico en la dieta influyó de manera negativa sobre el tamaño de las áreas de campeo a diferentes intensidades de uso espacial (HR y CA), teniendo una menor influencia los niveles de antropización del paisaje y la densidad de lobos. En paisajes dominados por el hombre, el efecto encontrado del alimento de origen antrópico sobre el tamaño de las áreas de campeo de los lobos se traduce en la posibilidad de mayores densidades de lobos en comparación con áreas naturales, factor que ha de tenerse en cuenta a la hora de gestionar la especie.


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ABSTRACT

This PhD thesis has focused on the study of the ecology of large carnivores in human-dominated landscapes. To do this, we have chosen as study subject the persistence of the wolf (*Canis lupus*) in human-dominated landscapes in Galicia, NW Iberian Peninsula. Galician context is a good example of a humanized territory with historical presence and persistence of wolves, steadily occupying most of Galicia, at least from the second half of XIX century. This thesis is structured in five chapters dealing with different aspects of wolf ecology in these contexts, trying to provide information on the mechanisms that explain the presence and persistence of wolves in human-dominated landscapes.

Understanding which human or environmental factors interact to enable or to limit the occurrence and persistence of large carnivores in human-dominated landscapes is an important issue for their effective conservation, especially under the current scenario of global change where most of their former habitat is being transformed by humans and size of protected areas is, most of the time, too small to maintain viable populations of large carnivores

In the first chapter, we have combined data on the distribution of Iberia wolves, obtained in several wolf monitoring conducted between 1999 and 2003 in Galicia, with environmental and human factors to investigate the relative importance of three sets of predictors and their interactions: food availability, human pressure (density, density of settlements and road density) and landscape attributes (altitude, roughness and refuge) in order to understand the factors that determine the presence of the wolf in human-dominated landscapes. We have used variation and partitioning methods to identify the relative importance of individual predictors or groups of predictors and their joint effects, combined with generalized linear models. In order to consider the effects associated with spatial autocorrelation of the explanatory variables in our analysis, we included a spatial term (polynomial) in all analyzes.

We found that the group of predictors related with landscape attributes (altitude, roughness and refuge) strongly determined wolf occurrence (16.4%), followed by human pressure (11.17%) and food availability (9.6%). Final models for the occurrence of wolves from the three predictor groups showed that i) for food availability, the model predicted an

increasing probability of wolf occurrence with increased densities of horses and wild ungulates; ii) with respect to human pressure, the model predicted an increasing probability of wolf occurrence with lower densities of buildings and roads; finally, iii) with respect to the attributes of the landscape, we have detected a positive effect for all predictors (altitude, roughness and refuge).

Variance partitioning analysis revealed that the three most important components determining wolf occurrence were related with landscape attributes: (i) the joint effects of the three predictor groups, (ii) the joint effect of humans and landscape attributes and (iii) the pure effect of landscape attributes. Altitude had the main independent contribution to explain the probability of wolf occurrence. These results demonstrate the complex interaction among several environmental and humans factors that determine wolf occurrence in human-dominated areas. Landscape features such as elevation, roughness and refuge, allow that wolves go unnoticed by humans, playing a key role in the occurrence and persistence of this species.

In the second chapter of this thesis, we have studied the effects of changes in sanitary and environmental policies could have onto the species and its coexistence with humans. Although sometimes the consequences for the conservation of biodiversity are evident beforehand or could emerge soon after the implementation of regulations, conflicts between new policies and human-wildlife coexistence are not always easy to predict. In our study area, wolves feeding on anthropogenic food sources (cattle depredation, carrion, garbage), which sometimes involve the whole of the diet for some packs, generating a conflict with humans, mainly due to predation on livestock. However, the availability of anthropogenic food sources can be influenced by different policies leading to diet shifts. Depending on the type and magnitude of these changes is expected to emerge or intensify certain conflicts between humans and wolves. This chapter illustrates this fact by showing a long-term shift in the diet of wolves in the northwest of the Iberian Peninsula, that could result from changes in sanitary, environmental and socioeconomic regulations occurred during the last three decades.

To study changes in the diet of wolves in last decades we compared two periods, 1970-1985 and 2002-2014. We use the data published by Cuesta *et al*., (1991) on the diet of wolves in western Galicia based on the analysis of 102 stomachs collected between 1970-1985 and the data from 93 wolf stomachs collected between 2002-2014 in the same study area described by Cuesta and colleagues. We have used hair samples (cuticular patterns identification) and bone remains to identify prey items. We compared the frequency of

occurrence of different prey items between periods using a chi-square test. We calculated prey diversity using the Shannon index of diversity ‘H’. Moreover, diet breadth was estimated using the Levin’s measure of niche breadth ‘B’. Z-tests (proportions) were used to compare the importance of the different anthropogenic food sources in the wolf diet between periods.

Our results show that wolves have persisted in western Galicia by feeding on anthropogenic food sources, accounting more than 94% of the diet at least during the last four decades. We detected a shift in the diet of wolves across anthropogenic food sources, from a broad diet, including more feedlot species (pigs, chickens) to a more narrow diet based primarily on large domestic ungulates (cattle and horses). We discuss the potential implications of the observed shift in the diet of wolves on human-wolf conflicts. We also call attention on the pressing need to integrate policies into biodiversity conservation to anticipate future conservation and management dilemmas.

It is exemplified in the third chapter, by analyzing the patterns of homesite wolf selection, the need to improve the interface between landscape planning and conservation of this large carnivore. In human-dominated landscapes, large carnivore recovery and conservation is often hindered by the large spatial requirements of these species and by human land use. Since protected areas are isolated within a human land-use matrix, and they are usually too small to support viable populations, conservation requires planning on very a large scale, increasing the focus on the matrix beyond incremental connectivity among protected areas.

Most of the critical factors determining the persistence of large carnivores (e.g., food, vulnerability) interact synergically in space and time during the breeding season. In this thesis we studied the factors determining homesites wolf selection in relation to food availability, human pressure and refuge availability. To do this, we used the information of 33 homesites detected in Western Galicia between 2003 and 2011.

Homesites were located using three procedures, i) simulated howling was used in order to stimulate the response of the pups (17 cases), ii) direct observation of pups in rendezvous sites (n = 12) and iii) data from GPS-GSM collared wolves was used to identify homesites (n = 4). In order to analyze homesite wolf selection, we compared the characteristics of 33 homesites with 151 random points on two spatial scales (1 km^2 and 9 km^2). Firstly, the influence of anthropogenic food availability on homesite selection was assessed by comparing the observed food availability in homesites with the average food availability of randomized sites within territories (n = 10). Then, we built three different sets

of Generalized Linear Models (GLMs) to assess: the influence of human-related predictors only, ii) the influence of landscape-related predictors only, and iii) the influence of both blocks pooled (combined model), on homesite selection patterns by wolves in human-dominated landscapes. In addition, taking into account those variables retained in the selected candidate model from the set of combined models, we performed a hierarchical partitioning analysis to identify the independent and conjoint contribution of each variable with all other significant variables.

Homesite wolf selection was not determined by food availability in the immediate vicinity. Our results show that wolves placed their homesites in areas with a high availability of unfragmented refuge, low accessibility and low human activity levels. Predictors related to the refuge’s qualitative attributes made up the greater proportion of independent contributions to explaining homesite selection patterns. The prevalence of refuge quality over refuge quantity reflects that the availability of high-quality refuge patches, even at very small spatial scales, could compensate for moderate levels of human activities in the vicinity of the homesites. Moreover, the strength of selection changed according to the immediate context, following a hierarchical selection process at small spatial scales. By temporally restricting human use on homesites and very small portions of surrounding lands (1 km^2), and by maintaining several high-quality refuge areas of this size at the landscape scale, we could favor wolf occupancy and persistence in human-dominated landscapes without reducing land availability for other uses, working toward coexistence between large carnivores and humans.

Centuries of persecution have influenced the behaviour of large carnivores. For those populations persisting in human-dominated landscapes, complete spatial segregation from humans is not possible, as they are in close contact with people even when they are resting, when their vulnerability increase remarkably. As a consequence, the selection of resting sites is expected to be critical for large carnivore persistence. In the fourth chapter of this thesis, we studied resting site wolf selection in humanised landscapes of Galicia. We hypothesised that selection of resting sites by wolves in human-dominated landscapes will be not only influenced by human activities, but also strongly determined by dense vegetation covers providing concealment, which allow them rest and go unnoticed of the humans. We investigated the selection of resting sites by wolves in this human-dominated landscape by studying the spatial behaviour of 16 wolves equipped with GPS-GSM collars. The criteria used to define a resting site were successive locations during at least a 6 h period with a maximum distance between hourly locations of less than 30 m. Moreover, within each wolf territory, calculated as the minimum convex polygon considering 100% of locations, we

generated around 35 random points to contrast with observed resting sites. Once we selected resting sites and generated the random points, we characterized each point regarding a set of 10 variables related to topography, vegetation and human activities. We used general linear mixed models to test for the influence of those ten selected predictors on wolf resting site selection in human-dominated landscapes of Galicia. Next, considering those variables included in the best candidate model, we run a hierarchical partitioning analysis to identify the independent and conjoint contribution of each predictor with all other predictors.

Half of resting sites (50.8%) were found in forests (mainly forest plantations, 73.1%), 43.4% in scrublands, and only 5.8% in croplands. Wolves located their resting sites away from paved and large unpaved roads and from settlements; in addition, they significantly selected areas with high availability of horizontal (refuge) and canopy cover. All variables, excepting altitude and slope, significantly differed between resting sites and random points. The importance of refuge was remarkably high, with its independent contribution alone being more important than the contribution of all the variables related to human pressure (distances) pooled (50.7% vs. 42.6%, respectively). The strength of refuge selection in human-dominated landscapes allowed wolves even to rest relatively close to manmade structures (sometimes less than 200m). Maintaining high-quality refuge areas becomes an important element for both favouring the persistence of large carnivores and for human-carnivore coexistence in human-dominated landscapes, which can easily be integrated in landscape planning.

Despite humans influencing the factors that shape the spatial ecology of large carnivores, such as food availability or intraspecific competition, the impact of human activities on certain parameters of the spatial ecology of these species, and in particular to the wolf, still remains poorly studied in certain contexts. For example, in human-dominated landscapes, game hunting, livestock practices, and human-caused predator mortality are expected to impact the spatial ecology of large carnivores. Multiple factors have been correlated with the spatial behaviour of large carnivores such as wolves in different systems, but rarer has such evaluation been when livestock comprised the most important fraction of the predator diet.

Finally, in the fifth chapter of this thesis, we have identified the determinants of home range size variation in wolves in human-dominated landscapes of NW Spain. We used spatial information from 29 wolves equipped with GPS-GSM collars (mean 4,884 locations by wolf). To estimate home range sizes (HR) and core areas (CA) were chosen the isopleths containing 90% and 50% of the locations, respectively, after applying fixed kernel method. For every

subadult or adult wolf, we classified its social status by means of exploring its spatial behaviour in relation to the location of homesites and packs in the area as well as direct observations of pack members. A wolf with recurrent locations in the vicinity or within a given homesite with pups or being observed with other pack members or pups was considered as a pack member (n=19), whereas 7 individuals were considered as non-pack individuals.

To identify the key determinants of home range size variation in wolves in highly human-dominated landscapes, we explored basic variations in home range size in relation to gender, age, status and seasons (breeding season vs. mating season), and focusing on territorial subadult/adult wolves, we explored the explanatory power of several non-mutually exclusive groups of factors that potentially could affect home range size as the anthropogenic influence, landscape configuration, the amount of available refuge and its structural composition. Furthermore, we have checked the effect of anthropogenic food availability on the home range size variation and the importance of anthropogenic food sources in the diet, because the diet of packs with collared wolves in the study area consisted basically livestock species - more than 85% in all cases-. Finally, we analyzed effects of intraspecific competition (wolf density). Using generalized linear models, we evaluated the influence of gender, age, social status, as well as interaction between gender and age on home range size variation. We used general linear mixed models to evaluate seasonal variations in home range size according to gender, age, their interaction, and season (two levels: breeding and mating seasons). For wolves integrated in packs, we built generalized linear models to compare a set of seven competing models explaining home range size variation and considering i) null model, ii) landscape configuration, iii) quantity and quality of refuge within the home range (refuge quantity and fragmentation level), iv) human pressure (densities of paved roads, unpaved roads, and human settlements), v) food availability, vi) the importance of livestock in the diet of wolves (percentage of livestock in the diet) and vii) intraspecific competition (wolf pack density).

We have observed similar spatial requirements in wolves regardless of gender and age classes. However, adult and sub-adult pack members showed on average an annual home range size four times smaller than non-pack members. Seasonal differences were also observed in range sizes, being larger during the mating season compared to the breeding season. We found that the importance of livestock in the diet of wolves influenced home range and core area sizes. The proportion of livestock in the diet showed negative and significant influence on range sizes. Small range sizes in human-dominated landscapes modulated by the importance of livestock in the diet translate into the potential for higher wolf densities in these landscapes compared to natural areas.

1.

INTRODUCCIÓN


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1. INTRODUCCIÓN

La plasticidad ecológica que presenta el lobo (*Canis lupus*) le ha posibilitado ocupar la mayor parte del hemisferio norte (Mech y Boitani, 2003). Dicha capacidad de adaptación le ha permitido establecerse en hábitats con condiciones ambientales muy distintas y en ocasiones extremas. Así, los lobos pueden encontrarse desde regiones árticas (Riewe, 1975; Mech, 1988; Mech, 1995a), bosques boreales de Norteamérica y Eurasia (Pulliainen, 1980; Wabakken *et al.*, 2001; Mech and Boitani, 2003; Houle *et al*., 2010; Lesmerises *et al*., 2012) hasta grandes estepas y desiertos asiáticos (Bibikow, 1973; Stepanov y Pole, 1996; Hefner y Geffen, 1999; Hovens *et al*., 2000; Wronski y Macasero, 2008; Davie *et al*., 2014), e incluso han persistido en áreas muy humanizadas de Eurasia (Mendelssohn, 1982; Blanco *et al*., 1990; Petrucci-Fonseca, 1990; Jhala y Giles, 1991; Adamakopoulos y Adamakopoulos, 1993; Boitani, 2000; Iliopoulos *et al*., 2009; Reichmann y Salts, 2005; Agarwala y Kumar, 2009; Ahmadi *et al*., 2014; Chapron *et al*., 2014). Los principales condicionantes de la distribución de esta especie no han estado relacionados con el ambiente, sino con el hombre (Chapron *et al*., 2014). Los lobos son capaces de persistir en cualquier lugar donde el hombre no provoque su desaparición y haya un mínimo de disponibilidad de alimento (Boitani, 2000). Solo la intensa persecución humana ha supuesto la extinción de la especie en grandes territorios de Norteamérica, la mayor parte de Europa occidental y algunas regiones de Asia (Mech y Boitani, 2003).

Teniendo en cuenta su ecología trófica, los lobos pueden comportarse como grandes predadores capturando presas silvestres dentro de un amplio rango de tamaños (desde alces *(Alces alces)*, bisontes (*Bison bison*) o caballos (*Equus ferus caballus*) hasta lagomorfos y roedores (Reig y Jedrzejewski, 1988; Okarma, 1995; Mech y Boitani, 2003; López-Bao *et al*., 2013; Mech *et al*., 2015). En sistemas con poca intervención humana se ha demostrado como los lobos juegan un papel importante en la regulación de las poblaciones de ungulados silvestres y su interacción con la dinámica de los hábitats (efectos cascada; Estes *et al*., 2011; Ripple y Beschta, 2012; Ripple *et al*., 2014; Mech *et al*., 2015). Dentro de este espectro trófico, los ungulados domésticos pueden llegar a suponer una parte importante en la dieta de la especie (Cuesta *et al*., 1991; Meriggi y Lovari, 1996; Llaneza *et al*., 1996; Vos 2000; López-Bao *et al*., 2013; Tinoco *et al*., 2015). Además, los lobos muestran comportamientos claramente carroñeros (Jhala y Giles, 1991; Meriggi and Lovari, 1996; Hovens *et al.*, 2000; Vos, 2000; Anwar *et al.*, 2012; Tourani *et al.*, 2014), particularmente en determinados contextos locales, como por ejemplo zonas de la estepa cerealista de España y del oeste de Galicia (Guitián *et al.*, 1979; Cuesta *et al.*, 1991; Cortes, 2001; Lagos, 2013), así como otras áreas mediterráneas (Meriggi and Lovari, 1996).

Los lobos han sido capaces de adaptarse y persistir en áreas muy humanizadas de Asia, como en la India (Jhala y Giles, 1991; Agarwala y Khumar, 2009), Israel (Reichmann *et al.*, 2005) e Irán (Ahmad *et al.*, 2013; Ahmadi *et al.*, 2014), así como en las penínsulas mediterráneas europeas (Blanco *et al.*, 1990; Petrucci-Fonseca, 1990; Adamakopoulos y Adamakopoulos, 1993; Boitani, 2000; Chapron *et al.*, 2014), llegando a estar presentes, en ocasiones, en áreas con más de 200 personas por km^2. Incluso en algunos contextos, como es el caso que nos ocupa, este gran carnívoro ha sido capaz de persistir en ausencia de ungulados silvestres de mediano/grande tamaño por un periodo de tiempo considerable – varias décadas - (Núñez-Quirós *et al.*, 2007; Vos, 2000; López-Bao *et al.*, 2013; Tourani *et al.*, 2015). En estos paisajes de elevada humanización, los lobos han mostrado una enorme resilencia, siendo capaces de persistir en situaciones con unos denominadores comunes que *a priori* no predecirían la presencia y viabilidad de poblaciones de esta especie, como una fuerte persecución humana, o una elevada antropización del territorio. Sin embargo, estos ambientes también proporcionan una elevada disponibilidad de alimento de origen antrópico, uno de los factores claves para la presencia y persistencia de la especie.

En Europa, la intensa persecución tanto legal como ilegal a la que estuvo sujeta el lobo en tiempos modernos, supuso su erradicación de muchos países como Alemania, Francia, Noruega, Suecia, Países Bajos, Dinamarca, etc., quedando poblaciones residuales en los países del este y en las penínsulas mediterráneas (Chapron *et al.*, 2014). En respuesta a este elevado nivel de persecución durante siglos, como en otros grandes carnívoros (p.ej., Zedrosser *et al.*, 2011), los lobos que han persistido en ambientes humanizados han desarrollado pautas comportamentales especificas que han facilitado su permanencia en estos contextos (Fuller y Sievert, 2001), sobre todo minimizando el contacto con el hombre (Ciucci *et al.*, 1997; Tehuerkauf *et al.*, 2003; Wittington *et al.*, 2005; Habib y Kumar, 2007; Lesmerises *et al.*, 2013; Ahmadi *et al.*, 2014). Sin embargo, la persistencia de la especie en algunos ambientes humanizados va acompañada de un elevado conflicto socioeconómico, dado que en algunos casos existen individuos, manadas o poblaciones que producen un impacto sobre el ganado o nuestras mascotas notable (Mech, 1995b; Kaltenborn *et al.*, 1999;

Vos, 2000; Blanco y Cortés, 2002; Naughton-Treves *et al*., 2003; Ericsson y Herberlein, 2003; Espirito-Santo, 2007; Iliopoulos *et al*., 2009; Houston *et al*., 2010; López-Bao *et al*., 2013; entre otros muchos).

Desde tiempos históricos, la depredación directa del lobo sobre el ganado en la Península Ibérica, donde en algunas zonas la abundancia de ungulados silvestres ha sido relativamente baja durante décadas (López-Seoane, 1861; Cabrera, 1914; Nores y Vázquez, 1987; Nores *et al*., 1995), desencadenó una fortísima persecución de la especie, alcanzándose unos niveles de persecución extraordinariamente elevados a mediados del s. XIX, con más de 13.000 lobos muertos en España para el periodo 1855-1859 (Rico y Torrente, 2000). Tal situación llevó a la desaparición del lobo en la mayor parte de la Península Ibérica a principios del siglo XX, quedando relegado a principios de los años 70 del pasado siglo a unos reducidos efectivos poblacionales en el NW de la Península Ibérica y Sierra Morena (Valverde, 1971; Petrucci-Fonseca, 1990; Chapron *et al*., 2014). Tras la puesta en marcha y aplicación de diversas normativas legales de carácter nacional y europeo (p.ej., Convenio de Berna de 1979, Ley de Caza y su Reglamento de 1971 – que supuso que el lobo no fuese considerado como una alimaña a la que se podía matar de múltiples maneras y durante cualquier época del año – o la Directiva Habitats 92/43/CEE), la población de lobo ibérico se fue recuperando en las décadas siguientes, adaptándose a un paisaje muy dinámico. El proceso de recuperación de las poblaciones de lobo en las últimas décadas ha estado favorecido además por el despoblamiento del medio rural acaecido en los últimos 50 años, junto con el incremento de las poblaciones de ungulados silvestres y una creciente opinión social favorable a la conservación de la especie (Chapron *et al*., 2014).

El área de estudio en el que se ha desarrollado esta tesis ha mantenido presencia histórica de la especie (Núñez-Quirós *et al*., 2007), en un contexto de continuos cambios paisajísticos en los últimos 60-100 años, pasando de paisajes eminentemente agrícolas y ganaderos, a un descenso de la actividad agrícola y un incremento de las plantaciones forestales de pinos y eucaliptos (Corbelle y Crecente, 2008; 2014; Corbelle-Rico *et al*., 2012), acompañado por un proceso de abanado rural, particularmente acusado en áreas de montaña (López-Bao *et al*., 2015a). Además, parejo a estos cambios ha habido un crecimiento constante de las infraestructuras humanas (carreteras, pistas, etc.) en el medio rural y natural (Ministerio de Fomento, 2014).

En Galicia, en la actualidad, se estima que alrededor de 84 manadas de lobos están presentes en el territorio gallego (Llaneza *et al.,* 2014), en un paisaje dominado por el hombre, con multitud de asentamientos humanos (≥ 10 edificios juntos) muy dispersos por todo el territorio gallego (de hecho, casi el 50% de los asentamientos humanos de España se encuentran en Galicia) y una densidad de población humana alrededor 93 habitantes / km^2 (INE, 2009). El 16,5 % de los habitantes de Galicia viven en pequeñas aldeas (<10 edificios), mientras que este porcentaje para el conjunto del estado español en general es cuatro veces menor. Esta alta dispersión geográfica de los asentamientos humanos se traduce en el desarrollo de una amplia red vial (2,7 km de carreteras asfaltadas / km^2). De hecho, los lobos que viven en Galicia tienen una de las mayores densidades de carreteras, a nivel mundial, dentro sus áreas de campeo (1,92 km carreteras asfaltadas / km^2, Dennehy, 2013).

La presencia y persistencia de lobos en un contexto de elevada humanización, básicamente, dependerá de una serie de factores que afectan a la reproducción, como la disponibilidad de alimento, y a la supervivencia, como puede ser, aparte del alimento, la actividad humana, tanto de manera directa (p.ej. persecución ilegal), como de manera indirecta (p.ej. efectos sobre la disponibilidad de alimento o sobre las características del hábitat) (Fuller, 1989; Mladenoff *et al*., 1995; Massolo y Meriggi, 1998; Woodroffe y Gingsberg, 1998; Fuller y Sievert, 2001; Jedrzejewski *et al.*, 2008; Musiani *et al*., 2010; entre otros). Además, la heterogeneidad paisajística, que en algunos casos se genera en paisajes humanizados, consecuencia de la fragmentación de hábitats derivada de la actividad humana (Vitousek *et al*., 1997; Crooks, 2002; Prugh *et al*., 2008; Soga y Koike, 2013), juega un papel crucial en la persistencia del lobo en ambientes humanizados (Amahdi *et al*., 2014).

La persistencia de los grandes carnívoros en ambientes humanizados ha suscitado un gran interés en los últimos años (Carter *et al*., 2012; Athreya *et al*., 2013; Dellinger *et al*., 2013; López-Bao *et al*., 2013; Fernández-Gil, 2013; Bouyer *et al*., 2014; Ahmadi *et al*., 2014; Ripple *et al*., 2014; Chapron *et al.*, 2014; López-Bao *et al*., 2015b), y empezamos a conocer los factores y mecanismos que influyen sobre dicha persistencia en diversos contextos dominados por el hombre. No obstante, las adaptaciones comportamentales de los lobos en paisajes humanizados con baja disponibilidad de presas silvestres, como es el caso de Galicia, permanecen poco explorados (Agarwala y Kumar, 2009; López-Bao *et al*., 2013; Ahmadi *et al*., 2014). En este sentido, en esta tesis se ha estudiado cómo diferentes grupos de predictores que representan la disponibilidad de alimento, las características del paisaje y la presión humana, explican de manera independiente o conjunta la presencia del lobo en paisajes dominados por el hombre, como es el caso de Galicia (**capítulo 1**).

En contextos ibéricos como el gallego, los lobos han sido capaces de persistir durante décadas en zonas con densidades muy bajas de ungulados silvestres, incluso en su completa ausencia, como es el caso de algunas regiones de la meseta cerealista castellana (Barrientos, 1989; Blanco y Cortés, 2002) o la mayor parte del Oeste de Galicia (Guitián *et al*., 1975; Munilla *et al*., 1991; SGHN, 1995). Por lo tanto, aunque en tiempos recientes las poblaciones de presas silvestres han ido en aumento en la mayor parte de la Península Ibérica (Fernández-Llario, 2006; Mateos-Quesada, 2011; Fandos y Burón, 2013), el alimento de origen antrópico ha jugado un papel clave en el mantenimiento de la especie en muchas zonas del NW de la Península Ibérica (Guitián *et al*., 1979; Cuesta *et al*., 1991; Llaneza *et al*., 1996; Sazatornil, 2008; Alvares, 2011; Lagos, 2013; López-Bao *et al*., 2013, Lázaro, 2014), siendo probablemente muy importante durante el mínimo poblacional que sufrió la especie en los años setenta (Valverde, 1971). El manejo tradicional del ganado en la Península Ibérica llevaba parejo el abandono de las carcasas de los animales muertos *in situ* en el campo, o arrojados en las inmediaciones de las explotaciones ganaderas o en muladares (Guitián *et al*., 1979; Cuesta *et al*., 1991; López-Bao *et al*., 2013). Ello suponía una importante disponibilidad de alimento potencial para los lobos. Sin embargo, esta dependencia de fuentes de alimento de origen antrópico puede generar situaciones complejas que afectan a la conservación y gestión de la especie. Por ejemplo, a raíz del brote de encefalopatía espongiforme bovina ("*enfermedad de las vacas locas*", periodo 1996-2000) se implementó una nueva normativa sanitaria en Europa (Reglamento CE 1774/2002) cuya aplicación obligó a los ganaderos a retirar del campo y destruir todas las carcasas de ganado en plantas autorizadas. Ello generó un nuevo escenario de disponibilidad de alimento para los lobos que, en un contexto de baja disponibilidad de presas silvestres, como sucede en el Oeste de Galicia (López-Bao *et al*., 2013), puede tener importantes consecuencias en el conflicto hombre-lobo. Relacionado con el efecto de diferentes regulaciones y políticas sanitarias y ambientales sobre el lobo, en esta tesis, bajo una perspectiva temporal, se ha evaluado cómo diferentes normativas podrían haber influido en cambios en la dieta del lobo en los últimos 30 años en el área de estudio (**capítulo 2**), y se discuten las implicaciones potenciales que ello puede suponer para la coexistencia entre el hombre y el lobo.

La viabilidad de poblaciones de lobos presentes en paisajes dominados por el hombre está condicionada con la capacidad que tenga la especie de reproducirse con éxito en una matriz paisajística muy heterogénea en cuanto a los usos del paisaje por parte del hombre, así como de su habilidad para pasar desapercibidos, incrementado así la probabilidad de supervivencia, tanto individual como de la manada (Theuerkauf *et al*., 2003; Dellinger *et al*., 2013; Iliopoulos *et al*., 2014; Ahmadi *et al*., 2014; Chapron *et al*., 2014; López-Bao *et al*., 2015b). Numerosos factores pueden estar interactuando de modo sinérgico durante el periodo de cría de los lobos, siendo, por tanto, uno de los periodos más comprometidos para la persistencia de la manada. El conocimiento de los condicionantes ambientales y humanos que afectan a la selección de los lugares de cría de los lobos, en paisajes dominados por el hombre, son cruciales para establecer medidas adecuadas de gestión del territorio y conservación de la especie (Habib and Kumar, 2007; Dellinger *et al*., 2013; Ahmadi *et al*., 2014). Aportar información al respecto ha sido uno de los objetivos de esta tesis (**capítulo 3**).

Del mismo modo, los lobos en paisajes humanizados han tenido que desarrollar mecanismos comportamentales que les hayan permitido ser capaces de minimizar el riesgo de contacto con el hombre (Ciucci *et al*., 1997; Theuerkauf *et al*., 2003; Ahmad *et al*., 2013; Iliopoulos *et al*., 2014; Ahmadi *et al*., 2014). Los lobos en ambientes humanizados presentan, principalmente, actividad nocturna y crepuscular (Vilá *et al*., 1995; Ciucci *et al*., 1997), permaneciendo refugiados y descansando durante las horas centrales del día. Estos lugares donde los lobos descansan y se refugian durante el día, conocidos como encames, deberán reunir una serie de características que les confieran protección para contrarrestar el potencial riesgo que supone un encuentro con el hombre a plena luz del día. Los factores que influyen en la selección de los lugares de descanso-refugio (encames) están escasamente descritos para las poblaciones de lobos euroasiáticas. En este sentido, en esta tesis se han estudiado los factores que determinan la selección de encames en los paisajes dominados por el hombre de Galicia (**capítulo 4**).

Otro de los aspectos de la ecología del lobo que puede verse influenciado por las adaptaciones comportamentales de la especie a paisajes dominados por el hombre es su ecología espacial, como puede ser, entre otros, el tamaño de sus áreas de campeo. En sistemas naturales, los principales factores que determinan el tamaño de las áreas de campeo de los lobos son la disponibilidad de alimento y los factores individuales y sociales (Fuller, 1989; Fuller, 1995, Wydeven *et al*., 1995; Fuller *et al*., 2003 Okarma *et al*., 1998; Jedrzejewski *et al*., 2007, entre otros). En áreas antropizadas con bajas densidades de ungulados silvestres y con una marcada dependencia del alimento de origen antrópico, como nuestra área de estudio (López-Bao *et al*., 2013; Lázaro, 2014), el tamaño de las áreas de campeo de los lobos podría estar influido por la presencia del ganado (abundancia y vulnerabilidad) y por los niveles de actividad e infraestructuras humanas (Mattison *et al*., 2013). Son escasos los estudios que han evaluado los factores que determinan el tamaño de las áreas de campeo de los lobos en paisajes dominados por el hombre (Ciucci *et al*., 1997; Kusak *et al*., 2005; Rich *et al*., 2012; Mattisson *et al*., 2013), pero menos aún en áreas donde la dieta del lobo está dominada por ungulados domésticos. Finalmente, en esta tesis, se han evaluado los factores que determinan el tamaño de las áreas de campeo de los lobos en paisajes dominados por el hombre en Galicia a diferentes niveles de intensidad del uso del espacio (**capítulo 5**).

La viabilidad de las poblaciones de grandes carnívoros y su conservación en ambientes dominados por el hombre debe considerar la necesidad de plantear estrategias de conservación a escalas espaciales grandes y transfronterizas (Linnel & Boitani, 2011; Chapron *et al*., 2014; López-Bao *et al*., 2015b). Estos planteamientos no solo deben focalizarse sobre territorios destinados a la conservación de la biodiversidad, como parques nacionales o reservas naturales, sino que se debe asumir implícitamente un modelo de convivencia entre grandes carnívoros y hombres (Linnell y Boitani, 2011; Chapron *et al*., 2014; López-Bao *et al*., 2015b) en aquellos paisajes donde el mantenimiento de grandes territorios bien conservados no sea un requisito clave para la persistencia de estas especies (López-Bao *et al*., 2015b). Estos nuevos retos de conservación de los grandes carnívoros en ambientes humanizados no resultan una tarea sencilla. La persistencia del lobo en medios rurales con actividad agropecuaria intensa, como es el caso de la mayor parte del área de distribución del lobo en la Península Ibérica, depende críticamente de la tolerancia humana a la predación del ganado y de una adecuada gestión del conflicto hombre-lobo. Por lo tanto, conocer los factores que determinan los niveles de humanización que los grandes carnívoros pueden tolerar, y su vulnerabilidad, son un primer paso fundamental para establecer medidas efectivas de gestión y conservación encaminadas a asegurar la viabilidad de las poblaciones de grandes carnívoros para las generaciones futuras. Un reto al que nos enfrentamos en nuestro tiempo.

1.1. REFERENCIAS

Adamakopoulos, P. & Adamakopoulos, T. (1993). *Wolves in Greece: current status and prospects*. (In: *Wolves in Europe-status and perspectives.* Eds. Promberger, C. & Schröder, W.). P. 56-61.

Ahmad M., Kaboli, M., Nourani, E., Alizadeh, A. & Ashrafi, S. (2013). A predictive spatial model for gray wolf (Canis lupus) denning sites in a human-dominated landscape in western Iran. *Ecol. Res*. 28(3):513-521.

Ahmadi, M., López-Bao, J.V. & Kaboli, M. (2014). Spatial heterogeneity in human activities favors the persistence of wolves in agroecosystems. *PloS one*, 9(9), e108080.

Agarwala, M. & Khumar, S. (2009). Wolves in Agricultural Landscapes in Western India. *Tropical Resources: Bulletin of the Yale Tropical Resources Institute*, *28:*48-53.

Alvares, F. (2011). *Ecología e Conservaçao do Lobo (Canis lups, L.) no Noroeste de Portugal*. Tesis de Doutoramente em Biologa. Universidade de Lisboa.

Anwar, M.B., Nadeem M.S., Shah, S.I., Kiayani, A.R. & Mushtaq, M. (2012). A note on the diet of Indian wolf (*Canis lupus*) in Baltistan, Pakistan. *Pak. J. Zool*. 44:588-591.

Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J., & Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One*, 8(3): e57872.

Barrientos, L. M. (1989). Situación del lobo en la provincia de Valladolid. *Quercus*, 45:22-26.

Bibikov, D. I. (1973). *The Wolf in the USSR*. IUCN Publications New Series. Supplementary Paper No 43, 5.

Blanco, J.C., Cuesta, L., & Reig, S. (1990). *El lobo (Canis lupus) en España. Situación, problemática y apuntes sobre su ecología. ICONA, Madrid. 118pp*.

Blanco, J.C., & Cortés, Y. (2002). *Ecología, censos, percepción y evolución del lobo en España: análisis de un conflicto*. SECEM. Málaga

Boitani, L. (2000). *Action plan for the conservation of wolves in Europe (Canis lupus)* (No. 18-113). Council of Europe.

Bouyer, Y., Gervasi, V., Poncin, P., Beudels-Jamar, R.C., Odden, J, & Linnell, J.D.C. (2014). Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Animal Conservation*, DOI:10.1111/acv.12168

Cabrera, A. (1914). *Fauna Ibérica. Mamíferos*. Museo Nacional de Ciencias Naturales. Madrid.

Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B. & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *PNAS*, 109(38): 15360–15365.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., ... & Nowak, S. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*(6216): 1517-1519.

Ciucci P., Boitani, L., Francisc, F. & Andreoli, G. (1997). Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology*. 243(4):803-819.

Corbelle, E., & Crecente, R. (2008). Abandono de terras: concepto teórico e consecuencias. *Revista Galega de Economía*, 17 (2):47-62.

Corbelle, E., & Crecente, R. (2014). Urbanización, forestación y abandono. Cambios recientes en el paisaje de Galicia, 1985-2005. *Revista Galega de Economía*, 23 (1):35-52.

Corbelle-Rico, E., Crecente-Maseda, R. &, Santé-Riveira, I. (2012). Multi-scale assessment and spatial modelling of agricultural land abandonment in a European peripheral region: Galicia (Spain), 1956–2004. *Land Use Policy*, 29:493– 501.

Cortés, Y. (2001). *Ecología y conservación del lobo (Canis lupus) en medios agrícolas*. Tesis Doctoral. Universidad Complutense de Madrid.

Cuesta, L., Bárcena, F., Palacios, F. & Reig, S. (1991) The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia*. 55:239-254.

Crooks, K.R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, *16*(2):488-502.

Davie, H.S., Murdoch, J.D., Lhagvasuren, A. & Reading, R.P. (2014). Measuring and mapping the influence of landscape factors on livestock predation by wolves in Mongolia. *Journal of Arid Environments*, *103*: 85-91.

Dellinger, J.A., Proctor, C., Steuryc, T.C., Kelly, M.J. & Vaughan, M.R. (2013). Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biological Conservation*, 157:324–330.

Dennehy, E. (2013*). The case of Iberian Wolf Canis lupus signatus persistence in the high road density region of galicia, north-west spain*. Research Dissertation. MSc Wildlife Biology and Conservation. School of Life, Sport and Social Sciences. Edinburgh Napier University

Ericsson, G. & Heberlein, T. A. (2003). Attitudes of hunters, locals and the general public in Sweden now that the wolves are back. *Biological Conservation*, 111: 149-159.

Espirito-Santo, C. (2007). *Human dimensions in Iberian Wolf Management in Portugal: attitudes and beliefts of interest groups and the public Howard a fragmented wolf* *population*. (A Requeriments for the Degree of Master of Science). Geography Department, memorial University of New foundland. St John`s, Newfoulnland, Canada.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... & Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, *333*(6040):301-306.

Fandos, P. & Burón, D. 2013. *Corzos*. Edición propia. Sevilla. España. ISBN: 978-84-616-5775-9

Fernández Gil, A. (2013). *Comportamiento y conservación de grandes carnívoros en ambientes humanizados. Osos y lobos en la Cordillera Cantábrica.* PhD Thesis. University of Oviedo.

Fernández-Llario, P. 2006. Jabalí – *Sus scrofa*. En: Enciclopedia Virtual de los Vertebrados Españoles. Carrascal, L. M., Salvador, A. (Eds.). Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/

Fuller, T. K. (1989). Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105.

Fuller, T. K. (1995). *Guidelines for gray wolf management in the northern Great Lakes region* (Vol. 271). International Wolf Center.

Fuller, T.K. & Sievert, P.R. (2001) *Carnivore demography and the consequences of changes in prey availability*. Carnivore Conservation (ed. by J.L. Gittleman, S.M. Funk, D. Macdonald and R.K. Wayne). pp. 163-178. Cambridge University Press.

Fuller A, Mech L.D. & Cochrane J.F. (2003) *Wolf populations dynamics*. In: Mech LD, Boitani L (eds) *Wolves behaviour, ecology, and conservation*. University of Chicago Press, Chicago, pp 161–191.

Guitián, J., Sánchez-Canals, J.L., de Castro, A., Bas, S., Rodríguez, J. & Bermejo, A. (1975). *El Inventario cinegético de la provincia de la Coruña*. Report to Xunta de Galicia.

Guitián, J., de Castro, A., Bas, S. & Sánchez, J.L. (1979). Nota sobre la dieta del lobo (*Canis lupus* L.) en Galicia. *Trabajos Compostelanos de Biología*, 8:95-104.

Habib, B. & Kumar, S. (2007). Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. *Journal of Zoology*, 272: 259–265.

Hefner, R., & Geffen, E. (1999). Group size and home range of the Arabian wolf (Canis lupus) in southern Israel. *Journal of Mammalogy*, 80(2):611-619.

Houle, M., Fortin, D., Dussault, C., Courtois, R., & Ouellet, J.P. (2010). Cumulative effects of forestry on habitat use by gray wolf (Canis lupus) in the boreal forest. *Landscape ecology*, 25(3):419-433.

Houston, M.J., Bruskotter, J.T. & Fan, D.P. (2010). Attitudes Toward Wolves in the United States and Canada: A Content Analysis of the Print News Media, 1999-2008 *Human Dimensions of Wildlife*, 15(5):389-403.

Hovens, J.P.M., Tungalaktuja, K.H., Todgeril, T. & Batdorj, D. (2000). The impact of wolves Canus lupus (L., 1758) on wild ungulates and nomadic livestock in and around the Hustain Nuruu Steppe Reserve (Mongolia). *Lutra*, 43(1):39-50.

Iliopoulos, Y., Sgardelis, S., Koutis, V., & Savaris, D. (2009). Wolf depredation on livestock in central Greece. *Acta theriologica*, 54(1):11-22.

Iliopoulos, Y., Youlatos, D. & Sgardelis, S. (2014). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *Eur. J. Wildlife Res*. 60:23-34.

INE (2009). *Censo de población y vivienda.* Instituto Nacional de Estadística de España.

Jhala Y. V. & Giles, R. H. (1991). The status and conservation of the wolf in Gujarat and Rajasthan, India. *Conserv. Biol*. 5:473-83.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B. & Kowalczyk, R. (2007). Territory size of wolves Canis lupus: linking local (Bialowieza Primeval Forest, Poland) and Holarctic-scale patterns. *Ecography*, 30:66–76

Jędrzejewski, W., Jędrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S., & Mysłajek, R. W. (2008). Habitat suitability model for Polish wolves based on long-term national census. *Animal Conservation*, 11(5): 377-390.

Kaltenborn, B.P., Bjerke, T. & Vitterso, J. (1999). Attitudes toward large carnivores among sheep farmers, wildlife managers and research biologists in Norway. *Human dimensions of wildlife*, 4(3):57-73.

Kusak, J. , Skribinsek, A.M. & Huber, D. (2005). Home ranges, movement, and activity of wolves (Canis lupus) in the Dalmatian part of Dinarids, Croatia. *Eur. J. Wildl. Res*. 1:254–262.

Lagos L (2013) *Ecología del lobo (Canis lupus), del poni salvaje (Equus ferus atlanticus) y del ganado vacuno semi-extensivo (Bos taurus) en Galicia: interacciones depredador - presa*. PhD Thesis. University of Santiago de Compostela. 486 p.

Lázaro, A. (2014). *Ecología trófica del lobo (Canis lupus) en un ambiente humanizado y multipresa: Variación geográfica*. MSc thesis. University of Cordoba, Spain.

Lesmerises F., Dussault, C. & St-Laurent, M.H. (2012). Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management,* 276: 125–131.

Linnell, J. D., & Boitani, L. (2011). Building biological realism into wolf management policy: the development of the population approach in Europe. *Hystrix*, *23*(1):80-91.

Llaneza, L., Fernández, A. & Nores, C. (1996). Dieta del lobo en dos zonas de Asturias (España) que difieren en carga ganadera. *Doñana Act. Vert*. 23(2): 201-213.

Llaneza L., E.J. García, V. Palacios & López-Bao (2014). *Trabajos de apoyo para la coordinación tecnico-científica del censo de lobo ibérico en la Comunidad Autónoma de Galicia*. Tragsatec-Ministerio de Agricultura, Alimentación y Medio Ambiente. Informe inédito. 48 pp.

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013) Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters*, 6: 448-455.

López-Bao, J. V., González-Varo, J. P., & Guitián, J. (2015a). Mutualistic relationships under landscape change: Carnivorous mammals and plants after 30 years of land abandonment. *Basic and Applied Ecology*, *16*(2), 152-161.

López-Bao, J. V., Kaczensky, P., Linnell, J.D., Boitani, L., & Chapron, G. (2015b). Carnivore coexistence: wilderness not required. *Science*, *348*(6237): 871.

López Seoane, V. (1861). *Fauna mastológica de Galicia ó Historia natural de los mamíferos de este antiguo reino: aplicada a la medicina, a la agricultura, a la industria, a las artes y al comercio*. Imprenta de Manuel Mirás. Santiago de Compostela.

Massolo, A., & Meriggi, A. (1998). Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. *Ecography*, *21*(2), 97-107.

Mateos-Quesada, P. 2011. Corzo – *Capreolus capreolus*. En: *Enciclopedia Virtual de los Vertebrados Españoles.* Salvador, A., Cassinello, J. (Eds.). Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J. D., Rauset, G.R. & Pedersen, H. C. (2013). Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia*, 173(3):813-825.

Mech, L. D. (1988). *The arctic wolf: living with the pack*. Voyageur Press. Stillwater, MN.

Mech, L. D. (1995a). A ten-year history of the demography and productivity of an arctic wolf pack. *Arctic*,329-332.

Mech, L. D. (1995b). The Challenge and opportunity of recovering wolf populations. *Conservation Biology*, 9 (2):270-278.

Mech, L.D. & Boitani, L. (2003). *Wolves: behavior, ecology, conservation*. University of Chicago Press, Chicago, IL.

Mech, L. D., Smith, D. W. & MacNulty, D.R. (2015). *Wolves on the Hunt: Behavior of Wolves Hunting Wild Prey*. University of Chicago Press.

Mendelssohn, H. (1982). *Wolves in Israel*. In: *Wolves of the world:Perspectives of behavior, ecology and conservation*. Harrington, F.H. & Paquet, P.C. (Eds.) Noyes Publications, New Jersey, 173-195.

Meriggi, A. & Lovari, S. (1996). A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*, 1561-1571.

Ministerio de Fomento. (2014). Catálogo y evolución de la red de carreteras. www.fomento.gob.es/mfom/lang_castellano/direcciones_generales/carreteras/catyevo_red_carreteras.

Mladenoff, D. J., Sickley, T. A., Haight, R. G., & Wydeven, A. P. (1995). A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology*, 9(2): 279-294.

Munilla, I., Romero, R. & de Azcárate, J.G. (1991). *Diagnóstico de las poblaciones faunísticas de interés cinegético de la provincia de Pontevedra.* Report to Xunta de Galicia.

Musiani, M., Anwar, S.M., McDermid, G.J., Hebblewhite, M. & Marceau, D. J. (2010). How humans shape wolf behavior in Banff and Kootenay National Parks, Canada. *Ecological Modelling*, 221(19): 2374-2387.

Naughton-Treves, L., Grossberg, R. & Treves, A. (2003). Paying for Tolerance: Rural Citizens' Attitudes toward Wolf Depredation and Compensation. *Conservation Biology*, 17(6):1500–1511.

Nores C. & Vázquez, V.M. (1987). La conservación de los vertebrados terrestres asturianos. MOPU. Madrid.

Nores, C., González, F. & García, P. (1995). Wild boar distribution trends in the last two centuries: an example in northern Spain. *Ibex, J.M.E.* 3:137-140

Nuñez-Quirós, P., García-Lavandera, R. & Llaneza, L. (2007) Analysis of historical wolf (*Canis lupus*) distributions in Galicia: 1850, 1960 and 2003. *Ecología*, 21:195-205.

Okarma, H. (1995). The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriologica*, 40: 335-386.

Okarma H., Jedrzejewski W., Schmidt K., Sniezko S., Bunevich A.N., & Jedrzejewska B. (1998). Home ranges of wolves in Bialowieza primeval forest, Poland, compared with other Eurasian populations. *J. Mammal.* 79:842–852

Petrucci-Fonseca, F. (1990). *O lobo (Canis lupus signatus Cabrera, 1907) em Portugal. Problemática da sua conservação* (Doctoral dissertation, Tese de Doutoramento, Faculdade de Ciências da Universidade de Lisboa, Lisboa).

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E. & Brashares, J.S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proc. Nat. Acad. Sci. U.S.A.* 105:20770–20775.

Pulliainen, E. (1980). *The status, structure and behaviour of populations of the wolf (Canis l. lupus L.) along the Fenno-Soviet border*. In *Annales zoologici fennici* (pp. 107-112). Finnish Academy of Sciences, Societas Scientiarum Fennica, Societas pro Fauna et Flora Fennica and Societas Biologica Fennica Vanamo.

Reichmann, A., & Saltz, D. (2005). The Golan wolves: the dynamics, behavioral ecology, and management of an endangered pest. *Israel Journal of Zoology*, 51(2), 87-133.

Reig, S., & Jędrzejewski, W. (1988). Winter and early spring food of some carnivores in the Białowieża National Park, eastern Poland. *Acta Theriologica*, 33: 57-65.

Rich, L.N., Mitchell M.S., Gude J.A. & Sime C.A. (2012) Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. *J. Mammal*. 93:722–731

Rico, M. & Torrente, J.P. (2000). *Caza y rarificación del lobo en España: investigación histórica y conclusiones biológicas*. Galemys, 12, 163-179.

Riewe, R.R. (1975). The high arctic wolf in the Jones Sound region of the Canadian High Arctic. *Arctic*, 28(3): 209-212.

Ripple, W.J. & Beschta, R.L. (2012). Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* 145: 205–213.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343(6167),1241484.

Sazatornil, V. (2008) *Alimentación del lobo (Canis lupus) en zonas del Occidente de Galicia con presencia de ganado equino en régimen de semi-libertad.* Msc Thesis. University of A Coruña.

SGHN (Sociedade Galega de Historia Natural) (1995). *Atlas de Vertebrados de Galici*a Tomo I. Consello da Cultura Gallega. Santiago de Compostela.

Soga, M., & Koike, S. (2013). Mapping the potential extinction debt of butterflies in a modern city: implications for conservation priorities in urban landscapes. *Animal Conservation*, 16(1): 1-11.

Stepanov, Y. V. & Pole, S. B. (1996). Numbers of wolves and the attitude towards them in Kazakhstan during recent decades. *J. Wildl. Res*, 1: 321-322.

Theuerkauf J., Rouys, S. & Jedrzejewski, W. (2003). Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Can. J. Zool.* 81:163–167

Tinoco, R., Silva, N., Brotas G. & Fonseca, C. (2015). To Eat or Not To Eat? The Diet of the Endangered Iberian Wolf (Canis lupus signatus) in a Human-Dominated Landscape in Central Portugal. *PLoS ONE* 10(6): e0129379. doi:10.1371/journal.pone.0129379.

Tourani, M, Moqanaki, E.M., Boitani, L. & Ciucci, P. (2014). Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia* 78:117-121.

Valverde, J. A. (1971). El lobo español. *Montes*, 159:229-241.

Vilà, C., Urios, V., Castroviejo, J. (1995). *Observations on the daily activity patterns in the Iberian wolf*. In *Ecology and conservation of wolves in a changing world* (Carbyn, L.N., Fritts, S.H. & Seip, D.R. (Eds.). Occasional Publication No. 35, Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada. pp. 335-340.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997). Human domination of Earth's ecosystems. *Science*, 277(5325): 494-499.

Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs in the North of Portugal. *Journal of Zoology*, 251: 457-62.

Wabakken, P., Sand, H., Liberg, O., & Bjärvall, A. (2001). The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology*, 79(4):710-725.

Whittington, J., St. Clair, C. C., & Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications*, 15(2):543-553.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, 280:2126-2128.

Wronski, T. & Macasero, W. (2008). Evidence for the persistence of Arabian Wolf (Canis lupus pallipes) in the Ibex Reserve, Saudi Arabia and its preferred prey species. *Zoology in the Middle East*, 45(1): 11-18.

Wydeven A.P., Schultz R.N. & Thiel R.P. (1995) Monitoring of a gray wolf (Canis lupus) population in Wisconsin, 1979–1991. In: Carbyn LH, Fritts SH, Seip DR (eds) *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Edmonton, pp. 147–156.

Zedrosser, A., Steyaert, S. M., Gossow, H., & Swenson, J. E. (2011). Brown bear conservation and the ghost of persecution past. *Biological Conservation*, 144(9): 2163-2170.


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2.

OBJETIVOS


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2. OBJETIVOS

1. Comprender como diferentes factores ambientales (características del paisaje, disponibilidad de alimento) y humanos interactúan para permitir o limitar la presencia del lobo en paisajes dominados por el hombre.

2. Evaluar la existencia de cambios a largo plazo en la dieta del lobo en paisajes antropizados del NW Ibérico, y su relación con cambios en las políticas ambientales y sanitarias ocurridos durante las últimas tres décadas.

3. Determinar qué factores ambientales y humanos están implicados en la selección de los lugares de cría por parte de los lobos en paisajes humanizados.

4. Conocer qué factores determinan la selección de los lugares de descanso y refugio (encames) que hacen los lobos en función del riesgo de interacción con el hombre en paisajes dominados por el hombre.

5. Identificar los principales factores que explican la variación del tamaño del área de campeo de los lobos en paisajes humanizados relacionados con atributos individuales, sociales y ambientales a diferentes niveles de intensidad de uso del espacio.


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3.

INSIGHTS INTO WOLF PRESENCE IN HUMAN-DOMINATED LANDSCAPES: THE RELATIVE ROLE OF FOOD AVAILABILITY, HUMANS AND LANDSCAPE ATTRIBUTES


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3. INSIGHTS INTO WOLF PRESENCE IN HUMAN-DOMINATED LANDSCAPES: THE RELATIVE ROLE OF FOOD AVAILABILITY, HUMANS AND LANDSCAPE ATTRIBUTES

ABSTRACT

Understanding which human or environmental factors interact to enable or to limit the occurrence and persistence of large carnivores in human-dominated landscapes is an important issue for their effective conservation, especially under the current scenario of global change where most of their former habitat is being transformed by humans. We combine data on the distribution of Iberian wolves *(Canis lupus signatus)* living in a human-dominated landscape in NW Spain and variation and partitioning methods to investigate the relative importance of three groups of predictors: food availability, humans and landscape attributes - each group expected to have unequal effects on wolf reproduction and survival - and their interactions on the occurrence of this species. We found that the group of predictors related with landscape attributes (altitude, roughness and refuge) strongly determined wolf occurrence, followed by humans and food availability. Variance partitioning analysis revealed that the three most important components determining wolf occurrence were related with landscape attributes: (i) the joint effects of the three predictor groups, (ii) the joint effect of humans and landscape attributes and (iii) the pure effect of landscape attributes. Altitude had the main independent contribution to explain the probability of wolf occurrence. In human-dominated landscapes, the occurrence of wolves is the result of a complex interaction among several environmental and human factors. Our results suggest that the characteristics of the landscape (spatial context) – factors associated with the security of wolves facilitating that animals go unnoticed by humans, wolf movements, dispersal events and short-time colonization – become more important in human-dominated landscapes and may have played a key role in the occurrence and persistence of this species throughout decades modulating the relationship between humans and wolf distribution.

KEYWORDS: *Canis lupus signatus*, carnivore conservation, carnivore persistence, human-dominated landscapes, landscape context, refuge, wolf presence.

3.1. INTRODUCTION

The ability of large carnivores to persist in human-dominated landscapes has aroused debate in recent years (Woodroffe, 2000; Linnell *et al.*, 2001; Basille *et al.*, 2009). Large carnivores are particularly sensitive to human development, with human density, human activities and associated human-carnivore conflict being key factors determining their occurrence and persistence (Woodroffe, 2000; Woodroffe *et al.*, 2005). However, in some areas, these species are able to persist at high human densities and at high levels of landscape transformation, suggesting a regional variation in the species' sensitivity to humans and their activities, driven by other human, biological or environmental factors (Woodroffe, 2000; Linnell *et al.*, 2001; Cardillo *et al.*, 2004; Blanco & Cortés, 2007; Basille *et al.*, 2009; Agarwala *et al.*, 2010). In anthropogenic landscapes, the occurrence and persistence of large carnivores seem to be modulated by strong interactions among factors that affect reproductive rates, such as food availability (Fuller & Sievert, 2001; Basille *et al.*, 2009), and factors that affect survival such as human activity or landscape context, which can reduce human pressure (Woodroffe & Gingsberg, 1998). However, the relative importance of these blocks (sometimes composed by several factors) and their interactions in determining the occurrence of these predators in human-dominated landscapes remains poorly understood (e.g. Boitani, 2000).

Along these lines, wolves (*Canis lupus*) living in human-dominated landscapes are a good model species to tackle this question. Broadly, wolf habitat tolerance is shaped by food availability and mortality risk (Fuller, 1989; Mech, 1995; Mladenoff *et al.*, 1995; Massolo & Meriggi, 1998; Fritts *et al.*, 2003; Jedrzejewski *et al.*, 2008; Musiani *et al.*, 2010). However, a lack of knowledge remains about how these factors interact to enable or to limit wolf presence in human-dominated landscapes (Boitani, 2000). In Eurasia, wolves persist in some areas where human densities are remarkably higher (> 30 inhabitants/km^2 and > 1 km of roads/km^2; Massolo & Meriggi, 1998; Blanco & Cortés, 2007; Theurkauf *et al.*, 2007; Agarwala *et al.*, 2010) than the upper threshold value reported in North America (< 13 inhabitants/km^2 and < 0.7 km of roads/km^2; Thiel, 1985; Mech, 1989; Mladenoff *et al.*, 1995; Mladenoff *et al.*, 2009; but see Merrill 2000). Moreover, these high human and road densities are accompanied by high levels of human activity and settlements (Massolo & Meriggi, 1998; Ciucci *et al.*, 2003; Blanco & Cortés, 2007; see below).

In Europe, as consequence of severe persecution during the last two centuries, wolves were reduced to few small isolated populations (Promberger & Schroder, 1993). In the Iberian Peninsula, a remnant wolf population (*Canis lupus signatus*) reached its lowest point in the 1970s, with wolves surviving mainly in the northwest (Blanco & Cortés, 2002; Fig. 3.1a). Subsequently, this population started to increase and expanded southward and eastward (Blanco & Cortés, 2002). Interestingly, wolves persisted in an area - Galicia, NW Spain (Fig. 1a,b) - with high levels of human density and activity (around 80-90 inhabitants km^{-2} during the last 5 decades; 93 inhabitants km^{-2} and 1 settlement km^{-2} in the last decade; INE, 2009; see Agarwala *et al.*, 2010, for a similar scenario), and where the human-wolf conflict has been evident for a long time (Blanco & Cortés, 2002). In fact, recent studies suggest that wolf range in Galicia did not vary remarkably in the last 1.5 centuries (Núñez-Quirós *et al.*, 2007). For example, at the beginning of the 2000s wolf presence and abundance in Galicia were remarkable with at least 68 different wolf packs identified (c. 2.25 wolf packs per 1000 km^{2}; Llaneza & Ordiz, 2003; Llaneza *et al.*, 2004, 2005a).

Thus, wolves living in Galicia provide a good opportunity to investigate how a group of predictors representing food availability, humans and landscape attributes, along with their interactions, determine the occurrence of a large predator in a human-dominated landscape. We expected that (i) wolves should select areas with high prey abundance, (ii) taking into account previous wolf habitat models, wolves should avoid the areas of highest human densities and activity levels (in most known cases, during the study period wolf mortality was caused by humans in 91% of cases: 65% were road killed, 20% died by poaching or illegal hunting, and 6% were legally hunted; Llaneza & Ordiz, 2003; Llaneza *et al.*, 2004, 2005a), but showing higher tolerance levels for these factors than previously reported in non-human-dominated landscapes, and (iii) wolves should strongly select inaccessible and safe places (i.e. refuge) to decrease human-mediated mortality risks. Human density and the type of human activities carried out in a given area may be important factors determining the level and the type of human pressure on a wolf population (Fuller, 1989; Mech, 1995), but landscape attributes may drive this human-wolf interaction by providing protection from humans. The availability of areas that are hardly accessible to humans may ensure the occurrence of large predators such as wolves by decreasing human pressure (Corsi *et al.*, 1999; Glenz *et al.*, 2001). In this regard, we predicted that landscape attributes should be a key group of predictors enabling the occurrence of this species in human-dominated landscapes.

3.2. METHODS

Study site

Fieldwork was carried out in Galicia (NW Spain; Fig. 3.1a,b), covering c. 30.000 km^2. The study area is characterized by a human-dominated landscape with human settlements (≥ 10 buildings) widely scattered (1 human settlement km^{-2}; c. 50% of human settlements of Spain are located in Galicia) and a mean human population density around 93 inhabitants km^{-2} (INE, 2009). The percentage of people living in small villages in Galicia (< 10 buildings) is 16.5%, whereas this percentage for the overall country is four times lower. Consequently, the high geographical dispersion of human settlements implicitly requires a well-developed paved road network (mean paved road density 2.7 km/km^2). Most human settlements in the area are placed at medium-low altitudes in the valleys and/or in flat areas. As a result, human activities decrease with increasing altitude and topographic roughness (see also Glenz *et al.*, 2001 for a similar scenario; Fig. 3.1c).

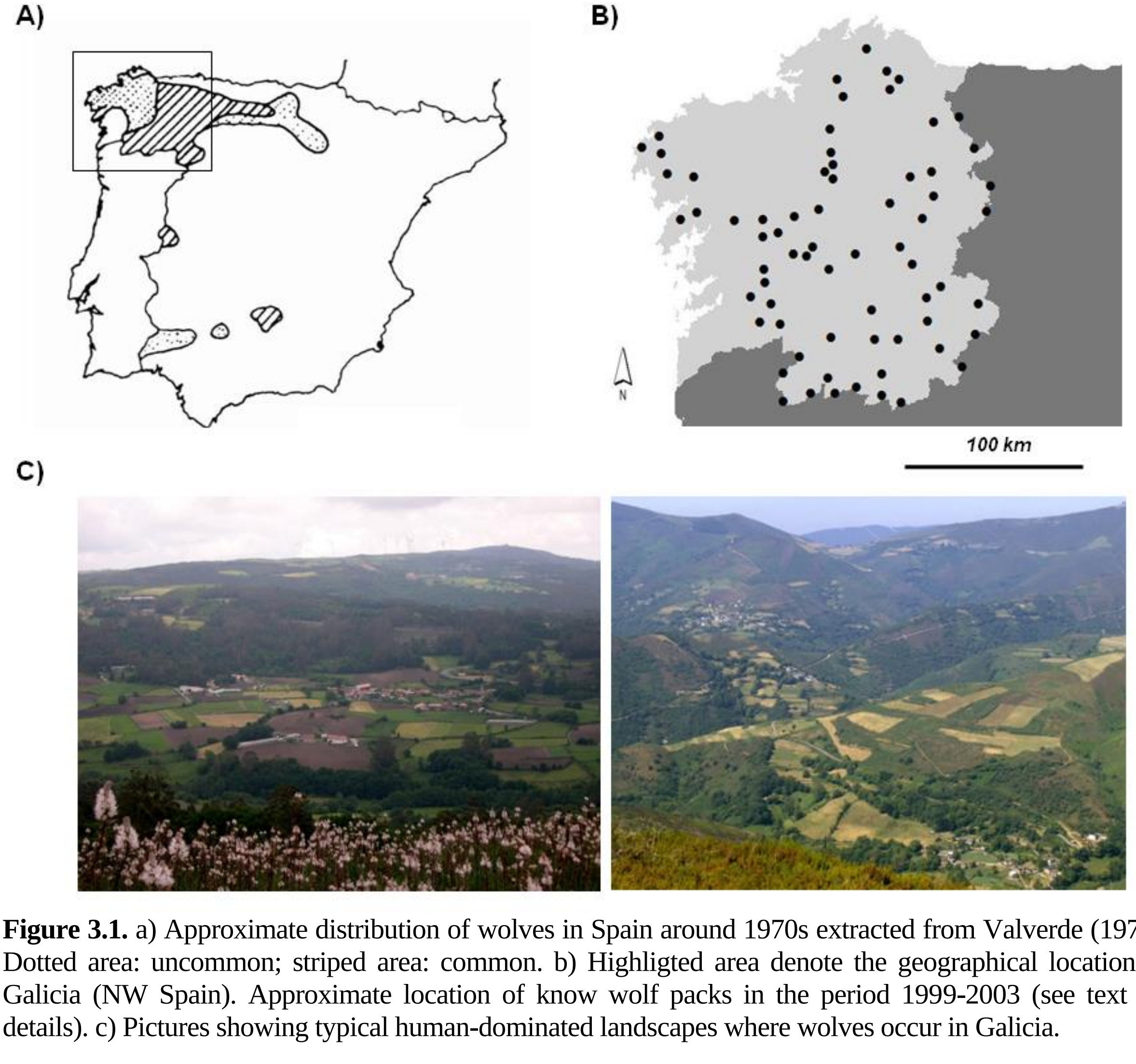

Figure 3.1. a) Approximate distribution of wolves in Spain around 1970s extracted from Valverde (1971). Dotted area: uncommon; striped area: common. b) Highligted area denote the geographical location of Galicia (NW Spain). Approximate location of know wolf packs in the period 1999-2003 (see text for details). c) Pictures showing typical human-dominated landscapes where wolves occur in Galicia.

As a result of long-standing traditional human management for agriculture and livestock in Galicia, most of the territory is comprised of a patchy and heterogeneous landscape (Fig. 3.1c) made up of cropland, pasture, scrub, semi-natural deciduous forest (*Quercus robur, Quercus pyrenaica* and *Betula alba*) and forest plantations (*Eucalyptus* spp. and *Pinus* spp.). It is worth mentioning that the cover percentage of pastures and crops in Galicia is 39%, 23% for forest plantations and 26.6% for scrublands, which have been transformed by human activities. Less than 10% of this area is occupied by woodland deciduous forest and most of them have been managed for long time (i.e. timber harvest). As in many rural areas of Europe, dramatic declines in livestock and the swift process of depopulation and land abandonment during the last third of the twentieth century (Gómez-Sal *et al.*, 1993; Roura-Pascual *et al.*, 2005; Munilla-Rumbao *et al.*, 2008) led to an increase in the cover of scrubland and forest plantations and a decrease in agricultural fields (see Munilla-Rumbao *et al.*, 2008 for an example in the East part of Galicia).

Wolf survey

Data on the distribution of wolves come from regional wolf surveys carried out in the summer-autumn periods (breeding and pre-dispersal periods) between 1999 and 2003 (Llaneza & Ordiz, 2003; Llaneza *et al.*, 2004, 2005a). Wolf presence was determined by means of indirect signs such as faeces and ground scratch marks, excluding tracks owing to the difficulty of differentiating dog tracks from wolf tracks (Harris & Ream, 1983). Shape, size, contents, smell and spatial position were, in combination, diagnostic attributes of wolf faeces. The criteria used were considered reliable since a trial using these criteria to assign wolf faeces and a parallel DNA analyses confirmed that 90% of faeces (n = 108) were correctly assigned to wolves (R. Godinho *et al.*, unpublished data). Ground scratching is a form of territorial marking, which in addition to olfactory information involves a visible sign and it is commonly placed on paths (Zub *et al.*, 2003). Size, length, intensity and the presence of other wolf signs such as faeces are commonly used to determine the identity of these marks. Overall, 1689 wolf signs (1594 faeces and 95 scratch marks; 100% of positive grid-cells by scratch marks were also confirmed by faeces) were located and used to determine wolf presence.

As random sampling is not effective to locate wolf signs (e.g. Llaneza *et al.*, 2005b), surveys were focused on landscape features often used by wolves as marking places. We therefore searched for wolf signs along transects, on foot or using a vehicle (< 10 km h-1) following paths, dirt roads, forest trails, firebreaks and crossroads, because wolves locate most of their faecal marking sites (territorial marking sites) in these places (Mech & Boitani, 2003; Barja *et al.*, 2004; Llaneza *et al.*, 2005b). Further details about the monitoring procedure are given in Llaneza et al. (2005b). The total number of transects used was 1204 with a total of 5631.4 km surveyed (a mean ± SD of 4.7 ± 3 km per transect).

We took the Universal Transverse Mercator (UTM) coordinates of all wolf signs to determine the presence of this species on a 5 x 5 km grid-cell basis. Out of the 1323 grid-cells that make up the study area, 862 (65%; 21550 km^2) were searched and wolf signs were located in 31% of them (47% of the total grid-cells sampled). Transect length in all grid-cells was > 1km with a mean of 6.5 km (range 1 - 8 km) and a mean of 4.2 wolf signs were found by positive cell (SD = ±3.5; range 1 – 34). Because of the extensive movements of wolves, often occupying territories several times larger than our survey grid-cells (> 100 km^2; Blanco & Cortés, 2007; Jedrzejewski *et al.*, 2007) and the constraints associated with our sampling protocol (focused on territorial marks), we excluded from analyses all grid-cells where wolf presence was not detected but which adjoined grid-cells with wolf presence, with the aim of reducing misidentification of wolf absence grid-cells.

Human and environmental variables

We used twelve predictors grouped into three blocks: food availability, humans and landscape attributes, each expected to have unequal effects on wolf reproduction and survival.

Food availability

Dietary studies carried out in Galicia have shown that the most important food resources for wolves in this area were livestock, mainly horses (*Equus caballus*), cattle (*Bos taurus*), sheep *(Ovis aries)*, pigs (*Sus scrofa domesticus)*, goats (*Capra hircus)* and carrion (Guitián *et al.*, 1979; Cuesta *et al.*, 1991; Sazatornil, 2008). Locally, wild ungulates (i.e. game species), particularly wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) can be also important (Guitián *et al.*, 1979; Cuesta *et al.*, 1991; Barja, 2009). Generally, anthropogenic food resources are more important than wild prey (Guitián *et al.*, 1979; Cuesta *et al.*, 1991; Sazatornil, 2008). In fact, excluding some local context (Guitián et al., 1979; Barja 2009), several studies showed that wild prey composed > 15% of the diet of wolves (Cuesta *et al*., 1991; Sazatornil, 2008; Palacios *et al*., 2009).

We estimated food availability as the densities of wild and domestic ungulates within each sampled grid-cell (i.e. an estimate of the biomass available of each food type). Data on approximate numbers of wild ungulates come from the official game statistics held by the Environmental Council of Galicia between 1999 and 2004 at the level of game preserve (mean area = 59 km^2; range 1 – 459 km^2; n = 501; 50% of game preserves have an area < 50 km^2; Xunta de Galicia, 2005) and were corrected by hunting effort (number of beats). In the case of Galicia, official game statistics are reliable as regards the differences in wild ungulate abundance among different zones. Since wolves mainly fed on human-origin food sources, we pooled together wild boar and roe deer in a variable representing the density of game species (i.e. wild prey). Data on livestock were taken from the Rural Council of Galicia at the level of council (mean area = 90 km^2; range 1 – 430 km^2; n = 323; 31% of councils have an area < 50 km^2; Xunta de Galicia, 2003). We used five variables representing those most important domestic species in the diet of wolves either in number of prey items or in biomass: horse, cattle, sheep, goat and pig (e.g. Guitián *et al*., 1979; Sazatornil, 2008). All variables were transformed to number of heads of animals per square kilometre. As a grid-cell often overlap more than one game preserve or council, data on wild prey or livestock from each overlapping administrative figure were weighted for each grid-cell in relation to their proportion of the total cell area.

Humans

We used density of human population, density of buildings and density of roads as measures of human presence and activity within each sampled grid-cell. Data on density of population and density of buildings were taken from the National Institute of Statistics (INE, 2009) at the level of parish (mean area = 7.8 km^2; range 0.08 – 75 km^2; n = 3797; 76% of parish have an area < 10 km^2 whereas 97% have an area < 25 km^2), and were measured as number of inhabitants per square kilometre and number of buildings per square kilometre, respectively. Again, for each grid-cell, we weighted data on human and settlement densities from each overlapping parish in relation to their proportion of the total cell area. Data on road density were taken from Environmental Council of Galicia (Xunta de Galicia, 2003). We grouped all types of paved roads in a single predictor representing accessibility of humans and risk of road mortality. We did not consider unpaved roads. We generated this variable as the ratio between the sum of the total lengths of all roads and the surface area of each grid-cell (km/km^2).

Landscape attributes

We compiled three variables associated with low human densities and activities, and safe places for wolves: mean altitude, roughness and refuge. We calculated the mean altitude (meters) by averaging altitudes of all 100 x 100 m raster cells included in each sampled grid-cell. We calculated roughness (meters) as the standard deviation of the altitudes of all 100 x 100 m raster cells included in each sampled grid-cell. Finally, in spite of the fact that wolves are highly adaptable to a wide range of vegetation types (even areas without plant cover; Boitani, 1982; Mech & Boitani, 2003; Jedrzejewski *et al.*, 2008), we counted as refuge sites only those vegetation types that could effectively conceal wolves (vegetation > 50 cm high): scrublands, woodlands and forest plantations. Functionally, these vegetation types provide similar conditions of refuge and resting site for wolves (L. Llaneza, J.V. López-Bao & V. Sazatornil, unpublished data), and therefore were pooled together in a single variable denominated *"refuge"*. This variable was the sum of the surface occupied by scrublands, woodlands and forest plantations within each sampled grid-cell. Data on vegetation types and the proportions of the different plant covers were obtained from the Spanish Forest Map (scale 1:200000; Ruiz de la Torre, 2001).

Statistical analyses

We used variation and hierarchical partitioning methods that allow the addressing of collinearity problems which sometimes can hinder the detection of key factors underlying studied processes (Mac Nally, 2000; Mac Nally & Horrocks, 2002). These statistical methods decompose the variation in response variables into independent components, which reflect the relative importance of individual predictors or groups of predictors and their joint effects (Anderson & Gribble, 1998; Heikkinen *et al.*, 2005).

Before carrying out analyses, we built matrices of Spearman correlation coefficients to explore collinearity between predictors. Only the pair of variables density of buildings and density of population showed high correlation ($r_s = 0.8$), but we retained both predictors due to their different biological meanings (Green, 1979).

We used a variance partitioning approach to decompose the variation in the occurrence of wolves among the three groups of predictors: food availability, humans and landscape attributes. We used a series of generalized linear models (GLM) with binomial errors and logit link to decompose the deviance among these three groups of predictors (i.e. partial models; Borcard *et al.*, 1992; Heikkinen *et al.*, 2005). Within each block, forward stepwise procedures, starting from a full model including all predictors, were performed to exclude within each group variables that did not contribute significantly ($P > 0.05$) to the explained deviance. Thus, final candidate models included only significant variables. In addition, we checked for Akaike`s information criterion (AIC) differences in all steps of the models (Burham & Anderson, 2002). We obtained the total explained variation in the occurrence of wolf in our data set by carrying out a GLM with all the selected statistically significant variables of the three groups of predictors (i.e. general model). The deviance explained by each of the previous models was calculated as the percentage of the total deviance explained by the respective general model. Variation partitioning led to eight fractions (Anderson & Gribble, 1998; Heikkinen *et al.*, 2005): (i) pure effect of food availability alone; (ii) pure effect of humans alone; (iii) pure effect of landscape attributes alone; and combined variance due to the joint effects of (iv) food availability and humans; (v) food availability and landscape attributes; (vi) humans and landscape attributes; (vii) the three groups of predictor variables and finally (viii) unexplained variance (see Fig. 3.2).

Values of human and environmental variables for neighboring grid-cells may be more similar than they would be for random. Therefore, to separate the independent effects of explanatory variables from those accounting for spatial autocorrelation, we corrected for spatial autocorrelation in all models by including a spatial term of the form “$x + y + x^2 + xy + y^2 + x^3 + x^2y + xy^2 + y^3$” (Legendre & Legendre, 1998). The spatial coordinates of the sampled grid-cells (lower-right “x” and “y” UTM coordinates) were centered on their respective means to reduce collinearity with higher order terms (Legendre & Legendre, 1998) and standardized to unit variance.

Then, we performed a hierarchical partitioning including only those predictors retained as significant in previous models to identify their independent and conjoint contributions with all other significant variables (Chevan & Sutherland, 1991; Mac Nally, 2000). Hierarchical partitioning was conducted using logistic regression and log-likelihood as the goodness-of-fit measure. This statistical procedure allowed us to identify those predictors with an important independent – not partial – correlation with the probability of wolf occurrence (Mac Nally & Horrocks, 2002). Statistical significances of the independent contributions of selected predictors were tested by a randomization procedure (100 randomizations), which yielded Z-scores for the generated distribution of randomized independent contributions and an indication of statistical significance ($P < 0.05$) based on an upper 0.95 confidence limit ($Z \geq 1.65$; Mac Nally & Horrocks, 2002). We used the R 2.8.1 statistical software (R Development Core Team, 2008) and the hier.part package (Walsh & Mac Nally, 2008) for all the regression and partitioning analyses.

3.3. RESULTS

The group of predictors that accounted the highest proportion of the variation in the wolf distribution data was landscape attributes (16.4 %), followed by humans (11.7 %) and food availability (9.6 %; Fig. 3.2). Final models for the occurrence of wolves from the three predictor groups are shown on Table 3.1. For food availability, the model predicted an increasing probability of wolf occurrence only with increased densities of horses and wild ungulates (Table 3.1; Fig. 3.3). For humans, the model predicted an increasing probability of wolf occurrence with lower densities of buildings and roads (Table 3.1; Fig. 3.3). Interestingly, human density was not selected in the final model of humans. In fact, mean human population density in grid-cells with wolf presence was highly variable (mean ± SD of 28 ± 32 inhabitants km^{-2}, range 0.6-247.6). Wolves occurred in Galicia in areas with remarkably high densities of paved roads (mean ± SD of 1.2 ± 0.7 km km^{-2}, range 0-3.7) and settlements (mean ± SD of 14.3 ± 12.1 buildings km^{-2}, range 0-131.7). Finally, we detected a positive effect for all predictors tested within the landscape attributes group (mean altitude, roughness and refuge) on the probability of wolf occurrence (Table 3.1; Fig. 3.3).

Together, food availability, humans and landscape attributes models explained 18.8% of the deviance in the data set (Fig. 3.2). Of the total deviance explained (Fig. 3.2), the most important components were the joint effect of the three predictor groups (vii = 35%), followed by the joint effect of humans and landscape attributes (vi = 24%) and the pure effect of landscape attributes (iii = 22%). The spatial term accounted for a high proportion of variability in the data set (Fig. 3.4), being more important for food availability (79%) than for humans and landscape attributes (43% and 47% respectively; Fig. 3.4).

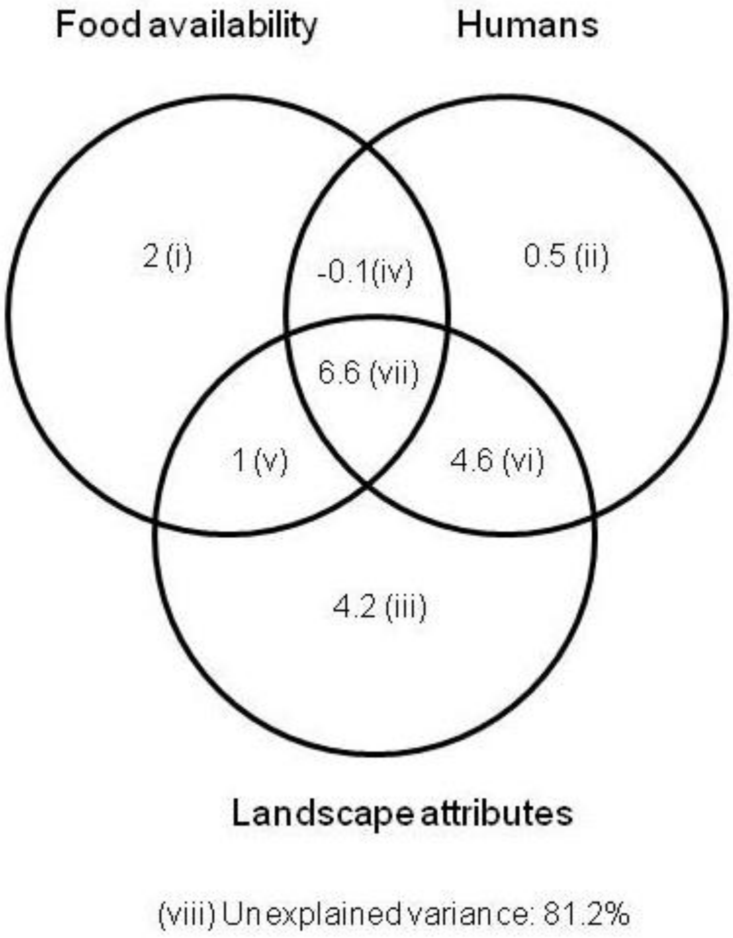

Figure 3.2. Results of variance partitioning for the occurrence of wolves in Galicia (NW Spain) in terms of the fractions of variance explained. Variance is explained by three groups of predictors: food availability, humans and landscape attributes; (i), (ii), and (iii) are unique effects of food availability, humans and landscape attributes, respectively; while (iv), (v), (vi) and (vii) are fractions indicating their joint effects. (viii) refer to undetermined variance.

Table 3.1. Generalized linear models obtained for the probability of wolf occurrence in Galicia (NW Spain). Models were built separately for each of the predictor groups before applying the variance partitioning approach. The spatial correction term was included in all the models but is not shown in the table for simplicity. Degrees of freedom: 64. Final candidate models were always those with the best AIC or with a difference < 1 with regard to the best model (models with a difference < 2 units are commonly considered as alternatives; Burnham & Anderson, 2002).

PREDICTOR GROUP	VARIABLE	ESTIMATE	SE	Z	*P*
Food availability	Density of horses	0.02	0.01	5.33	<0.0001
	Density of game species	0.73	0.29	2.42	0.015
Humans	Density of roads	-0.14	0.03	-4.96	<0.0001
	Density of buildings	-0.03	0.01	-4.22	<0.0001
Landscape attributes	Mean altitude	0.01	0.01	7.94	<0.0001
	Refuge	0.15	0.05	2.72	0.006
	Roughness	0.01	0.01	2.05	0.040

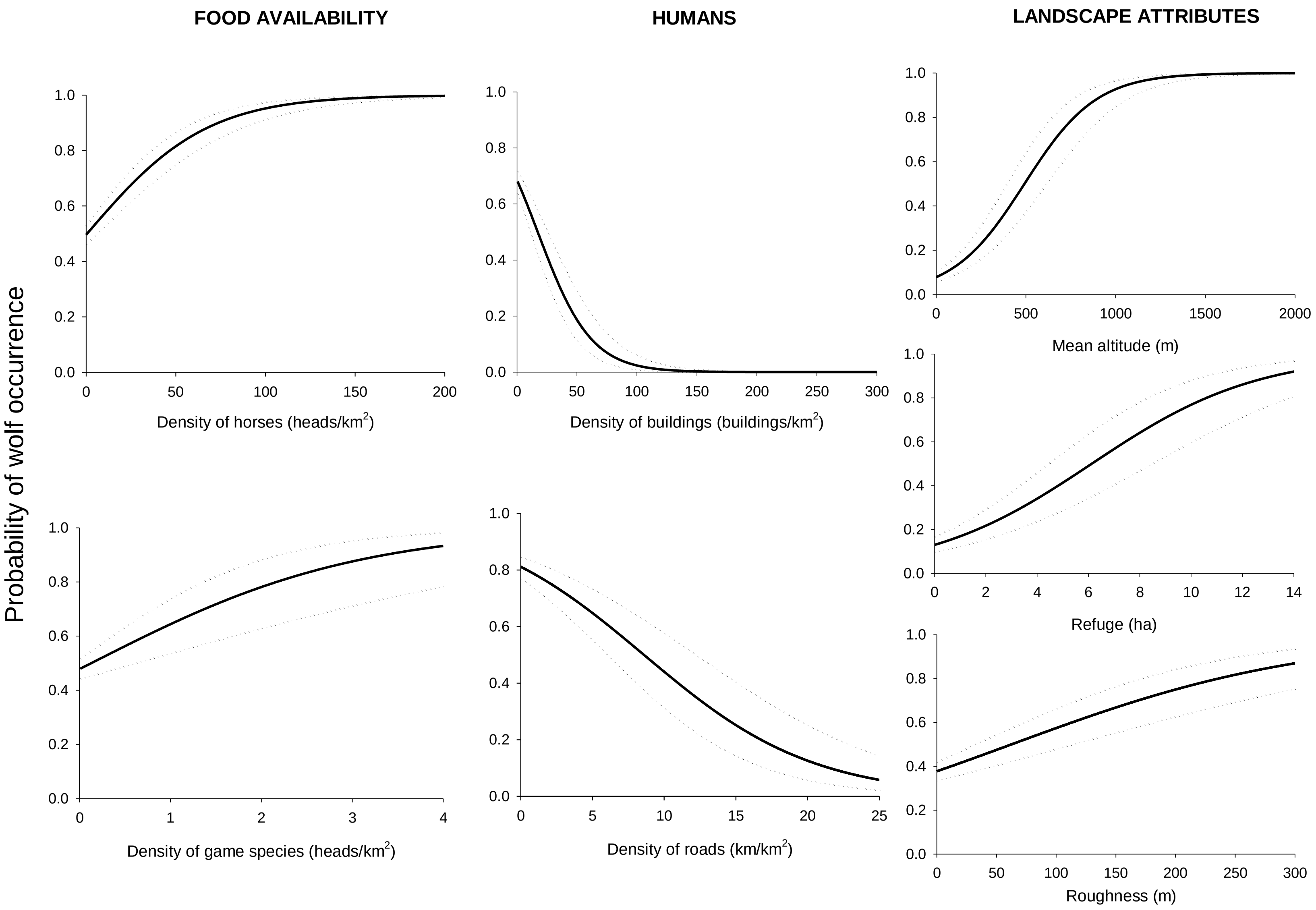

Figure 3.3. Predicted probability of wolf occurrence in Galicia (NW Spain) against the selected statistically significant variables of the three groups of predictors (food availability, humans and landscape attributes).

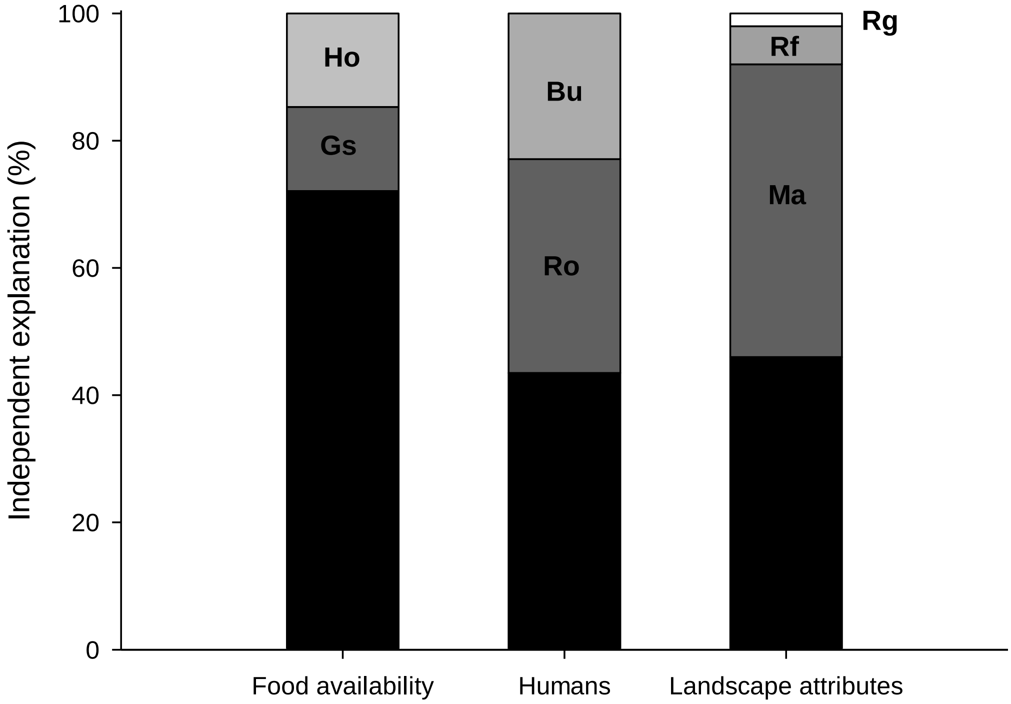

Figure 3.4. Results of the deviance partitioning analysis performed to assess the independent contribution of the explanatory variables included in the final models. Black: deviance explained by the spatial pattern of the sampled grid-cells. Ho: density of horses; Gs: density of game species; Bu: density of buildings; Ro: density of roads; Rg: roughness; Rf: refuge and Ma: Mean altitude.

Results of hierarchical partitioning were in accordance with those of variation partitioning. Hierarchical partitioning analysis revealed that mean altitude had the highest proportion of independent contribution to explaining the probability of wolf' occurrence (35.6 %), followed by density of buildings (23.8 %), density of horses (13.4 %) and density of roads (11.2 %; Fig. 3.5). The remaining predictors showed independent contributions < 10% (Fig. 3.5). All predictors showed remarkable proportions of joint contributions (> 48% of explained variance excluding density of horses; Fig. 3.5). The independent effects of all included variables were statistically significant (Table 3.2). Overall, landscape attributes was the group of predictors most important in explaining wolf occurrence (48%), followed by humans (35%) and food availability (17%).

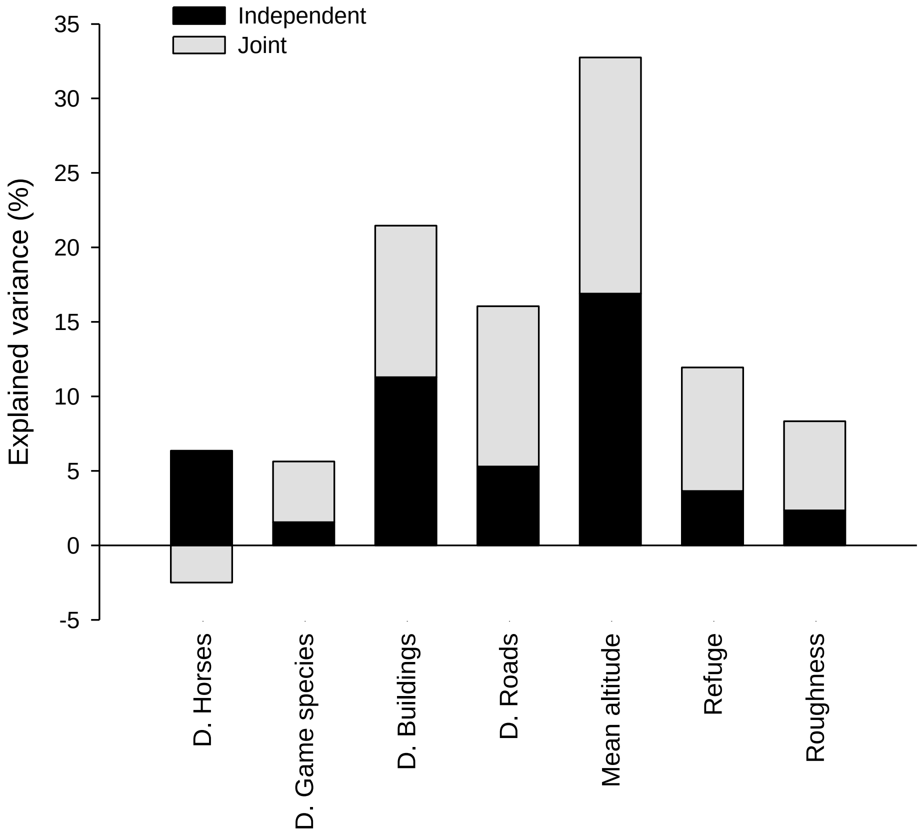

Figure 3.5. The independent and joint contributions (percentage of the total explained variance) of the variables selected for the probability of wolf occurrence in Galicia (NW Spain), as estimated from hierarchical partitioning.

Table 3.2. Results of the randomization tests for the independent contributions of separate predictor variables in hierarchical partitioning to explaining variation in the occupancy of wolves in Galicia (NW Spain).

VARIABLE	Z-score	*P*
Density of horses	8.94	< 0.05
Density of game species	2.33	< 0.05
Density of buildings	35.94	< 0.05
Density of roads	7.72	< 0.05
Mean altitude	37.69	<0.05
Refuge	4.44	< 0.05
Roughness	4.55	< 0.05

3.4. DISCUSSION

Studies on the factors that enable or limit the occurrence of wolves have yielded similar results throughout its range (e.g. Fuller, 1989; Mladenoff *et al.*, 1995; Massolo & Meriggi, 1998; Corsi *et al.*, 1999; Jedrzejewski *et al.*, 2008; Mladenoff *et al.*, 2009). Generally, the importance of human-related factors (human density, settlements or road density) has been emphasized along with the abundance of prey and the presence of refuge areas. Accordingly, despite the observational character of this study, we found that wolves selected areas with abundant prey (prediction 1), low human presence (prediction 2) and less access for humans (prediction 3).

The complexity of the behaviour of wolves and the fact that this species can adapt to a wide range of environments provided that food and refuge are available (Mech & Boitani, 2003) may explain the relatively low percentage of deviance explained together by food availability, humans and landscape attributes models (see also Mech 2006). Our results suggest that food availability did not seem to be a limiting factor for wolves in our study area, and we point out that this fact may be linked to the low percentage of deviance explained. Alternatively, we can not exclude the possibility that important determinants of wolf presence not considered in this study caused the large amount of unexplained variance. We suggest that in human-dominated landscapes just above the minimal requirements of food availability and refuge, which make the presence of this species possible, the level of tolerance towards wolves within each local context will play an important role driving the occurrence and persistence of wolves (Naughton-Treves *et al.*, 2003; Karlsson & Sjöström, 2011). In this regard, we stress that future research about which human or environmental factors interact to enable or to limit the persistence of large carnivores in human-dominated landscapes should try to integrate this human dimension.

On the other hand, some problems associated with differences in the spatial scale in which some variables were measured (particularly food availability) regarding to the spatial scale we used to determine wolf occurrence could be also partly responsible for the large amount of unexplained variance. In fact, the influence of this factor is probably the rule in many studies about distribution or habitat modeling using large vertebrate species as study models. A possible solution to reduce this source of bias would be matching all the spatial scales in which the different factors are measured (for example counting the livestock within each grid-cell in the field); however, which this procedure entails several logistic constraints given the spatial scale of these type of studies (around 30,000 km^2 in this study or even at the scale of entire countries).

Wild boar and roe deer are the main wild prey of wolves in Galicia, although their role in the diet of wolves is only locally significant (Guitián *et al.*, 1979; Sazatornil, 2008; Barja, 2009). Both species can adapt to remarkable levels of human activity living in agricultural landscapes (Sáez-Royuela & Tellería, 1986; Andersen *et al.*, 1998), particularly after the swift process of depopulation and land abandonment occurred during the last third of the 20th century. Thus, the adaptability of wild ungulates to human activity is facilitating the occurrence, persistence and recolonization of large predators in anthropogenic areas (e.g. Ensenrink & Vogel, 2006; Basille *et al.*, 2009; Mladenoff *et al.*, 2009). Moreover, this fact may be buffering potential negative effects in wolf populations coexisting with humans related to changes in animal husbandry and livestock practices at short-medium term.

We found that horses living in semi-wild conditions in Galicia may be a key factor determining wolf occurrence in areas of low abundance of wild prey or other livestock species. Our results regarding the important contribution of the spatial correction term to the total variance explained in the food availability model suggest that the significant selected food types seemed to be rather aggregated than randomly distributed in Galicia. Moreover, the negative joint contribution of density of horses indicates that a proportion of the relationships between this factor and the other predictors are suppressive and not additive (Chevan & Sutherland, 1991), particularly for those variables within the group of humans.

Regarding humans, two important differences appear in human-dominated landscapes when compared with other areas. First, human density was not selected as a determinant factor of wolf occurrence, contrary to the findings of other habitat suitability or predictive models (e.g. Mladenoff *et al.*, 1995; Corsi *et al.*, 1999; but see Theuerkauf *et al.*, 2009 about the relationship between nocturnal activity of wolves and human density), with wolves occurring even in areas of high human density (247.6 inhabitants km^{-2}). This fact shows the complex relationship between human density and the presence and persistence of large predators (Woodroffe, 2000; Linnell *et al.*, 2001). Our results suggest that this factor itself is not decisive, but the spatial dispersion of human settlements, which could be a key factor determining the occurrence of large carnivores in human-dominated landscapes. In addition, the lack of relationship between human density and wolf presence could also be associated with the link between humans and the most important food sources for wolves (livestock and carrion) in the area. Second, threshold values for settlements and roads from which wolves are absent were remarkably higher than in other areas (e.g. Thiel, 1985; Mech, 1989; Mladenoff *et al.*, 1995; Merrill, 2000; Theuerkauf *et al.*, 2009). For example, the threshold value for paved road density is one of the highest values reported in the literature (Merrill, 2000; Blanco & Cortés, 2007). Wolves in Galicia were present even in areas with remarkably high densities of paved roads (3.7 km/km^2). Our results support the hypothesis that wolves show higher tolerance values for human factors in human-dominated landscapes compared with non-human-dominated landscapes. On the other hand, the fact that wolves showed higher threshold values in human-dominated landscapes than in other areas alternatively suggests that wolves may have become more habituated to human presence over time in those areas of Europe where wolves have persisted for a long time (Nuñez-Quirós *et al.*, 2007; see Thiel *et al.*, 1998 for North America).

Wolves showed a strong positive selection towards elevated and hardly accessible sites as well as areas where vegetation structure provided refuge. The relatively new dense vegetation patches in much of the area (see for example Munilla-Rumbao *et al.*, 2008) are favoring that wolves to go unnoticed by humans. Overall, these variables indirectly reflect safe places from the human perspective (low human pressure) (Mladenoff *et al.*, 1995; Jedrzejewski *et al.*, 2008), although these places could also provide wild prey. The importance of landscape attributes may be exacerbated in human-dominated landscapes. Landscape attributes may facilitate wolf resting-refuge sites, movements, dispersal events and short-time colonization in areas where wolves were extinct (Gula *et al.*, 2009).

Variation partitioning showed the importance of landscape attributes in determining the occurrence of wolves in human-dominated landscapes. In fact, this block was involved in the three most important pure and joint effects determining the occurrence of this species. Likewise, hierarchical partitioning identified landscape attributes as the most important determinant of wolf occurrence. The large amount of joint effects and their importance across predictors of the three blocks provides evidence that in human-dominated landscapes the occurrence of wolves is the result of a complex interaction among several environmental and human factors, perhaps resulting in a regional variation in the species' sensitivity to humans.

Our results suggest that the strength of human persecution (indirectly estimated using landscape attributes) in determining wolf occurrence is more important than humans per se. Humans might not fully determine wolf occurrence except when additional factors facilitate wolf persecution. The occurrence of wolves in our study area seems to be highly influenced by landscape attributes and their interaction with humans, with food availability perhaps playing a secondary role reflecting the generalist trophic character of this species and a high availability of food resources for wolves in anthropogenic systems. Once food is available wolves will occur and persist in any place where human persecution is low (Boitani, 2000; Linnell *et al.*, 2001, Musiani *et al.*, 2010), even in human-dominated landscapes provided these areas fulfill this requirement (Blanco & Cortés, 2007; Theuerkauf *et al.*, 2007; this study). Landscape attributes may also facilitate spatio-temporal segregation of wolves from humans in anthropogenic landscapes (Theuerkauf *et al.*, 2003).

Furthermore, the importance of landscape attributes along with their joint effects with humans in both variation partitioning and hierarchical partitioning suggest that the relationship between humans and wolf occurrence is modulated by the spatial context. In fact, the occupied grid-cells seemed aggregated rather than distributed (see Fig. 3.6), making evident the importance of the landscape context in determining wolf occurrence. This is also borne out by the important contribution of the spatial correction term to the total variance explained (38% in the general model).

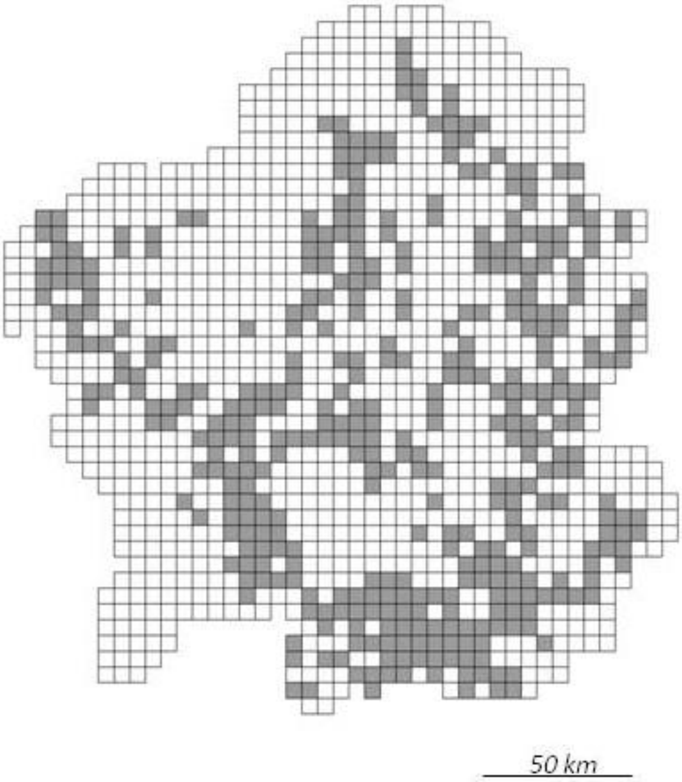

Figure 3.6. Spatial distribution of the positive grid-cells for the presence of wolves (grey cells) in Galicia between 1999 and 2003.

In summary, in human-dominated landscapes, factors associated with the security of wolves (refuge) become more important. This fact may be particularly important in areas like Galicia where the human-wolf conflict is noticeable and where mortality seems to be mainly associated with humans. Thus, in our human-dominated landscape, the characteristics of the landscape – inaccessible sites with a remarkable amount of refuge - may have played a key role in the occurrence and persistence of this large predator throughout decades, even in those periods where human persecution was highest (around 1970s).

3.5. REFERENCES

Agarwala, M., Kumar, S., Treves, A. & Naughton-Treves, L. (2010). Paying for wolves in Solapur, India and Wisconsin, USA: Comparing compensation rules and practice to understand the goals and politics of wolf conservation. *Biological Conservation*, 143:2945-2955.

Andersen, R., Duncan, P. & Linnell, J.D.C. (1998). *The European roe deer: The biology of success.* Scandinavian University Press, Oslo.

Anderson, M.J. & Gribble, N.A. (1998). Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Australian Journal of Ecology*, 23:158-167.

Barja, I., de Miguel, F.J. & Bárcena, F. (2004). The importance of crossroads in faecal marking behaviour of the wolves. *Naturwissenschaften*, 91: 489-492.

Barja, I. (2009). Prey and prey-age preference by the Iberian wolf Canis lupus signatus in a multiple-prey ecosystem. *Wildlife Biology*, 15:147-154.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Arild Høgda, K. & Gaillard, J. (2009). What shapes Eurasian lynx distribution in human dominated landscapes: Selecting prey or avoiding people? *Ecography*, 32:683-691.

Blanco, J.C. & Cortés, Y. (2002). *Ecología, censos, percepción y evolución del lobo en España: Análisis de un conflicto*. SECEM, Málaga.

Blanco, J.C. & Cortés, Y. (2007). Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. *Journal of Zoology*, 273:114-124.

Boitani, L. (1982). Wolf management in intensively used areas of Italy. *Wolves of the world. Perspectives of behaviour, ecology, and conservation* (ed. by F.H. Harrington and D.C. Paquet), pp. 158-172. Noyes Publications, Park Ridge.

Boitani, L. (2000). *Action plan for the conservation of wolves (Canis lupus) in Europe.* Council of Europe Publishing, Strasbourg, France.

Borcard, D., Legendre, P. & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73:1045–1055.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference.* Springer-Verlag Inc., New York.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology*, 2:909-0914.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *American Statistician*, 45, 90-96.

Ciucci, P., Masi, M. & Boitani, L. (2003). Winter habitat and travel route selection by wolves in the northern Apennines, Italy. *Ecography*, 26:223-235.

Corsi, F., Dupre, F. & Boitani, L. (1999). A large-scale model of wolf distribution in Italy for conservation planning. *Conservation Biology*, 13:150-159.

Cuesta, L., Bárcena, F., Palacios, F. & Reig, S. (1991). The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia*, 55:239-254.

Ensenrink, M. & Vogel, G. (2006). The carnivore comeback. *Science*, 314:746–749.

Fritts, S.H., Stephenson, R.O., Hayes, R.D. & Boitani, L. (2003). *Wolves and Humans*. Wolves: Behavior, Ecology, and Conservation. (ed. by L.D. Mech and L. Boitani). Pp. 289-316. University of Chicago Press.

Fuller, T.K. (1989). Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs*, 105:1-41.

Fuller, T.K. & Sievert, P.R. (2001). *Carnivore demography and the consequences of changes in prey availability*. Carnivore Conservation (ed. by J.L. Gittleman, S.M. Funk, D. Macdonald and R.K. Wayne). pp. 163-178. Cambridge University Press.

Glenz, C., Massolo, D., Kuonen, D. & Schlaepfer, R. (2001). A wolf habitat suitability prediction study in Valais (Switzerland). *Landscape and Urban Planning*, 55:55-65.

Gómez-Sal, A., Álvarez, J., Muñoz-Yanguas, M.A. & Rebollo, S. (1993). *Patterns of change in the agrarian landscape in an area of the Cantabrian Mountains (Spain). Assessment by transition probabilities*. Landscape Ecology and Agrosystems (ed. by R. Bunce, L. Ryzskowski & M. Paoletti). pp. 141-152. CRC Press.

Green, R.H. (1979). *Sampling design and statistical methods for environmental biologists.* John Wiley and Sons, New York.

Guitián, J., De Castro, A., Bas, S. & Sánchez, J.L. (1979). Nota sobre la dieta del lobo (*Canis lupus* L.) en Galicia. *Trabajos Compostelanos de Biología*, 8:95-104.

Gula, R., Hausknecht., R. & Kuehn., R. (2009). Evidence of wolf dispersal in anthropogenic habitats of the Polish Carpathian Mountains. *Biodiversity and Conservation*, 18:2173-2184.

Harris, R.B. & Ream, R.R. (1983). *A method to aid in discrimination of tracks from wolves and dogs*. Wolves in Canada and Alaska (ed. by L.N. Carbyn). pp. 120-124. Canadian Wildlife Service. Report Series, 45.

Heikkinen, R.K., Luoto, M., Kuussaari, M. & Pöyry, J. (2005). New insights into butterfly–environment relationships using partitioning methods. *Proceedings of the Royal Society of London. B*, 272:2203-2210.

INE (2009). *Censo de población y vivienda.* Instituto Nacional de Estadística de España.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B. & Kowalczyk, R. (2007). Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns. *Ecography*, 30:66-76.

Jedrzejewski, W., Jedrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S. & Mysajek, R.W. (2008). Habitat suitability model for Polish wolves based on long-term national census. *Animal Conservation*, 11:377-390.

Karlsson, J. & Sjöström, M. (2011). Subsidized fencing of livestock as a means of increasing tolerance for wolves. *Ecology and Society*, 16 (1):16.

Legendre, P. & Legendre, L. (1998). *Numerical Ecology, 2º edition.* Elsevier Science, Amsterdam.

Linnell, J.D.C., Swenson, J. & Andersen, R. (2001). Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, 4:345-349.

Llaneza, L. & Ordiz, A. (2003). Distribución y aspectos poblacionales del lobo ibérico en la provincia de Lugo. *Galemys*, 15:55-66.

Llaneza, L., Álvares, F., Ordiz, A., Sierra, P. & Uzal, A. (2004). Distribución y aspectos poblacionales del lobo ibérico en la provincia de Ourense. *Ecología*, 18:227-238.

Llaneza, L., Palacios, V., Uzal, A., Ordiz, A., Sazatornil, V., Sierra, P. & Álvares, F. (2005a). Distribución y aspectos poblacionales del lobo ibérico *(Canis lupus signatus)* en las provincias de Pontevedra y A Coruña. *Galemys*, 17:61-80.

Llaneza, L., Ordiz, A., Palacios, V. & Uzal, A. (2005b). Monitoring Wolf populations using points combined with sign surveys transects. *Wildlife Biology in Practice*, 1:108-117.

Mac Nally, R. (2000). Regression and model building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘‘predictive” and ‘‘explanatory” models. *Biodiversity and Conservation*, 9:655-671.

Mac Nally, R. & Horrocks, G. (2002). Relative influences of patch, landscape and historical factors on birds in an Australian fragmented landscape. *Journal of Biogeography*, 29:395-410.

Massolo, A. & Meriggi, A. (1998). Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): A model of habitat suitability. *Ecography*, 21:97-107.

Mech, L.D. (1989). Wolf population survival in an area of high road density. *American Midland Naturalist*, 121:387-389.

Mech, L.D. (1995). The challenge and opportunity of recovering wolf populations. *Conservation Biology*, 9:270-278.

Mech, L.D. & Boitani, L. (2003). *Wolves: behavior, ecology, conservation.* University of Chicago Press.

Mech, L.D. (2006). Prediction failure of a wolf landscape model. *Wildlife Society Bulletin*, 34:874-877.

Merrill, S.B. (2000). Road densities and Gray Wolf, *Canis lupus*, habitat suitability: An exception. *Canadian Field Naturalist*, 114:312-313.

Mladenoff, D., Sickley, T.A., Haight, R.G. & Wydeven, A.P. (1995). A regional landscape analysis and prediction of favourable gray wolf habitat in the northern great lakes region. *Conservation Biology*, 9:279-294.

Mladenoff, D., Clayton, M.K., Pratt, S.P., Sickley, T.A. & Wydeven, A.P. (2009). *Change in occupied wolf habitat in the northern Great Lakes region*. Recovery of Gray wolves in the Great Lakes region of the United States (ed. by A.P. Wydeven, T.R. van Deelen & A.J. Heske). pp. 119-138. Springer Science and Business Media.

Munilla-Rumbao, I., López-Bao, J.V., González-Varo, J.P. & Guitián, J. (2008). Long-term changes in the breeding bird assemblages of two woodland patches in northwest Spain. *Ardeola*, 55:221-227.

Musiani, M., Boitani, L. & Paquet, P. (2010). *The world of wolves. New perspectives on ecology, behaviour and management*. University of Calgary Press.

Naughton-Treves, L., Grossberg, R. & Treves, A. (2003). Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, 17:1500-1511.

Nuñez-Quirós, P., García-Lavandera, R. & Llaneza, L. (2007) Analysis of historical wolf (*Canis lupus*) distributions in Galicia: 1850, 1960 and 2003. *Ecología*, 21:195-205.

Palacios, V., García, E. & Llaneza, L. (2009). *Seguimiento del lobo en el norte de Lugo, 2008–2009*. Technical report from the Consellerí do Medio Rural. Xunta de Galicia.

Promberger, C. & Schroder, W. (1993). *Wolves in Europe: Status and perspectives.* Munich Wildlife Society, Ettal, Germany.

R Development Core Team. (2008). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Roura-Pascual, N., Pons, P., Etienne, M. & Lambert, B. (2005). Transformation of a rural landscape in the Eastern Pyrenees between 1953 and 2000. *Mountain Research and Development*, 25:254-263.

Ruíz de la Torre, J., (2001). *Mapa Forestal de España. Escala 1:200.000*. Ministerio de Agricultura. Pesca y Alimentación, Madrid.

Sáez-Royuela C. & Tellería, J.L. (1986). The increased population of wild boar (*Sus scrofa* L.) in Europe. *Mammal Review*, 16:97-101.

Sazatornil, V. (2008). *Alimentación del lobo (Canis lupus) en zonas del Occidente de Galicia con presencia de ganado equino en régimen de semi-libertad.* Msc Thesis. University of A Coruña.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K. & Gula, R. (2003). Spatiotemporal segregation of wolves from humans in the Białowieża Forest (Poland). *Journal of Wildlife Management*, 67:706-716.

Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S. & Radler, S. (2007) Human impact on wolf activity in the Bieszczady Mountains, SE Poland. *Annales Zoologici Fennici*, 44:225-231.

Theuerkauf, J. (2009). What drives wolves: Fear or hunger? Humans, diet, climate and wolf activity patterns. *Ethology*, 115:649-657.

Thiel, R.P. (1985). Relationship between road densities and wolf habitat suitability in Wisconsin. *American Midland Naturalist*, 113:404-407.

Thiel, R.P., Merrill, S. & Mech, D. (1998). Tolerance by denning Wolves, *Canis lupus*, to human disturbance. *Canadian Field Naturalist*, 112:340-342.

Valverde, J.A. (1971) El lobo español. *Montes*, 159:229-241.

Walsh, C. & Mac Nally., R. (2008). *hier.part: Hierarchical partitioning*. R package version 1.0.3.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280:2126-2128.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, 3:165-173.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005). *People and Wildlife: Conflict or Coexistence?* Cambridge University Press.

Xunta de Galicia. (2005). *Official Game Statistics, 2005*. Environmental Council of Galicia, Santiago de Compostela, Spain.

Zub, K., Theuerkauf, J., Jedrzejewski, W., Jedrzejewska, B., Schmidt, K. & Kowalczyk, R. (2003). Wolf pack territory marking in the Bialowieza Primeval Forest (Poland). *Behaviour*, 140:635-648.

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4.

INDIRECT EFFECTS OF CHANGES IN ENVIRONMENTAL AND AGRICULTURAL POLICIES ON THE DIET OF WOLVES


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4. INDIRECT EFFECTS OF CHANGES IN ENVIRONMENTAL AND AGRICULTURAL POLICIES ON THE DIET OF WOLVES

ABSTRACT

Policies have the potential to affect human-wildlife coexistence. However, despite consequences being evident beforehand or emerging soon after their implementation, potential conflicts between policies and biodiversity conservation are not always easy to predict. Wolves feeding on anthropogenic food sources (AFS) usually fall into conflict with humans, mainly due to predation on livestock. But the availability of AFS can be influenced by different policies leading to diet shifts, which could trigger new conflicts or exacerbate existing ones. Here, we show a long-term shift in the diet of wolves in northwestern Iberia over the last three decades, and discuss its potential connection to changes in sanitary, environmental and socio-economic policies. Wolves persisted for a long time due to the activity of humans with AFS accounting for >94% of their diet. Our results suggest a connection between a diet shift in wolves and changes in policies, from a broad diet including more feedlot (pigs, chickens) and medium-size (goats and dogs) species, mainly in the form of carrion, to a more narrow diet based primarily on large domestic ungulates (cattle and horses). We discuss the potential implications of the observed shift in the diet of wolves on human-wolf conflicts. We also call attention on the pressing need to integrate policies into biodiversity conservation to anticipate future conservation and management dilemmas.

KEYWORDS: long-term diet shift; EU policies; sanitary regulations, rural economy; *Canis lupus*; livestock predation; cattle; scavenging; free-ranging horses; human-wildlife conflicts.

4.1. INTRODUCTION

Wolves *(Canis lupus)* preying on livestock fall into a permanent conflict with humans, being a general conservation and management concern throughout its range (Mech and Boitani, 2010), and a key factor that has shaped the wolf range in human-dominated landscapes (Chapron *et al*., 2014). Conflict mitigation requires understanding how multiple factors interact in influencing livestock predation rates and the human-wolf conflict; factors such as the ecology and behavior of wolves (Mech and Boitani, 2010), livestock attributes and handling (Mech et al. 2000), wild prey availability (Meriggi *et al*., 2011), costs for rural economies (Steele *et al*., 2013), compensation and subsidies schemes (Boitani *et al*., 2010), human attitudes (Stronen *et al*., 2007), human-caused mortality (Wielgus *et al*., 2014) or even political interests (Chapron and López-Bao, 2014). But wolf management should also integrate those policies with potential to affect all of the abovementioned factors, such as environmental and agriculture policies in Europe. For example, changes in policies may influence the availability of different sources of food and the intensity of livestock predation, and ultimately, wolf persistence and human-wolf coexistence (López-Bao *et al*., 2013). However, how different unrelated policies may affect biodiversity conservation is commonly overlooked (Margalida *et al*., 2012; López-Bao *et al*., 2013).

The outcome of the implementation of either environmental or non-environmental policies can prompt unexpected changes in the behaviour of species, for instance, diet shifts as a consequence of their impacts on the availability of anthropogenic food sources (hereafter AFS) in human-dominated landscapes. This example is particularly important in cases where contentious species, such as wolves, have fed on AFS for a long time because diet shifts could trigger new conflicts or exacerbate existing ones (López-Bao *et al*., 2013). The abovementioned scenario for wolves is not a focalized problem since we can find wolves feeding remarkably on AFS (livestock, carrion, waste) in different European, Middle East and Asian countries (e.g. Cuesta *et al*., 1991; Meriggi and Lovari, 1996; Agarwala *et al*., 2010; Anwar *et al*., 2012; Tourani *et al*., 2014; Newsome *et al*., 2015). In fact, they have even persisted, sometimes for decades, in areas with a very low level or complete absence of wild prey (López-Bao *et al*., 2013).

However, despite consequences that can be evident beforehand or could emerge soon after the implementation of policies, conflicts between new policies and human-wildlife coexistence are not always easy to predict (López-Bao *et al*., 2013). The impact of European sanitary regulations on necrophagus birds represents a well-documented example of time-delayed unperceived side effects of policies on biodiversity, ecosystem services and human-wildlife coexistence. The dramatic reduction in the availability of livestock carcasses after the implementation of the CE 1774/2002 Regulation in Europe translated into declines in vulture populations and juvenile survival, as well as an increase in the number of reported vulture attacks on livestock, among others (Margalida *et al*., 2010, 2011; Margalida and Colomer, 2012).

Here we show an example of a long-term shift in the diet of wolves in a rural region of northwestern Iberia (western Galicia; Fig. 4.1) that could result from changes in agricultural and environmental policies during the last three decades. We draw attention to its potential implications on human-wolf coexistence in a context where wolves have traditionally persisted in an area where the abundance of wild ungulates has been extremely low or even absent until recently (at least since the 1960s; Guitián *et al*., 1975; Munilla *et al*., 1991; SGHN, 1995).

4.2. METHODS

A human-dominated landscape without enough wild prey

Our study case is located in western Galicia (ca. 13,000 km^2; Fig. 4.1) and is characterized by a human-dominated landscape with settlements (i.e. ≥10 buildings) widely scattered (1.4 settlements/km^2) and a mean human population density around 160 inhabitants/km^2 (INE, 2009). In Spain, wolves north of river Douro are in Annex V of the European Habitats Directive (92/43/EEC), being listed as game species in Galicia; whereas in south of river Douro the species is protected being in Annexes II and IV (Trouwborst 2014). At the beginning of the 2000s at least 68 different wolf packs were identified in Galicia (ca. 2.25 wolf packs per 1,000 km^2; Llaneza *et al*., 2012). This figure is similar to the scenario in the late 1980s, when at least 71 different wolf packs were identified (Bárcena, 1990). In the study area, at least 30 wolf packs have been estimated between 1999 and 2004 (Llaneza *et al*., 2012; López-Bao *et al*., 2013; Fig.4.1).

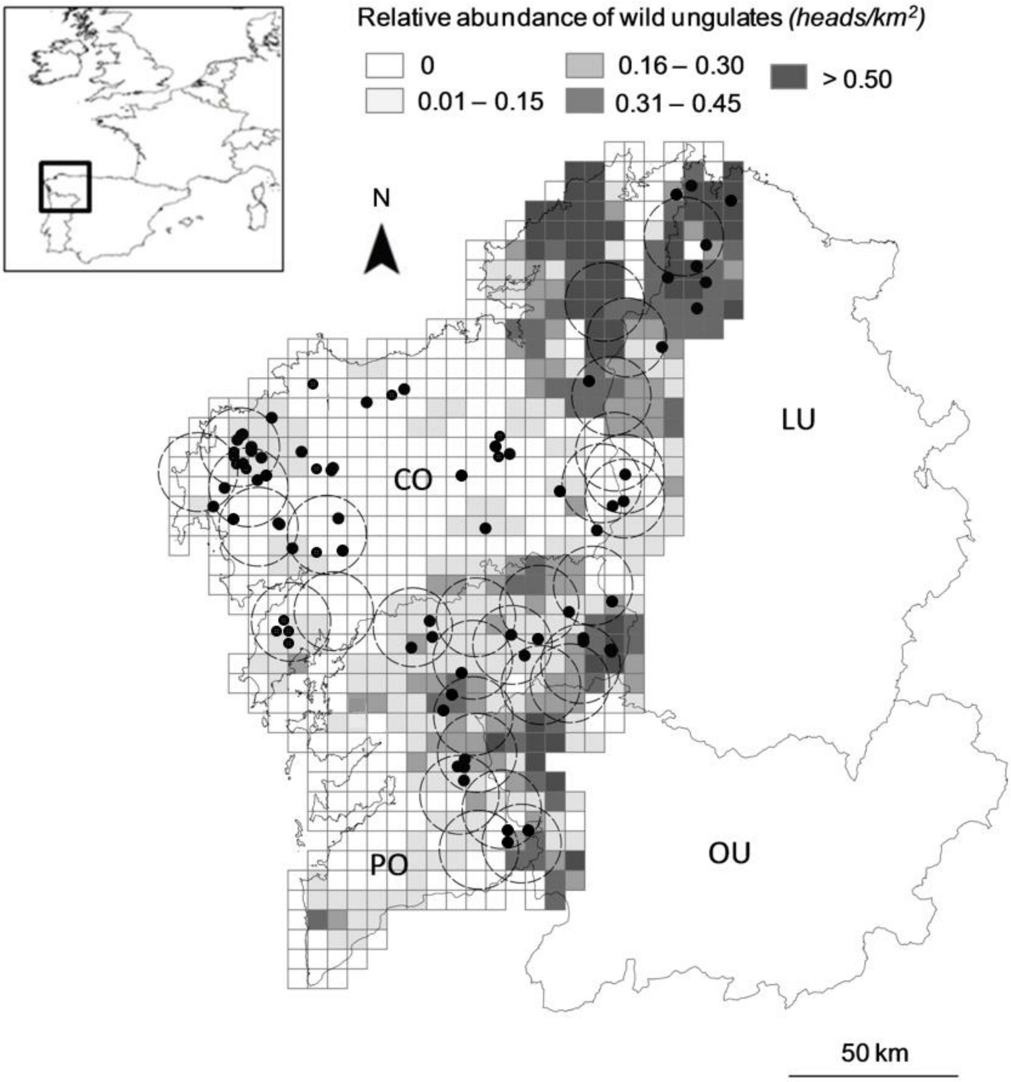

Figure 4.1. Location of the wolf stomachs with prey remains collected between 2002 and 2014 (black points). We also show the relative abundance of wild ungulates (heads/km^2) in the study area on a 5x5 km grid-cell basis based on hunting bags between 2002-2003 (Official Game Statistics; Regional Government of Galicia, 2004) as well as the simulated territories (ca. 300 km^2) of the packs detected in this area between 1999-2003 (n=30; Llaneza *et al*., 2012). Seventy-five per cent of stomachs with prey remains were collected in areas with low abundance or absence of wild ungulates (<0.15 heads/km^2). Provinces: CO (A Coruña); LU (Lugo); OU (Ourense) and PO (Pontevedra). The mean number of animals hunted per season between 2000 and 2010 have been small: 0.07 heads/km^2 for roe deer, range 0.01–0.14 and 0.08 heads/km^2 for wild boar, range 0.04–0.18 (Official Game Statistics provided by the Regional Government of Galicia in 2010). The relative abundance of wild ungulates is shown in five categories of relative abundance.

Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), the only two wild ungulates present in western Galicia nowadays, have been absent or extremely low at least since the 1960s (Guitián *et al*., 1975; Munilla *et al*., 1991; SGHN, 1995). However, during the last years both species have slightly increased their range and abundance. Assuming that hunting bags reflect variations in the abundance of ungulates (Merli and Meriggi, 2006) during the last decade a positive trend has been observed in their numbers (Spearman's rank correlation analyses, both $r_s>0.90$; $P<0.001$, n=10; Regional Government of Galicia), mainly as a consequence of the outcome of the rural depopulation process occurred in Galicia during the last decades (e.g. López-Bao *et al*., 2015). But still the availability of both ungulates for wolves is very low (Fig. 4.1).

On the contrary, the abundance of livestock has been high in the past (Rof-Codina, 1952) and still remains the most important economic mainstay in rural areas. Cattle breeding (*Bos taurus*) is the primary livestock activity, being abundant both in intensive (mainly dairy cattle) and extensive (mainly beef cattle) production (0.6 vs. 1.1 farms/km^2 and 24.1 vs. 10.1 heads/km^2, respectively), followed by sheep (*Ovis aries*) and goats (*Capra hircus*) (1.1 farms/km^2 and 6.4 heads/km^2, both species pooled). Sheep and goat flocks are relatively small (an average of 15 and 10 heads per farms for sheep and goats, respectively; INE, 2009). They are handled in semi-extensive management regimes usually roaming in the pastures close to the houses during the day and often, but not always, guarded during the night. Free-ranging horses *(Equus caballus*) are a traditional extensive livestock practice and can be abundant locally (>40 heads/km^2) (López-Bao *et al*., 2013). Free-ranging horses form small herds that roam and breed freely and unattended in communal lands all year round (Pose-Nieto and Vázquez-Varela, 2005). Finally, pig (*Sus scrofa domesticus*) and chicken (*Gallus gallus*) farms have been traditionally abundant (1.2 and 0.1 farms/km^2, respectively; data extracted from the Livestock Census, Regional Government of Galicia, 2010), but wolves could only use these two feedlot species, kept mainly under intensive and enclosed conditions, by scavenging on animal remains in small dumps around farms (Cuesta *et al*., 1991).

Changes in European, national and regional policies over time

Carrion can be an important source of food for wolves (Meriggi and Lovari, 1996). In western Galicia, as in the rest of Iberia, traditionally when livestock died, farmers abandoned animal carcasses *in situ*, around stock farms or in uncontrolled dumps, the latter being very common for dead animals that were kept indoors. As a consequence, carrion was highly available and it was an important food source for wolves (Guitián *et al*., 1979; Cuesta *et al*., 1991). However, in recent times, a new scenario emerged as a consequence of three main events related to changes in regional, national and European policies. First, the outbreak of bovine spongiform encephalopathy (*"mad cow disease",* 1996-2000) in Europe prompted the implementation of the CE 1774/2002 Regulation which obliged farmers to destroy all livestock carcasses at authorized plants. Second, the strict implementation of regional (Regional Government of Galicia 1998; Galician Decree 153/1998) and national (Spanish Decree 2110/2000) environmental and sanitary regulations closed uncontrolled dumps and obliged to destroy pet carcasses at the beginning of the 2000s decade. Finally, after the integration of Spain into the EU in 1986, a reorientation in livestock production systems occurred where predominant and traditional smallholding systems were replaced by an intensification in some livestock practices.

Implications of these changes on the availability of AFS were substantial. For example, after 2002, a mean of ca. 53,000 tons of carrion was being removed from farms in Galicia every year (period: 2002-2012, excluding 2004; Regional Government of Galicia); whereas such collection and destruction of carcasses at authorized plants did not exist before mad cow disease. This figure gives an idea about the potential availability of carrion for wolves in the past. On the other hand, as a result of changes in livestock production systems there was a dramatic reduction in the number of farms, and an increase in average farm size, although in Galicia small family farms still remained important locally. For example, out of the 40,562 cattle farms surveyed in 2009 in Galicia, 57.2% had less than 10 heads (Livestock Census, Regional Government of Galicia 2010). Moreover, some livestock practices were particularly promoted to the detriment of other traditional forms (e.g. traditional free-ranging horse husbandry; López-Bao *et al.*, 2013) and less profitable or subsidized livestock species or breeds (Otuño-Perez and Fernández-Cávada, 1995). For example, in Galicia, the number of dairy cattle decreased from 663,620 to 353,276 heads between 1986 and 2008, whereas beef cattle (usually handled in semi-extensive or extensive regimes) increased from 53,588 to 228,273 heads (a total number of 1,147,883 heads of cattle in 1986 and 839,457 heads in 2008; Livestock Census, Regional Government of Galicia 2010).

Considering a thirteen-year period before and after the 1986-2002 period, when the abovementioned changes in European, national and regional policies occurred, the annual census of cattle in Galicia significantly decreased by 5% (from an annual mean of 1,047,249±44,313 heads in 1973-1985 to 991,328±63,511 heads in 2003-2014; Mann-Whitney U-test, P = 0.018) and the annual census of sheep did not change over time (266,926±30,109 *vs.* 269,986±52,322 heads, respectively; Mann-Whitney U-test, P = 0.724). However, there was an important and significant decrease in the annual census of goats, decreasing by 28% (from an annual mean of 75,960±9,712 heads in 1973-1985 to 54,706±12,748 heads in 2003-2014; Mann-Whitney U-test, $P = 0.001$).

Determining long-term changes in wolf diet

We characterized the diet of wolves before (1970-1985; Cuesta *et al*., 1991) and after (2002-2014) the abovementioned changes in policies/regulations were implemented and the main socio-economic changes occurred in this rural area. We used the data published by Cuesta *et al*., (1991) on the diet of wolves in western Galicia, based on the analysis of 102 stomachs, to characterize the diet in the past. On the other hand, between 2002 and 2014, ninety-three wolf stomachs were collected as part of a long-term collection protocol of wolf samples approved by the Regional Government of Galicia and all stomachs with prey remains (n = 85) were used to characterize the diet of wolves in recent times. The origin of animals was diverse: road-kill (55%), poached (15%), lethal control (10%), and others/unknown (25%); but animals were never specifically killed for this study. Comparisons were methodologically acceptable since: i) the area where stomachs were collected in both periods was the same (Cuesta *et al*., 1991; Fig. 4.1), ii) the origin of animals was similar, decreasing potential bias associated with a heterogeneous distribution of individual age classes (e.g. juveniles, territorial animals) across different causes of death (wolf diet did not differ among causes of death between 2002 and 2014; Chi-square test = 10.8, $P = 0.837$; Monte Carlo simulation with 100,000 replicates), and iii) samples were collected continuously throughout both study periods.

Moreover, our sample can be considered representative of the diet of wolves in recent times based on two facts: first, the minimum convex polygon generated using the locations of the stomachs used was ca. 11,500 km^2 (88% of the study area) and second, considering the number and location of the different wolf packs located within this polygon (Fig. 4.1) as well as a simulated pack territory size of ca. 300 km^2 (based on the mean minimum convex polygon for 24 GPS collared subadult/adult wolves in Galicia, considering 100% of locations; García et al. 2012) centred on the position of their *rendezvous sites*, we collected at least one stomach in the territory or vicinity of 93% of the detected wolf packs (Fig. 4.1).

In both periods, identical standardized procedures were applied to identify prey items to the species level whenever possible using hair samples and bone remains (Teerink, 1991;

unpublished reference collections). We excluded fish, insects and fruits reported by Cuesta *et al.* (1991) for subsequent analyses.

Data analyses

We considered the stomach as the sample unit and we characterized the diet of wolves by calculating the frequency of occurrence of each prey item in stomachs. We evaluated changes in the diet of wolves through the number and type (wild vs. domestic species) of prey items found and the frequency of occurrence of each prey item. We compared the frequency of occurrence of the different prey items between periods using a randomization test of independence as expected frequencies for some prey items were small (<5%). We used a Monte Carlo randomization with 100,000 replicates to produce a null distribution of the Chi-square test statistic and to calculate P-values. We calculated prey diversity using the Shannon index of diversity 'H' (Shannon and Weaver, 1949). Moreover, diet breadth was estimated using the Levin's measure of niche breadth 'B' (Levins, 1968). Finally, Z-tests (proportions) were used to compare the importance of the different AFS in the wolf diet between periods. All statistical analyses were performed in R 3.0.2 (R Core Team, 2013).

4.3. RESULTS

Between 1970 and 1985, wolves fed on at least ten prey items (small mammals were pooled, and fish, insects and fruits were excluded; Cuesta et al. 1991; Fig. 4.2) and AFS accounted for nearly 98.5% in their diet. Pigs and chickens were the two main sources of food (18.5% and 15%, respectively) accounting for 33.5% in the diet, along with dogs (14%) (Fig. 4.2). On the other hand, between 2002 and 2014, we identified nine prey items, but still AFS accounted for 94% in the diet of wolves (Fig. 4.2). All stomachs with prey remains (n = 85) showed a single prey item and the averaged prey biomass was 0.8 kg (SD = 0.9, range 0.1 - 4.3 kg). Large livestock species, horses and cattle, were the dominant prey items in recent times (35.3% and 27.1%, respectively), comprising > 62.3% of the diet (around two times of the two main prey items detected in the past; Fig. 4.2). Wild ungulates were absent in the diet of wolves in the past and, in spite of the expansion processes suffered by wild boar and roe deer in this area in recent times, they were still rare in the diet (around 5%; Fig. 4.2).

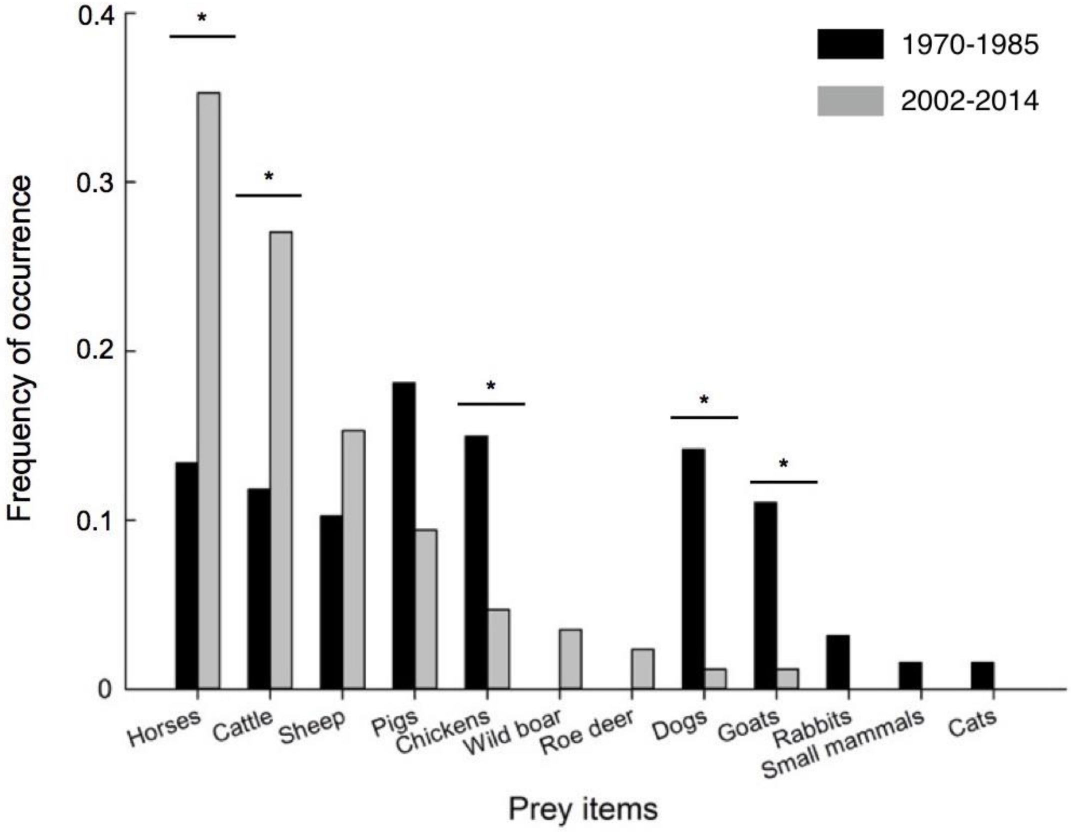

Figure 4.2. Frequency of occurrence of different prey items between 1970 and 1985 (black bars) and between 2002 and 2014 (grey bars) in the diet of wolves in the western part of Galicia. Significant comparisons of the proportion of each prey item between periods (Z-test; $P < 0.05$) are denoted by asterisks.

Although overall, we observed significant differences in the diet of wolves between periods (Chi-square test = 55.7, d.f. = 11, $P < 0.001$), the importance of AFS (all domestic prey pooled) was similar over time (Z-test, $P = 0.248$). Compared to four decades ago, we found a significant increase in the proportion of the consumption of large domestic ungulates, horses and cattle (an increment of 163% and 129%, respectively; Z-test, $P = 0.0003$ and 0.008, respectively; Fig. 4.2). On the other hand, we detected significant decrease in the importance of chickens, dogs and goats over time (Z-tests, $P = 0.033$, 0.003, and 0.013, respectively; Fig. 4.2) Prey diversity and niche breadth were higher four decades ago (H = 2.1 *vs.* 1.6; B = 7.6 *vs.* 4.2 in 1970-1985 and 2002-2014, respectively).

4.4. DISCUSSION

Wolves have persisted in western Galicia by feeding on AFS, despite most wild ungulates were exterminated, with AFS accounting for >94% of the diet at least during the last four decades. However, we observed a different use of AFS by wolves over time. We detected a shift in the diet of wolves across AFS, from a broad diet, including more feedlot species (pigs, chickens) and medium-size prey (goats, dogs), to a more narrow diet based primarily on large domestic ungulates (cattle and horses). Although our methodological procedures did not allow for distinguishing between predation and scavenging events, knowing that carrion was fully available in the past owing to the traditional management of animal carcasses, and that scavenging is a common wolf behaviour, makes it plausible to suggest that scavenging may have been important in the past, as has been highlighted by several other authors in the same area (Guitián *et al*., 1979; Cuesta *et al*., 1991; Lagos, 2013). The fact that the main AFS were feedlot species (pigs and chickens, mainly accessible by scavenging on animal remains in small dumps around farms) and that prey diversity (H) and niche breath (B) were higher four decades ago, supports this idea.

In the past, the low percentage of cattle found in the diet could be associated with its limited availability as live prey. Cattle were valuable working animals and farmers actively guarded this livestock more frequently at that time (Guitián *et al*., 1979; Álvares *et al*., 2014), particularly calves which are more vulnerable to wolf predation (Meriggi *et al*, 1996, 2011). Moreover, calves were kept mainly in stables or in the villages during the first six months of life (Álvares *et al*., 2014). Although horses were more abundant, being handled in a similar way as they are at present (i.e. unguarded; Iglesias, 1973; López-Bao *et al*., 2013), this livestock was also found in a low proportion in the diet in the past on a broad scale (although their role in supporting particular wolf packs was already important locally; López-Bao *et al*., 2013), possibly as other AFS in the form of carrion were more easily available at the time.

However, the proportion of cattle and horses in recent times was significantly higher than four decades ago, being the most important AFS even when carcasses from the former species should not be available owing to health rules. Three non-mutually exclusive interpretations might account for the observed frequency of cattle in the diet at present. First, such a remarkable proportion of cattle in the diet would reflect a low enforcement of sanitary legislations, with farmers still abandoning some animal carcasses in the field. The presence of low proportions of feedlot species found at present supports the idea that wolves still have access to carcasses and may evidence a cultural character of the abandonment of carcasses, perhaps also being reinforced by the associated costs of implementing sanitary regulations for farmers (ca. 20 € per animal; Margalida *et al.*, 2012). Second, cattle carcasses may also be on the field longer before they are detected by the owners and removed, increasing the opportunities for wolves to scavenge. This is particularly important for cattle in semi-extensive or extensive regimes such as beef cattle. Third, our findings would alternatively suggest an increase in wolf predation events on cattle at present (see also Álvares *et al.*, 2014 showing in Fig. 4.3 an increase in the relative importance of cattle in wolf damages in a similar scenario, Peneda-Gerês National Park, Portugal, from 1996 to 2012). The lower availability of cattle carcasses after health rules would predict a reduction in the frequency of occurrence of cattle in the diet, but the opposite was observed. Although no reliable data is available on the number of cattle killed by wolves in the past in the study area, only in 2011, 147 cattle were verified as being killed by wolves and compensated by the Regional Government of Galicia (Regional Government of Galicia, 2011).

Changes in livestock practices may have also contributed to the observed increment in the frequency of cattle in the diet of wolves. For example, promoting beef cattle in the extensive regime, along with a low implementation of damage prevention measures, could lead to higher predation rates on this livestock. Further data about wolf kill rates on livestock and how animal carcasses are being managed will help to increase our understanding on the mechanisms behind such increment in the importance of cattle and horses for wolves in this area over time. On the other hand, the fact that horses have been handled without any sanitary regulation until recently (López-Bao *et al.*, 2013), resulting in a lack of obligation to remove horse carcasses from the field, kept wolves both preying and scavenging on this prey. As a consequence, this non-profitable livestock practice has probably become a key resource for wolves in recent times after the health rules (CE 1774/2002 Regulation) were in place (López-Bao et al. 2013).

Contrary to the significant increase in the frequency of occurrence of large domestic ungulates and the decrease in feedlot species (only significant for chickens), we observed a significant decrease in the importance of goats and dogs in the diet over time (Fig. 4.2). Wolves not only prey on dogs (Butler *et al.*, 2013), but they also scavenge on their carcasses (Cuesta *et al.*, 1991). No information is available on the number of dogs (both feral and pets) in this area. Moreover, dogs have been handled without any sanitary regulation in the past. Cuesta *et al.*, (1991) highlighted that dogs were probably consumed more often as carrion in our study area in the past. In fact, a common practice by owners was to abandon pet carcasses in uncontrolled dumps. However, after sanitary regulations (Galician Decree 153/1998; Spanish Decree 2110/2000) uncontrolled dumps were closed and pet carcasses removed and destroyed. Although wolf predation on dogs still occur at present, and wolves have access to dog carcasses, for instance, from road-killed dogs, we argue that the implementation of sanitary regulations affecting the management of pet carcasses might have contributed to this result. On the other hand, reorientation in livestock practices together with the significant decrease in the number of goats in the study area over the past few decades (mean annual census decrease by 28% between periods in Galicia) may have caused the observed decrease in the frequency of occurrence of goats in the diet (see also Álvares *et al*., 2014).

The consequences of changes in the availability of AFS are unknown for wolves (e.g. changes in demographic parameters, spatial ecology, foraging behaviour), but we call attention to their potential influence on human-wolf coexistence. Wolves feeding on carrion may positively influence tolerance levels towards their presence in this human-dominated landscape. Under this scenario without abundant populations of wild prey during the last decades, wolves could go unnoticed or could be better tolerated if their economic impact was low. However, if wolves would increase feeding on valuable large livestock such as cattle, this fact would translate into an increase in economic loss for rural economies. For example, the estimated value of cattle (218 - 1,635 € depending on the age class and breed) is several times higher than the estimated value of goats (31 – 131 €; data extracted from the damage compensation program of the Regional Government of Galicia in 2013). On the other hand, the annual average number of verified and compensated cattle killed by wolves in Galicia between 2006 and 2011 was 132 animals, whereas it was 87 goats (Regional Government of Galicia 2011). Annually, this means an economic loss associated with wolf predation ranging between 28,776 and 215,820 € for damages on cattle, and between 2,697 and 11,397 € for damages on goats. As a result, we hypothesize that an increase in the economic loss associated with a higher consumption of valuable species such as cattle, may decrease tolerance and increase human pressure on wolves.

In western Galicia, where 30 wolf packs have been detected during the last decade (Llaneza *et al*., 2012; Fig. 4.1), the abundance of wild ungulates is still too low as to promote a diet shift in wolves towards natural prey (Meriggi *et al*., 2011), which is also not guaranteed if efficient damage prevention methods are not adopted. If this substantial wolf population were to resort to predation of livestock to make up for the loss of carrion food sources, the impact on livestock activities, and therefore likely on levels of tolerance towards wolves, could be significant illustrating the scale of the unperceived consequences of policies on human-wolf coexistence.

Our results suggest how changes in environmental and sanitary policies were possibly accompanied by shifts in wolf diet. We draw attention to the unexpected impacts that seemingly unrelated policy changes might have on conservation outcomes. Conservation should take into account and anticipate the potential impacts of changes in the broader policy context. The conflict exemplified with the case of necrophagus birds in Europe (Margalida *et al.*, 2012) is a good example illustrating a pressing need for a better integration of both environmental and non-environmental policies into conservation planning to anticipate future conservation and management dilemmas (López-Bao *et al.*, 2013). Such an integration effort will require a decisive commitment by all stakeholders and authorities to forecast potential unperceived consequences of changes in policies on biodiversity conservation and human-wildlife coexistence. This point is particular important as unperceived consequences of these policies can emerge late (López-Bao *et al.*, 2013). Scientifically sound research will be key to provide answers regarding possible consequences of changing policies on biodiversity conservation and human-wildlife conflicts.

4.5. REFERENCES

Álvares, F., Blanco, J.C., Salvatori, V., Pimenta, V., Barroso, I. & Ribeiro, S. (2014). *Exploring traditional husbandry methods to reduce wolf predation on free-ranging cattle in Portugal and Spain*. Final Report to the European Comission. 42 p.

Anwar, M.B., Nadeem, M.S., Shah, S.I., Kiayani, A.R. & Mushtaq, M. (2012) A note on the diet of Indian wolf (*Canis lupus*) in Baltistan, Pakistan. *Pak. J. Zool*. 44:588-591.

Agarwala, M., Kumar, S., Treves, A. & Naughton-Treves, L. (2010). Paying for wolves in Solapur, India and Wisconsin, USA: Comparing compensation rules and practice to understand the goals and politics of wolf conservation. *Biol. Cons.* 143:2945-2955.

Bárcena, F. (1990). *El lobo en Galicia*. In: Blanco JC, Cuesta L, Reig S (Eds.). El lobo en España. ICONA, Madrid. Pp: 11-18.

Boitani, L., Ciucci, P. & Raganella-Pelliccioni, E. (2010). Ex-post compensation payments for wolf predation on livestock in Italy: A tool for conservation? *Wildlife Res*. 37:722-730.

Butler, J.R., Linnell, J.D., Morrant, D., Athreya, V., Lescureux, N. & McKeown, A. (2014). *Dog eat dog, cat eat dog: social-ecological dimensions of dog predation by wild carnivores*. In: Gomper, M.E. (Ed.) *Free-Ranging Dogs and Wildlife Conservation*, Oxford University Press, pp. 117-143.

Cuesta, L. Bárcena, F., Palacios, F. & Reig, S. (1991). The trophic ecology of the Iberian wolf (*Canis lupus signatus*, Cabrera, 1907). A new analysis of stomach's data. *Mammalia*, 55:239-254.

Chapron, G. & López-Bao, J.V. (2014) Conserving carnivores: politics in play. Science, 343:1199-1200.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., ... & Nowak, S. (2014). Recovery of large carnivores in Europe’s modern human-dominated landscapes. *Science*, 346:1517-1519.

García, E., Llaneza, L., Palacios, V., López-Bao, J.V., Sazatornil, V., Rodríguez, A., Rivas, O. & Cabana, M. (2012). *Primeros datos sobre la ecología espacial del lobo en Galicia*. Abstract-book of the III Iberian Wolf Congress, pp.44.

Guitián, J., Sánchez-Canals, J.L., de Castro,A., Bas, S., Rodríguez, J. &, Bermejo, A. (1975). *El Inventario cinegético de la provincia de la Coruña*. Report to Xunta de Galicia.

Guitián, J., de Castro, A., Bas, S. & Sánchez, J.L. (1979). Nota sobre la dieta del lobo (*Canis lupus* L.) en Galicia. *Trabajos Compostelanos de Biología* 8:95-104.

Iglesias, P. (1973). *Los caballos gallegos explotados en régimen de libertad o caballos salvajes de Galicia*. PhD Thesis. Universidad Complutense de Madrid, Madrid.

INE (2009). *Censo de población y vivienda*. Instituto Nacional de Estadística de España.

Lagos, L. (2013). *Ecología del lobo (Canis lupus), del poni salvaje (Equus ferus atlanticus) y del ganado vacuno semi-extensivo (Bos taurus) en Galicia: interacciones depredador - presa*. PhD Thesis. University of Santiago de Compostela. 486 p.

Levins, R. (1968). *Ecology in Chicago environments: some theoretical explorations*. Princeton University Press, Princeton, NJ.

Llaneza, L., López-Bao, J.V. & Sazatornil, V. (2012). Insights into wolf presence in highly human-dominated landscapes: The relative role of food availability, human activity and landscape attributes. *Divers. Distrib*. 18:459-469.

López-Seoane, V. (1863). *Fauna mastozoológica de Galicia*. Santiago de Compostela, España.

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013) Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conserv. Lett*. 6:448-455.

López-Bao, J.V., González-Varo, J.P. & Guitián, J. (2015). Mutualistic relationships under landscape change: Carnivorous mammals and plants after 30 years of land abandonment. *Basic Appl. Ecol*. 16:152-161.

Margalida, A., Donázar, J.A., Carrete, M. &Sánchez-Zapata, J.A. (2010). Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *J. Appl. Ecol*. 47:931-935.

Margalida, A., Campion, D. & Donázar, J.A. (2011). European vultures' altered behaviour. *Nature*, 480:437.

Margalida A, Colomer MA (2012) Modelling the effects of sanitary policies on European vulture conservation. Nature Scientific Reports 2:753.

Margalida, A., Carrete, M., Sánchez-Zapata, J.A. & Donázar, J.A. (2012). Good news for European vultures. *Science*, 335:284.

Mech, L.D., Harper, E.K., Meier, T.J. & Paul, W.J. (2000). Assessing factors that may predispose Minnesota farms to wolf depredations on cattle. *Wildlife Soc. Bull*. 28:623-629.

Meriggi, A. & Lovari, S. (1996). A review of wolf predation in southern Europe: Does the wolf prefer wild prey to livestock? *J. Appl. Ecol*. 33:1561-1571.

Meriggi, A., Brangi, A., Schenone, L., Signorelli, D. & Milanesi, P. (2011). Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethol. Ecol. Evol.* 23:195-210.

Merli, E. & Meriggi, A. (2006). Using harvest data to predict habitat population relationship of the wild boar (*Sus scrofa*) in Northern Italy. *Acta Theriol*. 51:338-389.

Munilla, I., Romero & R., de Azcárate, J.G. (1991). *Diagnóstico de las poblaciones faunísticas de interés cinegético de la provincia de Pontevedra.* Report to Xunta de Galicia.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. & Dickman, C.R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24:1-11.

Otuño-Perez, S.F. & Fernández-Cávada, J.L. (1995). Perspectivas económicas de las producciones ganaderas extensivas en las áreas desfavorecidas ante la liberalización de los mercados. *Revista Española de Economía Agraria*, 174:165-191.

Pose-Nieto, H. & Vázquez-Varela, J.M. (2005). Nuevos datos y perspectivas sobre la domesticación del caballo: los caballos criados en régimen de libertad en Galicia, Noroeste de España. *Munibe*, 57:487-493.

R Core Team. (2013). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rof-Codina, J. (1952). *Importancia social del veterinario en Galicia*. Publicación de la Cátedra de divulgación pecuaria.

Shannon, C.E. & Weaver, W. (1949). *The mathematical theory of communication*. University of Illinois Press.

SGHN (Sociedade Galega de Historia Natural). (1995). *Atlas de Vertebrados de Galicia*: Tomo I. Consello da Cultura Gallega. Santiago de Compostela.

Steele, J.R., Rashford, B., Foulke, T.K., Tanaka, J.A. &Taylor, D.T. (2013). Wolf predation impacts on livestock production: Direct effects, indirect effects, and implications for compensation ratios. *Rangeland Ecol. Manage*. 66:539-544.

Stronen, A.V., Brook, R.K., Paquet, P.C. & McLachlan, S.M. (2007). Farmer attitudes toward wolves: implications for the role of predators in managing disease. *Biol. Cons*. 135:1-10.

Teerink, B.J. (1991). *Atlas and identification key hair of West-European mammals*. Cambridge University Press. Cambridge.

Tourani, M., Moqanaki, E.M., Boitani, L. & Ciucci, P. (2014). Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia*, 78:117-121.

Trouwborst, A. (2014). The EU Habitats Directive and wolf conservation and management on the Iberian Peninsula: a legal perspective. *Galemys*, 26:15-30

Wielgus, R.B. & Peebles, K.A. (2014). Effects of wolf mortality on livestock depredations. PLOS ONE, 9:e113505.


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5.

IMPROVING THE INTERFACE BETWEEN LANDSCAPE PLANNING AND LARGE CARNIVORE CONSERVATION: ACCOUNTING FOR FINE-SCALE HABITAT SELECTION PATTERNS

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ABSTRACT

In human-dominated landscapes, large carnivore recovery and conservation is often hindered by the large spatial requirements of these species and by human land use. Since protected areas are isolated within a human land-use matrix, and they are usually too small to support viable populations, conservation requires planning on very a large scale, increasing the focus on the matrix beyond incremental connectivity among protected areas. Many large carnivores require not large-scale habitat preservation but an approach identified at the proper scale. Most of the critical factors determining the persistence of large carnivores (e.g., food, vulnerability) interact synergically in space and time during the breeding season. Here, using a wolf population persisting in a human-dominated landscape in northwest Iberia and feeding as case study, we studied large carnivore breeding site (homesite) selection in multi-use landscapes in relation to food availability, human pressure, and refuge availability. Within territories, homesite selection was not determined by food availability in the immediate vicinity. However, wolves placed their homesites in areas with a high availability of unfragmented refuge, low accessibility, and low human activity levels in the vicinity at a 1 km^2 scale. Predictors related to the refuge's qualitative attributes made up the greater proportion of independent contributions to explaining homesite selection patterns. The prevalence of refuge quality over refuge quantity reflects that the availability of high-quality refuge patches, even at very small spatial scales, compensate for moderate levels of human activities in the vicinity of the homesites. Moreover, the strength of selection changed according to the immediate context, following a hierarchical selection process at small spatial scales. Understanding the main factors used to determine that a given site is suitable for large carnivores' breeding sites is important in a landscape-sharing approach that demands the integration of behavioural patterns into landscape planning. By temporally restricting human use on homesites and very small portions of surrounding lands (1 km^2), and by maintaining several high-quality refuge areas of this size at the landscape scale, we could favor wolf occupancy and persistence in human-dominated landscapes without reducing land availability for other uses, working toward coexistence between large carnivores and humans.

KEYWORDS: Breeding, *Canis lupus*, carnivore conservation, homesite selection, human-dominated landscapes, landscape planning, refuge.

5.1. INTRODUCTION

Conserving large carnivores in human-dominated landscapes has become a major challenge for biodiversity conservation in modern societies (Chapron *et al.*, 2014). Traditionally, large carnivore conservation relied on the connectivity of protected areas (i.e. metapopulation management approach; Noss *et al.*, 1996; Mech and Hallet, 2001; Crooks and Sanjayan, 2006). However, in human-dominated landscapes, such figures are isolated within a matrix of multiple human land uses, and these areas are usually too small as to support demographically and functionally viable populations of large carnivores (Wikramanayake *et al.*, 1998; Santini *et al.*, 2014). Small populations, on the other hand, are potentially influenced by multiple processes, such as edge or Allee effects, even when food availability is not limiting (Woodroffe and Ginsberg, 1998; Stephens and Sutherland, 1999; López-Bao *et al.*, 2010) or subjected to high intensity of management actions (e.g. translocations). Because large carnivores occur at low densities and have large spatial requirements (Fuller and Sievert, 2001), their conservation needs to be planned on very large scales outside reserves, implicitly assuming a land sharing model of coexistence and a landscape-scale conservation approach in human-dominated landscapes (Linnell and Boitani, 2012; Carter *et al.*, 2012; Chapron *et al.*, 2014).

Beyond human attitudes towards large carnivores and the willingness to share the landscape with these species (Kleiven *et al.*, 2004; Bruskotter and Wilson, 2014; Treves and Bruskotter, 2014; López-Bao *et al.*, 2015*a*), the success of a landscape-scale approach to the persistence of large carnivore populations in human-dominated landscapes depends largely on the ability of these species to reproduce and persist outside protected and remote areas (Naves *et al.*, 2003; Llaneza *et al.*, 2012; Dellinger *et al.*, 2013; Ahmadi *et al.*, 2014; Chapron *et al.*, 2014; López-Bao *et al.*, 2015*b*). Disentangling the mechanisms of coexistence is therefore very important in determining to what extent large carnivores can tolerate living in human-dominated landscapes while considering different spatial and ecological constraints and levels of conflict. An optimum decision-making process is crucial, understanding where and when to establish limits on sharing the landscape. In human-dominated landscapes, such a coexistence approach will require delineating appropriate landscape planning measures (i.e. landscape configuration affect species persistence in fragmented landscapes, the norm in human-domianted landscapes, Prugh *et al.*, 2008; Soga and Koike, 2013) integrating large carnivore conservation with human activities.

The ability of large carnivores to persist in human-dominated landscapes, and the consequences of this persistence have attracted muach attention in recent times (Basille *et al.*, 2009; Carter *et al.*, 2012; Llaneza *et al.*, 2012; Athreya *et al.*, 2013; Dellinger *et al.*, 2013; López-Bao *et al.*, 2013; Bouyer *et al.*, 2014; Ahmadi *et al.*, 2014; Ripple *et al.*, 2014; Chapron *et al.*, 2014). The behavior of large carnivores in human-dominated landscapes can be strongly influenced by the history of human persecution of these species (Habib *et al.*, 2007; Zedrosser *et al.* 2011; Ordiz *et al.*, 2013; Amahdi *et al.*, 2014); triggered mainly by conflicts associated with the large species´ predatory behavior. Their persistence in humanized landscapes seems to be modulated by strong interactions among multiple factors affecting reproductive rates and survival (Woodroffe and Ginsberg, 1998; Fuller and Sievert, 2001; Llaneza *et al.*, 2012). Notably, most such critical factors interact synergically in space and time during the breeding season, turning this into one of the most sensitive periods for determining the persistence of large carnivores.

This is the case with wolves (*Canis lupus*) persisting in human-dominated landscapes. As a consequence of a long history of persecution, they have adopted different behavioral adaptations to minimize their vulnerability to humans, such as the location of breeding sites (homesites) in areas that reduce pack members´ risk of mortality (Ciucci *et al.*, 1997; Theuerkauf *et al.*, 2003; Whittington *et al.*, 2005; Habib *et al.*, 2007; Lesmerises *et al.*, 2013; Ahmadi *et al.*, 2014). Previous information suggests that the location of homesites in non human-dominated landscapes would be the outcome of a tradeoff between food and refuge availability (Mech and Boitani, 2003). Nevertheless in human-dominated landscapes, because wolves have been pursued using a wide variety of lethal methods, such as the rewarded removal of litters (Fernández and Azua, 2010), and people targeting homesites to kill wolves (Chapman and Buck, 1910), it is expected that wolves´ homesite selection would be strongly influenced by exposure risk and disturbance associated with humans (Ermala, 2003; Ahmad *et al.*, 2013; Dellinger *et al.*, 2013; Iolopoulus *et al.*, 2014; Ahmadi *et al.*, 2014). Food avaialability thus may play a secondary role once minimum requirements are fulfilled at the territory level. Actually, in such landscapes, food availability may not be a constraining factor because wolves may use anthropogenic sources of food to a large extent (Cuesta *et al.*, 1991; Meriggi and Lovari, 1996; López-Bao *et al.*, 2013).

The cumulative effects of human activities during the breeding season and the capability of wolves for coping with these disturbing factors are still poorly understood

(Habib and Kumar, 2007; Dellinger *et al.*, 2013; Ahmadi *et al.*, 2014). Identifying the main factors that allow a given site to be suitable for large carnivores´ homesites is very important in a landscape sharing approach in order to ensure the persistence of these species in multi-use landscapes, for instance, by adapting knowledge for landscape planning, and for protecting or restricting human access to crucial wolf breeding sites.

In this study, using as study case a wolf population persisting in a human-dominated landscape in NW Iberia (Llaneza *et al.*, 2012) that has a low abundance of wild ungulates (López-Bao *et al.*, 2013), we hypothesized that wolves´ homesite selection will be strongly driven not only by the quantity of refuge available but also by its quality (limits on human access) and by the level of human activity in the surrounding areas. As food availability may not be a limiting factor in such multi-use landscapes, we predict that as soon as food requirements are guaranteed at the territory level, the selection of homesites by wolves will be mainly driven by their vulnerability to humans. Thus, wolves will select areas with low human accessibility and activity; and the location of refuge areas will be determinant in placing homesites. In human-dominated landscapes, those areas will be, by definition, of small size. According to the hierarchical habitat selection hypothesis (Rettie and Messier, 2000), we also predict that factors influencing wolves´ homesite selection will be more important at finer spatial scales. We therefore expect hierarchical effects of human and landscape attributes on homesite selection patterns.

5.2. METHODS

Study area

This study was carried out in western Galicia – the A Coruña and Pontevedra provinces - (NW Spain), in an area of ca. 12,500 km^2. The study area is characterized by a human-dominated landscape with widely scattered human settlements (2.8 human settlements km^{-2}) and a mean human population density of ca. 169 inhabitants km^{-2} (INE, 2010). Moreover, the high geographical dispersion of human settlements implicitly requires a well-developed paved road network (mean paved road density 3.6 km/km^2). Habitat transformation dominates the landscape, mainly because of agriculture and livestock activities. As a consequence, Western Galicia is comprised of a patchy landscape made up of croplands (32%), managed scrublands (11%) and forest plantations (*Eucalyptus globulus* and *Pinus* spp.) (43%). Only less than 8% of the landscape is occupied by semi-natural forests (*Quercus robur, Quercus pyrenaica, Castanea sativa* and *Betula alba*). Wolves in Western Galicia show a continuous distribution with 29 and 31 wolf packs estimated in this area in 2003 and 2013 (0.23-0.25 packs/100km^2) (Llaneza *et al.*, 2005, 2014*a*, following the procedure described by Llaneza *et al.*, 2014*b*).

Location of homesites

We used information from 33 homesites detected in Western Galicia between 2003 and 2011 by different regional wolf surveys and research projects. We defined a homesite as an area selected by wolves for giving birth and rearing the pups in their first months of life, from May to early October (Scott and Fuller, 1965; Theuerkauf *et al.*, 2003; Llaneza *et al.*, 2014*b*). Homesites were located using three different procedures. For one group of sites, simulated howling was used in order to stimulate the response of the pups (n = 17) (see details in Harrington and Mech, 1982). The selection of the locations to carry out howling sessions was based on the availability of refuge and areas with low human activity (Ausband *et al.*, 2010), the meteorology (avoiding rainy or windy nights), and the information gathered during previous wolf surveys (i.e., accumulation of wolf marks; Llaneza *et al.*, 2014*b*). Howling sessions started at sunset and spanned the early nighttime hours, and were carried out between August and October (Harrington and Mech 1982). For the second group, we carried out direct observation points to detect pups in potential *rendezvous sites* (n = 12). The selection of the locations to carry out observations was also based on the landscape configuration and the information obtained in previous wolf surveys (Llaneza *et al*. 2014*b*). The observer used 8X or 10X binoculars and telescopes with 20–60X zoom lenses to scan potential *rendezvous sites* and the surrounding areas for at least one hour. Observation points were carried out at sunrise and sunset.

Finally, data from GPS collared wolves was also used to identify homesites (n = 4). Wolves were captured with Belisle® leg-hold snares (Edouard Belisle, Saint Veronique, PQ, Canada) and chemically immobilized, from 2006 to 2007. Snares were monitored twice every day, in the early morning and late afternoon. Wolves included here were captured in the context of research projects on the ecology of the species in Galicia under permit 019/2006 from the Regional Government of Galicia (Spain). Clusters of GPS positions overlapping in space and time in consecutive days during May and June were assumed to identify den sites.

In addition, we confirmed the presence of pups in these areas by carrying out howling and observation points.

Once a homesite was detected, we georeferenced a point representing that either, taking the center of GPS position clusters or by locating the places where pups replied to simulated howling or were observed, in high-resolution ortophoto images. We considered that this procedure did not influence our results since we were interested in small-scale patterns of homesite selection (1 km^2 and 9 km^2, see below), not in micro-scale selection patterns.

Estimating anthropogenic food availability for wolves

Because of the very low abundance of wild prey (Guitián *et al.*, 1975; Munilla *et al.*, 1991; SGHN, 1995), the frequency of wild ungulates in the wolf's diet is very small or almost absent. The most important food resources for wolves in this area are horses (*Equus caballus*), cattle (*Bos taurus*), sheep *(Ovis aries)*, goats (*Capra hircus)*, and carrion (Guitián *et al.*, 1979; Cuesta *et al.*, 1991; Sazatornil, 2008; López-Bao *et al.*, 2013). To estimate food avaialability for wolves, we gathered data from livestock censuses at the parish level (mean area of parish in Galicia = 7.5 km^2; range 0.1–65 km^2; n = 1,604; 58% of parish have an area <7 km^2. Data on livestock were taken from the Rural Council of Galicia in 2011). Considering the different livestock practices in this area, we assumed that this measure was positively correlated with the availability of food for wolves. For example, most beef cattle (228,273 heads in Galicia in 2008) are handled in semi-extensive and extensive regimes, as are all Galician mountain ponies (López-Bao *et al.*, 2013). Although some beef cattle farmers use prevention methods (e.g., fences or livestock guarding dogs), these cattle are vulnerable to wolf attacks. In addition, wolves often feed on sheep, goats, and dairy cattle in this area (Sazatornil, 2008; López-Bao *et al.*, 2013; Lázaro, 2014), and they can have access to carcasses from all these livestock species (Cuesta *et al.*, 1991).

To estimate anthropogenic food availability for wolves, we selected the four domestic species most represented in the diet of wolves based on contemporary studies (Sazatornil, 2008; López-Bao *et al.*, 2013, Lázaro, 2014); horses, cattle, sheep and goats. Next, considering the location of the homesite, we simulated 33 wolf pack territories of areas similar to the mean home range size reported for sub-adult/adults wolves in Galicia (ca. 170 km^2, 90% kernel estimate; García *et al.*, 2012). Then, we generated a 1 km^2 buffer centered on each homesite location. In addition, we generated 10 non-overlapping random buffers within each simulated pack territory. We calculated the abundance of every livestock species (number of heads) considering all parishes overlapping with observed homesites and random buffers. We converted the number of heads into biomass by considering the average weight of every livestock species and age class (horse: 300 kg, foal: 100 kg, cattle: 500 kg, calf: 160 kg, sheep: 30 kg and goat: 36 kg; Llaneza *et al.*, 1996). We finally estimated the potential available biomass per buffer zone (metric tons/km^2).

Human and landscape predictors

For each homesite, we generated a 1x1 km (1 km^2) and a 3x3 km (9 km^2) grids. In addition, we generated between four and five nonoverlapping associated random grids for each area (n = 151). Thus, we analysed homesite selection by comparing 33 observed homesites to 151 random sites. We calculated a set of 26 predictors as surrogates for wolf vulnerability, risk of mortality and human disturbance in homesites at different small spatial scales (1 km^2 and 9 km^2; Table 5.1). Predictors were grouped into two blocks: human pressure and landscape attributes. These blocks were expected to have unequal effects on the wolves´ behavioral response in selecting homesites in human-dominated landscapes (Table 5.1).

We used different variables reflecting human pressure in homesites, based on paved and unpaved roads, buildings, human activity, and human population density (Table 5.1). First, we used density of unpaved roads (paths) and paved roads, pooling in the latter category all types of paved roads (e.g., national roads or highways). Data on unpaved roads (km) were obtained by manually checking high-resolution orthophoto images and creating specific spatial layers. We opted for this procedure because public GIS layers were incomplete and underestimated the real density of infrastrucutre, particularly paths, which could affect our analyses.

Table 5.1. Predictors used to study wolf homesite selection in human-dominated landscapes of Western Galicia, Spain.

		VARIABLE	DESCRIPTION
Landscape attributes	Topographic features	Altitude 1 km^2	Average value of the altitude in 1x1 km grid based on 5x5 m cells
		Altitude 9 km^2	Average value of the altitude in 3x3 km grid based on 5x5 m cells
		Ratio Altitude 1 km^2 /Mean altitude study area	Ratio between Altitude 1 km^2 and the average value of the altitude in the study area
		Ratio Altitude 9 km^2/Mean altitude study area	Ratio between Altitude 9 km^2 and the average value of the altitude in the study area
		Roughness 1 km^2	Average value of the roughness in 1x1 km grid based on 5x5 m cells
		Roughness 9 km^2	Average value of the roughness in 3x3 km grid based on 5x5 m cells
		Ratio Roughness 1 km^2/ Roughness 9 km^2	Ratio between the average value of the roughnes in 1x1 km grid regard to average value of the roughnes in 1x1 km grid
		Ratio Roughness 1 km^2/Mean Roughness study area	Ratio between Roughness 1 km^2 and the average value of the roughness in the study area
		Ratio Roughness 9 km^2/Mean Roughness study area	Ratio between Roughness 9 km^2 and the average value of the roughness in the study area
	Refuge	Refuge quality mean distance 1 km^2	Mean distance value from all the 30x30 m refuge pixels to the nearest patch edge within the 1 km^2 grid
		Refuge quality upper quartile 1 km^2	Value of the upper quartile of the distance from all the 30x30 m refuge pixels to the nearest patch edge within the 1 km^2 grid
		Refuge quality percentile 10th 1 km^2	Value of percentile 10th of the distance from all the 30x30 m refuge pixels to the nearest patch edge within the 1 km^2 grid
		Proportion of pixels with refuge 1 km^2	Number of 30x30 m refuge pixels within the 1 km^2 grid (transformed to area)
		Proportion of refuge 1 km^2	Area covered by scrublands, woodlands and forest plantations within the 1 km^2 grid
		Proportion of refuge 9 km^2	Area covered by scrublands, woodlands and forest plantations within the 9 km^2 grid
Human pressure	Settlements	Number of buildings at 1 km^2	
		Number of 100x100 m cells with buildings	Number of 100x100m cells with buildings wihtin the 1 km^2 grid
		Number of central 100x100 m cells with buildings	Number of 100x100 m cells in the center of the 1 km^2 (< 400 m from the homesite) grid with buildings
		Number of buildings in central 100x100 m cells	Number of buildings in the 100x100 central cells (< 400 m from the homesite)
	Roads	Paved Roads 1 km^2	Paved roads length (m) within the 1 km^2
		Paved Roads 9 km^2	Paved roads length (m) within the 9 km^2
		Paths 1 km^2	Unpaved roads length (m) within the 1 km^2
		Paths 9 km^2	Unpaved roads length (m) within the 9 km^2
	F. land	Farming land 1 km^2	Proportion of the 1km^2 covered by farming lands
		Farming land 9 km^2	Proportion of the 9km^2 covered by farming land
	People	Human population density 9 km^2	Weighted data on human density from each overlapping paris relation to its proportion of the total 9 km^2 grid area

Second, we considered the density of buildings (at 1 km^2) and their spatial distribution. We were interested to test the effect of the buildings´ spatial dispersion on the risk perception of wolves towards human presence/activity when selecting low-risk places to locate homesites. To do this, we subdivided every 1 km^2 grid into 100 x 100 m cells (n = 100), and we counted all the buildings inside each cell. Then, we calculated four different variables representing human presence and its spatial dispersion in the vicinity of homesites: i) number of buildings at 1 km^2, ii) number of 100 x 100 cells with buildings, iii) number of cells in the center of the 1 km^2 grid with buildings, and iv) the total number of buildings in the central cells. Central cells were considered to be those that were no more than 400 m away from the location of the homesite (Table 5.1).

Third, we measured the proportion of farming land at both spatial scales. Farming lands were identified from the Spanish Forest Map (DGCN, 2000) and double-checked by using high-resolution orthophoto images. Finally, at the 9 km^2, we also calculated the density of the area´s human population. Data on population density were taken from the National Institute of Statistics (INE, 2010) at the parish level and measured as the number of inhabitants per square kilometer. For each 9 km^2 grid, we weighted data on human density from each overlapping parish in relation to its proportion of the total grid area.

Regarding landscape variables, we first calculated altitude and roughness for all grids at both spatial scales, which are negatively correlated with human densities and activities (Glenz *et al.*, 2001). We calculated the mean altitude (in meters) by averaging altitudes of all 5 x 5 m raster cells included in each grid. We also calculated roughness (also in meters) as the standard deviation of the altitudes of all 5 x 5 m raster cells included in each grid. We then combined these two variables, measured at different spatial scales, to create a set of five variables characterizing each site in relation to the accessibility and/or remoteness of each specific spatial context and the study area (Table 5.1). We calculated the ratio between the mean altitudes and the roughness on both spatial scales, and the mean altitude and roughness of the study area, as well as the ratio between roughnesses values at both spatial scales (Table 5.1).

On the other hand, we measured two different attributes of the refuge available for wolves around homesites: the quantity and the quality of refuge. To date, most studies on homesite selection have been focused on the type and amount of refuge available (Norris *et al.*, 2002; Theuerkauf *et al.*, 2003; Jêdrzejewski *et al.*, 2005; Capitani *et al.*, 2006; Houle *et* *al.,* 2010¸ Kaartinen *et al.,* 2010), and less on the quality of such refuges (Illiopoulus *et al.,* 2014). However, in human-dominated landscapes, where the norm is expected to be a constraint in the amount of refuge continuously available in large areas, the quality of the refuge may be more important than the quantity. The landscape is dominated by a high heterogeneity of high- and low-risk areas on a small scale for wolves. As wolves are highly adaptable to a wide range of vegetation types (even areas without plant cover) (Mech and Boitani, 2003; Ahmadi *et al.,* 2014), we counted as refuge those vegetation types that could effectively conceal wolves: dense and high scrublands (mainly represented by *Ulex sp* and *Erica sp*), woodlands and forest plantations. Functionally, all these vegetation types provide similar conditions of refuge for wolves in the study area (Llaneza *et al.*, 2012). As a first step, refuge size was estimated at both spatial scales by summing the surface areas occupied by scrublands, woodlands, and forest plantations. Data on vegetation types and the proportions of the different vegetation covers were obtained from the Spanish Forest Map, Land Use Map (DGCN, 2000).

However, in order to gain new insights into the relative importance of refuge quantity (total area occupied) and quality (fragmentation/edge effect) within each 1 km^2 grid, we delineated all refuge patches using high-resolution orthophoto images. Next, all paved and unpaved roads and all patch borders between refuge areas and any other land use (e.g., farmlands or grasslands) were identified and considered as patch edges. Thus, beyond the absolute refuge area, we weighted refuge area on the basis of human accessibility and wolf vulnerability. After rasterizing all the identified refuge patches in a 30 x 30 m cell-size raster, we calculated the number of pixels with refuge at 1 km^2 (quantitative estimate of refuge availability). The number of pixels with refuge and the refuge estimated from vegetation cover were highly correlated (Spearman rank correlation, $r_s = 0.788$, $P < 0.001$, $n = 184$). We then calculated the distance from each pixel of refuge to the nearest patch edge. Based on the set of distances obtained, we calculated the mean, the upper quartile and the 10th percentile distance values for each 1 km^2 grid. These metrics were used as different proxies of refuge quality. The mean distance values provided information about the average quality of refuge in the grid. The upper quartile values (above the median of the upper half of the dataset), and the 10th percentile values (the value below which 10 percent of the observations were found) were useful for identifying grids with high-quality refuge (i.e., large and continuous refuge patches).

Data analyses

We tested if wolves selected the location of their homesites in relation to the perceived availability of anthropogenic food resources. To do this, we performed a test evaluating whether wolves selected homesites within their territories with more food availability in the immediate vicinity (1 km^2) than by random (*third order selection*; Johnson, 1980). The influence of anthropogenic food availability on homesite selection was assessed by comparing the observed food availability (metric tons/km^2) in homesites with the average food availability of randomized sites within territories (n = 10) using a Wilcoxon signed-rank test.

To explore the influence of human and landscape attributes on the behavioral response of wolves locating their homesites, we first carried out univariate analyses (Mann–Whitney U-tests) to test for significant differences between homesites and random sites for all the predictors measured, excepting for proportions, for which Z-proportions tests were used. Before carrying out multivariate analyses, we built matrices of Spearman correlation coefficients to explore colinearity between predictors. Only mean value distance and upper-quartile values showed high correlation ($r_s = 0.9$), but we retained both predictors because of their different functional meanings (see above; Green, 1979). Then, we built three different sets of Generalized Linear Models (GLMs) with binomial error distribution and complementary log-log link (allowing for a more assymetrical number of presence and absence cases) to assess: i) the influence of human-related predictors only, ii) the influence of landscape-related predictors only, and iii) the influence of both blocks pooled (combined model), on homesite selection patterns by wolves in human-dominated landscapes. We implemented this modeling approach on both spatial scales. We also included in both the human and combined sets of models the interaction between human population density and the sum of unpaved and paved roads.

Forward stepwise procedures were performed to exclude within each block those variables that did not contribute significantly ($P > 0.05$) to the explained deviance. For each set of GLMs, we used an information theoretic framework to rank competing models based on AIC. Models within ΔAIC <2 were considered to have substantial empirical support (Burham and Anderson, 2010). From among these models, we selected the most parsimonious. In addition, we used Akaike weights (w_i values) as evidence in favor of a given model being the best of the competing models (Burham and Anderson, 2010).

In a further step, taking into account those variables retained in the selected candidate model from the set of combined models at 1 km^2, we performed a hierarchical partitioning analysis to identify the independent and conjoint contribution of each variable with all other significant variables (Chevan and Sutherland, 1991; Mac Nally, 2000). Hierarchical partitioning was conducted using logistic regression and log-likelihood as the goodness-of-fit measure. This statistical procedure allowed us to identify those variables with an important independent – not partial – correlation with the homesite selection patterns (Mac Nally and Horrocks, 2002). The statistical significances of the independent contributions of selected predictors were tested by a randomization procedure (100 randomizations), which yielded Z-scores for the generated distribution of randomized independent contributions and an indication of statistical significance (P <0.05) based on an upper 0.95 confidence limit (Z ≥1.65; Mac Nally and Horrocks, 2002).

We additionally explored the existence of hierarchical effects in human and landscape factors determining wolves´ homesite selection patterns. To do this, we built two sets of GLMs including interaction terms for each human or landscape predictor at both spatial scales to account for such potential hierarchical effects. Forward stepwise procedures and an information theoretic framework based on AIC as described above were used.

We used the R 3.2.0 statistical software (R Development Core Team 2015) and the “*hier.part”* package (Walsh and Mac Nally, 2008) for all the analyses.

5.3. RESULTS

The density of livestock in western Galicia was remarkable (cattle = 35.4 heads/km^2, sheep-goats = 7.1 heads/km^2 and horses = 2.5 heads/km^2; Livestock Census, Regional Government of Galicia, 2011); translating into high potential biomass availability from anthropogenic sources of food for wolves at the landscape scale (ca. 30 metric tons/km^2), as reflected in the diet of wolves in this area (Cuesta *et al.*, 1991; Sazatornil, 2008; López-Bao *et al.*, 2013; Lázaro, 2014). Potential availability of biomass in the buffers around homesites and random sites ranged between 0.07 and 174.68 metric tons/km^2 (mean = 46.8; SD = 50.6), and 4.1 and 129.3 metric tons/km^2 (mean = 43.8; SD = 31.3), respectively. Within territories, only in 8 out of 33 cases (24%), food availability values at homesites were above the upper limit of the 95% CI of the randomized values from the ten random buffers (Table 5.A1). Homesite selection was not determined by food availability in the immediate vicinity (Wilcoxon signed-rank test: Z = -0.027, *P* =0.979, n =33; Table 5.A1).

Wolves placed their homesites in areas with high availability of unfragmented refuge, low accessibility and with low human activity levels in the vicinity (Table 5.2). At the 1 km^2 spatial scale, four models showed a ΔAIC <2 in the block of human pressure (Table 5.A2), with the best model including paved roads, farm land, number of buildings and the interaction between roads and human population density (Table 5.A2). The probability of a given area being selected as a homesite by wolves was elevated in areas with low human presence (negative estimation for all selected predictors, paved roads and the interaction between roads and human population density showed 95% confidence intervals that did not overlap with zero; Table 5.A3). The role of vulnerability in this landscape was also reflected in the block of landscape attributes, with four models having ΔAIC <2 (Table 5.A4). Variables representing the quantity (proportion of pixels with refuge), quality (refuge quality: mean distance and 10th percentile), and location (the ratio of the 1 km^2 altitude to the mean altitude study area) of refuge were included in the best model (Table 5.A4), with positive parameter estimates for all except the refuge 10th percentile, which was a surrogate of highly fragmented refuge areas (all parameters showing 95% confidence intervals that did not overlap with zero; Table 5.A5).

The selection of areas minimizing exposure risk was evident when we combined both blocks (seven models showed ΔAIC <2; Table 5.A6). From the best candidate model, the probability of wolves selecting a given area as a homesite was strongly determined by the homesite's spatial location (the ratio of the 1 km^2 altitude to the mean altitude study area had a positive effect). Homesite locations had minimal human activities in the vicinity (paved roads had a negative effect) and a high availability of good-quality refuge (refuge quality mean distance had a positive effect and the 10th percentile had a negative effect; Table 5.A7). The proportion of pixels with refuge and paved roads showed 95% confidence intervals that did not overlap with zero (Table 5.A7).

Table 5.2. Descriptive statistics (mean and standard deviation) for the selected variables to study homesite selection by wolves in human-dominated landscapes of NW Iberia for both homesites and random sites. Significance levels from Mann-Whitney U-tests comparing resting sites *vs.* random points are shown (* $P < 0.001$).

		Variable	Home site		Random site		p
			Mean	SD	Mean	SD	
Landscapes attributes	Topographic features	Altitude 1 km^2	508.9	179.1	335.3	199.2	*
		Roughness 1 km^2	40.9	19.9	28.6	15.5	*
		Ratio Altitude 1 km^2 /Mean altitude study area	1.3	0.4	0.9	0.5	*
		Ratio Roughness 1 km^2/Mean roughness study area	1.3	0.6	0.9	0.5	*
		Ratio Roughness 1 km^2/ Roughness 9km^2	0.6	0.2	0.5	0.2	n.s.
		Altitude 9 km^2	494.6	186.7	331.3	195.1	*
		Roughness 9 km^2	71.9	36.4	54.3	26.1	*
		Ratio Altitude 9 km^2/Mean Altitude study area	1.3	0.5	0.9	0.5	*
		Ratio Roughness 9 km^2/Mean Roughnes study area	1.2	0.6	0.9	0.4	*
	Refuge (quality)	Refuge quality mean distance 1 km^2	222.4	190.6	94.8	70.9	*
		Refuge quality upper quartile 1 km^2	308.1	237.8	129.5	98.9	*
		Refuge quality percentile 10th 1 km^2	79.1	118.1	36.5	32.6	*
	Refuge (quantity)	Proportion of pixels with refuge 1 km^2	56.6	19.4	31.9	22.5	*
		Proportion of refuge 1 km^2	90.4	15.8	59.5	29.8	*
		Proportion of refuge 9 km^2	730.3	127.5	583.9	175.6	*
Human pressure	Settlements	Number of buildings	2.3	5.5	36.4	60.7	*
		Number of 100x100 m cells with buildings	1	2.2	13	16.8	*
		Number of 100x100 m cells with buildings	0.1	0.3	2.1	3.7	*
		Number of buldings central 100 x 100 m grid	0.1	0.5	6.1	14.4	*
	Roads paved	Paved Roads 1 km^2	326.2	485.3	1898.1	1558.2	*
		Paved Roads 3 km^2	9875.9	5025.1	21166.9	11186.2	*
	Roads unpaved	Paths 1 km^2	2516.9	1423.4	2298.3	1511.6	n.s.
		Paths 9 km^2	16762.7	7887.9	19831.1	7233.7	*
	Farming lands	Farming land 1 km^2	8.7	14.7	36.4	27.6	*
		Farming land 9 km^2	167.9	125.1	288.7	164.6	*
	Human density	Human population density 9 km^2	1005.8	1178.5	2914.4	4783.3	*

Hierarchical partitioning analysis performed on the best combined model (human and landscape blocks pooled; Table 5.A8) showed that paved roads and the predictors related to the quality of refuge (refuge quality mean distance and 10th percentile, pooled) had the highest proportion of independent contribution to explaining homesite selection patterns in this human-dominated landscape (34.3% and 30.6%, respectively). These were followed by the quantity of refuge (20.9%) and its location (14.1%; Fig. 5.1). All predictors showed remarkable proportions of joint contributions (at least 42% of explained variance; Fig. 5.1). The independent effects of all predictors were statistically significant (Table 5.A8).

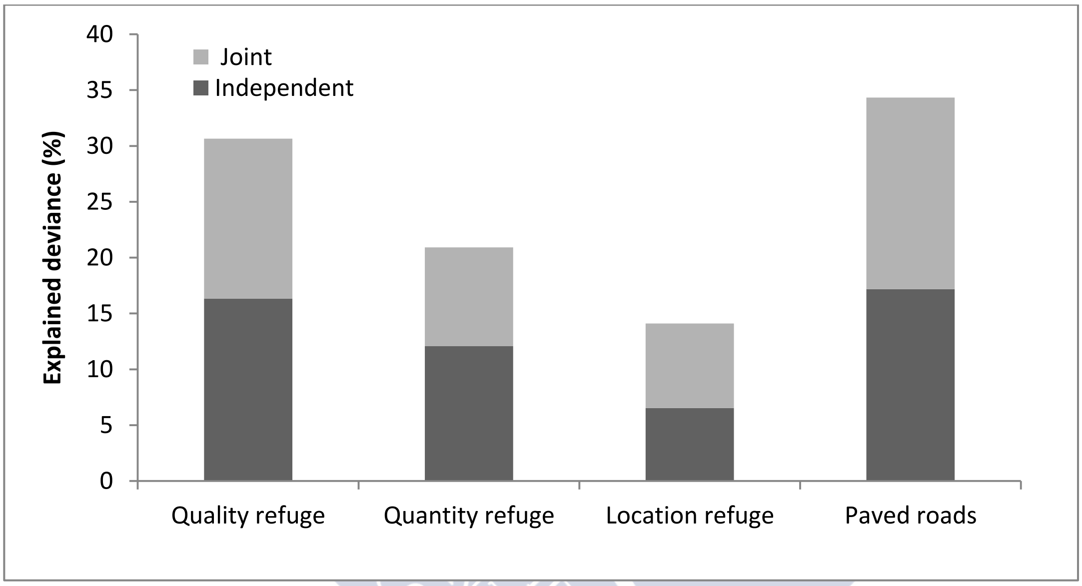

Figure 5.1. Independent and joint contributions (percentage of the total explained variance) of the variables selected in the best candidate model of the combined model (human and landscape blocks pooled). Quality refuge represents two refuge variables pooled: Refuge quality percentile 10th and Refuge quality mean distance.

At the 9 km^2 spatial scale, three models had ΔAIC <2 in the block of human pressure (Table 5.A9), with the best model including paved roads and the interaction between linear infrastructures and human population density; contrary to the 1 km^2 scale, unpaved roads were selected in the best model (Table 5.A9). All predictors showed negative parameter estimations, and paved and unpaved roads showed 95% confidence intervals that did not overlap with zero (Table 5.A10). Regarding the landscape attributes, the selection of remote, safe, and inaccessible areas prevailed at this spatial scale. Three models showed ΔAIC <2 (Table 5.A11), with the best model including the proportion of refuge and the ratios between a given area's altitude/roughness and the mean values observed in the study area. All predictors had a positive parameter estimation but only refuge and the altitude ratio had 95% confidence intervals that did not overlap with zero (Table 5.A12). Finally, considering the combined model at this spatial scale, five models had ΔAIC <2 (Table 5.A13), with the best model including paved and unpaved roads, roughness, and the interaction between linear infrastructures and human population density (Table 5.A13). All predictors except roughness showed negative parameter estimations and paved and unpaved roads, as well as roughness, showed 95% confidence intervals that did not overlap with zero (Table 5.A14).

When evaluating hierarchical spatial effects for human pressure, from the best model (Table 5.A15), hierarchical effects in homesite selection patterns arose for the avoidance of areas with a high density of paved roads (Table 5.A15). Avoidance of paved roads at 1 km^2 was modulated by the density of paved roads at the larger scale, with the strength of avoidance of paved roads at 1 km^2 increasing as the density increased at the larger scale (the negative parameter estimation for this predictor showed 95% confidence intervals that did not overlap with zero; Table A16). Other variables included in the best model were paved and unpaved roads at the 9 km^2 spatial scale and farmlands at both spatial scales (Tables 5.A15 and 5.A16). Similarly, we detected hierarchical spatial effects regarding selection for landscape attributes (Table 5.A17). Wolves located their homesites in inaccessible areas, but this selection was modulated by the spatial context. The selection for rough areas at 1 km^2 increased as the roughness at 9 km^2 decreased (95% confidence intervals that did not overlap with zero; Table 5.A18). In the best candidate model, the rest of the predictors that showed 95% confidence intervals not overlapping with zero were related to selection at the smallest spatial scale: proportion of refuge and the ratios between altitude or roughness and their mean values for the study area (Tables 5.A17 and 5.A18). This indicates the importance of landscape attributes at small spatial scales as a means to cope with human-related risk.

5.4 DISCUSSION

In human-dominated landscapes, the persistence of large carnivores is modulated by the outcome of the interaction of multiple factors affecting reproductive rates, such as food availability, and survival, such as human activities and conflict levels (Woodroffe and Ginsberg, 1998; Fuller and Sievert, 2001; Basille *et al.*, 2009; Chapron *et al.*, 2014). Heterogeneity in human activities at the landscape level provides large carnivores with different spatially explicit survival chances depending on the behavioral responses they adopt in relation with spatio-temporal habitat uses (Habib and Kumar, 2007; Ahmadi *et al.*, 2014; Oriol-Cotterill *et al.*, 2015). Our findings suggest that, once food availability is ensured within the territory, wolves´ homesite selection in human-dominated landscapes is primarily determined by human-related factors. Homesite selection was not determined by food availability in the immediate vicinity. This result may be explained by the generally high spatio-temporal availability and predictability of anthropogenic food sources for wolves in these contexts compared to natural areas (Heard and Williams, 1992; Meriggi and Lovari, 1996; Capitani *et al.*, 2006; López-Bao *et al.*, 2013).

Our results broadly support previously reported patterns showing selection for less accessible areas when wolves share the landscape with humans, either by means of refuge-providing vegetation (Theuerkauf *et al.*, 2003, Jêdrzejewski *et al.*, 2004; Capitani *et al.*, 2006; Kaartinen *et al.*, 2010; Illopoulus *et al.*, 2014) or topographic features, such as high elevation and slope (Norris *et al.*, 2002; Capitani *et al.*, 2006; Trapp *et al.*, 2008; Unger *et al.*, 2009; Person and Russell, 2009). Wolves avoided infrastructures associated with human presence, especially roads (Theuerkauf *et al.*, 2003; Jêdrzejewski *et al.*, 2004, 2005; Capitani *et al.*, 2006; Kaartinen *et al.*, 2010; Houle *et al.*, 2010). Wolf homesite areas, compared with random points, were characterized by lower densities of settlements and paved roads (Theuerkauf *et al.*, 2003; Capitani *et al.*, 2006; Lesmerises *et al.*, 2012; Ahmadi *et al.*, 2014). Hierarchical partitioning analysis showed that predictors related to qualitative refuge attributes had a greater proportion of independent contribution to homesite selection patterns than other factors. The stronger effect of refuge-providing habitats and the prevalence of refuge quality over refuge quantity, show that the availability of high-quality refuge patches, even at very small spatial scales, compensate for moderate levels of human activities in the vicinity of homesites.

Wolves seem to perceive the existence of a spatial mismatch between exposure risk and the attributes of the habitat patches related to vegetation structure, which is probably driven primarily by the vulnerability associated with edge effects (Woodroffe and Ginsberg, 1998). High vulnerability associated with low-quality refuge patches is compensated for an increased distance to the edge. Such edge effects introduce spatial heterogeneity of risk within refuge patches, as sites distant from refuge edges are more secure locations for wolf homesites. The availability of functional refuge is reduced in fragmented landscapes in comparison to areas where the same amount of refuge-providing vegetation is distributed in larger, more continuous patches. Our results indicate that, for wolves, the size and distribution of high-quality refuge habitat patches becomes more important than just the total extent of refuge in locating homesites. Functional vegetation structure, together with quality, prevailed over particular vegetation types (Theuerkauf *et al.*, 2003; Jêdrzejewski *et al.*, 2004; Kaartinen *et al.*, 2010). Wolves can breed in sunflower *(Helianthus annus)* fields in Russia (Ryabov, 1987) and cereal fields in central Spain (Barrientos *com. pers*. and Llaneza and Blanco, 2005) or agroecosystems in India (Agarwala and Khumar, 2009) or Iran (Ahmadi *et al.*, 2014). Interestingly, such human and habitat factors operate at very small spatial scales relative to wolves' territory size: between 0.6% and 5% of wolf territories (ca. 170 km^2, 90% kernel estimate; García *et al.*, 2012).

The spatial dispersion of buildings tends to homogenize exposure risk in space, reducing the availability of low-risk areas for use by wolves as homesites. At the spatial scale considered, for an equal density of buildings, a higher aggregation of human activity (buildings) increases the heterogeneity of risk, resulting in higher availability of low-risk areas for wolves. Although we detected a similar response at the 1 and 9 km^2 scales, the strength of the selection changed according to the immediate context following a hierarchical selection process. For example, avoidance of paved roads at 1 km^2 was modulated by the density of paved roads at 9 km^2, and the selection for rough areas at 1 km^2 increased as the roughness at 9 km^2 decreased. The lack of an effect of the length of unpaved roads at 1 km^2 (but not at 9 km^2) between homesites and random sites suggests a decreasing exposure risk along with the scale of the main surrogates of human activities (paved roads and buildings or areas with intense human land use; Ahmadi *et al.*, 2014). Wolves may use unpaved roads with low human activity for ease of travel and territorial marking around homesites (Dellinger *et al.*, 2013; Llaneza *et al.*, 2014b). Multiple spatial, habitat and human factors affect homesite location, and how refuge quality and buildings are distributed at the scales considered determines the suitability of a given site as a potential homesite. Thus, spatial changes in risk heterogeneity will determine the abandonment of a given area as a homesite.

Effective large carnivore conservation in a human-dominated landscape matrix outside of formally protected areas is of paramount importance in the Anthropocene (Chapron *et al.*, 2014; López-Bao *et al.*, 2015b). Such conservation has been often hindered by the need to preserve large areas of suitable habitat (Woodroffe and Ginsberg, 1998; Linnell *et al.*, 2001; Chapron *et al.*, 2014; López-Bao *et al.*, 2015b). However, some large carnivores do not necessarily require such large-scale habitat preservation, if the preserved habitats are identified at the proper scale. The vulnerability of large carnivores in human-dominated landscapes could be compensated for by the existence of spatial heterogeneity in human activities (Amahdi *et al.,* 2014). Our results provide new insights for sustainable landscape planning that integrates human land uses and large carnivores´ requirements (Ciuci *et al*., 2012; Ahmadi *et al*., 2014; White *et al*., 2015), favoring a land-sharing model with coexistence between large carnivores and people (Chapron *et al*., 2014).

Identifying minimum requirements for large carnivore conservation in human-dominated landscapes is of paramount importance for delineating appropriate landscape planning measures and policies (Sanderson *et al*., 2002; Pressey *et al*., 2007). In the case of wolves, although protected areas may play an important role in wolf persistence at a local scale (Capitani *et al.*, 2006), none of the homesites identified in our study area were located in strictly protected areas aside from the Natura 2000 network, which is not a network of strict protection where all human activities are excluded (European Union, 2013).

Landscape planning has been traditionally focused on increasing the connectiviy between protected areas, making recommendations to enhance potential corridors or to extend the networks of protected areas (Wikramanayake *et al.*, 1998; Tischendorf and Fahrig, 2000; Wikramanayake *et al*., 2004; Crooks and Sajayan, 2006; Epps *et al.*, 2011; Brodie *et al.*, 2015). Moreover, the strategy adopted to increase the viability of many species has been focused on functional connectivity through dispersal across broad landscapes (Tischendorf and Fahrig, 2000).

However, in human-dominated landscapes, the conservation of many large carnivore populations, including wolves, does not primarily depend on high connectivity between such areas, but rather on other landscape management approaches that integrate large carnivore habitat requirements and planning transportation networks, forestry and land development and use. Our results suggest that in the case of wolves by temporally restricting human use on homesites and very small portions of the surrounding lands (1 km^2), as well as maintaining several high quality refuge areas of this size at the landscape scale, we could favor wolf occupancy and persistence in human-dominated landscapes without reducing availability for other land uses. This approach is expected to be successful for other large carnivore species (e.g., Elbroch *et al.*, 2015; White *et al*., 2015).

5.5. REFERENCES

Ahmad, M., Kaboli, M., Nourani, E., Alizadeh A. & Ashrafi S. (2013). A predictive spatial model for gray wolf (*Canis lupus*) denning sites in a human-dominated landscape in western Iran. *Ecol. Res*. 28:513-521.

Ahmadi, M., López-Bao, J.V. & Kaboli, M. (2014). Spatial Heterogeneity in Human Activities Favors the Persistence of Wolves in Agroecosystems. *PLoS One*, 9, e108080.

Agarwala, M. & Khumar S. (2009). Wolves in Agricultural Landscapes in Western India.Tropical Resources: *Bulletin of the Yale Tropical Resources Institute*, 28:48-53.

Athreya, V., Odden, M., Linnell, J.D., Krishnaswamy, J. & Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One*. *8,* e57872.

Ausband, D.E., Mitchell, M.S., Doherty, V., Zager, P., Mack, C.M. & Holyan, J. (2010). Surveying Predicted Rendezvous Sites to Monitor Gray Wolf Populations. *J. Wildlife Management*, 74:1043-1049

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Høgda, K. & Gaillard, J. (2009). What shapes Eurasian lynx distribution in human dominated landscapes: Selecting prey or avoiding people? *Ecography*, 32:683-691

Bruskotter, J.T. & Wilson, R.S. (2014). Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. *Conservation Letters*, 7:158-165.

Bouyer, Y., Gervasi, V., Poncin, P., Beudels-Jamar, R.C., Odden J, & Linnell, J.D.C. (2014). Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Animal Conservation*. DOI:10.1111/acv.12168

Brodie, J.F., Giordano, A.J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J., Anderson, J., & Ambu, L. (2015). Evaluating multispecies landscape connectivity in a threatened tropical mammal community. *Conservation Biology*, 29:122-132.

Burnham, K.P. & Anderson, D.R. (2010). Model selection and multimodel inference. A practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Capitani C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., Scandura, M., Viviani, A. & Apollonio, M. (2006). Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. *Acta Theriologica*, 51:395–404.

Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B. & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *PNAS*, 109:15360–15365

Chapman, A. & Buck, W.J. 1910. *Unexplored Spain*, London.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., ... & Nowak, S. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346:1517-1519

Chevan, A. & Sutherland, M. (1991). Hierarchical partitioning. *American Statistician*, 45:90-96.

Ciucci, P., Boitani, L., Francisc, F. & Andreoli, G. (1997). Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology*, 243:803-819.

Cuesta, L., Bárcena, F., Palacios, F. & Reig, S. (1991). The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia*, 55:239-254.

Crooks, K.R., & Sanjayan, M. (Eds.). (2006). *Connectivity conservation* (Vol. 14). Cambridge University Press.

D.G.C.N., 2000. *Tercer Inventario Forestal Nacional, 1997-2006: Galicia*. Ministerio de Medio Ambiente, Dirección General de Conservacion de la Naturaleza, Madrid.

Dellinger, J.A., Proctor, C., Steuryc, T.D., Kelly, M.J. & Vaughan, M.R. (2013). Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biological Conservation*, 157:324–330

Ermala, A. (2003). A survey of large predators in Finland during the 19th–20th centuries. *Acta Zoologica Lituanica*, 13:15-20.

Fernández, J.M., & De Azua, N.R. (2010). Historical dynamics of a declining wolf population: persecution vs. prey reduction. *European Journal of Wildlife Research*, 56:169-179.

Fuller, T.K. & Sievert, P.R. (2001). *Carnivore demography and the consequences of changes in prey availability*. Carnivore Conservation (ed. by J.L. Gittleman, S.M. Funk, D. Macdonald and R.K. Wayne). pp. 163-178. Cambridge University Press.

García, E., Llaneza, L., Palacios, V., López-Bao, J.V., Sazatornil, V., Rodríguez, A., Rivas, O. & Cabana, M. (2012*) Primeros datos sobre la ecología espacial del lobo en Galicia.* Abstract-book of the III Iberian Wolf Congress, pp.44.

Glenz, C., Massolo, D., Kuonen, D. & Schlaepfer, R. (2001) A wolf habitat suitability prediction study in Valais (Switzerland). *Landscape and Urban Planning*, 55:55-65.

Green, R.H. (1979). *Sampling design and statistical methods for environmental biologists.* John Wiley and Sons, New York.

Guitián, J., Sánchez-Canals, J.L., de Castro, A., Bas, S., Rodríguez, J. & Bermejo, A. (1975) *El Inventario cinegético de la provincia de la Coruña*. Report to Xunta de Galicia.

Guitián, J., de Castro, A, Bas, S & Sánchez, J.L. (1979). Nota sobre la dieta del lobo (*Canis lupus* L.) en Galicia. *Trabajos Compostelanos de Biología*, 8:95-104.

Habib B. & S. Kumar (2007). Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. *Journal of Zoology*, 272:259–265.

Elbroch, L.M., Lendrum, P.E., Alexander, P. & Quigley, H. (2015). Cougar den site selection in the Southern Yellowstone Ecosystem. *Mammal Research*, 60*:*89-96.

Epps, C.W., Mutayoba, B.M., Gwin, L., & Brashares, J.S. (2011). An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa. *Diversity and Distributions*, 17:603-612.

Harrington, F.H. & Mech, L.D. (1982). An analysis of howling response parameters useful for wolf pack censusing. *J. Wildl. Manage*. 46:686–693.

Heard, D.C., & Williams, T.M. (1992). Distribution of wolf dens on migratory caribou ranges in the Northwest Territories, Canada. *Canadian Journal of Zoology*, 70:1504-1510.

Houle, M., Fortin, D., Dussault, C., Courtois, R., & Ouellet, J.P. (2010). Cumulative effects of forestry on habitat use by gray wolf (Canis lupus) in the boreal forest. *Landscape Ecology*, 25:419–433.

Iliopoulos, Y., Youlatos, D., & Sgardelis, S. (2014). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *European* Journal of Wildlife Research, 60:23-34.

INE (2010) Censo de población y vivienda. Instituto Nacional de Estadística de España.

Jêdrzejewski W., Niedzia£kowska, M., Myslajek, R.W., Nowak, S. & Jêdrzejewska, B. (2004). Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. *Acta Theriologica*, 50:417–428.

Jêdrzejewski W., Niedzia£kowska, M., Myslajek, R.W., Nowak, S. & Jêdrzejewska, B. (2005). Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. *Diversity Distribution*, 10:225–233.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61:65-71.

Kaartinen S., Luoto, M. & Kojola, I. (2005). Selection of den sites by wolves in boreal forests in Finland. *Journal of Zoology*, 281:99–104.

Kleiven, J., Bjerke, T. & Kaltenborn, B. (2004). Factors influencing the social acceptability of large carnivore behaviours. *Biodiversity and Conservation*, 13:1647–1658.

Lázaro, A. (2014). *Ecología trófica del lobo (Canis lupus) en un ambiente humanizado y multipresa: Variación geográfica*. MSc thesis. University of Cordoba, Spain.

Lesmerises, F., Dussault, C. & St-Laurent, M.H. (2012). Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management*, 276:125–131

Linnell, J.D.C. & Boitani, L. (2012). Building biological realism into wolf management policy: the development of the population approach in Europe. *Hystrix,* 23:80-91.

Llaneza, L., Fernández, A. & Nores, C. (1996). Dieta del lobo en dos zonas de Asturias (España) que difieren en carga ganadera. *Doñana Acta Vertebrata* 23:201-213.

Llaneza, L., Palacios, V., Uzal, A., Ordiz, A., Sazatornil, V., Sierra, P. & Álvares, F. (2005) Distribución y aspectos poblacionales del lobo ibérico *(Canis lupus signatus)* en las provincias de Pontevedra y A Coruña. *Galemys*, 17:61-80.

Llaneza, L., López-Bao, J.V. & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions*. 18:459–469.

Llaneza L., García, E.J., Palacios, V. & López-Bao, J.V. (2014a). *Trabajos de apoyo para la coordinación tecnico-científica del censo de lobo ibérico en la Comunidad Autónoma de Galicia.* Tragsatec-Ministerio de Agricultura, Alimentación y Medio Ambiente. Informe inédito. 48 pp.

Llaneza, L., García, E.J. & López-Bao, J.V. (2014b) Intensity of territorial marking predicts wolf reproduction: implications for wolf monitoring. *PLOS ONE*, 9, e93015.

López-Bao, J.V., Palomares, F., Rodríguez, A. & Delibes, M. (2010). Effects of food supplementation on home range size, reproductive success, productivity and recruitment in a small population of Iberian lynx. *Animal Conservation*, 13:35-42.

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013). Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters,* 6:448-455.

López-Bao, J.V., Kaczensky, P., Linnell, J.D.C., Boitani, L. & Chapron, G. (2015a). Carnivore coexistence: wilderness not required. *Science, 348*:871-872.

López-Bao, J.V., Blanco, J.C., Rodríguez, A., Godinho, R., Sazatornil, V., Alvares, F., García, E.J., Llaneza, L., Rico, M., Cortés, Y., Palacios, V. & Chapron, G. (2015b). Toothless wildlife protection laws. *Biodiversity and Conservation*. In press.

Mac Nally, R. (2000). Regression and model building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘‘predictive” and ‘‘explanatory” models. *Biodiversity and Conservation*, 9:655-671.

Mac Nally, R. & Horrocks, G. (2002). Relative influences of patch, landscape and historical factors on birds in an Australian fragmented landscape. Journal of *Biogeography*, 29:395-410.

Mech, S.G., & Hallett, J.G. (2001). Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology*, 15:467-474.

Mech, L.D. & Boitani, L. (2003) *Wolf social ecology*. In: Mech L.D., Boitani L. (eds) *Wolves: behaviour, ecology, and conservation*. University of Chicago Press, Chicago, pp 1–34

Meriggi, A., & Lovari, S. (1996). A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock?. *Journal of Applied Ecology*, 33:1561-1571.

Munilla, I., Romero, R. & de Azcárate, J.G. (1991). *Diagnóstico de las poblaciones faunísticas de interés cinegético de la provincia de Pontevedra.* Report to Xunta de Galicia.

Naves, J., Wiegand, T., Revilla, E. & Delibes, M. (2003). Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. *Conservation Biology*, 17:1276–1289.

Norris, D.R., Theberge, M.T & Theberge, J.B. (2002). Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park, Ontario. *Can. J. Zool*. 80:866–872

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., & Paquet, P.C. (1996). Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, 10:949-963.

Ordiz, A., Bischof, R., & Swenson, J.E. (2013). Saving large carnivores, but losing the apex predator? *Biological Conservation*, 168:128-133.

Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., & Macdonald, D.W. (2015). Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, in press

Person, D.K. & Russell, A.L. (2009) Reproduction and den site selection by wolves in a disturbed landscape. *Northwest Science*. 83:211-224.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., & Wilson, K.A. (2007). Conservation planning in a changing world. *Trends in Ecology & Evolution*, 22:583-592.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E. & Brashares, J.S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proc. Nat. Acad. Sci. U.S.A.*, 105: 20770–20775.

R Core Team (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rettie, W.J., & Messier, F. (2000). Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, *2*3:466-478.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world’s largest carnivores. *Science*, 343(6167):1241484.

Ryabov, L.S. (1987). On the wolf synanthrophy in the Central Black Earth Belt. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdelene Biologii*, 92 (1):3–12

Santini, L., Di Marco, M., Boitani, L., Maiorano, L. & Rondinini, C. (2014). Incorporating spatial population structure in gap analysis reveals inequitable assessments of species protection. *Diversity and distributions*, 20:698-707.

Sanderson, E.W., Redford, K.H., Vedder, A., Coppolillo, P.B. & Ward, S.E. (2002). A conceptual model for conservation planning based on landscape species requirements. *Landscape and urban planning*, 58:41-56.

Sazatornil, V. (2008). *Alimentación del lobo (Canis lupus) en zonas del Occidente de Galicia con presencia de ganado equino en régimen de semi-libertad.* Msc Thesis. University of A Coruña.

Scott, J.P. & Fuller, J.L. (1965). *Genetics and the Social Behavior of the Dog*. Chicago Press, Chicago.

S.G.H.N. (Sociedade Galega de Historia Natural) (1995). *Atlas de Vertebrados de Galicia.* Tomo I. Consello da Cultura Gallega. Santiago de Compostela.

Soga, M., & Koike, S. (2013). Mapping the potential extinction debt of butterflies in a modern city: implications for conservation priorities in urban landscapes. *Animal Conservation*, 16:1-11.

Stephens, P.A., & Sutherland, W.J. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution*, 14*:*401-405.

Theuerkauf, J., Rouys, S. & Jêdrzejewski, W. (2003). Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Can. J. Zool*. 81:163–167 .

Tischendorf, L. & Fahrig, L. (2000). How should we measure landscape connectivity?. *Landscape Ecology*, 15*:*633-641.

Trapp J.R., Beier, P., Mack, C., Parsons, D.R. & Paquet, P.C. (2008). Wolf, *Canis lupus*, den site selection in the Rocky Mountains. *Canadian Field-Naturalist*. 122:49-56

Treves, A. & Bruskotter, J. (2014). Tolerance for predatory wildlife. S*cience*, 344:475-476.

Unger, D.E., Keenlance, P.W., Kohn, B.E. & Anderson, E.M. (2009) *Factors Influencing Homesite Selection by Gray Wolves in Northwestern Wisconsin and East-Central Minnesota*. In Wydeven, A.P. et al. (eds.). *Recovery of Gray Wolves in the Great Lakes* Region of the United States (pp. 175-189). Springer New York.

Walsh, C. & Mac Nally, R. (2008) *hier.part: hierarchical partitioning. R package version 1.0.3*. R Foundation for Statistical Computing, Vienna, Austria.

Wikramanayake, E.D., Dinerstein, E., Robinson, J.G., Karanth, U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Conner, M., Hemley, T. & Bolze, D. (1998). An ecology based method for defining priorities for large mammal conservation: the tiger as case study. *Conservation Biology*, 12:865-878.

Wikramanayake, E., McKnight, M., Dinerstein, E., Joshi, A., Gurung, B. & Smith, D. (2004). Designing a conservation landscape for tigers in human-dominated environments. *Conservation Biology*, 18:839-844.

White, S., Briers, R.A., Bouyer, Y., Odden, J. & Linnell, J.D.C. (2015). Eurasian lynx natal den site and maternal home-range selection in multi-use landscapes of Norway. *Journal of Zoology*. In press.

Whittington, J., St. Clair, C.C. & Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications*, 15:543-553.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, 280:2126-2128.

Zedrosser, A., Steyaert, S.M., Gossow, H. & Swenson, J.E. (2011). Brown bear conservation and the ghost of persecution past. *Biological Conservation*, 144:2163-2170.


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Supporting information

Table 5.A1. Mean potential food availability (biomass estimated considering cattle, horses, sheep and goats) in homesites (biomass observed) compared to the average food availability of randomized sites within territories (mean randomized, n = 10).

Pack	Biomass observed	Mean randomized	95% CI		Observed > 95% CI
1	16.6	33.4	9.3	57.5	
2	18.3	61.8	12.6	111.1	
3	68.9	62.5	42.4	82.6	
4	7.7	54.8	7.7	101.9	
5	71.4	49.9	24.6	75.2	
6	149.4	129.3	79.4	179.2	
7	17.9	17.7	10.5	24.9	
8	24.9	12.3	7.8	16.9	*
9	97.8	50.7	29.7	71.7	*
10	84.6	55.8	35.5	76.1	*
11	174.6	73.1	38.1	108.1	*
12	4.1	25.6	0.6	50.7	
13	45.4	16.3	5.8	26.9	*
14	25.2	23.7	8.5	39.0	
15	2.4	12.1	6.7	17.5	
16	14.3	64.4	28.1	100.7	
17	84.1	87.6	52.8	122.4	
18	38.4	49.6	11.1	88.1	
19	9.3	6.6	1.1	12.1	
20	1.1	9.8	5.4	14.2	
21	14.4	20.1	2.6	37.7	
22	31.2	83.7	57.3	110.1	
23	6.8	21.9	10.1	33.7	
24	1.6	10.4	4.8	15.9	
25	22.2	5.7	3.0	8.3	*
26	20.5	50.9	21.4	80.5	
27	160.0	75.6	44.5	106.6	*
28	100.7	92.2	61.7	122.6	
29	0.07	4.0	0	8.1	
30	117.7	83.4	33.4	133.3	
31	99.4	47.6	32.0	63.2	*
32	1.8	8.6	0.2	17.1	
33	11.8	43.2	19.7	66.8	

Table 5.A2. Results of Generalized Linear Models evaluating homesite selection by wolves in NW Spain at 1 km^2 in relation to human pressure. Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i).

VARIABLES	**AIC**	**ΔAIC**	w_i
Paved Roads 1 km^2 + Farming land 1 km^2 + Number of buildings 1 km^2+ Total roads*human density interaction	127.54	0	0.30
Paved Roads 1 km^2+ Farming land 1 km^2+ Total roads*human density interaction	127.97	0.43	0.24
Paved Roads 1 km^2+ Paths 1 km^2+ Farming land 1 km^2+ Number of buildings 1 km^2+ Total roads*human density interaction	128.74	1.2	0.16
Paved Roads 1 km^2+ Paths 1 km^2+ Farming land 1 km^2	129.16	1.62	0.13
Paved Roads 1 km^2	130.60	3.06	0.06
Paved Roads 1 km^2 + Paths 1 km^2+ Farming land 1 km^2+ Number of buildings 1 km^2. Number of 100x100 m cell with buildings + Total roads*human density interaction	130.65	3.11	0.06
Paved Roads 1 km^2+ Paths 1 km^2+ Farming land 1 km^2+ Number of buildings 1 km^2. Number of 100x100 m cell with buildings + Number of buildings central 100 x 100 m cells + Total roads*human density interaction	132.64	5.1	0.02
Null model	175.11	47.57	0.00

Table 5.A3. Parameter estimates in the best candidate model testing the influence of human pressure at 1 km^2 on wolf homesite selection patterns in NW Spain. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

HUMAN PRESSURE	**1 km^2**		
Predictors	*B*	CI 2.5%	CI 97.5%
Number of buildings 1 km^2	-0.043	-1.29	0.19
Paved Roads 1 km^2	-0.723*	-1.57	-0.028
Farming land 1 km^2	-0.017	-0.04	0.006
Total roads*human density interaction	-6.27e-05*	-0.0001	3.48e-06

Table 5.A4. Results of Generalized Linear Models evaluating homesite selection by wolves in NW Spain at 1 km^2 in relation to landscape attributes. Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i).

VARIABLES	AIC	ΔAIC	w_i
Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality percentile 10th 1 km^2 + Refuge quality mean distance 1 km^2 + Proportion of pixels with refuge 1 km^2	122.59	0	0.31
Ratio Altitude 1 km^2 /Mean Altitude study area. Altitude 1 km^2 + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality percentile 10th 1 km^2 + Refuge quality mean distance 1 km^2+ Proportion of pixels with refuge 1 km^2	122.59	0	0.31
Refuge quality percentile 10th 1 km^2 + Refuge quality mean distance 1 km^2 + Proportion of pixels with refuge 1 km^2	123.67	1.08	0.18
Altitude 1 km^2 + Ratio Roughness 1 km^2/ Roughness 3km^2 + Refuge quality upper quartile 1 km^2 + Refuge quality percentile 10th 1 km^2 + Refuge quality mean distance 1 km^2+ Proportion of pixels with refuge 1 km^2	124.46	1.87	0.12
Altitude 1 km^2 + Ratio Roughness 1 km^2/ Roughness 3km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality upper quartile 1 km^2 + Refuge quality percentile 10th 1 km^2 + Refuge quality mean distance 1 km^2 + Proportion of pixels with refuge 1 km^2	126.34	3.75	0.04
Altitude 1 km^2 Roughness 1 km^2 + Ratio Roughness 1 km^2/ Roughness 3km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality upper quartile 1 km^2 + Refuge quality percentile 10th 1 km^2 + Refuge quality mean distance 1 km^2 + Proportion of pixels with refuge 1 km^2	128.33	5.74	0.01
Null model	175.11	52.52	0.00

Table 5.A5. Parameter estimates in the best candidate model testing the influence of landscape attributes at 1 km^2 on wolf homesite selection patterns in NW Spain. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

LANDSCAPES ATTRIBUTES	1 km^2		
Predictors	*B*	CI 2.5%	CI 97.5%
Refuge quality mean distance 1 km^2	0.013*	0.005	0.020
Refuge quality percentile 10th 1 km^2	-0.020*	-0.032	-0.005
Proportion of pixels with refuge 1 km^2	0.026*	0.008	0.043
Ratio Roughness 1 km^2/Mean Roughness study area	1.032*	0.308	1.775

Table 5.A6. Results of Generalized Linear Models evaluating homesite selection by wolves in NW Spain at 1 km^2 in relation to landscape attributes and human pressure factors pooled (combined model). Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i). For simplicity, only models with ΔAIC < 2 are showed.

VARIABLES	**AIC**	**ΔAIC**	w_i
Ratio Altitude 1 km^2 /Mean Altitude study area + Refuge quality percentile 10th 1 km^2 + Proportion of pixels with refuge 1 km^2 + Refuge quality mean distance 1 km^2 + Paved Roads 1 km^2	114.79	0	0.18
Altitude 1 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality percentile 10th 1 km^2 + Proportion of pixels with refuge 1 km^2 + Refuge quality mean distance 1 km^2 + Paved Roads 1 km^2 + Farming land 1 km^2 + Number of buildings 1 km^2	114.95	0.16	0.16
Altitude 1 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality percentile 10th 1 km^2 + Proportion of pixels with refuge 1 km^2 + Refuge quality mean distance 1 km^2 + Paved Roads 1 km^2 + Farming land 1 km^2	115.26	0.47	0.14
Altitude 1 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality percentile 10th 1 km^2 + Proportion of pixels with refuge 1 km^2 + Refuge quality mean distance 1 km^2 + Paved Roads 1 km^2 + Farming land 1 km^2 + Number of buildings 1 km^2 + Total roads*human density interaction.	115.32	0.53	0.13
Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality percentile 10th 1 km^2 + Proportion of pixels with refuge 1 km^2 + Refuge quality mean distance 1 km^2 + Paved Roads 1 km^2	115.4	0.61	0.13
Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Refuge quality percentile 10th 1 km^2 + Proportion of pixels with refuge 1 km^2 + Refuge quality mean distance 1 km^2 + Paved Roads 1 km^2 + Farming land 1 km^2	115.76	0.97	0.11
Refuge quality percentile 10th 1 km^2 + Proportion of pixels with refuge 1 km^2 + Refuge quality mean distance 1 km^2+ Paved Roads 1 km^2	116.28	1.49	0.08

Table 5.A7. Parameter estimates in the best candidate model testing the influence of landscape attributes and human pressure factors pooled at 1 km^2 (combined model) on wolf homesite selection patterns in NW Spain. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

COMBINED MODEL		**1 km^2**	
Predictors	*B*	CI 2.5%	CI 97.5%
Refuge quality mean distance 1 km^2	0.008	-0.0006	0.0180
Refuge quality percentile 10th 1 km^2	-0.013	-0.0293	0.0022
Proportion of pixels with refuge 1 km^2	0.024*	0.0066	0.0425
Ratio Altitude 1 km^2 /Mean Altitude study area	0.7682	-0.037	1.596
Paved Roads 1 km^2	-0.997*	-1.785	-0.3664

Table 5.A8. Results of hierarchical partitioning analysis carried out on the best model evaluating homesite selection by wolves in NW Spain at 1 km^2 in relation to landscape attributes and human pressure factors pooled (combined model).

VARIABLES	Interpretation	Z-Score	P
Refuge quality mean distance 1 km^2	Quality refuge	9.62	<0.05
Refuge quality upper quartile 1 km^2	Quality refuge	2.86	<0.05
Proportion of pixels with refuge 1 km^2	Quantity refuge	13.21	<0.05
Ratio Altitude 1 km^2 /Mean Altitude study area	Location refuge	4.67	<0.05
Paved Roads 1 km^2	Paved Roads	12.42	<0.05

Table 5.A9. Results of Generalized Linear Models evaluating homesite selection by wolves in NW Spain at 9 km^2 in relation to human pressure. Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i).

VARIABLES	AIC	ΔAIC	w_i
Total roads*human density interaction + Paved Roads 9 km^2+ Paths 9 km^2	130.74	0	0.52
Paved Roads 9 km^2 + Paths 9 km^2	131.95	1.21	0.28
Total roads*human density interaction + Farming land 9 km^2+ Paved Roads 9 km^2 + Paths 9 km^2	132.69	1.95	0.19
Null model	175.11	44.37	0

Table 5.A10. Parameter estimates in the best candidate model testing the influence of human pressure at 9 km^2 on wolf homesite selection patterns in NW Spain. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

HUMAN PRESSURE	9 km^2		
Predictors	*B*	CI 2.5%	CI 97.5%
Paved Roads 9 km^2	-0.136*	-0.201	-0.776
Paths 9 km^2	-0.054*	-0.107	-0.0026
Total roads*human density interaction	-8.401e-06	-2.112e-05	4.951e-07

Table 5.A11. Results of Generalized Linear Models evaluating homesite selection by wolves in NW Spain at 9 km^2 in relation to landscape attributes. Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i).

VARIABLES	**AIC**	**ΔAIC**	w_i
Ratio Altitude 9 km^2/Mean Altitude study area + Ratio Roughness 9 km^2/Mean + Proportion of refuge 9 km^2	152.37	0	0.36
Ratio Altitude 9 km^2/Mean Altitude study area + Proportion of refuge 9 km^2 +	152.42	0.05	0.35
Roughness 9 km^2 + Ratio Altitude 9 km^2/Mean Altitude study area Ratio Roughness 9 km^2/Mean Roughness study area + Proportion of refuge 9 km^2	153.71	1.34	0.18
Altitude 9 km^2 + Roughness 9 km^2 + Ratio Altitude 9 km^2/Mean Altitude study area + Ratio Roughness 9 km^2/Mean Roughness study area + Proportion of refuge 9 km^2	155.07	2.7	0.09
Null model	175.11	22.74	0

Table 5.A12. Parameter estimates in the best candidate model testing the influence of landscape attributes at 9 km^2 on wolf homesite selection patterns in NW Spain. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

LANDSCAPES ATTRIBUTES	**9 km^2**		
Predictors	*B*	CI 2.5%	CI 97.5%
Ratio Altitude 9 km^2/Mean Altitude study area	0.809*	0.150	1.463
Ratio Roughness 9 km^2/Mean	0.535	-0.202	1.245
Proportion of refuge 9 km^2	0.003 *	0.0004	0.006

Table 5.A13. Results of Generalized Linear Models evaluating homesite selection by wolves in NW Spain at 9 km^2 in relation to landscape attributes and human pressure factors pooled (combined model). Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i). For simplicity, only models with ΔAIC < 2 are showed.

VARIABLES	AIC	ΔAIC	w_i
Roughness 9 km^2 + Total roads*human density interaction + Paved Roads 9 km^2 + Paths 9 km^2	128.2	0	0.28
Roughness 9 km^2 + Proportion of refuge 9 km^2 + Total roads*human density interaction + Paved Roads 9 km^2+Paths 9 km^2	128.79	0.59	0.21
Roughness 9 km^2 + Proportion of refuge 9 km^2 + Total roads*human density interaction + Farming land 9 km^2 + Paved Roads 9 km^2+Paths 9 km^2	129.21	1.01	0.17
Roughness 9 km^2 + Ratio Altitude 9 km^2/Mean Altitude study area + Proportion of refuge 9 km^2 + Total roads*human density interaction + Farming land 9 km^2 + Paved Roads 9 km^2 + Paths 9 km^2	129.62	1.42	0.14
Roughness 9 km^2 + Paved Roads 9 km^2 + Paths 9 km^2 + Roughness 9 km^2	129.98	1.78	0.11

Table 5.A14. Parameter estimates in the best candidate model testing the influence of landscape attributes and human pressure factors pooled at 9 km^2 (combined model) on wolf homesite selection patterns in NW Spain. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

COMBINED MODEL	**9 km^2**		
Predictors	*B*	CI 2.5%	CI 97.5%
Paved Roads 9 km^2	-0.118*	-0.182	-0.059
Paths 9 km^2	-0.058*	-0.127	-0.006
Roughness 9 km^2	0.014*	0.001	0.027
Total roads*human density interaction	-9.737e-06	-2.305e-05	2.491e-09

Table 5.A15. Results of Generalized Linear Models evaluating hierarchical spatial effects on homesite selection by wolves in NW Spain in relation to human pressure. Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i). For simplicity, only models with ΔAIC < 2 are showed.

VARIABLES	AIC	ΔAIC	w_i
Paved Roads 9 km^2 + Paths 9 km^2 + Farming land 1 km^2 + Farming land 9 km^2 + Paved Roads 1 km^2* Paved Roads 9 km^2	118,05	0	0,229
Paths 9 km^2+ Paved Roads 1 km^2* Paved Roads 9 km^2	118,47	0,42	0,186
Paved Roads 9 km^2+ Paths 9 km^2+ Paved Roads 1 km^2* Paved Roads 9 km^2	118,63	0,58	0,172
Paved Roads 9 km^2+ Paths 9 km^2+ Farming land 1 km^2+ Paved Roads 1 km^2* Paved Roads 9 km^2	119,71	1,66	0,100
Paths 1 km^2+ Paved Roads 9 km^2+ Paths 9 km^2+ Farming land 1 km^2+ Farming land 9 km^2+ Paved Roads 1 km^2* Paved Roads 9 km^2+ Paths 1 km^2* Paths 9 km^2	119,94	1,89	0,089
Paved Roads 9 km^2+ Paths 9 km^2+ Farming land 1 km^2+ Farming land 9 km^2+ Paved Roads 1 km^2* Paved Roads 9 km^2+ Paths 1 km^2* Paths 9 km^2	119,96	1,91	0,088
Paths 1 km^2+ Paved Roads 9 km^2+ Paths 9 km^2+ Farming land 1 km^2+ Farming land 9 km^2+ Total roads*human density interaction 9 km^2+ Paved Roads 1 km^2* Paved Roads 9 km^2+ Paths 1 km^2* Paths 9 km^2+	120,43	2,38	0,070

Table 5.A16. Parameter estimates in the best candidate model testing the existence of hierarchical spatial effects on homesite selection by wolves in NW Spain in relation to human pressure. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

HUMAN PRESSURE			
Predictors	*B*	CI 2.5%	CI 97.5%
Paved Roads 9 km^2	-0.089*	-0.189	-0.002
Paths 9 km^2	-0.070*	-0.122	-0.020
Farming land 1 km^2	-0.034*	-0.072	-0.0005
Farming land 9 km^2	0.004	-0.0001	0.008
Paved Roads 1 km^2* Paved Roads 9 km^2	-0.056*	-0.122	-0.006

Table 5.A17. Results of Generalized Linear Models evaluating hierarchical spatial effects on homesite selection by wolves in NW Spain in relation to landscape attributes. Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC weights (w_i). For simplicity, only models with ΔAIC < 2 are showed.

VARIABLES	AIC	ΔAIC	w_i
Roughness 1 km^2*Roughness 9 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area*Ratio Altitude 9 km^2 /Mean Altitude study area + Refuge 1 km^2 + Roughness 9 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Altitude 9 km^2 /Mean Altitude study area + Ratio Roughness 9 km^2/Mean Roughness study area	136,21	0	0,166
Roughness 1 km^2*Roughness 9 km^2 + Roughness 1 km^2 + Roughness 9 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Ratio Roughness 9 km^2 / Mean Roughness study area	136,24	0,03	0,164
Roughness 1 km^2*Roughness 9 km^2 + Refuge 1 km^2 + Roughness 9 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area	136,58	0,37	0,138
Roughness 1 km^2*Roughness 9 km^2 + Ratio Altitude 1 km^2 /Mean Altitude study area * Ratio Altitude 9 km^2/Mean Altitude study area + Refuge 1 km^2 + Altitude 1 km^2 + Roughness 9 km^2 + Ratio Altitude 1 km^2/Mean Altitude study area + Ratio Roughness 1 km^2/Mean Roughness study area + Ratio Roughness 9 km^2/Mean Roughness study	136,76	0,55	0,126
Refuge 1 km^2 + Ratio Altitude 1 km^2/Mean Altitude study area	137,02	0,81	0,111
Roughness 1 km^2*Roughness 9 km^2 + Refuge 1 km^2 + Ratio Altitude 1 km^2/Mean Altitude study area	137,03	0,82	0,110
Roughness 1 km^2*Roughness 9 km^2 + Refuge 1 km^2 + Roughness 9 km^2 + Ratio Altitude 1 km^2/Mean Altitude study area	137,55	1,34	0,085

Table 5.A18. Parameter estimates in the best candidate model testing the existence of hierarchical spatial effects on homesite selection by wolves in NW Spain in relation to landscape attributes. *B*: regression coefficients, CI 2.5% and CI 97.5%: confidence intervals computed at the 95% interval. Predictors with coefficients with CI 95% non-overlapping with zero are denoted with an asterisk.

LANDSCAPE ATTRIBUTES			
Predictors	*B*	CI 2.5%	CI 97.5%
Refuge 1 km^2	0.048*	0.024	0.076
Roughness 9 km^2	-1.888	-4.497	0.614
Ratio Altitude 1 km^2 /Mean Altitude study area	2.939*	0.121	6.348
Ratio Roughness 1 km^2/Mean Roughness study area	-1.698	-3.552	0.083
Ratio Roughness 9 km^2/Mean Roughness study area	1.055	-3.677	2.536
Roughness 1 km^2*Roughness 9 km^2	0.0008*	0.0002	0.001
Ratio Altitude 1 km^2 /Mean Altitude study area*Ratio Altitude 9 km^2 /Mean Altitude study area	-0.707	-1.829	0.247

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6.

RESTING IN RISKY ENVIRONMENTS: THE IMPORTANCE OF COVER FOR A LARGE CARNIVORE TO COPE WITH EXPOSURE RISK IN HUMAN-DOMINATED LANDSCAPES


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6. RESTING IN RISKY ENVIRONMENTS: THE IMPORTANCE OF COVER FOR A LARGE CARNIVORE TO COPE WITH EXPOSURE RISK IN HUMAN-DOMINATED LANDSCAPES

ABSTRACT

Centuries of persecution have influenced the behaviour of large carnivores. For those populations persisting in human-dominated landscapes, complete spatial segregation from humans is not possible, as they are in close contact with people even when they are resting, when their vulnerability increase remarkably. As a consequence, the selection of resting sites is expected to be critical for large carnivore persistence, where resting sites must offer protection to counteract exposure risk. Using wolves *(Canis lupus)* as a model species, we hypothesised that selection of resting sites by large carnivores in human-dominated landscapes will be not only influenced by human activities, but also strongly determined by dense vegetation covers providing concealment. We studied the fine-scale attributes of 546 resting sites and confronted them to 571 random points in NW Iberia. Half of resting sites (50.8%) were found in forests (mainly forest plantations, 73.1%), 43.4% in scrublands, and only 5.8% in croplands. Wolves located their resting sites away from paved and large unpaved roads and from settlements, whereas they significantly selected areas with high availability of horizontal (refuge) and canopy cover. The importance of refuge was remarkably high, with its independent contribution alone being more important than the contribution of all the variables related to human pressure (distances) pooled (50.7% vs. 42.6%, respectively). The strength of refuge selection in human-dominated landscapes allowed wolves even to rest relatively close to manmade structures (sometimes less than 200m). Maintaining high-quality refuge areas becomes an important element for both favouring the persistence of large carnivores and for human-carnivore coexistence in human-dominated landscapes, which can easily be integrated in landscape planning.

KEYWORDS: *Canis lupus*, carnivore persistence, human-wildlife interactions, human-dominated landscapes, landscape planning, refuge, resting behaviour, human-wildlife interactions.

6.1. INTRODUCTION

Historically, human societies have invested huge efforts to persecute and exterminate large carnivores (Boitani, 1995; Frank and Woodroffe, 2001). As a result, In Europe by the first half of the last century, wolves (*Canis lupus*), bears (*Ursus arctos*) or lynx (*Lynx lunx*) were absent from most of the continent (Chapron *et al.*, 2014). For example, in the nineteenth-century in Spain, wolves were intensively persecuted using poison, firearms or wolf traps and removing litters, and only between 1855 and 1859, ca. 15,000 wolves were officially killed (Rico and Torrente, 2000). Although a positive trend has been observed for some large carnivore populations in recent times (Chapron *et al.*, 2014), humans are still behind the main causes of mortality for large carnivores (Woodfroffe and Ginsberg, 1998), and sometimes such mortality sources can even curb, slow down or prevent the recovery process of large carnivore populations (Goodrigh *et al.*, 2008; Creel and Rotella, 2010; Liberg *et al.*, 2012; López-Bao *et al.*, 2015).

Centuries of persecution have influenced large carnivore life-history patterns and behaviour, with these species becoming, for instance, more vigilant and actively avoiding contact with humans (Swenson, 1999; Linnell *et al.*, 2002; Zedrosser *et al.*, 2011). As a consequence, many large carnivore populations have been able to persist in human-dominated landscapes by adapting their behaviour to share the landscape with humans (Habib and Kumar, 2007; Ordiz *et al.*, 2011; *Llaneza et al.*, 2012; Athreya *et al.*, 2013; López-Bao *et al.*, 2013; Ahmadi *et al.*, 2014; Chapron *et al.*, 2014; Bouyer *et al.*, 2015). Such persistence is driven to a large extent by the ability of large carnivores to minimise the probability of a risky situation with humans. Chances of survival and persistence will therefore depend on the adoption of different behavioural mechanisms involving both temporal and spatial segregation, such as becoming more nocturnal (Vilá *et al.*, 1995; Ciucci *et al.*, 1997), avoiding areas with high human activities (Theuerkauf *et al.*, 2003; Llaneza *et al.*, 2012; Iliopoulos *et al.*, 2013; Ahmadi *et al.*, 2014) or maximising the selection of refuges facilitating that animals go unnoticed by humans (Ordiz *et al.*, 2011; Llaneza *et al.*, 2012; Cristescu *et al.*, 2013).

For large carnivores persisting in multi-use landscapes, complete spatial segregation from humans is not always possible, being in close contact with people even when they are resting. In humanised landscapes, large carnivores are mainly active at night or at twilight (Ciucci *et al*., 1997; Moe *et al*., 2007; Theuerkauf, 2009; Heurich *et al*., 2014), resting or sleeping mainly during daylight. When resting or sleeping, risk perception decreases; therefore, the vulnerability of animals can increase remarkably (Lima *et al*., 2005). As a consequence, the selection of resting sites in human-dominated landscapes is expected to be critical for large carnivores, where resting sites must offer protection to counteract exposure risk (Podgorski *et al*., 2008; Ordiz *et al*., 2011; Cristescu *et al*., 2013).

Wolves are highly resilient to persist in humanised landscapes compared to other large carnivore species (Chapron *et al*., 2014) by perceiving mortality risks associated with humans, adjusting, for instance, the use of the space at different scales over time (Habib and Kumar, 2007; Agarwala and Kumar, 2009; Ahmadi *et al*., 2014). However, the risk of being detected while resting is high because of the costs associated with fleeing in daylight (Ordiz *et al*., 2011). Therefore, it is expected that wolves will strongly minimise the chance of detection when selecting resting sites. In human-dominated landscapes, this would translate into the avoidance of manmade infrastructures where the probability of interaction with humans is high, as well as a strong selection for dense and inaccessible vegetation covers (i.e., refuge).

Here, we have evaluated the characteristics of resting sites for Iberian wolves equipped with GPS collars in human-dominated landscapes of Galicia, NW Iberia. Iberian wolves have been traditionally pursued using a great variety of methods (Rico and Torrente, 2000; Fernández and De Azúa, 2010; Álvares *et al*., 2011). Nevertheless, they have persisted in areas with high levels of human activities such as Galicia (mean human population density: 93 inhabitants/km^2, 1 human settlement/km^2; mean paved road density: 2.7 km/km^2; INE 2014), and where the human–wolf conflict has been evident for a long time, considering the feeding ecology of the species (here, feeding considerably on livestock; Cuesta *et al*., 1991; López-Bao *et al*., 2013). Indeed, wolf abundance in Galicia is remarkable, with an estimate of 2.25 and 2.8 wolf packs per 1,000 km^2 between 1999 and 2003 and between 2013 and 2014, respectively; Llaneza *et al*., 2005; 2014).

We aimed to increase our understanding of the mechanisms allowing the persistence of large carnivores in human-dominated landscapes. In particular, if wolves select resting sites according to perceived exposure risk, we hypothesised that selection of resting sites will be not only influenced by human activities, but also strongly determined by environmental attributes such as dense vegetation cover providing concealment. By comparing resting sites of wolves with random points, we therefore predicted that i) resting sites would be located in more concealed places than random points, and furthermore that the strength of the effect of vegetation cover should be stronger compared to other fine scale attributes; ii) wolves would actively avoid locating their resting sites close to those manmade structures where human activity will be more predictable; iii) wolves would avoid locating their resting sites close to forest edges and in small patches of refuge, which are expected to increase exposure risk. We additionally explored whether individual attributes (sex and age) influenced the selection of resting sites.

6.2. METHODS

Study area

This study was carried out in Galicia, NW Spain (ca. 30,000 km^2) (specifically in A Coruña, Lugo and Pontevedra provinces; 22,500 km^2). The outcome of the interaction between a human-dominated patchy landscape and the fact that wolves here can feed remarkably on anthropogenic sources of food (wolves in the study area feed remarkably on livestock; Cuesta *et al*., 1991; López-Bao *et al*., 2013), translates into a risky scenario where it is expected that wolves will maximise the concealment of resting sites in relation to human-derived risk.

The study area was characterised by a patchy landscape highly transformed by agriculture and livestock activities. During the twentieth century, for instance, the landscape experienced an important transformation because of a generalised increment of forest plantations (*Eucalyptus* spp. and *Pinus* spp.). As a result, the cover percentage in Galicia of forest plantations rose to 23% in recent times, whereas less than 10% of the area is covered by woodland deciduous forests and most of them have been managed for a long time (i.e., timber harvest). The remainder of the land in the area mainly is used as pastures and crops (40%) and scrublands (27%). The dynamism of this landscape is considerable. Between 2006 and 2013, a mean of 26,500 ha (range *ca*. 6,400–96,000 ha) burned annually in Galicia because of forest fires (Regional Government of Galicia, 2014), which is evidence of the dynamism that wolves have to cope with in this area.

Studying wolf resting behaviour

We investigated the selection of resting sites by wolves in this human-dominated landscape by studying the spatial behaviour of 16 wolves equipped with GPS-GSM collars (Followit, Sweden). Between 2006 and 2011, wolves were captured with Belisle® leg-hold snares (Edouard Belisle, Saint Veronique, PQ, Canada) and chemically immobilised by intramuscular injection of medetomidine (Dormitor®, Merial, Lyon, France). Immobilisation was reversed by the intramuscular injection of atipamezole (Revertor®, Merial, Lyon, France). Sex and age were determined *in situ*, and age was estimated by dental pattern and tooth wear (Gipson *et al*., 2000) and wolves were classified into two categories, juvenile/sub-adults (< 2 yr) and adults (> 2 yr).

All wolves were evaluated as clinically healthy at the moment of capture, and they only presented minor lesions associated with trapping. Snares were monitored twice every day, in the early morning and late afternoon. Wolves included in this study were captured under permits 19/2006, 71/2009 and 86/2011 from the Regional Government of Galicia (Spain). All fieldwork procedures were adhered to the animal welfare regulations. GPS collars were scheduled to take a position every hour during the diurnal period (from 8:00 to 20:00 GTM), and every two hours during night-time. Four days a month, locations were taken every 20 minutes. Thus, we used a dataset of 57,837 total locations (mean number of locations per wolf=3,615, range 755-10,181).

Although wolves can rest during short time periods even a night-time, in this study, we focused on long-term resting sites, assuming that when wolves rest for long periods, they will maximise concealment. We therefore studied diurnal resting sites. We identified wolf resting sites by identifying clusters of locations. Wolf locations were plotted over high-resolution orthoimages in ArcGIS (ESRI, California, USA). Then, we studied the spatial distribution of consecutive locations to identify potential resting sites. The criteria used to define a resting site were successive locations during at least a 6 h period with a maximum distance between hourly locations of less than 30 m to account for GPS location errors (Fig. 6.1; Dussault *et al*., 2001). As a resting site will be defined by multiple locations, we calculated the centroid to characterise each resting site. Next, we randomly selected around 30 resting sites per wolf (mean=34). Moreover, within each wolf territory, calculated as the minimum convex polygon considering 100% of locations, we generated around 35 random points (mean=36) to contrast with observed resting sites. As a result, a total of 1,117 points were considered in this study, 546 resting sites and 571 random points.

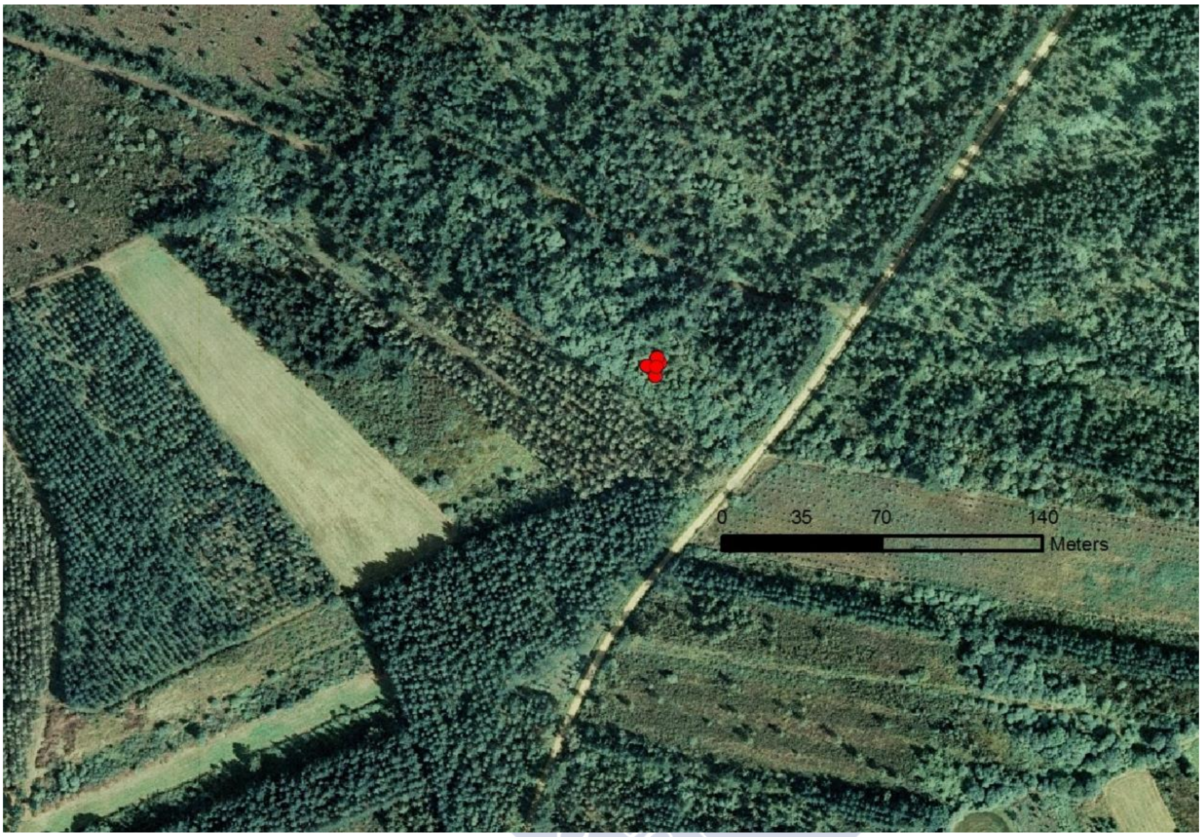

Figure 6.1. Example of a wolf resting site in the study area, NW Spain, in a forest plantation (*Eucalyptus* spp.), defined using the criteria of successive locations during at least a 6 h period with a maximum distance between hourly locations of less than 30 m.

Characterising resting sites and random points

Once we selected resting sites and generated the random points, we investigated the 1,117 points in the field in order to characterise each point in relation to different topographic, vegetation (cover) and human attributes (Table 6.1). First, we compiled two variables associated with low human densities and activities, altitude and slope (Glenz *et al*., 2001; Llaneza *et al*., 2012). For each point, we calculated the altitude (m) of the 25x25 m cell of each resting site and random point location from the Spanish Digital Elevation Model (Ministerio de Fomento, 1999) as well as the slope using ArcGIS (ESRI, California, USA).

Second, by using high-resolution orthoimages, we measured the distance from each resting site and random point to four manmade structures related to potentially human-wolf interactions. We focused on the distance to: i) the nearest settlement with more than 5 buildings, ii) the nearest paved road, iii) the nearest unpaved road wider than 4 m (large unpaved roads) and iv) the nearest small unpaved road. We considered that the predictability of human activity was correlated with ease of driving with a car, being different across linear infrastructures as follows: paved roads > large unpaved roads > small unpaved roads.

Finally, we measured a set of variables related to cover and refuge provided by vegetation, which have been shown to be determinant factors in locating resting sites in large carnivores (Podgorski *et al*., 2008; Ordiz *et al*., 2011; Cristescu *et al*., 2013), allowing wolves to go unnoticed by humans and decreasing exposure risk. First, for descriptive purposes, we recorded whether a resting site was located in forest, scrubland or cropland, and the dominant species in each case. Second, we delineated the habitat patch where each point was located using high-resolution orthoimages in ArcGIS. Next, we calculated the size of the patch and the distance from the location of the point to the nearest edge patch.

We secondly measured, *in situ*, the concealment offered by each site by focusing on the cover of different functional vegetation structures minimizing exposure risk for wolves. To do this, considering the location of each site as a central point, we generated four other points, 20 m separated from the central point, in the cardinal directions, and we generated a sampling area of 5 m radius for each point. Thus, we estimated the cover on a 50 x 50 m area with five points of measurement (Fig. 6.2). Despite the fact that wolves are adaptable to a wide range of vegetation types (even areas without plant cover; Boitani, 1982; Jedrzejewski *et al*., 2008; Mech and Boitani, 2003; Ahmadi *et al*., 2014), we counted as refuge only those vegetation types that could effectively conceal wolves (vegetation types >50 cm high): scrublands, woodlands and forest plantations. Functionally, we assumed that these vegetation types provided similar conditions of refuge for wolves (Llaneza *et al*., 2012), and therefore, we measured the proportion of these three vegetation types *in situ* being pooled together in a single variable denominated '*refuge*'. This measure was considered as horizontal cover. Moreover, to account for the effect of vertical cover on resting site selection, we also measured the proportion of canopy cover in the five sampling points. This measure was considered as vertical cover. We estimated the refuge and canopy cover as the average values obtained in the five sampling points for each site (Table 6.1).

Table 6.1. The selected variables to study resting site selection by wolves in human-dominated landscapes of NW Iberia.

GROUP	VARIABLE	DEFINITION
Topographic features	Altitude	Altitude in the 25 x 25 m cell where the central point of the resting or random site was located (see Fig. S2).
	Slope	Slope in the 25 x 25 m cell where the central point of the resting or random site was located (see Fig. S2).
Vegetation features	Patch size	Size (ha) of the vegetation patch where the central point of the resting or random site was placed.
	Distance to the edge patch	Euclidean distance (m) from the central point of the resting or random site to the edge patch.
	Canopy cover (vertical cover)	Proportion of canopy cover in a radius of 5 m (averaged value from the 5 points, see Fig. S2).
	Refuge (horizontal cover)	Proportion of forest and dense shrub >50 cm in a radius of 5 m (averaged value from the 5 points, see Fig. S2).
Human pressure	Distance to small unpaved roads	Euclidean distance (m) from the border to the central point of the resting or random site.
	Distance to large unpaved roads (> 4 m wide)	Euclidean distance (m) from the border to the central point of the resting or random site.
	Distance to paved roads	Euclidean distance (m) from the border to the central point of the resting or random site.
	Distance to settlements	Euclidean distance (m) from the central point of the resting or random site to the nearest settlement with >5 buildings.

Data analyses

We used general linear mixed models (GLMMs) with binomial error distribution and logit link using the '*lme4*' package (Bates *et al*., 2014) in R (R Core Team 2014) to test for the influence of the ten selected predictors (Table 1) on wolf resting site selection in human-dominated landscapes of Galicia. We created a set of candidate models (including the null model) considering all possible combinations among these predictors and compared them using the Akaike Information Criterion and the AIC weights (w_i) calculated using the '*MuMIn*' package (Barton, 2013) in R, to determine the relative strength of support for each candidate model. Models within ΔAIC<2 from the highest-ranked model were combined to calculated model-averaged parameter estimates in order to reduce model selection bias effects on regression coefficient estimates (Burnham and Anderson, 2010). In addition, we used AIC weights to generate Relative Variable Importance weights (RVI) for each predictor (Burnham and Anderson, 2010). We standardised the predictors before running analyses. We also estimated the marginal and the conditional R^2 of the top-ranking model following Nakagawa and Schielzeth (2013). Marginal R^2 represented the variance explained by fixed predictors, whereas Conditional R^2 is interpreted as the variance explained by both fixed predictors and the random factor, the individual in this case. Thus, we were able to assess the variability in our dataset associated with the individual-level effect.

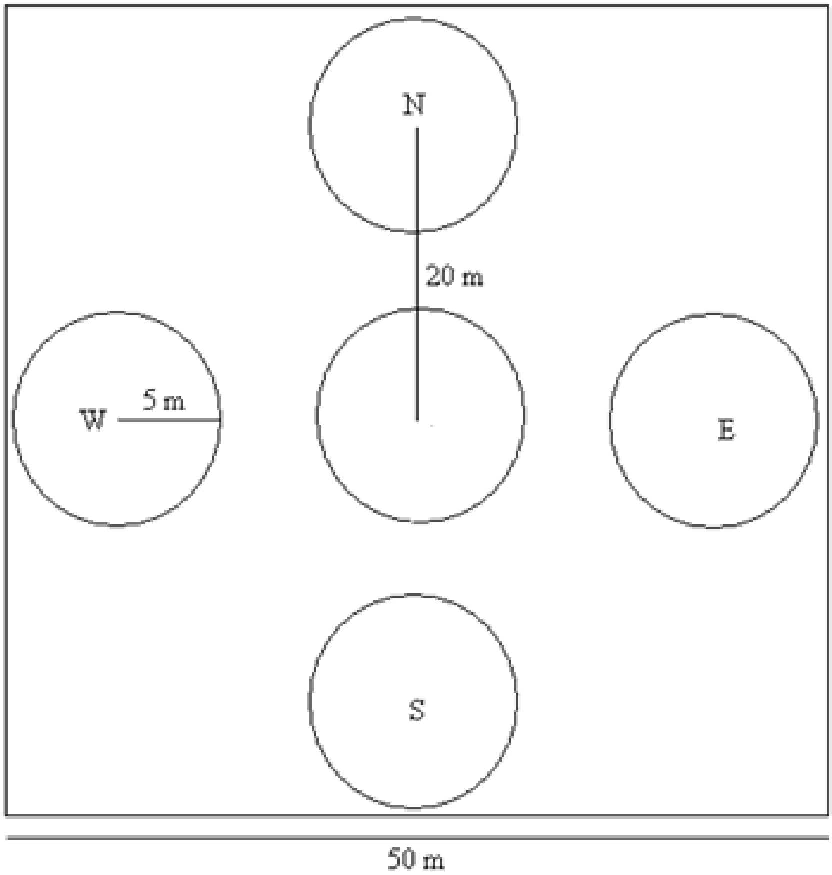

Figure 6.2. Scheme showing the field procedure used to characterise resting sites and random points in human-dominated landscapes of NW Iberia. The central circle corresponds to the centroid of all locations used to define a resting site, or with the generated random points. Considering the location of each resting and random site as the central point, we generated four other points, 20 m separated from the central (centroid) point in the cardinal directions, and we generated a sampling area of 5 m radius for each point. Vegetation features for each den and random site resulted from averaging the five sampling plots within the 50 x 50 m area.

Next, considering those variables included in the best candidate model, we run a hierarchical partitioning analysis to identify the independent and conjoint contribution of each predictor with all other predictors (Chevan and Sutherland, 1991; Mac Nally, 2000). Hierarchical partitioning was conducted using logistic regression and log-likelihood as the goodness-of-fit measure. This statistical procedure allowed us to identify those predictors with an important independent correlation to the selection of resting sites by wolves (Mac Nally and Horrocks, 2002). Statistical significances of the independent contributions of selected predictors were tested by a randomization procedure (100 randomizations), which yielded Z-scores for the generated distribution of randomised independent contributions, and an indication of statistical significance ($P < 0.05$) based on an upper 0.95 confidence limit ($Z \geq 1.65$; Mac Nally and Horrocks, 2002). Hierarchical partitioning analyses were carried out using the *"hier.part"* package (Walsh and Mac Nally, 2008).

Finally, to evaluate the influence of individual attributes on the selection of resting sites, we tested the influence of sex and age (two levels), and their interaction, on those predictors showing the highest independent contribution obtained in the hierarchical partitioning analyses. In this case, we treated such predictors as the explanatory variables in this second block of analyses. We used GLMMs in the '*glmmADMB*' package (Skaug *et al*., 2014) in R with a Beta distribution and logit link function to model proportions, and with a gamma distribution and the inverse link function to model distances. Individual identity was included as random effect in all models to account for repeated measures.

6.3. RESULTS

Out of the 546 resting sites we visited *in situ*, half of them (50.8 %) were found in forested areas (41.7% and 31.4% were in forest plantations of *Pinus* spp. and *Eucalyptus* spp., respectively), 43.4% were found in scrublands (48.2%, 17.6% and 15.4% were in gorses [*Ulex* spp.], ferns and heaths [*Erica* spp.], respectively), and only 5.8% were found in croplands (64.5% and 32.3% were in grasslands and corn fields). Wolves located their resting sites far away from paved and large unpaved roads, and settlements, compared to random points, as well as in areas with high availability of horizontal (refuge) and vertical (canopy) cover (Table 6.2;). All variables, excepting altitude and slope, significantly differed between resting sites and random points (Table 6.2).

Six candidate models showed $\Delta AIC<2$ (Table 6.3), and the best model included the distances to roads, large unpaved roads and settlements, as well as refuge, canopy cover and slope (Table 6.3). These six predictors were the most important fine-scale predictors determining resting site selection by wolves based on their relative variable importance weight (RVI; Table 6.4). The other two variables included in the selected set of candidate models were altitude and distance to small unpaved roads (Table 6.3), although their RVI was small (Table 6.4). Averaging the coefficient estimates of the six selected candidate models showed that wolves significantly avoided choosing resting sites close to human settlements and paved or large unpaved roads, whereas they significantly selected areas with high availability of refuge and canopy cover (Table 6.4). Considering the best candidate model, marginal R^2 was 0.351 and conditional R^2 was 0.352, indicating that the explained variance attributed to individual variability was negligible.

Table 6.2. Descriptive statistics (mean, standard deviation and 95% confidence intervals) for the ten selected variables to study resting site selection by wolves in human-dominated landscapes of NW Iberia for both resting and random points. Significance levels from Mann-Whitney U-tests comparing resting sites *vs*. random points are shown (* $P < 0.001$).

	RESTING SITES				RANDOM POINTS				
	Mean	SD	95% CI		Mean	SD	95% CI		P
Distance to small unpaved roads	126.3	117.9	116.4	136.2	92.7	96.7	84.7	100.6	*
Distance to large unpaved roads	273.2	250.5	252.2	294.3	173.3	176.6	158.8	187.9	*
Distance to roads	619.2	413.9	584.4	653.9	373.1	377.7	342.1	404.2	*
Distance to settlements	859.1	462.6	820.2	897.9	621.1	550.0	575.8	666.3	*
Distance to the edge patch	208.8	330.9	181.0	236.6	183.0	325.5	155.9	210.1	*
Patch size	177.6	237.8	157.6	197.5	191.2	489.8	150.4	232.1	*
Slope	10.1	43.9	6.5	13.8	6.7	9.3	5.9	7.5	n.s.
Altitude	467.8	188.3	451.9	483.6	461.5	195.6	445.4	477.6	n.s.
Canopy cover	16.8	19.4	15.2	18.5	12.4	18.4	10.9	13.9	*
Refuge	70.7	30.1	68.2	73.2	42.0	37.2	38.9	45.1	*

Hierarchical partitioning analysis run on the best candidate model (Table 6.3) revealed that the predictor showing the highest proportion of independent contribution to explaining the selection of resting sites by wolves in this human-dominated landscape was refuge (50.8%), followed by distance to roads (19.5%), distance to large unpaved roads (12.4%) and distance to settlements (11%). The remaining predictors showed independent contributions <5% (canopy cover=4.8%; slope=1.5%). The importance of refuge was remarkably high in this human-dominated landscape, the independent contribution of this predictor alone being more important than the contribution of all the variables related to human pressure (distances) pooled (50.7% vs. 42.6%, respectively). Indeed, the joint contribution of refuge was small (5%) compared to human-related predictors (between 9% and 19% of joint contribution). The independent effects of all included predictors were statistically significant (Table 6.S1).

Considering those predictors with important independent contribution (refuge, distance to roads, distance to large unpaved roads and distance to settlements), we only detected two significant differences in resting site selection patterns associated with individual attributes (Table 6.S2). We found that males tended to rest far away from large unpaved roads compared to females (mean distance to large unpaved roads of 263 m vs. 173 m for males and females, respectively, Table 6.S2). Accordingly, selection of refuge was stronger in females compared to males (mean refuge cover of 0.62 vs. 0.52 for females and males, respectively). We did not find any effect of the age on resting site selection by wolves (Table 6.S2).

Table 6.3. Selected candidate Generalized Linear Mixed Models explaining wolf resting site selection in NW Spain. Models are ranked based on AIC, difference in AIC relative to the highest-ranked model (ΔAIC) and AIC-weights (w_i). By simplicity, we show only those models with ΔAIC < 2.

COMPETING MODELS	df	AIC	ΔAIC	w_i
2/5/6/7/8/10	**8**	**1228.45**	**0**	**0.28**
1/2/5/6/7/8/10	9	1228.93	0.48	0.22
2/4/5/6/7/8/10	9	1229.52	1.07	0.16
1/2/4/5/6/7/8/10	10	1230.00	1.54	0.13
2/3/5/6/7/8/10	9	1230.33	1.87	0.11
2/5/6/7/8/9/10	9	1230.44	1.98	0.10

Term codes: Altitude (1), Canopy cover (2), Distance to the edge patch (3), Distance to small unpaved roads (4), Distance to large unpaved roads (5), Distance to roads (6), Distance to settlements (7), Refuge (8), Patch size (9), Slope (10).

Table 6.4. Model averaged coefficient estimates (Estimate), adjusted standard errors, level of significance and relative variable importance weight (RIV) for the predictors included in the selected candidate models explaining resting site selection by wolves in human-dominated landscapes of NW Iberia (models with ΔAIC < 2).

VARIABLE	ESTIMATE	ADJUSTED SE	P	RIV
(Intercept)	-0.03	0.07	<0.0001	
Altitude	-0.19	0.15	n.s.	0.35
Canopy cover	0.48	0.14	0.002	1
Distance to small unpaved roads	0.17	0.17	n.s.	0.29
Distance to large unpaved roads	0.79	0.18	<0.0001	1
Distance to roads	1.05	0.21	<0.0001	1
Distance to settlements	0.43	0.21	0.003	1
Refuge	1.73	0.15	<0.0001	1
Slope	0.42	0.30	n.s.	1
Distance to the edge patch	-0.03	0.16	n.s.	0.11
Patch size	0.02	0.15	n.s.	0.11

6.4. DISCUSSION

In risky environments such as the study area (wolves remarkably use anthropogenic food sources and suffer from poaching, e.g., 20% of poaching in known wolf mortality cases between 1999 and 2003, Llaneza *et al*., 2012; lethal control actions to remove some individuals from areas with recurrent wolf attacks on livestock are occasional; López-Bao *et al.*, 2013), the persistence of wolves is probably favoured by multiple behavioural adaptions to cope with risk and positively affects the chances of survival (Theuerkauf *et al*., 2003; Chavez and Gese 2005; Kusak *et al*., 2005; Capitani *et al*., 2006; Llaneza *et al*., 2012; Ahmadi *et al*., 2014). Among these adaptations, as we predicted, our results supports the idea that wolves adaptively select resting sites to minimise exposure risk.

Humans influenced the selection of resting sites by wolves (Theuerkauf *et al*,. 2013). We found that resting sites were placed in dense cover areas (both in terms of horizontal and vertical cover) as well as further from manmade structures compared to random points. Interestingly, because human activities were spread over the entire study area, as we expected, the strength of the selection for refuge was stronger compared to single or pooled manmade structures. The lack of significant effects of patch size on resting site selection suggest that the selection of resting sites is a fine-scale process (Ordiz *et al*., 2011), with their selection being determined more by the quality of the refuge than by its quantity (i.e., extension). Indeed, wolves located their resting sites in places with abundant refuge at fine spatial scale, and we found resting sites in pine and eucalyptus forest plantations, semi-natural woodlands or scrublands (dense and prickly gorses, for instance, provide good concealment to wolves in this area; Fig. 6.3). The strength of refuge selection in human-dominated landscapes may be adaptive to compensate for uselessness defences during resting (Cristescu *et al*., 2013).

Figure 6.3. Gorses (*Ulex* spp.) in Galicia, NW Spain, are located in slopes of the hills, and are a suitable refuge for wolves in this area.

The observed strong selection for refuge allowed wolves to rest relatively close to manmade structures (Table 6.2), sometimes at distances of less than 200 m from roads or human settlements (e.g., in 15% and 7% of cases, wolves rested less than 200 m from roads and human settlements, respectively; n=546; Fig. 6.4), and occasionally even at less than 50 m from these manmade structures (2 and 0.5%, respectively; n=546; Fig. 6.4). However, whereas wolves were sensitive to roads with predictable human activity (roads and large unpaved roads), they did not avoid small unpaved roads. On the one hand, this result supports the idea that wolves are capable of perceiving different spatiotemporal exposure risks associated with different manmade structures (Ahmadi *et al*., 2014; Benson *et al*., 2015). On the other hand, as small unpaved roads are expected to have less human activity, this linear element may also facilitate wolf movement and escape in a risky situation (Latham *et al*., 2011; Zimmerman *et al*., 2014).

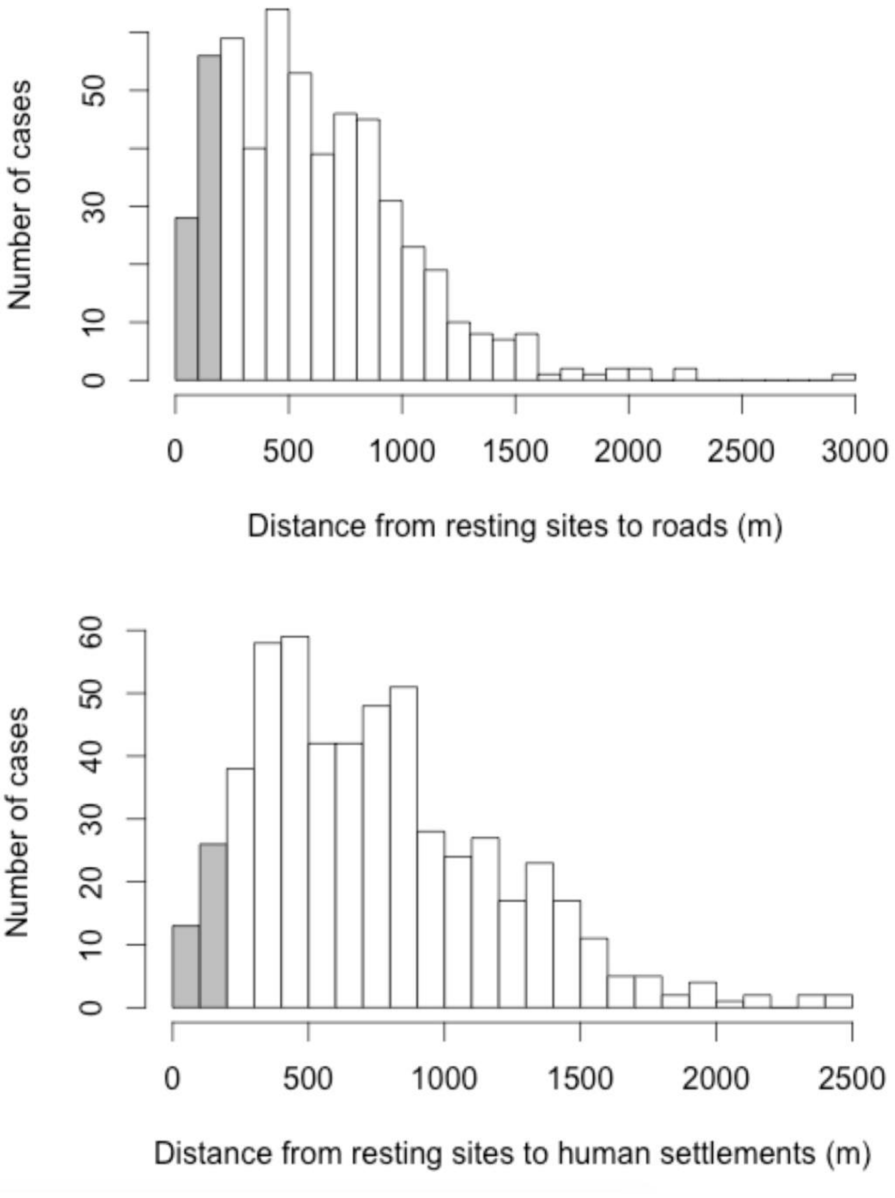

Figure 6.4. Distribution frequencies of the distances (intervals of 100 m) between wolf resting sites and manmade structures: roads and human settlements. Bars showing distances less than 200 m are highlighted in grey.

Contrary to the patterns observed in bears (black – *Ursus americanus* - and brown bears), where these species locate their beds close to habitat patch edges (Lyons *et al*., 2003; Moe *et al*., 2007; Ordiz *et al*., 2011), we did not find evidence of the influence of this factor on wolf resting site selection. Moreover, slope and elevation had poor predictive power for explaining resting site selection. This could be explained by the fact that the most important factor governing resting site selection, dense vegetation cover areas (refuge, horizontal cover), are not necessarily distributed at high altitudes or steep slopes in our study area (Spearman rank correlation analyses between refuge and altitude or slope, all *P*>0.622). Finally, we only found two effects of individual attributes on the selection of resting sites. On the one hand, our results suggest that males are more sensitive to roads than females (we compared data from 7 females *vs.* 9 males). On the other hand, female wolves selected resting sites with more refuge than males, which has also been observed in ungulates (Mysterud and Østbye, 1999).

Quantitative information on the mechanisms for wildlife to coexist with humans at fine spatial scales is scarce (Carter *et al*., 2012). Our results show that when wolves and humans share the landscape and overlap their activities at fine spatial scales, selection for refuge for concealment during the day may be an important mechanism favouring the persistence of the species in human-dominated landscapes (similar to the microhabitat use by subordinate carnivores when coexisting with apex predators; e.g., Viota *et al*., 2012). How wolves adapt this behaviour at different periods of human activity (e.g., hunting vs. non-hunting season) deserves further investigation (e.g., Ordiz *et al*., 2011).

Effective conservation of large carnivores in human-dominated landscapes depends on their conservation outside reserves (Chapron *et al*., 2014). In this regard, understanding the selection patterns of resting sites by wolves in such landscapes may add valuable information to delineate effective conservation measures for the species (Anthony and Blumstein, 2000), favoring human-wolf coexistence and mitigating the risk posed by humans (Cristescu *et al*., 2013). In this regard, our results provide basic information on the minimum requirements of wolf resting sites, which can easily be implemented in landscape planning. The selection for dense cover areas by wolves to rest may also favour human-wolf coexistence because this behavioural adaptation decreases the probability that people will have a direct experience with wolves (e.g., to spot a wolf at daylight resting). Because such types of experiences can contribute to changing attitudes of people toward wolves (Williams *et al*., 2002; Karlsson and Sjöström, 2007), maintaining high-quality refuge areas becomes an important element for both favouring the persistence of the species and for human-wolf coexistence in human-dominated landscapes.

6.5. REFERENCES

Ahmadi, M,, López-Bao, JV. & Kaboli, M. (2014). Spatial heterogeneity in human activities favors persistence of wolves in agroecosystems. *PLoS ONE*, 9:e108080.

Agarwala, M., & Khumar, S. (2009) Wolves in agricultural landscapes in Western India. *Tropical Resources: Bulletin of the Yale Tropical Resources Institute*, 28:48-53.

Álvares, F., Domingues, J., Sierra, P. &, Primavera, P. (2011). Cultural dimension of wolves in the Iberian Peninsula: implications of ethnozoology in conservation biology. *Innovation: The European Journal of Social Science Research*, 24:313-331.

Anthony, L. & Blumstein, D.T. (2000). Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e. *Biological Conservation*, 95:303-315.

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J. & Karanth, U. (2013). Big cats in our backyards: Persistence of large carnivores in a human-dominated landscape in India. *PLoS ONE*, 8:e57872.

Barton, K. (2013). *MuMIn: multi-model inference*. R package version 1.9. 5.

Bates, D., Maechler, M. & Bolker, B. (2014). *lme4: Linear mixed-effects models using S4 classes*. R package version 0.999999-0. http://CRAN.R-project. org/package=lme4

Benson, J.F., Mills, K.J. & Patterson, B.R. (2015). Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. *Biological Conservation*, 182:223-232.

Boitani, L. (1982). *Wolf management in intensively used areas of Italy*. In: Harrington, F.H., Paquet, P.C. (eds). *Wolves of the world, perspectives of behaviour, ecology and conservation*. Pp 158-172. Noyes Publishing, Park Ridge, New Jersey.

Boitani, L. (1995). *Ecological and cultural diversities in the evolution of wolf–human relationships*. In: Carbyn, L.N., Fritts, S.H. & Seip, D.R. (eds) *Ecology and conservation of wolves in a changing world*. Pp. 3–12. Edmonton, Alberta: Canadian Circumpolar Institute.

Bouyer, Y., Gervasi, V., Poncin, P., Beudels-Jamar, R.C., Odden, J. & Linnell, J.D.C. (2015). Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Anim Conserv*, Doi:10.1111/acv.12168.

Burnham, KP. & Anderson, D.R. (2010). *Model selection and multimodel inference. A practical information-theoretic approach*. Second edition. Springer, New York, New York, USA.

Capitani, C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., Scandura, M., Viviani, A. & Apollonio, M. (2006). Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. *Acta Theriol.* 51:395–404.

Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B. & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *PNAS*, 109:15360–15365.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., ... & Nowak, S. (2014). Recovery of large carnivores in Europe´s modern human-dominated landscapes. *Science*, 346:1517-1519.

Chevan, A. & Sutherland, M. (1991). Hierarchical partitioning. *Ameri. Stat*. 45:90-96.

Chavez, A.S. & Gese E.M. (2005). Landscape use and movements of wolves in relation to livestock in a wildland–agriculture matrix. *J. Wildlife Manage.* 70:1079-1086.

Ciucci, P., Boitani, L., Francisc, F. & Andreoli, G. (1997). Home range, activity and movements of a wolf pack in central Italy. *J. Zool.* 243:803-819.

Creel, S. & Rotella, J.J. (2010). Meta-analysis of relationships between human offtake, total mortality and population dynamics of Gray wolves (*Canis lupus*). *PLoS ONE*, 5:e12918.

Cristescu, B., Stenhouse, G.B. & Boyce, M.S. (2013). Perception of human-derived risk influences choice at top of the food chain. *PLoS ONE*, 8:e82738.

Cuesta, L., Bárcena, F., Palacios, F. & Reig, S. (1991). The trophic ecology of the Iberian wolf (*Canis lupus signatus*, Cabrera, 1907). A new analysis of stomach's data. *Mammalia*, 55:239-254.

Dussault, C., Courtois, R., Ouellet, J.P. & Huot, J. (2001). Influence of satellite geometry and differential correction on GPS location accuracy. *Wildlife Soc. Bull.* 29:171-179.

Fernández, J.M. & De Azúa, N.R. (2010). Historical dynamics of a declining wolf population: persecution vs. prey reduction. *Eur. J. Wildlife Res.* 56:169-179.

Frank, L.G. & Woodroffe, R. (2001). *Behaviour of carnivores in exploited and controlled populations*. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W. & Wayne, R.K. (eds). *Carnivore Conservation*. Cambridge University Press, pp. 419-442.

Glenz, C., Massolo, D., Kuonen, D. & Schlaepfer, R. (2001). A wolf habitat suitability prediction study in Valais (Switzerland). *Landscape Urban Plan,* 55:55-65.

Gipson, P.S., Ballard, W.B., Nowak, R.M. & Mech, L.D. (2000). Accuracy and precision of estimating age of gray wolves by tooth wear. *J. Wildlife Manage*. 64:752–758.

Goodrich, J.M., Kerley, L.L., Smirnov, E.N., Miquelle, D.G., McDonald, L., Quigley, H.B., Hornocker, M.G. & McDonald, T. (2008). Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *J. Zool*. 276:323-329.

Habib, B. & Kumar, S. (2007). Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. *J. Zool.* 272:259–265.

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattison, J., Odden, J., Persson, J., Rauset, G.R., Schmidt, K. & Linnell, J.D.C. (2014). Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS ONE*, 9:e114143.

I.N.E. (2014). Instituto Nacional de Estadística. Censo de población y vivienda.

Iliopoulos, Y., Youlatos, D. & Sgardelis, S. (2014). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *Eur. J. Wildlife Res*. 60: 23-34.

Jędrzejewski, W., Jędrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S. & Mysłajek R.W. (2008). Habitat suitability model for Polish wolves based on long-term national census. *Anim Conserv*. 11:377-390.

Karlsson, J. &, Sjöström, M. (2007). Human attitudes towards wolves, a matter of distance. *Biological Conservation*, 137:610-616.

Kusak, J., Skrbinšek, A.M. & Huber, D. (2005). Home ranges, movements, and activity of wolves (Canis lupus) in the Dalmatian part of Dinarids, Croatia. *Eur. J. Wildlife Res*. 51:254-262.

Latham, A.D.M., Latham, M.C., Boyce, M.S. & Boutin, S. (2011). Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications*, 21:2854-2865.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012). Shoot, shovel and shut up: Cryptic poaching slows restoration of a large carnivore in Europe. *Proc. R. Soc. Lond*. 279:910-915.

Lima, S.L., Rattenborg, N.C., Lesku, J.A. & Amlaner, C.J. (2005). Sleeping under the risk of predation. *Anim. Behav*. 70:723–736.

Linnell, J.D.C., Andersen, R., Andersone, Z., Balciauskas, L., Blanco, J.C., Boitani, L., Brainerd, S., Breitenmoser, U., Kojola, I., Liberg, O., Loe, J., Okarma, H., Pedersen, H.C., Promberger, C., Sand, H., Solberg, E.J., Valdman, H. & Wabakken, P. (2002). *The fear of wolves: a review of wolf attacks on people*. NINA Oppdragsmelding 731:65 p.

Llaneza, L., Palacios, V., Uzal, A., Ordiz, A., Sazatornil, V., Sierra, P. & Álvares, F. (2005). Distribución y aspectos poblacionales del lobo ibérico (*Canis lupus signatus*) en las provincias de Pontevedra y A Coruña. *Galemys*, 17:61-80.

Llaneza, L., López-Bao, J.V. & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distribution*, 18:459–469.

Llaneza, L., García, E.J., Palacios, V. & López-Bao J.V. (2014). *Wolf monitoring in Galicia, NW Spain, 2013-2014*. Report to TRAGSATEC and the Spanish Ministry of Agriculture, Food, and Environment. 56 p.

López-Bao J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013). Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters*, 6:448-455.

López-Bao, J.V., Blanco, J.C., Rodríguez, A., Godinho, R., Sazatornil, V., Álvares, F., García, E.J., Llaneza, L., Rico, M., Cortés, Y., Palacios, V. & Chapron, G. (2015). Toothless wildlife protection laws. *Biodiversity & Conservation*, 24:2105-2108.

Lyons, A.L., Gaines, W.L. & Servheen, C. (2003). Black bear resource selection in the northeast Cascades, Washington. *Biological Conservation*, 113:55-62.

Mac Nally, R. (2000). Regression and model building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘‘predictive” and ‘‘explanatory” models. *Biodiversity & Conservation*, 9:655-671.

Mac Nally, R. & Horrocks, G. (2002). Relative influences of patch, landscape and historical factors on birds in an Australian fragmented landscape. *J. Biogeogr*. 29:395-410.

Mech, L.D., Fritts, S.H., Radde, G.L. & Paul, W.J. (1988). Wolf distribution and road density in Minnesota. *Wild. Soc. Bull*. 16:85-87.

Mech, L.D. & Boitani, L. (2003). *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Ministerio de Fomento (1999). *Modelo Digital del Terreno 1:25000*. Dirección General del Instituto Geografico Nacional, Centro Nacional de Información Geográfica, Madrid.

Moe, T.F., Kindberg, J., Jansson, I. & Swenson, J.E. (2007). Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Can. J. Zool*. 85:518-525.

Mysterud, A. & Østbye, E. (1999). Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wild. Soc. Bull*. 27:385-394.

Nakagawa, S. &, Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol*. 4:133-142.

Ordiz, A., Støen, O.G., Delibes, M. & Swenson, J.E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166:59-67.

Podgórski, T., Schmidt, K., Kowalczyk, R. & Gulczyńska, A. (2008). Microhabitat selection by Eurasian lynx and its implications for species conservation. *Acta Theriol*. 53:97-110.

R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rico, M. & Torrente, J.P. (2000). Caza y rarificación del lobo en España: investigación histórica y conclusiones biológicas. *Galemys*, 12:163-179.

Skaug, H., Fournier, D., Magnusson, A. & Nielsen, A. (2014). *Generalized linear mixed models using AD model builder*. (R Package v0.8.0).

Swenson, J.E. (1999). Does hunting affect the behavior of brown bears in Eurasia? *Ursus*, 11:157-162.

Theuerkauf, J., Rouys, S. & Jedrzejewski, W. (2003). Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Can. J. Zool*. 81:163–167.

Theuerkauf, J. (2009). What drives wolves: fear or hunger? Humans, diet, climate and wolf activity patterns. *Ethology*, 115:649-657.

Valeix, M., Hemson, G., Loveridge, A.J., Mills, G. & Macdonald, D.W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *J. Appl. Ecol*. 49:73-81.

Vilà ,C., Urios, V. & Castroviejo, J. (1995). *Observations on the daily activity patterns in the Iberian wolf*. In: Carbyn LN, Fritts SH, Seip DR (eds). *Ecology and conservation of wolves in a changing world*. pp. 335-340., Occasional Publication No. 35, Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada.

Viota, M., Rodríguez, A., López-Bao, J.V. & Palomares, F. (2012). Shift in microhabitat use as a mechanism allowing the coexistence of victim and killer carnivore predators. *Open Journal of Ecology*, 2:21612.

Walsh, C. & Mac Nally, R. (2008) *hier.part: Hierarchical partitioning*. R package version 1.0.3.

Williams, C.K., Ericsson, G. & Heberlein, T.A. (2002). A quantitative summary of attitudes toward wolves and their reintroduction (1972-2000). *Wild. Soc. Bull*. 30:575-584.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280:2126-2128.

Zedrosser, A., Steyaert, S.M., Gossow, H. & Swenson, J.E. (2011). Brown bear conservation and the ghost of persecution past. *Biological Conservation*, 144:2163-2170.

Zimmermann, B. Nelson, L., Wabakken, P., Sand, H. & Liberg, O. (2014). Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behav. Ecol*. 25:1353-1364.


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Supporting information

Table 6.S1. Results of the randomization tests for the independent contributions of separate predictor variables included in the best candidate model explaining wolf resting site selection in human-dominated landscapes of NW Spain (see Table 3) in hierarchical partitioning analysis.

Variable	Z - score	P
Distance to large unpaved roads	31.47	< 0.05
Distance to roads	37.75	< 0.05
Distance to settlements	23.5	< 0.05
Slope	2.09	< 0.05
Canopy cover	9.3	< 0.05
Refuge	131.13	< 0.05

Table 6.S2. Generalized Linear Mixed Models evaluating the effect of individual attributes on the selection of resting sites. We tested the influence of sex and age (two levels), and their interaction, on those predictors showing the highest independent contribution obtained in the hierarchical partitioning analyses: Distance to large unpaved roads, distance to roads, distance to settlements and refuge (see text for details). The terms "*Males*" and "*Juveniles*" are included in the intercept.

Variable	Predictors	Estimate	S.E.	P
Distance to large unpaved roads				
	Intercept	55.39	0.13	
	Females	-0.60	0.19	<0.001
	Adults	-0.09	0.22	0.667
	Females x Adults	0.55	0.34	0.104
Distance to roads				
	Intercept	6.22	0.10	
	Females	-0.02	0.15	0.824
	Adults	-0.20	0.17	0.236
	Females x Adults	0.28	0.26	0.285
Distance to settlements				
	Intercept	6.41	0.12	
	Females	0.14	0.17	0.445
	Adults	-0.21	0.20	0.295
	Females x Adults	0.15	0.11	0.137
Refuge				
	Intercept	0.09	0.14	
	Adults	0.48	0.21	0.017
	Adults	-0.12	0.25	0.625
	Females x Adults	-0.49	0.38	0.203


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7.

DETERMINANTS OF WOLF HOME RANGE SIZE VARIATION IN HUMAN-DOMINATED LANDSCAPES


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7. DETERMINANTS OF WOLF HOME RANGE SIZE VARIATION IN HUMAN-DOMINATED LANDSCAPES

ABSTRACT

Despite humans influencing the factors that shape the spatial ecology of large carnivores, such as food availability or intraspecific competition, the anthropogenic influence on home range size variation in these species still remains an issue. For example, in human-dominated landscapes, game hunting, livestock practices, and human-caused predator mortality are expected to impact the spatial ecology of large carnivores. Multiple factors have been correlated with the spatial behavior of large carnivores such as wolves *(Canis lupus)* in different systems, but rarer has such evaluation been when livestock comprised the most important fraction of the predator diet. This study aims to identify the determinants of home range size variation in wolves in human-dominated landscapes of NW Spain. We used spatial information from 29 wolves and observed similar spatial requirements in wolves regardless of gender and age classes. However, adult and sub-adult pack members showed on average an annual home range size four times smaller than non-pack members (122.1 km^2 SD=93.6 *vs.* 554.7 km^2 SD=413.3, respectively). Seasonaly differences were also observed in range sizes, being larger during the mating season compared to the breeding season. We found that the importance of livestock in the diet of wolves influenced home range and core area sizes. The proportion of livestock in the diet showed negative and significant influence on range sizes. Small range sizes in human-dominated landscapes modulated by the importance of livestock in the diet translate into the potential for higher wolf densities in these landscapes compared to natural areas.

KEYWORDS: *Canis lupus*, carnivore conservation, core areas, home range, human-dominated landscapes, spatial ecology .

7.1 INTRODUCTION

Intraspecific variation in home range size has attracted great attention among ecologists (Schoener and Schoener, 1982; Gompper and Gittleman, 1991; Gittleman & Harvey, 1992; Börger *et al*,. 2006; 2008; Saïd *et al*., 2009). For example, in mammalian carnivores, home range size variation has been linked to the action of multiple intrinsic and extrinsic factors such as differences in sex and age classes, body size, diet, social organization, landscape configuration, food availability, or conspecific density (McNab, 1963; Kelt and Van Vuren, 2001; Dahle and Swenson, 2003; Jetz *et al*., 2004; Benson *et al*,. 2006; Jedrzejewski *et al*., 2007; López-Bao *et al*., 2010; van Beest *et al*., 2011; Rich *et al*., 2012).

Food availability and intraspecific competition have been identified as important drivers affecting home range size variation in carnivores (Sandell, 1989; Okarma *et al*., 1998; McLoughlin and Ferguson, 2000; Mitchell and Powell, 2004; Loveridge *et al*., 2009). However, despite humans influencing both factors, the anthropogenic influence on home range size variation in these species is poorly understood (Vanak and Gommper, 2010; Rich *et al*., 2012). In human-dominated landscapes, factors affecting home range size variation may be strongly influenced by human activities such as the impact of game hunting, livestock practices, and garbage on food availability (Bino *et al*., 2010; Newsome *et al*. 2013, 2015) or human-caused predator mortality on conspecific density (Rich *et al*., 2012; Maletzke *et al*., 2014). Different management actions are thus expected to influence the spatial behaviour of large carnivores.

Wolves *(Canis lupus)* show a remarkable capability to persist in human-dominated landscapes compared to other large carnivore species (Habib and Kumar, 2007; Agarwala and Kumar, 2009; Llaneza *et al*., 2012; Iliopoulos *et al*., 2014; Ahmadi *et al*., 2014; Chapron *et al*., 2014). Their ability to significantly exploit anthropogenic food sources (Cuesta *et al*., 1991; Papageorgiou *et al*., 1994; Llaneza *et al*., 1996; Meriggi and Lovari, 1996; Vos, 2000; López-Bao *et al*., 2013) is expected to impact wolf ecology and behavior (diet, population dymanics, social behavior, movements, dispersal patterns and home range size; Mech and Boitani 2003; Llaneza *et al*., 2012; Rich *et al*., 2012; Ahmadi *et al*., 2014; Newsome *et al*., 2015).

The influence of different intrinsic and extrinsic factors on the spatial behavior of wolves has been mainly explored in areas with low human impact. Several studies have been carried out in natural (protected) areas or landscapes with few humanization levels showing how home range size is influenced by individual attributes and social factors (Fritts and Mech, 1981; Peterson *et al.*, 1984; Ballard *et al.*, 1987; Fuller, 1989; Okarma *et al.*, 1998; Jedrzejewski *et al.*, 2001; 2007) as well as landscape context-dependent factors such as food (prey biomass) availability or land cover (Fuller, 1989; 1995; Wydeven *et al.*, 1995; Okarma *et al.*, 1998; Fuller *et al.*, 2003; Jedrzejewski *et al.*, 2007; Kittle *et al.*, 2015) or landscape configuration (Findo and Chovancova, 2004). However, only a few studies have evaluated how these factors affect wolf home range sizes in human-dominated landscapes (Ciucci *et al.*, 1997; Kusak *et al.*, 2005; Rich *et al.*, 2012; Mattisson *et al.*, 2013). But rarer has been such evaluation when livestock comprised an important fraction of the diet of wolves. Given that food availability influence home range size (Jedrzejewski *et al.*, 2007; Rich *et al.*, 2012; Mattisson *et al.*, 2013) livestock availability and the proportion of livestock in the diet is expected to strongly shape home range size.

The present study aims to identify the key determinants of home range size variation in wolves in highly human-dominated landscapes. First, we explored basic variations in home range size in relation to gender, age, status and seasons. We predicted higher home range sizes for non-territorial compared to territorial wolves as well as the existence of seasonal home range variations influenced by the wolf annual cycle, with seasonal home ranges being smaller at the breeding season compared to the mating season (Jedrzejewski *et al.*, 2007). Second, focusing on territorial subadult/adult wolves, we explored the explanatory power of several non-mutually exclusive groups of factors that potentially could affect home range size. We evaluated the following hypothesis: i) we first tested the null hypothesis that anthropogenic influences buffer the effect of known drivers of wolf home range size in human-dominated landscapes. Alternatively, we assessed whether home range size was shaped by ii) landscape configuration; for example, a positive correlation was shown between wolf home range size and roughness (Rich *et al.*, 2012); iii) the amount of available refuge and its structural compostition (Riley *et al.*, 2003; Hinam and Clair, 2008); iv) human pressure (paved and unpaved roads, and human settlements). Although wolves exhibit a remarkable resilience to persist in human-dominated landscapes (Agarwala and Khumar, 2009; Llaneza *et al.*, 2012; Ahmadi *et al.*, 2014; Chapron *et al.*, 2014), the level of humanization within territories may increase home range size (Riley *et al.*, 2003; Mattison *et* *al*., 2013); v) anthropogenic food availability; vi) the importance of anthropogenic food sources in the diet. Since vulnerability, abundance and predictability of anthropogenic food sources differs from wild prey and can be remarkably high, we predicted small home range sizes in areas where wolves fed mainly on anthropogenic food sources; and vii) intraspecific competition (wolf density). We expected the home range size of wolves being negatively correlated with the density of packs (Rich *et al*., 2012). Moreover, we compared whether the same determinants of home range size emerged at different spatial scales of intensity of home range use.

7.2 METHODS

Study area

This study was carried out in Galicia, NW Spain (specifically in A Coruña, Pontevedra and Lugo provinces; 22,500 km^2). Galicia is characterized by a human-dominated landscape with human settlements widely scattered (2.7 human settlements km^{-2}) and a mean human population density around 93 inhabitants km^{-2} (INE, 2010). The high geographical dispersion of human settlements implicitly requires a well-developed paved road network (mean paved road density 2.7 km/km^2). Habitat transformation dominates the landscape, mainly because of agriculture and livestock practices. As a consequence, Galicia is comprised of a patchy landscape made up of croplands (32%), managed scrublands (11%) and forest plantations (*Eucalyptus globulus* and *Pinus* spp.) (43%), with the dynamism of this landscape being remarkable due to human activities (e.g., fires, clearings). Only less than 8% of the landscape is occupied by semi-natural forests (e.g., *Quercus robur*, *Quercus pyrenaica*, *Betula alba*). At the beginning of the 2000s at least 68 different wolf packs were identified in Galicia (ca. 2.25 wolf packs per 1,000 km^2; Llaneza *et al*., 2012).

Wolves in the study area feed mainly on livestock (Cuesta *et al*., 1991; Sazatornil 2008; López-Bao *et al*., 2013; Lázaro, 2014). Livestock is the most important economic mainstay in rural areas. Cattle (*Bos taurus*) are the primary livestock activity (0.6 vs. 1.1 farms/km^2 and 24.1 vs. 10.1 heads/km^2 of dairy and beef cattle, respectively), followed by sheep (*Ovis aries*) and goats (*Capra hircus*) (1.1 farms/km^2 and 6.4 heads/km^2, both species pooled). Free-ranging mountain ponies *(Equus caballus*) are maintained in a traditional extensive practise and can be abundant locally (> 40 heads/km^2) (López-Bao et al. 2013).

Finally, pig (*Sus scrofa domesticus*) and chicken (*Gallus gallus*) farms have been traditionally abundant in this area (1.2 and 0.1 farms/km^2, respectively; Regional Government of Galicia, 2010). In the Western part of the study area (A Coruña and Pontevedra provinces), wild ungulates (roe deer *Capreolus capreolus* and wild boar *Sus scrofa*) were absent or extremely low at least since the 1960s (Guitián *et al*., 1975; Munilla *et al*., 1991; SGHN, 1995). However, during the last years both species are slightly increasing their range and abundance. Assuming that hunting bags reflect variations in the abundance of ungulates (Merli and Meriggi 2006) during the last decade a positive trend has been observed in their numbers (Spearman's rank correlation analyses, both $r_s > 0.90$; $P < 0.001$, $n = 10$; Regional Government of Galicia)**,** mainly as a consequence of the outcome of the rural depopulation process occurred in Galicia during the last decades (López-Bao *et al*., 2015). But still concumption of wild ungulates in the Western side of the study area is very low or absent **(**López-Bao *et al*., 2013; Lázaro, 2014).

Wolf captures and data collection

We used spatial information from 29 wolves (3 male pups, 8 subadult females, 8 subadult males, 4 adult females and 6 adult males) equipped with GPS-GSM collars (Followit, Sweden), T5H and T3H models, between 2006 and 2014. Wolves were captured with Belisle® leg-hold snares (Edouard Belisle, Saint Veronique, PQ, Canada) and chemically immobilized by intramuscular injection of medetomidine (Dormitor®, Merial, Lyon, France). Immobilization was reversed by the intramuscular injection of atipamezole (Revertor®, Merial, Lyon, France). All wolves were evaluated as clinically healthy at the moment of capture, and they only presented minor lesions associated with trapping. Snares were monitored twice a day, in the early morning and late afternoon. The wolves included in this study were captured under permits 19/2006, 71/2009, 86/2011, and 095/2013 from the Regional Government of Galicia (Spain). All fieldwork procedures adhered to the animal welfare regulations. GPS collars were scheduled to take a location every hour during the diurnal period (from 8:00 to 20:00 GTM) and every two hours during nighttime. We used a dataset of 141,652 total valid locations (mean number of locations per wolf = 4,884 locations).

Sex and age were determined *in situ*. Age was estimated by dental pattern and tooth wear (Gipson *et al*., 2000), and the wolves were classified into three categories, pups (< 1 yr), subadults (1-2 yrs), and adults (>2 yrs). Moreover, for every subadult or adult wolf, we classified its social status by means of exploring its spatial behavior in relation to the location of homesites and packs in the area as well as direct observations of pack members. A wolf with recurrent locations in the vicinity or within a given homesite with pups or being observed with other pack members or pups was considered as a pack member (4 adult females, 3 adult males; 7 subadult females and 5 subadult males); whereas 7 individuals were considered as non-pack individuals (2 adult males, 3 subadult males and 1 subadult female).

Estimations of home range size

We used the fixed kernel method to estimate the home range sizes of wolves (Seaman et al., 1996,; 1999; Swihart and Slade, 1997; Börger *et al*., 2006). For each individual, we calculated the size of the annual fixed kernel estimates of home ranges (hereafter HR, 90% probability contour of locations distribution; Börger *et al*., 2006) and core areas (hereafter CA, 50% probability contour of locations distribution) using the extension Home Range tools (Rodgers *et al*., 2007) for ArcGIS 9 (Esri Inc., Redlands, CA, USA) and the reference smoothing factor h_{ref}. Given that kernel estimations assume independence between locations, we subset our dataset by choosing two locations per day and wolf in order to maximize independence between locations without compromising the quality of the biological information (Reynolds and Laundre, 1990; Solla *et al*., 1999; Blundell *et al*., 2001; Fortin and Dale, 2005). For each wolf, we also estimated two seasonal home ranges at HR and CA levels to evaluate the influence of different phases of the annual cycle of wolves on home range size: breeding period (May-December) vs. matting season (January – April) (Mech and Boitani, 2003).

Environmental data

Considering only pack members, for each HR and CA we measured nine factors representing different competing models that could explain home range size variation in wolves in human-dominated landscapes. We focused this analysis on pack members because of the remarkable differences expected between the drivers (e.g., food availability *vs.* mating opportunities) of the spatial ecology of pack *vs.* non-pack members (e.g., dispersal individuals and floaters).

Landscape configuration was evaluated by calculating the percentage of HR and CA occupied by mountainous areas, which was considered as a surrogate of low human use areas favoring wolf movements (Llaneza *et al*., 2012; Rich *et al*., 2012). We used high-resolution ortophotoimages and elevation digital models (Ministerio de Fomento, 1999) to delineate mountainous areas. Mountainous areas were estimated by firstly identifying the axis of mountains using three-dimensional projections of high-resolution ortophotoimages overlapping with wolf territories, in combination with contour lines, and secondly detecting the contour lines where the slope increase notably in comparison with flat areas and bottom valleys. We considered as refuge those vegetation types that could effectively conceal wolves: dense and high scrublands (mainly represented by *Ulex* spp. and *Erica* spp.), woodlands, and forest plantations. Functionally, we assumed that all these vegetation types provide similar conditions of refuge for wolves (Llaneza *et al*., 2012). Data on vegetation types and covers were obtained from the Spanish Forest and Land Use Map (DGCN, 2000). We considered not only the refuge quantity (total area occupied by refuge) but also a simple proxy of its quality (fragmentation level) estimated by calculating the ratio between the number of patches of *i* habitat category and the total number of patches (Cardille and Tuner, 2002). In our case, we have pooled patches of different habitats according to their features as wolf refuge (Llaneza *et al*., 2012). The level of anthropization within the territory was evaluated by considering the densities of paved roads (pooling all types of paved roads) and unpaved roads (both in km/km^2) as well as human settlements per km^2 within territories. These variables were measured using public GIS layers facilitated by the Regional Government of Galicia and combined with a posterior double-checking process using high-resolution ortophotoimages in order to correct these layers (e.g., adding lacking unpaved roads).

To test the effect of livestock availability on home range size variation we selected the four most important livestock species in the diet of wolves in the study area: horse, cattle, sheep, and goat (Sazatornil, 2008; López-Bao *et al*., 2013; Lázaro, 2014). Together, these species can account for the totality of the wolf diet in some packs (López-Bao *et al*., 2013). Data on livestock availability were taken from the Rural Council of Galicia at the level of parishes, which was the smallest administrative level in the study area providing a high spatial resolution (mean area = 7.8 km^2; range 0.08–75 km^2; n = 3,797). For each HR and CA, we selected all overlapping parishes and calculated the total number of heads of every selected livestock species. Then, we converted the number of heads into biomass (metric tons/km^2). Only two wild ungulates exist in our study area, wildboar and roe deer, and their importance in the diet of the studied packs with collared wolves was small. In fact, livestock composed more than 85% of the diet in all the packs with collared wolves considered in this study (Lázaro, 2014; *unpub. results*). Therefore, we decided not to test the effect of wild prey availability on home range size (which, on the other hand, is the opposite of the importance of livestock in the diet). Nevertheless, we assessed the influence of the importance of anthropogenic food sources in the diet of wolves on home range size. To do this, for each collared wolf, we considered the percentage in the diet in every pack of all anthropogenic food sources pooled.

Finally, to test the effect of conspecific density on home range size variation, for each wolf we counted the number of packs occurring in a buffer radius of 20 km generated from the centroid of every wolf home range. Information on the number of packs was extracted from wolf surveys carried out during the last decade (Llaneza *et al*., 2012; 2014; *unpublished data*), considering for each wolf the closest estimate of the number of packs available.

Statistical analyses

We log-transformed all HR and CA estimates and removed the pups (n = 3) from the dataset for subsequent analyses. First, we built Generalized Linear Models (GLMs) with gaussian error distribution and identity link to test for the influence of gender, age, social status (pack/no pack member), and the interaction between gender and age on home range size variation. Secondly, we used General Linear Mixed Models (GLMMs) with gaussian error distribution and identity link to evaluate seasonal variations in home range size according to gender, age, their interaction, and season (two levels: breeding and mating seasons). We also included the interaction terms between season and gender, and between season and age to test for individual differences in seasonal home range sizes according to individual attributes. The identity of the individual was treated as a random factor in these models.

Finally, we built GLMs, with gaussian error distribution and identity link, to compare a set of seven competing models explaining home range size variation and considering i) the null model; ii) a model containing the variable describing the landscape configuration (proportion of mountainous areas within the home range); iii) a model considering the quantity and quality of refuge within the home range (refuge quantity and fragmentation level); iv) a model considering human pressure within home ranges (densities of paved roads, unpaved roads, and human settlements) and representing the degree of habitat anthropization; v) a model representing food availability in the area (livestock biomass); vi) a model representing the importance of livestock in the diet of wolves (percentage of livestock in the diet); and vii) a model considering the potential differences in home range size associated to intraspecific competition (wolf pack density). Due to limited sample size, we did not run the full covariate model to avoid overparameterization.

The monitoring period varied between wolves. Subadults and adults were followed between 52 and 397 days. Malfunction of collars, battery size, or mortality events influenced the number of monitoring days. A different number of monitoring days could influence our results, so, we previously tested whether the number of days of monitoring influenced the home range size estimates. We built a GLM with gaussian error distribution and identity link to test the relationship between the number of days each wolf was monitored and the log-transformed estimate of HR and CA. Since we did not detect a significant effect of sampling effort on home range size (P = 0.534), we excluded this covariate in our models. To test the effect of age, gender, and social status on wolf home range size we used all collared subadult/adult wolves (n=26), whereas the rest of the analyses were only focused on those wolves being classified as pack members (n=19). Akaike Information Criterion with a second order correction for small sample size (AICc) was used for model selection (Burnham & Anderson, 2010). We also used the AIC weights (w_i) to determine the relative strength of support for each competing model (Burnham and Anderson, 2010). AIC weights were calculated using the "*bbmle*" package for R (Bolker, 2012). We used the "*glmmADMB*" package (Fournier *et al.*, 2012) to run GLMMs. All statistical analyses were performed in R 3.0.2 (R Core Team, 2013).

7.3 RESULTS

Pups, with a monitoring period of ca. 3 months, showed a HR and CA size of 55.5 km^2 (SD=64.7) and 9 km^2 (SD=7.4), respectively. Subadults showed a HR and CA size of 275.7 km^2 (SD=337.3) and 75.1 km^2 (SD=95.6), respectively. Finally, adults showed a HR and CA size of 183.7 km^2 (SD=163.4) and 37.9 km^2 (SD=30.8), respectively (Table 7.1).

Table 7.1. Annual home range size (km^2) of wolves in NW Spain in the period 2006-2014 estimated by means of fixed kernel method. (1) Males and females pooled.

AGE	DAYS			K90		K50	
	Mean	SD	Sex	Mean	SD	Mean	SD
Adults > (2 yrs) (n=10)	202.4	105.7	M (n=6)	155.8	79.5	38.5	24.2
			F (n=4)	113.4	63.6	20.9	15.3
Subadults (1-2 yrs) (n=16)	187.6	100.1	M (n= 8)	309.2	392.2	73.7	96.2
			F (n= 8)	242.4	295.8	76.5	101.5
Pups (< 1 yr) (n=3)	84.6	39.3	M (n= 3)	55.5	64.7	8.9	7.4
Adults[1] pack				131.4	47.2	27.1	13.0
Adults[1] non pack				210.7	116.6	55.8	38.9
Subadults[1] pack				125.4	111.5	33.4	38.8
Subadults[1] non pack				726.7	402.2	200.3	110.7

When we evaluated the influence of individual attributes on home range size variation, we only detected a significant effect of social status on home range size at both HR and CA levels. In human-dominated landscapes of Galicia, we observed similar spatial requirements in wolves regardless of gender and age classes, but wolves that were not pack members showed larger range estimates compared to pack members (Table 7.1). Considering subadult and adult wolves, pack members showed on average, an annual home range size ca. four times smaller than non pack members (122.1 km^2 SD=93.6 *vs.* 554.7 km^2 SD=413.3, respectively).

For wolf pack members, we observed seasonal variations in home range size in relation to age classes and seasons (Table 7.2 and 7.3). On one hand, adult wolves showed larger seasonal home ranges at both HR and CA levels compared to subadults (199.8 km^2 SD=255.5 *vs.* 113.9 km^2 SD=106.3, respectively). On the other hand, ranges were larger for wolves in the mating season compared to the breeding season (216.3 km^2 SD=271.7 *vs.* 108.1 km^2 SD=85.9, respectively).

Table 7.2. Parameter estimates (± SE) for the models testing the influence of individual attributes on home range size variation in human-dominated landscapes on Galicia. The levels ‘‘sex (male)’’, “age (adult)” and “social status (pack) are included in the intercept.

	HR			CA		
	Estimate	SE	*P*	Estimate	SE	*P*
Parametric coefficients:						
Intercept	2.11	0.16		1.42	0.17	
Sex (female)	-0.14	0.25	n.s.	-0.20	0.25	n.s.
Age (subadult)	-0.18	0.20	n.s.	-0.16	0.21	n.s.
Social status (no pack)	0.57	0.18	**	0.67	0.19	**
Sex x Age	0.28	0.31	n.s.	0.42	0.31	n.s.

** Significant at P < 0.01.

Table 7.3. Parameter estimates (± SE) for the models testing the influence of seasonal period regarding to individual attributes on home range size variation in human-dominated landscapes on Galicia. The levels ‘‘sex (male)’’, “age (adult)” and “season (mating)" are included in the intercept.

	HR			CA		
	Estimate	SE	*P*	Estimate	SE	*P*
Parametric coefficients:						
Intercept	2.47	0.17		1.91	0.19	
Sex (female)	-0.29	0.24	n.s.	-0.34	0.26	n.s.
Age (subadult)	-0.52	0.22	*	-0.57	0.24	*
Season (breeding)	-0.43	0.17	**	-0.52	0.19	**
Sex x Age	0.35	0.26	n.s.	0.51	0.28	n.s.
Age x Season	0.20	0.19	n.s.	0.21	0.21	n.s.
Sex x Season	0.19	0.18	n.s.	0.17	0.21	n.s.

* Significant at P < 0.05; ** Significant at P < 0.01.

Different extrinsic factors explained range size variations in wolf pack members at different spatial scales of intensity of home range use. At the HR level, the most parsimonious model was the model considering the importance of livestock in the wolf diet (w_i = 0.43). Two additional models also showed ΔAICc <2 (Table 7.4), which are models considering the anthropization level of the landscape (w_i = 0.32) and intraspecific competition (w_i = 0.16). The proportion of livestock in the diet of wolves showed a negative and significant influence on home range size (P = 0.004). On the other hand, we observed an increase in the density of human settlements with increasing home range sizes (P <0.0001) (P-values for paved and unpaved roads > 0.715). Finally, we detected a decrease in HR size as the density of packs increased in the vicinity (P = 0.019). The importance of livestock in the diet of wolves determining range size was also observed at the CA level, where only the model considering the importance of livestock in the wolf diet was within ΔAICc <2 (w_i = 0.90) (Table 7.4). Again, we observed a significant and negative relationship between CA size and the proportion of livestock in the diet of wolves (P = 0.003, Table 7.4).

Table 7.4. Comparison of seven competing models built to understand home range size variation in human-dominated landscapes of Galicia, N Spain, at HR and CA levels.

	HR		CA	
HYPOTHESIS	ΔAICc	ω_i	ΔAICc	ω_i
Importance of livestock in the diet of wolves	0.0	0.44	0.0	0.90
Anthropization level	0.6	0.33	5.5	0.06
Intraspecific competition	1.9	0.17	6.8	0.03
Null model	4.4	0.05	9.4	0.01
Landscape configuration	7.1	0.01	11.0	<0.01
Refuge	9.0	<0.01	12.6	<0.01
Livestock biomass	11.3	<0.01	15.2	<0.01

7.4 DISCUSSION

In this study, we explored factors affecting home range size in wolves persisting in human-dominated landscapes of Galicia, NW Spain. Similar to other regions, we observed variability in home range size (e.g., Jedrzejewski et al. 2007; Mattisson et al. 2013). Wolves integrated in packs showed home ranges of similar size to those ranges obtained in other areas of the Iberian Peninsula (ca. 150 km^2 in Zamora province, Vilá, 1993), (ca. 260 km^2 in agroecoystems of Valladolid and Zamora provinces, Blanco, *com. pers.*) or European countries such as Portugal (ca. 160 km^2, Alvares, 2011; Rio-Maior *et al*., 2012), Italy (ca. 200 km^2, Ciuci *et al*., 1997), Croatia (ca. 150 km^2, Kusak *et al*., 2005), Poland (ca. 170-300 km^2, Bialowieza Primeval Forest; Okarma *et al*., 1998; Jedrzejewski *et al*., 2007) or Slovakia (ca. 150-190 km^2, Tatra Mountains; Findo and Chovancová, 2004). Moreover, such figures were similar to the home range sizes reported in several states of US (Mech, 1973; Fuller 1989; Wydeven *et al*., 1995). Generally, home range sizes of subadult/adult wolves ranged between 150 and 300 km^2. However, home ranges increased notably at higher latitudes (Okarma *et al*., 1998; Mech and Boitani, 2003; Jedrzejewski *et al*., 2007) such as the Scandinavian Peninsula (ca. 1000 km^2, Mattisson *et al*., 2013) and northern areas of America (Fuller and Keith, 1980; Ballard *et al*., 1987; Mech *et al*., 1998; Hayes and Harestad, 2000; Adams *et al*., 2008).

We did not detect an influence of individual attributes on annual home range size, at both HR and CA levels, except for social status. Wolves integrated in packs showed smaller range sizes compared to non-pack members (Mech and Boitani, 2003). Moreover, at the seasonal level, we detected larger home ranges for adults compared to subadult individuals, which was in contrast with the patterns observed on annual range estimates (Table 7.1). These findings suggest that subadults use different areas throughout the year compared to adult wolves, which may be more stationary. Seasonal variation in range sizes was observed at both HR and CA levels, probably associated to the presence of pups during the breeding season. Resident wolves during this period are spatially constrained due to pup presence in homesites (Jedrzejewski *et al*., 2007).

Although the relationship between the density of human settlements and home range size could be expected, considering the configuration of the landscape (distribution of settlements) in human-dominated landscapes, other alternative explanations may be behind this result. Wolves in most areas of S Europe occur in humanized landscapes. The increase of HR size in these areas in relation to human activity may reflect a behavioral response of wolves to cope with different human-associated disturbances such as the expansion of agricultural lands, forest fragmentation, and hunting activities, in addition to direct human persecution (Rich *et al*., 2012; Mattison *et al*., 2013; Maletzke *et al*., 2014). Although a negative influence of the density of roads on wolf presence in this area has been shown (Llaneza *et al*., 2012), we did not find evidence to support the idea that the densities of paved and unpaved roads influence range sizes (e.g., roads may reduce the cost of keeping a large home range; Mattisson *et al*., 2013).

However, the density of wolf packs in the vicinity negatively influenced the wolf range size at the HR level (Rich *et al*., 2012, but see Mattisson *et al*., 2013). The fact that wolf pack density influenced HR suggests a close-to-saturation scenario for wolves in this area, where pack density is a limiting factor of space use (Hayes and Harestad 2000; Rich *et al*., 2012; but see Mattisson *et al*., 2013). In fact, the wolf range in Galicia has not varied remarkably in the last 1.5 centuries (Nuñez-Quirós *et al*., 2007) and the estimated number of wolf packs in Western Galicia have been similar over the las decade, 29 and 31 wolf packs estimated in this area in 2003 and 2013, respectively (0.23-0.25 packs/100km^2) (Llaneza *et al*., 2005, 2014a, following the procedure described by Llaneza *et al*., 2014b).

Wolf home range size has been negatively correlated to prey biomass where food availability is, basically, wild prey (e.g., Fuller, 1989; 1995; Wydeven *et al*., 1995; Mech *et al*., 1998; Fuller *et al*., 2003; Rich *et al*., 2012; Mattisson *et al*., 2013). Contrary to natural areas or regions where wild prey is the basis of the wolf diet, in human-dominated landscapes where anthropogenic food sources comprise the basis of the diet of wolves, food availability (livestock biomass) did not affect the range size of the intensity of spatial use. Such a lack of relationship could be associated to the heterogeneity in livestock vulnerability to wolf predation, which deserves further investigation. In this case, we predict that variation in range sizes in human-dominated landscapes may reflect differences in livestock vulnerability rather than livestock abundance.

However, we observed how the importance of livestock in the diet influenced range size at both HR and CA levels (Newsome *et al*., 2015). In our study case, availability of anthropogenic food sources was high at the landscape scale, either as live prey (livesotck), carrion or garbage (Cuesta *et al*., 1991; Lagos, 2013); therefore, wolves may do not need to travel large distances to find food (Newsome *et al*., 2015). Because the importance of anthropogenic food sources in the diet modulated the range size, the landscape configuration and refuge did not affect range sizes, which were the significant factors affecting home range size when wild prey was the basis of the diet (Oakleaf *et al*., 2006; Rich *et al*., 2012; Kittle *et al*., 2015). The small home ranges observed in this human-dominated landscape, being modulated by the importance of anthropogenic food sources in the diet, translate into the potential for higher wolf densities in these landscapes compared to natural areas.

7.5 REFERENCES

Adams, L.G., Stephenson, R.O., Dale B.W., Ahgook, R.T. & Demma, D.J. (2008) Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildl. Monogr*. 170:1–25.

Agarwala, M. & Khumar, S. (2009). Wolves in Agricultural Landscapes in Western India. *Tropical Resources: Bulletin of the Yale Tropical Resources Institute*, 28: 48-53.

Ahmadi, M., López-Bao, J.V., & Kaboli, M. (2014). Spatial Heterogeneity in Human Activities Favors the Persistence of Wolves in Agroecosystems. *PLoS ONE*, 9, e108080.

Alvares, F. (2011). *Ecología e Conservaçao do Lobo (Canis lups, L.) no Noroeste de Portugal*. Tesis de Doutoramente em Biologa. Universidade de Lisboa.

Ballard, W.B., Whitman, J.S. & Gardner, C.L. (1987). Ecology of anexploited wolf population in south-central Alaska. *Wildl. Monogr*. 98:5–54.

Benson, J.F., Chamberlain, M.J. & Leopold, B. D. (2006). Regulation of space use in a solitary felid: population density or prey availability? *Animal Behaviour*, 71: 685-693.

Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D. & Kark, S. (2010). Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology*, 47: 1262-1271.

Blundell, G.M., Maier, J.A. & Debevec, E.M. (2001). Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological monographs*, 71:469-489.

Bolker, B. (2012). *bbmle: Tools for general maximum likelihood estimation*. *R package version*, *1*(5.2). R Development Core Team, 2014

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal Animal Ecology*, 75:1393-1405.

Börger, L., Dalziel, B.D., & Fryxell, J.M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology letters*, 11:637-650.

Burnham, K.P. & Anderson, D.R., (2010). *Model selection and multimodel inference. A practical information-theoretic approach*. Second edition. Springer, New York, New York, USA.

Cardille, J. A. & Turner, M. G. (2002). *Understanding Landscape Metrics I*. In: Gergel, S. E. & Turner, M. G. (eds). L*earning Landscape Ecology. A Practical Guide to Concept and Techniques*. pp: 85-111. Springer-Verlag New York, Inc.

Ciucci P., Boitani L., Francisci F, & Andreoli G. (1997) Home range, activity and movements of a wolf pack in central Italy. *J. Zool*. 243:803–819.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H., ... & Nowak, S. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216):1517-1519.

Cuesta, L., Bárcena, F., Palacios, F. & Reig, S. (1991). The trophic ecology of the Iberian wolf (Canis lupus signatus Cabrera, 1907). A new analysis of stomach's data. *Mammalia*, 55:239-254.

Dahle, B. & Swenson, J. E. (2003). Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. *J. Zool.* 260: 329-335.

D.G.C.N. (2000). *Tercer Inventario Forestal Nacional, 1997-2006: Galicia*. Ministerio de Medio Ambiente, Dirección General de Conservacion de la Naturaleza, Madrid.

Findo, S. & Chovancová, B. (2004). Home ranges of two wolf packs in the Slovak Carpathians. *Folia Zool*. 53(1):17-26.

Fortin, M.J. & Dale, M. (2005). *Spatial Analysis A Guide for Ecologists*. Cambridge University Press, Cambridge, UK.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A. & Sibert J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27: 233-249.

Fritts, S.H. & Mech, L.D. (1981) Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildl. Monog*. 80:1–79

Fuller, T.K. (1989). Population dynamics of wolves in north-central Minnesota. *Wildl. Mono*g. 3-41.

Fuller, T.K. (1995). *Guidelines for gray wolf management in the northern Great Lakes region* (Vol. 271). International Wolf Center.

Fuller, T.K. & Keith, L.B. (1980). Wolf population dynamics and prey relationships in northeastern Alberta. *J. Wildl. Manage*. 583-602.

Fuller, A., Mech, L.D. & Cochrane, J.F. (2003). *Wolf populations dynamics*. In: Mech L.D. & Boitani, L. (eds). *Wolves behaviour, ecology, and conservation*. University of Chicago Press, Chicago, pp 161–191

Gittleman, J.L. & Harvey, P.H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10:57-63.

Gompper, M.E. & Gittleman, J.L. (1991). Home range scaling: intraspecific and comparative trends. *Oecologia*, 87:343-348.

Guitián, J., Sánchez-Canals, J.L., de Castro, A., Bas, S., Rodríguez, J. & Bermejo, A. (1975). *El Inventario cinegético de la provincia de la Coruña*. Report to Xunta de Galicia.

Habib, B. & Kumar, S. (2007). Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. *J. Zool.* 272:259–265.

Hayes, R.D. & Harestad, A.S. (2000). Demography of recovering wolf population in the Yukon. *Can. J. Zool*. 78:36–48

Hinam, H.L. & Clair, C.C.S. (2008). High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls. *Biological Conservation*, 141:524-535.

I.N.E. (2010). *Censo de población y vivienda*. Instituto Nacional de Estadística de España.

Iliopoulos, Y., Youlatos, D., Sgardelis, S. (2014). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *Eur. J. Wildlife Res*. 60:23-34.

Jetz, W., Carbone, C., Fulford, J. & Brown, J. H. (2004). The scaling of animal space use. *Science*, 306:266-268.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B. & Okarma, H. (2001). Daily movements and territory use by radio-collared wolves (Canis lupus) in Bialowieza Primeval Forest in Poland. *Can. J. Zool*. 79:1993-2004.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B. & Kowalczyk, R. (2007). Territory size of wolves Canis lupus: linking local (Bialowieza Primeval Forest, Poland) and Holarctic-scale patterns. *Ecography*, 30:66–76.

Kelt, D.A. & Van Vuren, D.H. (2001). The ecology and macroecology of mammalian home range area. *American Naturalist*, 157:637-645.

Kittle, A.M., Anderson, M., Avgar, T., Baker, J.A., Brown, G.S., Hagens, J., Iwachewski, E., Moffatt, S., Mosser, A., Patterson, B.R., Reid, D.E., Rodgers, A.R., Shuter J., Street, G.M., Thompson, I.D., Vander Vennen, L.M., Fryxell, J.M. (2015). Wolves adapt territory size, not pack size to local habitat quality. *Journal of Animal Ecology*. doi: 10.1111/1365-2656.12366.

Kusak, J., Skribinsek, A.M. & Huber, D. (2005). Home ranges, movement, and activity of wolves (Canis lupus) in the Dalmatian part of Dinarids, Croatia. *Eur. J. Wildl. Res*. 1:254–262

Lázaro, A. 2014. *Ecología trófica del lobo (Canis lupus) en un ambiente humanizado y* *multipresa: Variación geográfica*. MSc thesis. University of Cordoba, Spain.

Lagos, L. (2013) *Ecología del lobo (Canis lupus), del poni salvaje (Equus ferus atlanticus) y del ganado vacuno semi-extensivo (Bos taurus) en Galicia: interacciones depredador - presa*. PhD Thesis. University of Santiago de Compostela. 486 p.

Llaneza, L., Fernández, A. & Nores, C. (1996). Dieta del lobo en dos zonas de Asturias (España) que difieren en carga ganadera. *Doñana Acta Vertebrata*, 23:201-213.

Llaneza, L., Palacios, V., Uzal, A., Ordiz, A., Sazatornil, V., Sierra, P. & Álvares, F. (2005) Distribución y aspectos poblacionales del lobo ibérico *(Canis lupus signatus)* en las provincias de Pontevedra y A Coruña. *Galemys*, 17:61-80.

Llaneza, L., López-Bao, J.V. & Sazatornil, V. (2012) Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions*. 18:459–469.

Llaneza, L., García, E.J., Palacios, V. & López-Bao, J.V. (2014a). *Trabajos de apoyo para la coordinación tecnico-científica del censo de lobo ibérico en la Comunidad Autónoma de Galicia*. Tragsatec-Ministerio de Agricultura, Alimentación y Medio Ambiente. Informe inédito. 48 pp.

Llaneza, L., García, E.J. & López-Bao, J.V. (2014b) Intensity of territorial marking predicts wolf reproduction: implications for wolf monitoring. *PLoS ONE*, 9, e93015.

López-Bao, J.V., Palomares, F., Rodríguez, A., & Delibes, M. (2010). Effects of food supplementation on home-range size, reproductive success, productivity and recruitment in a small population of Iberian lynx. *Animal Conservation*, 13:35-42.

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013). Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters*, 6:448-455.

López-Bao, J.V., González-Varo, J.P. & Guitián, J. (2015). Mutualistic relationships under landscape change: Carnivorous mammals and plants after 30 years of land abandonment. *Basic and Applied Ecology*, 16:152-161.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. (2009). Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography*, *32*(6):953-962.

Maletzke, B.T., Wielgus, R., Koehler, G.M., Swanson, M., Cooley, H. & Alldredge, J.R. (2014). Effects of hunting on cougar spatial organization. *Ecology and evolution*, 4:2178-2185.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R. & Pedersen, H.C. (2013). Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia*, 173(3):813-825.

McLoughlin, P.D. & Ferguson, S.H. (2000). A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*, 123-130.

McNab, B.K. (1963). Bioenergetics and the determination of home range size. *American Naturalist*, 133-140.

Mitchell, M.S. & Powell, R.A. (2004). A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, 177(1):209-232.

Mech, L.D. (1973). *Wolf numbers in the Superior National Forest of Minnesota*. USDA Forest Service Research paper NC-97. North Central Forest Experiment Station, St. Paul, MN.

Mech, L.D., Fritts, S.H., Radde, G.L. & Paul, W.J. (1988). Wolf distribution and road density in Minnesota. *Wildl. Soc. Bull*. 16:85-87.

Mech, L.D., Adams L.G., Meier T.J., Burch J.W. & Dale B.W. (1998). *The wolves of Denali*. University of Minnesota Press.

Mech, L.D. & Boitani, L. (2003). *Wolf social ecology*. In: Mech, L.D., Boitani, L. (eds) *Wolves: behaviour, ecology, and conservation*. University of Chicago Press, Chicago.

Meriggi, A. & Lovari, S. (1996). A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *Journal Applied Ecology*, 33:1561-1571.

Merli, E. & Meriggi, A. (2006). Using harvest data to predict habitat-population relationship of the wild boarSus scrofa in Northern Italy. *Acta Theriologica*, 51:383-394.

Munilla, I., Romero, R. & de Azcárate, J.G. (1991) *Diagnóstico de las poblaciones faunísticas de interés cinegético de la provincia de Pontevedra.* Report to Xunta de Galicia.

Newsome, T.M., Ballard, G.A., Dickman, C.R., Fleming, P.J.S. & Howden, C. (2013) Anthropogenic Resource Subsidies Determine Space Use by Australian Arid Zone Dingoes: An Improved Resource Selection Modelling Approach. *PLoS ONE* 8: e63931. doi:10.1371/journal.pone.0063931

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A. J. & Dickman, C.R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24:1-11.

Núñez-Quirós, P., García-Lavandera, R. & Llaneza, L. (2007). Analysis of historical wolf (*Canis lupus*) distributions in Galicia: 1850, 1960 and 2003. *Ecología*, 21:195-205.

Oakleaf, J.K., Murray, D.L., Oakleaf, J.R., Bangs, E.E., Mack, C.M., Smith, D.W., Fointanie, J.A., Jimenez, M.D., Meier, T.J. & Niemeyer, C. . (2006). Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. *J. Wildl. Manage*. 70:554-563.

Okarma H., Jedrzejewski W., Schmidt K., Sniezko S., Bunevich A.N. & Jedrzejewska B. (1998). Home ranges of wolves in Bialowieza primeval forest, Poland, compared with other Eurasian populations. *J. Mammal*. 79:842–852.

Papageorgiou, N., Vlachos, C., Sfougaris, A., & Tsachalidis, E. (1994). Status and diet of wolves in Greece. *Acta Theriologica*, 39:411-411.

Peterson R.O., Woolington J.D. & Bailey T.N. (1984) Wolves of the Kenai Peninsula, Alaska. *Wildl. Monogr*. 88:1–52.

R Development Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing,Vienna. http://www.R-project.org/

Reynolds, T.D. & Laundre, J.W. (1990). Time intervals for estimating pronghorn and coyote home ranges and daily movements. *J. Wildl. Manage*. 54(2):316-322.

Rich, L.N., Mitchell M.S., Gude J.A. & Sime C.A. (2012). Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. *J. Mammal*. 93:722–731.

Riley, S.P., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C. & Wayne, R.K. (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology*, 17:566-576.

Rio-Maior, H., Godinho, R., Nakamura, M. & Alvares, F. (2011). *Comportamento social e espacial de um núcleo de 5 alcateias no noroeste de Portugal*. III Congreso Ibérico del Lobo. p.29.

Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L. & Kie, J.G. (2007). *HRT: home range tools for ArcGIS*. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, ON, Canada.

Saïd, S., Gaillard, J.M., Widmer, O., Débias, F., Bourgoin, G., Delorme, D., & Roux, C. (2009). What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos*, 118:1299-1306.

Sandell, M. (1989) The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, Ecology, and Evolution,* (Gittleman, J.L. Ed.), pp. 64–82. Cornell University Press, New York.

Sazatornil, V. (2008) *Alimentación del lobo (Canis lupus) en zonas del Occidente de Galicia con presencia de ganado equino en régimen de semi-libertad*. Msc Thesis. University of A Coruña.

Schoener, T. W. & Schoener, A. (1982). Intraspecific variation in home-range size in some Anolis lizards. *Ecology*, 63(3):809-823.

Seaman, D.E. & Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77:2075–2085.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999). Effects of sample size on kernel home range estimates. J. Wildl. Manage. 63:739–747.

S.G.H.N. (Sociedade Galega de Historia Natural). (1995). *Atlas de Vertebrados de Galicia*. Tomo I. Consello da Cultura Gallega. Santiago de Compostela.

Solla, D.E., Shane, R., Bonduriansky, R., & Brooks, R.J. (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal Animal Ecology*, 68:221-234.

Swihart, R.K. & Slade, N.A. (1997). On testing for independence of animal movements. *Journal of Agricultural, Biological, and Environmental Statistics*, 2(1):48-63.

Van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M. & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology*, 80(4):771-785.

Vanak, A.T. & Gompper, M.E. (2010). Multi-scale resource selection and spatial ecology of the Indian fox in a human-dominated dry grassland ecosystem. *J. Zool.* 281:140-148.

Vilà, C. (1993). *Aspectos morfológicos y ecológicos del lobo ibérico Canis lupus L* Tesis doctoral. Universidad de Barcelona.

Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal. *J. Zool*. 251:457-462.

Wydeven, A.P., Schultz, R.N. & Thiel, R.P. (1995). *Monitoring of a gray wolf (Canis lupus) population in Wisconsin, 1979–1991*. In: Carbyn, L.H., Fritts, S.H. & Seip, D.R. (eds) *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Edmonton, pp 147–156.


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CONCLUSIONES


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8. CONCLUSIONES

1. En paisajes dominados por el hombre la presencia del lobo es el resultado de una compleja interacción entre varios factores ambientales y humanos.

2. Las características del paisaje, básicamente las relacionadas con la disponibilidad de refugio, han jugado un papel clave en la persistencia de esta especie a lo largo de décadas en ambientes humanizados de Galicia, modelando la relación entre la distribución del lobo y las actividades humanas. Además, en nuestra área de estudio los caballos mantenidos en régimen extensivo juegan un papel clave en la presencia del lobo en áreas con baja abundancia de presas silvestres.

3. La densidad de población humana no es un factor determinante *per se* de la presencia del lobo, pero sí la dispersión espacial de los asentamientos humanos.

4. Se sugiere una conexión entre los cambios observados durante las últimas décadas en la dieta del lobo en el área de estudio y la implementación de diferentes regulaciones sanitarias y ambientales regionales, nacionales y europeas. Así, se ha observado un cambio en la dieta de la especie, pasando de una dieta basada mayoritariamente en alimento en forma de carroña, a una dieta basada, principalmente, en grandes ungulados domésticos (ganado bovino y equino).

5. Las variaciones en la disponibilidad de carroña en el área de estudio han tenido un impacto sobre la dieta del lobo y probablemente sobre la relación hombre-lobo. Por lo tanto, se sugiere la necesidad de plantear y estudiar modificaciones a las actuales normativas que regulan la gestión de las carroñas.

6. Los lobos seleccionan sus lugares de cría en zonas con una alta disponibilidad de refugio no fragmentado (se observa una prevalencia de la calidad frente a la cantidad del refugio disponible), baja accesibilidad humana (baja densidad de carreteras) y bajos niveles de actividad humana. La disponibilidad de alimento en los alrededores de los lugares de cría no parece influir en dicha selección en el área de estudio.

7. La disponibilidad de refugio de alta calidad, incluso a pequeña escala (1 km^2), compensaría las actividades humanas en el entorno de las áreas de cría. Con su mantenimiento y protección se podría favorecer la persistencia de la especie en ambientes dominados por el hombre sin apenas reducir el uso del suelo para las actividades humanas.

8. Los lobos seleccionan los lugares de descanso-refugio (encames) evitando las carreteras asfaltadas y pistas, alejados de los asentamientos humanos y eligiendo significativamente lugares con alta disponibilidad de cobertura vegetal.

9. Los lobos (adultos y sub-adultos) integrados en manadas mostraron un área de campeo medio anual de media cuatro veces más pequeño que los lobos no integrados en una manada. Además, se ha observado que la clase de edad y el periodo anual (periodo de celo vs. reproducción) influyen en el tamaño del área de campeo.

10. Para lobos integrados en manadas, se ha observado que la proporción de ganado en la dieta afecta al tamaño de las áreas de campeo y de los centros de actividad (relación negativa). También se ha comprobado un efecto del nivel de antropización (relación positiva) y la densidad de lobos (relación negativa) sobre las áreas de campeo.


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Índice de Figuras

Índice de Tablas