

ECOLOGÍA ESPACIAL DEL ÁGUILA DE BONELLI (*Aquila fasciata*) EN ARAGÓN

SPATIAL ECOLOGY OF BONELLI'S EAGLE (*Aquila fasciata*) IN ARAGÓN



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Tesis Doctoral 2017

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Madrid, 2017
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Memoria presentada por Beatriz Martínez Miranzo para optar al grado de Doctor en Ciencias Biológicas, bajo la dirección del doctor José Ignacio Aguirre de Miguel y la doctora Eva Isabel Banda Rueda, de la Universidad Complutense de Madrid.

Madrid, 2017

El doctorando

V^o B^o del director

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Cover Front

Bonelli's Eagle (*Aquila fasciata*)

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Cover Chapters

Daniel Bustillo

A mis padres por su apoyo incondicional

Caminante, son tus huellas
el camino y nada más;
caminante, no hay camino:
se hace camino al andar.

Antonio Machado

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Acknowledgements

Cuando hace 12 años salí de mi Cuenca natal para emprender el camino de la Biología, nunca hubiese imaginado que este día llegaría. Haciendo memoria, tengo infinidad de recuerdos y experiencias que serían imposibles de escribir en unas líneas. Personas que han pasado o se han quedado durante estos años e incluso sin saberlo, han dejado huella en ese camino.

Mis padres, Juan y M^a Carmen, que son la parte más importante de esta tesis. Su esfuerzo y apoyo incondicional durante tantos años me han dado fuerzas en los momentos de debilidad. Todo esto no hubiese sido posible sin vosotros. Quizás no os lo digo tanto como os merecéis: gracias infinitas. Mi hermana Leticia, mi “escriba” favorita. Gracias por las horas de conejo, paloma y perdiz. Por todo lo compartido, sobre todo estos últimos años de convivencia en la capital, sin duda la mejor compañera que se puede tener.

Durante esta tesis he ganado una familia científica: mis directores Chechu y Eva, que confiaron en mí desde el primer momento. Ellos me han enseñado a caminar por la ciencia y por la vida, me han guiado y me han ayudado a recorrer este camino. Nunca podré agradecer lo suficiente la oportunidad que me habéis brindado. Gracias porque no solo he ganado unos directores, también una segunda familia. Andrea y Ernesto, todavía recuerdo la primera vez que nos conocimos, cuando yo no tenía ni idea de la vida de las Águilas perdiceras. Gracias por trasmitirme vuestra sabiduría, vuestra experiencia y vuestros consejos. Vosotros también formáis parte de esta familia.

Todo el sector becarial, “Los Veteranos” Sita Sofi, Irene, Antón, Joaquín, Ivan y Sheila; “Los Extranjeros” Mateja, Jasper y Michael; las “Nuevas Incorporaciones” María, Alex, Diego G. y Elena; el equipo gorrión Javi y Amparo, gracias por todos esos momentos, sobre todo por las risas, las cañas y los viajes, porque éstos son los que me llevo. Javi, ha pasado mucho desde aquella salida de Vertebrados, “Mapachín” gracias por todo lo vivido desde entonces. Guille, juntos empezamos y juntos terminamos. Compañero incansable y amigo, gracias por tu apoyo todo este tiempo. Recorrer este camino con una persona como tú lo hace mucho más fácil.

José Luis Tellería, gracias por tener siempre una palabra sabia, una palabra amable. Tomás, Pepe, Francisco, Javier, Álvaro, Carlos, Diego, Ainhoa, Carol, Paco y Jose porque todos habéis aportado algo a esta tesis. Empezasteis siendo profesores y termináis siendo compañeros, gracias por ayudar a formarme en este camino.

Todos los que vinieron, están y vendrán a ese “Esbirraje Ilustrado”. Los pata negra, Almu y Pelao, porque vosotros me abristeis las puertas de este grupo que tantas alegrías me ha dado, gracias por estar ahí todo este tiempo. Mi Pelusa, porque nunca entenderé como una cosa tan pequeña puede desprender tanto amor: gracias por cuidarme. Busti, mi nuevo artista favorito, gracias por dar vida a esas imágenes y por dibujarme una sonrisa todos estos años. Pablo Capilla, Pablo Salmón, Blanca, Paco, Alvar, Miky, Sergio, Miriam C., Patricia, Xabi, Cris, Alex, Miriam. Vosotros habéis hecho más llevaderos estos años.

Mi *team* perdicera: Jose Tendero, Elena, Abel, Irene, David, Pablo, Iván, Busti, Pelao, Almu, Patri, Javi y Amparo. Cientos de kilómetros recorridos, incontables horas de “cañonero”, pero sobre todo buenos momentos. Gracias, porque sin vosotros esta tesis no sería ahora realidad. Mención especial a Eduardo por nuestra siempre acogedora base de operaciones en Terrer.

Todavía recuerdo mi primera charla en La Alfranca con más de 40 APNs escuchando como todo su trabajo se veía reflejado en lo que empezaba a ser esta tesis. Gracias M. Alcántara por darme esta oportunidad. David G. y Jorge R. siempre dispuestos a ayudar. A todo el grupo de APNs, Mariló, Alberto, Álvaro, Jesús, Miguel, Juan, Tomás, Fco. Javier, Ángel, Javier, Damián y Juan Carlos involucrados en la conservación de la perdicera. Gracias por vuestro esfuerzo y dedicación, pero sobre todo por ayudarme a sobrevivir en tierras aragonesas.

Dicen que una tesis se completa con experiencias, como las que viví en mi estancia en Italia. Gracias Michelangelo por acordarte de “la chica de las águilas” y tenderme el puente a Palermo. Y gracias Maurizio Sarà por hacerme sentir como en casa. Me llevo las horas que pasamos en Gela, la búsqueda incansable del Lanario y de las Perdiceras, el entusiasmo que trasmites con tu trabajo, pero sobre todo con las personas: Laura, Daniela, “sabio” Totò y Rosanna gracias por hacerme disfrutar tanto en tan poco tiempo.

Cuando estás fuera de casa, todo lo que vives se magnifica y las personas que conoces se convierten en una parte importante de ti. Mis “F. con luce” llegaron en Palermo pero se mantienen en España. Casla, Inés y Lois lo que un aperitivo unió que no lo separe nadie.

Hay personas que llegan en el momento justo para quedarse. Olga e Isa, mis compis de Beca ECI, vosotras habéis dado un soplo de aire fresco a este final. Gracias por hacerme ver la vida desde otra perspectiva.

Mi “Mamá Gato”, nunca un café había dado para tanto. Tu sencillez y dulzura te hacen única. Sé que hay una Calpurnia dentro de ti y eso nunca lo perderás. Gracias por enseñármelo. Rami, el “Papá Gato”, porque detrás de una gran mujer, hay un gran hombre. Gracias por cuidarla.

Mis conquenses por el mundo, esas amigas de toda la vida que están ahí siempre, aunque sea a miles de kilómetros de distancia. Sara, porque desde el otro lado del charco no siento que estés lejos. Si la amistad infinita existe, ésta es la tuya. Laura, mi pavi, nunca un gol dio para tanto. Mi segunda hermana, gracias por estar ahí y sobre todo gracias por poner un poco de locura en mi vida. Cris, gracias por tu sensatez y tus consejos. Personas como tú valen millones. María, la otra Miranzo, gracias por poner a ese bebé tan precioso en nuestras vidas y dejarme formar parte de tu familia.

Y por último y no menos importante, la familia que se elige. Mis niñas “Estu Power”: Ceci, Huesca, Laura, Eli, Barbi, Andre, Boal, Tere y María. Creo que sois lo más importante que me ha pasado en Madrid. La nuestra es una amistad que se forja desde dentro. Podría enumerar una por una las cosas que os hacen únicas, pero lo que realmente importa es lo que somos cuando estamos juntas. Siempre seremos la “L del Quinto”.

Podría escribir otra tesis sobre todos aquellos que de una manera u otra habéis aportado algo a todo lo que viene a continuación. Esto es sólo el principio, todavía queda mucho por recorrer y espero que pueda seguir compartiéndolo con vosotros.

Beatriz Martínez Miranzo

Madrid, 2017



Abstract

Introduction

Spatial ecology has traditionally attempted to comprehend how the configuration of space affects organisms. This includes understanding how species used space and establishing themselves in a particular area. Findings from spatial ecology help applied ecology, especially in relation to the management and conservation of endangered territorial species.

Ecological processes restrict the movements of many animals to a particular area or territory. It not only depends on the individual characteristics but also on spatiotemporal scales under which these processes are interpreted. For conservation biology, scales are important in establishing guidelines for the management of endangered species. For example, patterns related to the use of space identified at large spatial scales might be masking others only detectable at smaller scales. The same can be applied to the temporal scales.

The use of a single approximation can also have a limiting effect. Therefore, ecologists and conservation biologists often include multiple approaches to understanding patterns and processes. This might be useful for the design of conservation strategies that provide a broader and more complete view of the factors that determine the spatial ecology of species.

Objectives and Results

The general objective of this study was to better characterise the spatial ecology of Bonelli's Eagle in the northeast of the Iberian Peninsula. Using long-term monitoring data gather by GPS satellite telemetry, we attempt to identify patterns and processes that will be informative for the design of novel conservation strategies for the species, and which can be applied to other species with similar characteristics.

In **Chapter 1**, we analyse basic aspects of territorial behaviour. We characterize home range size and shape of the Bonelli's Eagle breeding individuals at different periods of the year. Specifically, we focus on non-breeding, breeding seasons and chicks' dependence period. Also, we verify individuals' home range fidelity, a decisive

factor for territorial species. Home range fidelity was high for all individuals over the three periods in all years. Females changed home range size and its use throughout the year, with significant differences during the breeding season. Nevertheless, fidelity to nesting areas was low during the same periods.

Another important aspect to understand the spatial ecology of the territorial species is habitat selection. In **Chapter 2**, we study the habitat selection of the Bonelli's Eagle at different temporal (years and seasons) and spatial scales (Regional, Study Area or Territory) through habitat structure. Also, we investigate how habitat structure influences resource distribution. We found a heterogeneous selection of wooded, rocky and scrub areas alternating with agricultural areas at a regional scale. At the home range scale, individuals selected forests and scrubland over the entire year cycle, except during the breeding season, when, surprisingly, they selected humanized areas. Although Bonelli's Eagle is considered a forest raptor, during the breeding season they selected other habitat types, such as dense scrub and humanized areas, probably due to the high prey availability in these areas.

To understand how trophic resources condition home range behaviour, in **Chapter 3**, we test whether biomass availability acts as a limiting factor for the establishment of home ranges. Specifically, we test if there are biomass differences between home ranges and potentially favourable adjacent areas. Also, we check the annual and seasonal variation in biomass availability and how such variations determine the establishment of home ranges, as well as establishing which of these are important for conservation. We detected variations in biomass availability between territories but no annual or seasonal variation within territories. Differences in biomass availability were identified between each of the territories and their potential adjacent areas. Although biomass availability is lower inside the territories, it remains stable throughout the year, while strong fluctuations in biomass availability were detected outside of the territories. The Eagles, thus, might follow a strategy that we called *Trophic Stability Hypothesis*.

In an attempt to develop an integrative approach to the population dynamics of the species, **Chapter 4** relates species distribution and reproductive success. Specifically, it has been determined how biotic and abiotic variables condition the

distribution of the species and its reproductive success. To identify underlying dynamics in the population, we analyse the relationship between distribution and reproductive success. In the study population, biotic variables (presence of competitors, such as the Golden Eagle, or prey availability) are more important for the distribution of the species than breeding success. However, abiotic traits (related to habitat structure and climate), which negatively influence reproductive success, do not strongly condition the distribution of the species. Nevertheless, the replacement of one of the members of the breeding pairs affects reproductive success and population dynamics. We found ecological sink patterns in the population under study. In areas that are environmentally optimal for the presence of the species, breeding success is lower, mainly to because of the replacement of breeders within the population.

Conclusions and Relevance

- I. Breeders of Bonelli's Eagle in Aragón show high home range fidelity. However, they show less fidelity to the nesting areas within the same territory determined by each breeding pair.
- II. Home range behaviour of individuals in this population is influenced by seasonality and the sex of individuals.
- III. The use of different spatial and temporal scales reveals differences in habitat selection among the individuals of this population.
- IV. The habitat structure plays an important role in the establishment and maintenance of the territories.
- V. The use of space of individuals inside the territories depends on the habitat structure and the ecological requirements of the species during the different periods of the year.
- VI. The continuous and predictable trophic availability over the year contributes to the establishment and fidelity to the territory in the study population.
- VII. Bonelli's Eagle in Aragón seems to follow ecological sink dynamics within the Iberian population. Breeding pairs that establish their territories in presumably more suitable areas for the presence of the species, due to their favourable

ecological characteristics, show a low breeding success. This is conditioned mainly by the high replacement rate of individuals due to death or emigration of either member of the breeding pair.

- VIII. For endangered species conservation, we recommend long-term monitoring studies of the different aspects related to the management of the species. It is desirable to use several scales, both temporal and spatial, which might reveal underlying problems and provide specific patterns of management. Also, the use of integrative approaches can reveal population dynamics not previously identified.

Resumen

Introducción

La ecología espacial ha tratado de identificar los mecanismos y procesos que llevan a comprender cómo la configuración del espacio afecta a los organismos. Uno de los aspectos básicos dentro de esta disciplina, es conocer el uso que las especies hacen del espacio y comprender los mecanismos por los que se establecen en un lugar. Esto puede aportar numerosos beneficios en el campo de la ecología aplicada, sobre todo en lo relacionado con el manejo y conservación de especies territoriales amenazadas.

Muchos animales restringen sus movimientos a un área determinada o territorio. Éste área será el resultado espacial de una serie de procesos ecológicos que satisfagan las necesidades de esos animales para sobrevivir, que pueden depender no sólo de las características individuales, sino también de las escalas espacio-temporales a las que se interpreten esos procesos. Para la biología de la conservación, las escalas juegan un papel muy importante a la hora de establecer pautas para el manejo de las especies amenazadas. Patrones relacionados con el uso del espacio que son identificados a escalas espaciales amplias pueden estar enmascarando otros que solo se detectan a escalas más pequeñas. Lo mismo ocurre con las escalas temporales, largos periodos de tiempo pueden identificar aspectos y procesos que no son identificados a una escala temporal corta.

Al igual que la selección de múltiples escalas pueden revelar diferencias en el uso del espacio que no son perceptibles a una escala, abordar este tipo de estudios basándose en una única aproximación puede enmascarar determinados aspectos relacionados con el uso del espacio que podrían ser revelados con un enfoque integrado. Ecólogos y biólogos de la conservación han utilizado diferentes enfoques para intentar entender patrones y procesos de manera simultánea. Esto puede ser útil para el diseño de estrategias de conservación que den una visión más amplia y completa de los factores que determinan la ecología espacial de las especies.

Objetivos y Resultados

El objetivo general de este estudio es profundizar en diferentes aspectos relacionados con la ecología espacial del Águila de Bonelli en el Noreste de la Península Ibérica. Gracias a datos obtenidos mediante el marcaje y seguimiento a largo plazo de individuos reproductores con dispositivos GPS, se pretende descifrar patrones y procesos que ayuden a diseñar nuevas estrategias de conservación para la misma y que puedan ser aplicadas a otras especies con características afines.

En el **capítulo 1** se han analizado aspectos básicos del comportamiento territorial. Se ha caracterizado el tamaño y forma de los territorios en individuos reproductores de Águila de Bonelli en diferentes periodos del año, es decir, en los periodos no reproductor, reproductor y de dependencia de los pollos. Además se ha comprobado la fidelidad a los territorios por parte de los individuos, un factor determinante para especies territoriales. En la población de estudio no se han encontrado diferencias individuales en el comportamiento territorial. Las hembras presentan cambios en el tamaño y en el uso del espacio, marcada por la época de reproducción, donde disminuyen el tamaño de los territorios y el uso es más restringido. Existe una gran fidelidad al territorio por parte de los individuos durante los tres periodos anuales. Sin embargo, la fidelidad a las zonas de nidificación, dentro de un mismo territorio, es menor en las mismas épocas.

Otro aspecto importante para profundizar en la ecología espacial de las especies territoriales es la selección de hábitat. En el **capítulo 2** se ha explorado la selección de hábitat por parte del Águila de Bonelli a diferente escala temporal (años y temporadas) y espacial (regional, área de estudio y territorio) a través de la estructura del hábitat. Además se ha estudiado cómo la estructura espacial influye en la distribución de los recursos tróficos. Los resultados muestran, a escala regional, una selección heterogénea de zonas arboladas, rocosas y matorral salpicado de cultivos agrícolas. A escala de territorio, los individuos seleccionan activamente zonas boscosas y matorral durante todo el año, aunque sorprendentemente, seleccionan áreas humanizadas durante la época de cría. A pesar de que el Águila de Bonelli es considerada una rapaz forestal, durante la época de cría tiene preferencia por otras

áreas como el matorral denso o zonas antropizadas, posiblemente relacionadas con la presencia de determinados recursos tróficos.

Para conocer como los recursos tróficos condicionan el comportamiento territorial, en el **capítulo 3** se ha estudiado si la biomasa disponible para ser consumida actúa como factor limitante en el establecimiento del territorio. Se ha analizado si existen diferencias de biomasa disponible entre los territorios conocidos y las zonas próximas potencialmente favorables. También, se ha explorado si había diferencias anuales y estacionales en la disponibilidad de biomasa. Por último se ha estudiado como esa variación puede afectar en el establecimiento de los territorios y cual son sus implicaciones en la conservación de la especie. Se encontraron variaciones en la disponibilidad de biomasa entre los diferentes territorios. No se aprecian diferencias anuales ni temporales dentro de cada territorio, pero si entre las zonas próximas potenciales. La disponibilidad de biomasa es menor dentro de los territorios que fuera de ellos, sin embargo permanece estable a lo largo del año sin fuertes fluctuaciones, al contrario de lo detectado en áreas adyacentes. Esta población puede estar siguiendo una estrategia que hemos denominado *Hipótesis de la Estabilidad Trófica*.

Buscando un enfoque integrador que profundice en la dinámica poblacional de la especie, en el **capítulo 4** se relaciona la distribución de la especie con el éxito reproductor. Concretamente se ha establecido cómo determinadas variables (abióticas y bióticas) condicionan la distribución de la especie y su éxito reproductor. Con el fin de identificar dinámicas subyacentes en la población se ha explorado la relación entre distribución y éxito reproductor. Para la población aragonesa, las variables bióticas seleccionadas, presencia de competidores como el Águila Real (*Aquila chrysaetos*) y disponibilidad de presas, tienen más importancia en la distribución de la especie que en el éxito reproductor. No ocurre lo mismo con las abióticas, aquellas relacionadas con la estructura del hábitat o con el clima influyen en el éxito reproductor (de manera negativa) pero no tanto en la distribución de la especie. Sin embargo, el cambio en alguno de los miembros de la pareja reproductor tiene una gran influencia no solo en el éxito reproductor, sino también en la dinámica de la población. Se ha detectado que la población aragonesa puede estar siguiendo una dinámica de sumidero ecológico. En zonas que ambientalmente son óptimas para la presencia de la especie, el éxito

reproductor es menor, debido principalmente al reemplazo de individuos reproductores dentro de la población.

Conclusiones y aportaciones científicas

- I. Los individuos reproductores de Águila de Bonelli en Aragón, muestran una alta fidelidad al territorio. Sin embargo, presentan una menor fidelidad a las zonas de nidificación dentro de un mismo territorio determinado por cada pareja reproductora.
- II. El comportamiento territorial de los individuos de la población de estudio está influido por la estacionalidad y el sexo de los individuos.
- III. El uso de diferentes escalas, espaciales y temporales, revelan diferencias en la selección de hábitat por parte de los individuos de esta población.
- IV. La estructura del hábitat juega un papel muy importante en el establecimiento y mantenimiento de los territorios.
- V. El uso del espacio que los individuos hacen dentro de los territorios depende de la estructura del hábitat y de los requerimientos ecológicos de la especie en las diferentes épocas del año.
- VI. La disponibilidad trófica constante, continua y predecible a lo largo del tiempo es uno de los factores que determinan el establecimiento y fidelidad al territorio en la población de estudio.
- VII. La población de Águila de Bonelli en Aragón parece seguir una dinámica de sumidero dentro de la población Ibérica. Parejas que establecen sus territorios en zonas presumiblemente más adecuadas para la presencia de la especie debido a sus características ecológicas favorables, presentan un éxito reproductor bajo. Este bajo éxito está condicionado principalmente por el reemplazo de individuos por la muerte o la emigración de algún miembro de la pareja reproductora.
- VIII. Para la conservación de especies territoriales amenazadas, se recomienda un seguimiento a largo plazo de los diferentes aspectos relacionados con el uso del espacio. Es interesante el uso de varias escalas, temporal y espacial, que

revelan problemas subyacentes y dan pautas específicas de actuación. Además el uso de aproximaciones integradoras, puede mostrar dinámicas poblacionales que no son identificadas a priori.



General Introduction

Spatial ecology is the combination of landscape ecology and population dynamics. Spatial ecology focuses on how landscape configuration might influence population and community dynamics (Tilman and Kareiva 1997). The classical ecologist, evolutionary and conservation biologists have addressed these issues separately. Recently, these disciplines recognize the importance of the space in their research and try to understand patterns and process simultaneously. Such approaches provide useful tools for designing conservation strategies (Collinge 2001).

One basic topic in spatial ecology is the home range behaviour. Many animals restrict their movements to a particular area, the home range (Burt 1943). Home range is the spatial expression of the interaction among individual characteristics, individual states, and the external environment. This has fundamental consequences for many ecological processes, such as the distribution of organisms, habitat selection, predator-prey dynamics and population regulation (Börger et al. 2008). The resulting patterns of this dynamic process might have great relevance for space use behaviour at different spatiotemporal scales and population levels (Wang and Grimm 2007).

In this way, statistical modelling approaches aided spatial ecology research, and have become a promising method for studying the spatial patterns of animals (Moorcroft and Barnett 2008), especially since the advent of new technologies (Dale et al. 2002; Börger et al. 2008). The use of large data sets of animal locations obtained by satellite telemetry has been a breakthrough in space-use behaviour studies. This approach has even allowed long-term monitoring programs with accurate information to explain biological process related to the animal space use (Rhodes et al. 2005; Moorcroft and Barnett 2008; Martínez-Miranzo et al. 2016a, see Chapter 1). Also, combining these tools provides a unified approach to multi-scale home range behaviour research (Moorcroft and Lewis 2006): quantifying the influence of individual characteristics, states or external environments on home range behaviour, while also quantifying the spatiotemporal scales of variation related to ecological process (Collinge 2001).

In spatial ecology, and especially in home range behaviour, the question of how scale influences patterns is a recurrent topic (Levin 1992; Börger et al. 2008). The spatial scale might have important effects in space-use and might condition the resulting patterns. In the case of studies addressing changes of space use in a particular species or population, to choose an inappropriate spatial scale might mask some important patterns and lead the researcher to erroneous conclusions. Therefore, the scale must be chosen based on biological criteria depending on the purpose of the research, and not arbitrarily (Wiens 1989). The same criteria might be applied to temporal scales. Long-term studies conducted at reduced spatial scales show low predictive capacity. However, short-term studies at broader spatial scales have higher predictability (Wiens 1989).

Addressing the precise scales might be important for applied disciplines such as conservation biology. When addressing species with widespread populations with very precise requirements at a fine scale, a multiscale approach seems most useful (Dray et al. 2012; Mc Garigal et al. 2016), revealing patterns that might not be perceived at a single scale. This is true for the spatial ecology of endangered territorial species. Although the general ecological or environmental requirements for species distributions match at larger scales, they will be different at population level or home range level during different seasons. Such mismatch is determined by resource availability in a particular season and, in a directly way, the allocation of such resources are determined by habitat structure in each home range (Börger et al. 2008). For that reason, multiscale approaches about habitat structure or selection are necessary to improve our knowledge of home range behaviour (Börger et al. 2006a, 2006b).

Prey availability is a commonly accepted resource influencing space use (Benson et al. 2005). For a generalist top predator, the real limiting factor is not prey type, but the total amount of biomass available from all potential prey (Lourenço et al. 2015). Habitat structure plays an important role in prey distribution, and it will determine the size and shape of the home range (Morris, 1987). Therefore, biomass abundance might be conditioned not only by habitat structure but also by temporal variations in prey availability in relation to its biological cycles (Martínez-Miranzo et al. 2016b, see Chapter 2). This involves taking into account the spatial and the temporal

scales, which might influence not only the establishment of a home range and the use of it but also the fidelity to it (Börger et al. 2006b).

As mentioned above, for a species to be allocated in a particular place, certain factors must concur. To manage endangered populations, it is necessary to determine such factors, which might be abiotic, biotic or related to intrinsic factors of the species. Climatic or habitat structure variables are often considered abiotic factors in species distribution models (Krebs 1978; Brown et al. 1996; Channel and Lomolino 2000; Guisan and Zimmermann 2000; Pearce and Ferrier 2001). Biotic factors, such as thropic resources or presences of competitors, are not so widely used, mainly because they are difficult to obtain. Only a few studies combine both factors, screening for the importance of climate, habitat and resource availability in species distribution (Carrascal and Seoane 2009).

In addition to species distribution, climate and resource availability might also influence breeding success (Ontiveros and Pleguezuelo 2000, 2003; Gil-Sánchez et al. 2004), determining the population viability in the long term. This approach can be problematic when the resources are properly distributed, and climatic factors do not alter breeding success. However, a risky population dynamic arises. Such a scenario is typical in conservation biology, where populations tend to be established in adequate sites with enough resources, but are unable to prevail over time. In this case, it is necessary to identify which factors compromise (in an indirectly way) the population viability. Such factors might include the loss of breeders in the population, the lack of replacement rates of those problems derived from the habitat transformation. An understanding of these underlying dynamics is essential for the management and conservation of endangered populations (Pulliam 1988; Pulliam and Danielson 1991). However, many times, these underlying dynamics are difficult to find. Connecting different methodologies under a multivariate approach might provide an integrated view of the question (Horne et al. 2008). Trying to find a solution based on contributions provided by both theoretical and applied disciplines is currently popular in spatial ecology and conservation biology (Collinge 2001).

Under this theoretical framework, this study investigates how space use influences the population dynamics of an endangered top generalist predator, the

Bonelli's Eagle (*Aquila fasciata*). We attempt to understand which factors determine the establishment of their home range and the space-use at different spatial and temporal scales; identifying how resource availability and distribution determine home range behaviour. Ultimately, we will determine the principal factors influencing the distribution of the Bonelli's Eagle in the northeast of Spain, and how these challenge population viability. This integrated vision of the spatial ecology of this species in this particular region will likely help with the management conservation of other species with similar requirements or spatial distribution.

Methodology

Model Species

Bonelli's Eagle is a raptor that belongs to the Order Accipitriformes. Molecular studies separated this species from the *Hieraetus* genus and included it in the *Aquila* genus (Helbig et al. 2005; Lerner and Mindell 2005; Jiang et al. 2015). Two subspecies are normally recognized, *A. f. fasciata* (Vieillot 1822) and *A. f. renschi* (Stresemann 1932). *A. f. fasciata* is principally distributed through the Mediterranean areas (as well as the Middle East) and is a winter visitor to northwest Africa. *A. f. renschi* (Stresemann 1932) is distributed in Lesser Sunda (Sumbawa, Komodo, Flores, Besar, Timor, Wetar, Luang) in south-eastern Asia.

Because of its wide Palearctic distribution, the Bonelli's Eagle is listed as Least Concern (LC) by the International Union for Conservation of Nature (IUCN). However, a decrease in prey availability, habitat disturbance, electrocution and direct persecution by humans (shooting or poisoning) in certain populations (as in the case of the Iberian Peninsula), makes the Bonelli's Eagle especially vulnerable (Ontiveros 2016). In Spain, the Bonelli's Eagle is included in the National Catalogue of Endangered Species (RD 139/2011), in the vulnerable category. Similarly, the species is included in the Annex I of the Birds Directive (species subject to conservation measures), Annex II of the Berne Convention (species subject to regulation to keep their populations out of danger) and Annex II of the Bonn Convention (species with unfavourable conservation status that require international collaboration for conservation).

Although the extent of occurrence is large, most of the breeding pairs of the subspecies *fasciata* are located in the Mediterranean area, particularly in the Iberian Peninsula. *A. f. fasciata* is distributed unevenly throughout the country, occurring mainly in the south and east areas of the Iberian Peninsula, where the best-preserved populations of this species exist (Ontiveros 2016). Currently, *A. f. fasciata* is recovering on the Mallorca Island, where it bred for the last time in 1964, and it did again in 2014, thanks to reintroduction programs arranged by the Life Bonelli project (*LIFE 12 NAT/ES/000701*).

The distribution of Iberian breeding pairs is very heterogeneous. No clear habitat preferences for establishing their territories have been defined (Ontiveros 2016). Several factors seem to influence such selection, including climate (Ontiveros and Pleguezuelos 2003), type of habitat (Sánchez-Zapata et al. 1996; Sánchez-Zapata; Calvo 1999 and Rico-Alcázar et al. 2001), food resources and competition with other species (Gil-Sánchez et al. 2004). Only one factor is common to all breeding pairs: the presence of medium height crags where they can establish their nests (Ontiveros 1999; Rico-Alcázar et al. 2001; Román et al. 2005; López-López et al. 2006). Although this species also nests in trees (common in the Portuguese population [LIFE06 NAT/P/000194]) in the Spanish fraction of the population, such nesting site selection is not frequent.

Due to the heterogeneity of their territories, the trophic spectrum of this species is variable. In the Aragón region, the diet consists of rabbits (28.5%), pigeons (24.0%), partridges (15.3%), other birds (11.6%), other mammals (7.1%), corvids (7, 0%) and reptiles (6.4%) (Alcántara et al. 2003). In line with this pattern of exploitation of the most abundant resources in each season or area, the analysis of the possible prey selection by the Bonelli's Eagle has not shown a clear pattern of selection of any of them (Ontiveros 2016). Coupled with the scarcity of rabbit as main prey, Bonelli's Eagle makes a fairly generalist species.

Study area and population

The study was conducted in the Aragón region (Northeast Spain). The altitude in the area ranges from 130 to 1200 m. s. n. m. The study area landscape consists mainly of coniferous forests (*Pinus uncinata*, *Pinus sylvestris* and *Pinus nigra*) and holm oak (*Quercus ilex*) with large areas of Mediterranean scrub (*Juniperus communis* *Juniperus thurifera*, *Cistus ladanifer* and *Quercus coccifera*). Filled cultivation areas mostly include dry cereals, wheat (*Triticum spp.*) and barley (*Hordeum vulgare*), fruit trees, and Mediterranean crops (principally olive trees [*Olea europaea*] and vineyards [*Vitis vinifera*]).

Bonelli's Eagle population in Aragón is one of the northernmost of the Iberian

Peninsula. It occurs from the Ebro River to the foothills of the Iberian System in Zaragoza and Teruel, the Somontano of Huesca and the pre-Pyrenees mountains, avoiding the greater heights of the Pyrenees (view supplementary material for details). Medium height crags are mainly used for nesting sites, and only two cases of nests in trees are known in our study area.

This population has suffered a general decline in recent years. In the late 1980s, this area included about 60 breeding pairs. However, in the early 2000s, the population did not exceed 33-35 breeding pairs, assuming almost a decline of 50% of the population in only two decades. After a Life project (LIFEB4-3200/97/252) was carried out between 1998 and 2001, the population has re-stabilized and now consists of 34 breeding pairs distributed across three provinces (Zaragoza [18 pairs], Teruel [11 pairs] and Huesca [5 pairs]). Despite the stabilization of the population, different conservation problems resulting from space use by breeders, home range behaviour and habitat transformation put this population under a real conservation threat (Ontiveros 2016; Martínez-Miranzo et al. 2016b)

As in other Iberian populations, shortage of good food resources (especially by the reduction in rabbit abundance) has led to a change in the trophic spectrum of the species, with the domestic pigeons and partridges as potential prey (Alcantara et al. 2003). This change in the trophic spectrum produces a change in the use of space and forces an adaptation to the new requirements.

Trapping and monitoring birds

Between 2004 and 2014, 21 breeders of Bonelli's Eagle were trapped in the study area. According to the different methodological approaches, subsets of individuals were selected for each chapter of this thesis (see particular methods section in each chapter).

Government environmental technicians captured the Eagles using radio-controlled bow-net traps. Individuals were ringed with a metal ring and PVC distance lecture ring and were equipped with a 45-g Argos/GPS PTTs (Microwave Telemetry, MD, USA). Transmitters were powered by solar panels and fixed to the birds as

backpacks by a Teflon harness with a central ventral rupture point (Garcelon 1985). The weight of the transmitters represented just 2.25% of total body weight (Kenward 2001).

Data gathering and processing

The GPS devices were programmed from 6:00 to 21:00, thus obtaining as much data as possible and avoiding hours when the animals have little or no activity (e.g., hours without light where these animals are not active). The platform for obtaining these data was ARGOS. Periodically (every three days) the satellite sends the collected data to the processing centre. From there, they are sent in .txt format files to the researcher (an example of the ARGOS output is provided in the supplementary material section).

Around 50,000 locations were obtained, and different subsets of data have been used in the different chapters of this study. The transmitter provides two different types of data, GPS and ARGOS, based on their accuracy. We only used GPS data due to their higher accuracy (+/- 3 m.) and rejected ARGOS data. Any single satellite location was processed, eliminating those that led to a pseudoreplication problem (Kenward 2001). Even though the transmitter was programmed to record positions only during the daylight hours, we further filtered the data according to the season. We restricted the data between 8:00 and 18:00 during the winter season and 7:00 and 20:00 during the spring season. We also eliminated data allocated to the same position for an extended period or if problems with the transmitter were detected. Although the accuracy of the data obtained with these transmitters is high, a second data processing was performed using geographic information systems (GIS). All data were plotted on a map and the ones that showed a wrong geographical position, such as an ocean position or different country were rejected. By this approach, we were able to remove erroneous position data.

To extract as much information as possible from the spatial ecology of these individuals, the filtered locations have been used in different subsets in different chapters of this study. The particular processing and analyses of each of the single subsets are detailed in each of the chapters.

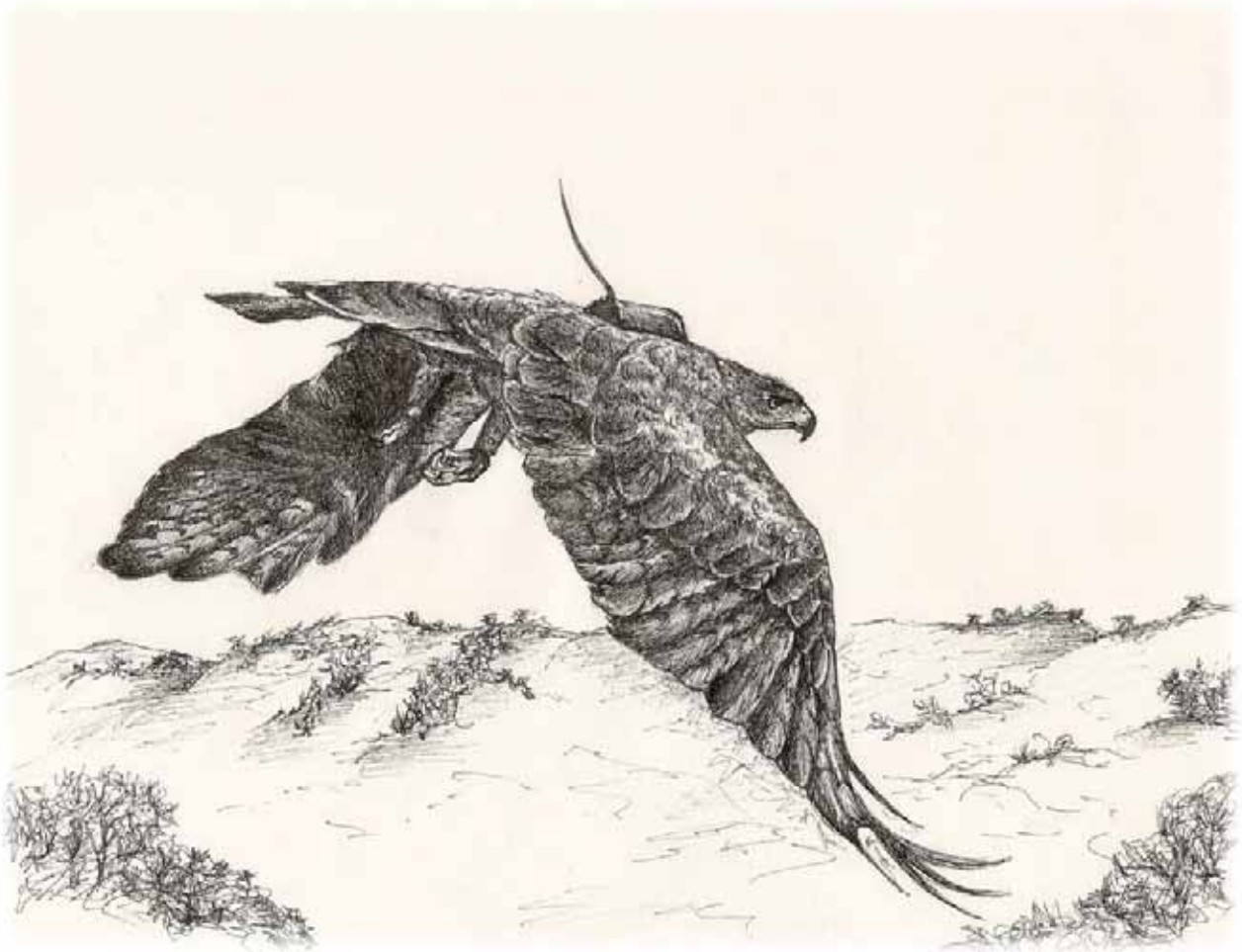
General Objectives

The general objective of this study is to make a significant contribution to the conservation of Bonelli's Eagle in Aragón based on the knowledge of spatial ecology of the species. To this end, we explore some aspect related to home range behaviour, habitat and resource selection and population dynamics. Particularly:

1. Evaluate the spatial and temporal variation in home ranges behaviour (**Chapter 1: Differential spatial use and spatial fidelity by breeders in Bonelli's Eagle (*Aquila fasciata*)**).
2. Determine habitat selection at different spatial and temporal scales and which factors determine long-term habitat selection (**Chapter 2: Multiscale analysis of habitat selection by Bonelli's Eagle (*Aquila fasciata*) in NE Spain**).
3. Insight into how prey availability affects the establishment and structure of home range (**Chapter 3: Home range requirements in a generalist top predator: prey abundance o trophic stability?**).
4. Identify optimal habitats for species occurrence and determine the relationship with breeding success (**Chapter 4: Mismatch between spatial distribution and breeding success reveals sink population dynamics in an endangered raptor species**).



Chapter 1: Differential spatial use and spatial fidelity by breeders in Bonelli's Eagle (*Aquila fasciata*)



This chapter is based on the manuscript: **Martínez-Miranzo B**, Banda E, Gardiazábal A, Ferreiro E, Aguirre JI. 2016. Differential spatial use and spatial fidelity by breeders in Bonelli's Eagle (*Aquila fasciata*). *Journal of Ornithology* 157: 971-979. doi:10.1007/s10336-016-1347-1

Differential spatial use and spatial fidelity by breeders in Bonelli's Eagle (*Aquila fasciata*)

Introduction

Home ranges are the spatial expressions of the behaviours that animals perform to survive and reproduce (Burt 1943). They are determined by a large number of single movement steps (Moorcroft and Lewis 2006), each of which results from the interactions among individual characteristics, individual states and the external environment, with fundamental consequences for ecological processes (Börger et al. 2008). Over the past few years, a new line of research has been opened in order to test the variations of home range behaviour (see the review in Börger et al. 2008). However, long-term monitoring studies about the spatial-temporal variations of the size and shape of home ranges are still limited (e.g. Adams 2001; Börger et al. 2006a). Long-term studies (Møller and Fiedler 2010) provide information about population dynamics, and may help identify conservation problems and suggest possible solutions. In addition, they are a useful tool to improve knowledge about home range behaviour and will play an important role in the conservation of long-lived territorial endangered species (Thomas 1996).

Recently, an increasing number of long-term studies about home range behaviour using telemetry devices have been published (Schradin et al. 2010; García-Ripollés et al. 2011; Hart et al. 2013). For example, studies of large raptors such as the Spanish Imperial Eagle (*Aquila adalberti*) (Fernández et al. 2009), Golden Eagle (*Aquila chrysaetos*) (Collopy and Edwards 1989; Marzluff et al. 1997) and Lesser Spotted Eagle (*Aquila pomarina*) (Meyburg et al. 2006) are having important applications in conservation.

Our research focuses on Bonelli's Eagle (*Aquila fasciata*), an endangered territorial raptor that has experienced a sharp population decline in Spain (Arroyo et

al. 1995; Ontiveros 2016) and other European countries such as Portugal, France (Hernández-Matías et al. 2013) and Italy (López-López et al. 2012). One of the most important causes of mortality is electrocution (Real et al. 2001), which is strongly related to the spatial ecology and land use of individuals. Therefore, home range behaviour studies are necessary when addressing conservation issues for this species.

Most studies about spatial ecology in Bonelli's Eagle focus on juvenile habitat use (Mañosa et al. 1998; Balbontín 2005; Cadahía et al. 2005; Balbontín and Ferrer 2009) but rarely treat breeding adults (Sanz et al. 2005; Bosch et al. 2009; Cabeza Arroyo and de la Cruz Solís 2011; Pérez-García et al. 2012).

Satellite radio-tracking systems to analyse spatial-temporal variation of adult Bonelli's Eagle territories have only been used in a few breeding individuals (Cabeza Arroyo and de la Cruz Solís 2011, Pérez-García et al. 2012), or the study is based on terrestrial radio-tracking data (Bosch et al. 2009). The latter provides useful information, but the accuracy of data is low compared to that obtained by modern systems of GPS satellite-tracking devices (Withey et al. 2001).

To our knowledge, this is the first investigation focusing on different spatial-temporal use and home range fidelity that includes large numbers of Bonelli's Eagle breeders of both sexes over a long time series of consecutive years and using GPS satellite telemetry. We divided the year into three periods due to the biological cycle of the animals. The territorial behaviour of breeders can be influenced by several factors like the breeding stage, the quality/quantity of food and the dependence stage of recently fledged juveniles (Real et al. 1998). The latter has not yet been studied.

We specifically evaluated the spatial and temporal variation in home ranges, examining the differences among individuals, sexes, years and the three annual periods, because this information may provide powerful applications in conservation highly necessary for this endangered species, not only in the Aragón Region (catalogued in critical danger, D 326/2011) but also in Spain as a whole (catalogued vulnerable, RD 139/2011) and Europe (least concern, IUCN Red List. Annex I of EU Bird Directive and/or SPEC 3 classification according to Tucker and Heath 1994).

Methods

Study area

The study was conducted in the Aragón Region (Fig. 1), Northeast Spain, over a 47,719 km² area which holds fewer than 30 Bonelli's Eagle breeding pairs representing 4 % of the entire Spanish population.

Land cover consists mainly of coniferous forests, large areas of Mediterranean scrub, steppe areas or crops, and crags and cliffs as nesting substrates in mid-mountain areas (Sampietro et al. 1998).

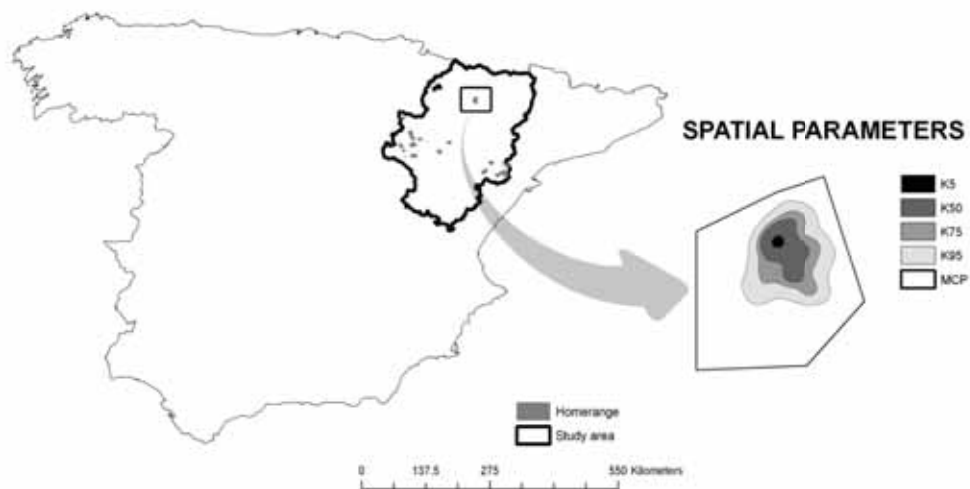


Fig 1 Study area and spatial parameters. 5% kernel (K5) nesting area, 50% kernel (K50) core area, 75% kernel (K75) critical area, 95% kernel (K95) and Minimum convex polygon (MCP).

Trapping and monitoring

During the years 2004–2011, 17 breeders of Bonelli's Eagle (10 males, seven females) were trapped in Aragón. The Eagles were trapped by a radio-controlled bow-net trap; all individuals were ringed with a metal ring and were equipped with a 45 g Argos/GPS PTTs (Microwave Telemetry, MD, USA). Transmitters were powered with solar panels and fixed to birds as backpacks by a Teflon harness with a central ventral rupture point (Garcelon 1985). The weight of the transmitters only represented 2.25 % of total body weight (Kenward 2001). PTTs were programmed to work between 06:00 h and 21:00 h. A total number of 48,000 locations from the 17 individuals were obtained (see supplementary material).

Spatial parameters and home range analysis

The spatial parameters and home ranges were estimated using Hawth's tools (Beyer 2004) in ArcGIS 9.3 (ESRI 1999–2009). Fixed kernel methods (Worton 1989) with a default smoothing factor (1) were used (Bosch et al. 2009; Fernández et al. 2009). Isopleths 5 % (K5) and isopleths 50 % (K50) were designated as the nesting and core areas, respectively (Samuel et al. 1985). Isopleths 75 % (K75) were calculated as the actively selected areas for hunting or roosting (critical areas) (Bosch et al. 2009), and isopleths 95 % (K95) were defined as an estimate of the total home range (Seaman and Powell 1996; Kenward 2001; Laver and Kelly 2008). Minimum convex polygon (MCP 100%) was defined as the maximum area used by individuals, which was calculated with all valid locations including outermost locations. Home range sizes were constructed using only diurnal locations. To avoid bias towards roosting areas, consecutively repeated locations in the early morning and late evening of inactive Eagles were excluded because they were considered to be non-independent (Swihard and Slade 1985; Seaman and Powell 1996; Kenward 2001).

For the temporal variation analysis we divided the year into three periods related to the biological cycle of the species (Arroyo et al. 1995). Period 1 was defined as the non-breeding season (NBr), from September 1 to February 14, when breeding individuals are less tied to their nesting area and accomplish long distance movements

(Newton 1979). In period 2, or the breeding season (Br) (from February 15 to June 14), both parents invest in clutches but females spend most of the time in the nest, and in general parents' movements are restricted (Ontiveros 2016). During period 3, or the post-fledging dependence period (Pfdp), between June 15 to August 31, parents continue to feed fledglings near nesting areas until the juveniles leave the territories where they were born and disperse (Real et al. 1998).

Home range fidelity analysis

We used the Kerneloverlap function in the AdehabitatHR package for R (Calenge 2006) to assess the degree of overlap over consecutive years and home range fidelity (range of 2–4 years depending on the individual tracked) in eight individuals (four males and four females) that had been tracked for more than two years. The index selected to estimate the home range overlap was the result of the intersection statistic index (VI) (Fieberg and Kochanny 2005). The VI index provides a measure of overlap that is a function of the full home range in different seasons. VI index ranged between zero (no overlap) and 1 (complete overlap).

Due to methodological limitations, the overlapping area for other spatial parameters (K5 and K50) was calculated as the percentage of any of the spatial parameters on an annual basis related to the maximum area that was used over all tracking years for each individual. To calculate the maximum area the Data Management module in ArcGIS 9.3 (ESRI 1999–2009) was used; merged polygons were obtained for each spatial parameter and the Dissolve function was used in such a way that duplicate values were deleted in overlapping areas to avoid overestimation of the area. To identify the degree of overlap, we calculated the percentage of area fidelity on a yearly basis. The spatial parameter K75 was not included in the analysis because these areas are randomly used by breeders and may change (Bosch et al. 2009).

Overlapping seasonal variation was determined in all of the three periods defined above.

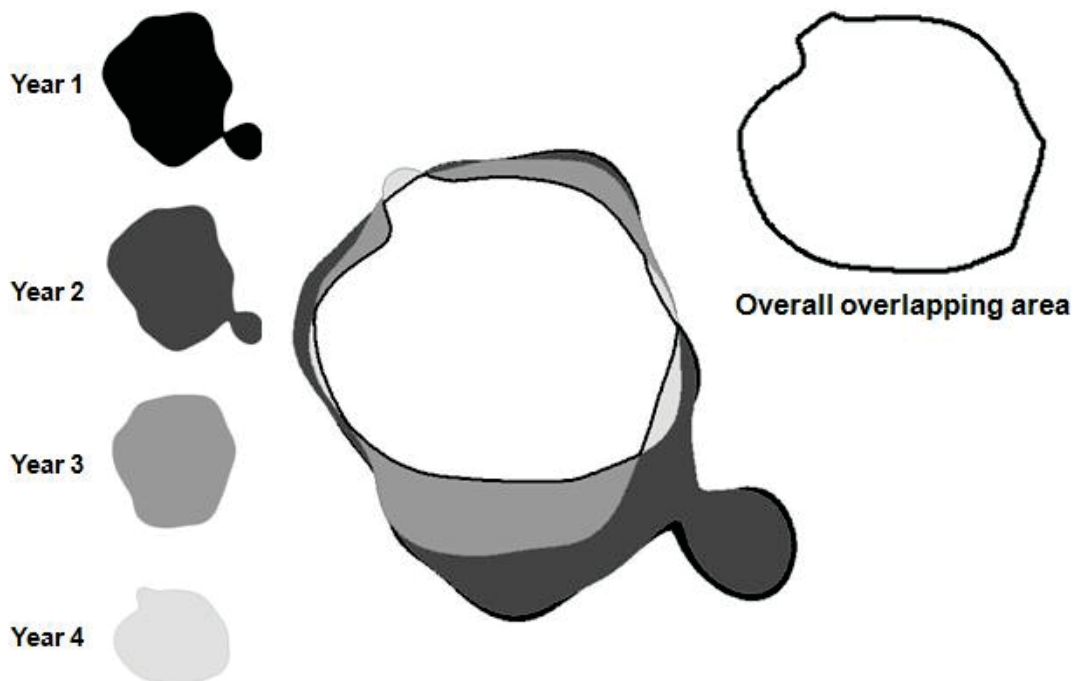


Fig 2 Example of overlapping areas for one individual over a 4-year period.

Statistical analysis

General linear mixed models (GLMM) in SAS statistical software (SAS 1989-96 Institute Inc., Cary, NC, USA) were conducted to analyse variations in home range according to individuals, sexes, years and annual periods. K5, K50, K75, K95 and MCP were used as response variables in all models and they were checked for normality (Kolmogorov–Smirnov, all $p > 0.05$).

Individual variations in home range behaviour were checked. The identity of individuals was considered as a fixed factor and year was included as a random factor. We studied differences between sex in home range using year and identity of the individual as random factors and sex as a fixed factor. To test annual variations in home range we used year as a fixed factor and the identity of the individual as a random factor. In addition, we studied variation among annual periods using year and identity of the individual as random factors and period and sex as fixed factors.

Home range fidelity by individuals was tested by chi-square analysis for all spatial parameters. In order to check differences between sexes, we used general linear models (GLM) in all periods for all spatial parameters. Sex was used as a fixed factor and year as a random factor.

The statistical significance of differences between categories of the same variable was computed using the LSMEANS statement of SAS. Degrees of freedom were calculated following the Satterthwaite method.

Results

Individual and sex size variations of home range

We found significant differences in all spatial parameters for all individuals (all $p < 0.001$).

There were significant differences when we compared males and females in all spatial parameters (Table 1).

The graphical representation shows that kernel areas are of irregular shape and the nesting area is often placed at one side of the total home range (Fig. 1). MCP is more than double the size of K95 (Table 1).

Temporal and interannual size variations of home range

Significant differences were found between the three annual periods in home range behaviour (K5 $F_{2,93} = 10.14$, $p = 0.0001$; K50 $F_{2,93} = 8.82$, $p = 0.0003$; K75 $F_{2,93} = 7.88$, $p = 0.0007$; K95 $F_{2,93} = 3.67$, $p = 0.029$) but not for MCP ($p > 0.05$), with all areas being smaller during the breeding season (LSMEANS, NBr and Pfdp > Br). When sex was included in the analysis, only females showed significant differences among periods for all spatial parameters (K5 $F_{2,39} = 11.03$, $p = 0.002$; K50 $F_{2,39} = 11.60$, $p = 0.0001$; K75 $F_{2,39} = 11.42$, $p = 0.0001$; K95 $F_{2,39} = 9.79$, $p = 0.0004$; MCP $F_{2,39} = 3.28$, $p = 0.0481$), with areas being smaller during the breeding season (LSMEANS, NBr and Pfdp > Br) (Fig. 3).

We did not find differences in home range sizes or other spatial parameters between years for all individuals (all $p > 0.05$).

| | K5 | K50 | K75 | K95 | MCP |
|---|---------------------|-----------------------|-----------------------|-------------------------|--------------------------|
| ♂ (n = 10) | 0.47 (0.23-0.89) | 8.45 (3.57-21.27) | 20.09 (7.99-60.16) | 55.05 (23.48-152.24) | 149.26 (26.97-563.45) |
| ♀ (n = 7) | 0.53 (0.20-0.98) | 10.11 (3.37-20.49) | 23.76 (8.32-43.78) | 59.44 (24.95-101.55) | 109.09 (27.18-414.98) |
| TOTAL (n = 17) | 0.5 (0.20-0.98) | 9.28 (3.37-21.27) | 21.93 (7.99-60.16) | 57.25 (23.48-152.24) | 131.22 (26.97-563.45) |
| ♂ (n = 10) F 9,48 | 7.07 | 6.66 | 6.62 | 6.29 | 4.16 |
| ♀ (n = 7) F 6,41 | 5.80 | 6.01 | 7.20 | 5.80 | 5.19 |
| TOTAL (n = 17) F _{16,95} | 6.04 | 6.24 | 6.86 | 6.45 | 4.82 |

Table 1 Mean values (Km²) and ranges (Min-Max) of sizes of all spatial parameters. F values of statistical differences (all $p < 0.001$) between the total of individuals and sexes for the designated spatial parameters. Sample size (n) and degrees of freedom (F) and number of cases are listed in the first column.

Home range fidelity

In general, home range fidelity showed stable patterns for periods and sexes. The degree of overlap for home range was 76.18 % in all periods during the study and similar between males and females (Table 2).

Core area fidelity was different between periods. More than 70 % of the core area was regularly used during the non-breeding season (Table 2). However, these values were smaller during the breeding season (mean = 58.60 %, range: 36.15–87.29 %) and during fledgling dependence (mean = 59.29 %, range: 41.01–80.27 %). We found a difference between males and females during breeding season ($F_{1,18} = 8.0152$, $p = 0.011457$). The degree of overlap in this period was higher in males than females.

Only 32.13 % of the nesting area was regularly used during all monitored seasons. Fidelity to the nesting area differed between individuals and periods, and was

even non-existent in some periods for some individuals (Table 2). We found sex differences during the non-breeding season ($F_{1,18} = 11.64350$, $p = 0.002777$), fidelity being higher in males than females.

| Sex | Years | K95 | | | K50 | | | K5 | | |
|-------------------------|-------|-------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| | | NBr | Br | Pfdp | NBr | Br | Pfdp | NBr | Br | Pfdp |
| ♂ | 4 | 78.15 | 73.24 | 74.18 | 73.82 | 71 | 74.8 | 0 | <u>57.71</u> | <u>30.15</u> |
| ♂ | 3 | 80.26 | 82.58 | 77.77 | 85.65 | 75.87 | 80.27 | 47.17 | <u>54.92</u> | <u>24.84</u> |
| ♂ | 2 | 79.17 | 71.79 | 75.58 | 82.47 | 53.24 | 59.22 | 50.77 | 3.24 | 0 |
| ♂ | 3 | 79.28 | 66.99 | <u>77.54</u> | 61.08 | 44.41 | <u>41.01</u> | 64.06 | <u>54.81</u> | 0 |
| ♀ | 4 | 77.96 | 68.31 | 82.24 | <u>79.51</u> | <u>40.22</u> | <u>61.27</u> | <u>4.16</u> | 0 | 0 |
| ♀ | 4 | 77.62 | 77.99 | 72.23 | 63.86 | <u>60.65</u> | 48.6 | <u>18.51</u> | <u>17.83</u> | <u>36.73</u> |
| ♀ | 2 | 78.28 | 64.66 | 80.94 | 66.47 | 36.15 | 47.13 | 76.52 | 40.90 | <u>58.89</u> |
| ♀ | 3 | 80.33 | <u>81.83</u> | 69.43 | 77.38 | 87.29 | 62.03 | <u>39.13</u> | 74.99 | <u>15.74</u> |
| Mean Males | | 79.22 | 73.65 | 76.27 | 75.75 | 61.13 | 63.82 | 40.50 | 42.67 | 13.75 |
| Mean Female | | 78.55 | 73.20 | 76.21 | 71.81 | 56.08 | 54.76 | 34.58 | 33.43 | 27.84 |
| Mean Total | | 78.88 | 73.42 | 76.24 | 73.78 | 58.60 | 59.29 | 37.54 | 38.05 | 20.79 |
| Mean all periods | | | 76.18 | | | 63.89 | | | 32.13 | |

Table 2 Overlapping percentage for the three designated periods over the study period. Mean values for each period and all periods are listed at the bottom of the table. Percentages in underline-blod show statistical differences (Chi square test, $p < 0.05$) in overlapping for that particular individual over the years of study.

Discussion

Our findings show the importance of long-term studies on movement ecology of endangered raptors like the Bonelli's Eagle. This allowed us to reveal that, although every individual has a different-sized home range, they show great home range fidelity, maintaining that size over time. Individuals make differential land use depending on the season. Females reduce the size of home ranges and other spatial parameters in the breeding season due to the presence of eggs and chicks in the nest.

Contrariwise to the fidelity to nesting areas, that changes depending on the time of the year.

Spatial patterns such as MCP or fixed kernel estimation are commonly used to calculate and characterize home range behaviour (Börger et al. 2006a). Many studies have used MCP for estimating the size of home ranges, but this method overestimates the areas that are used by the individuals and often makes inadequate biological assumptions such as a convex form of the home range determined only by the positions of the outermost locations (Worton 1995) (see Fig. 1). Therefore, the use of MCP, which includes long and peripheral movements, should be improved by the use of kernel fixed models (Worton 1989). Kernel estimators provide a better estimation and a more realistic view of the size and shape of the home range (Börger et al. 2006aa). In addition, the large and precise number of locations (48,000) obtained by GPS satellite telemetry and long-term monitoring over years shows the real area used. Our results highlight the differences between the two methods of analysis. The mean MCP would have been more than double the size of K95.

We obtained an average home range size of Bonelli's Eagles in Aragón (based on kernel estimation, K95 = 57.25 km²), with higher values than those obtained in other studies with terrestrial radio tracking in other regions of the Iberian Peninsula such as Catalonia (36.1 km², range: 33.4–110.7 km², Bosch et al. 2009) or Valencia (30.5 km², range: 15.82–44.48 km², Sanz et al. 2005). These differences could be due to the fact that GPS satellite telemetry provides more accurate information than that obtained in radio tracking studies. Pérez-García et al. (2012) found home range sizes of around 44.4 km² (range: 31.8–91.9 km²) in GPS-tracked Bonelli's Eagle in the Valencia-Tarragona area. This is in line with those described for large raptors such as Spanish Imperial Eagle (range: 2.06–139.19 km², Fernández et al. 2009) and Golden Eagle (32.76 km², range: 11.61–48.98 km², Collopy and Edwards 1989; 30.48 km², Marzluff et al. 1997) using conventional tracking methods, and Lesser Spotted Eagle (41.92 km², Meyburg et al. 2006) using GPS satellite telemetry. Despite differing methodologies, these values agree with those obtained in our study.

Individuals showed different home range size and shape as well as other spatial parameters. This difference may be influenced by several ecological and

environmental factors. Suitable habitats with favourable areas for nesting or hunting are very important in territorial species (Newton 1979). The presence of food resources and variation of prey abundances between areas will shape this variation. Besides this, the presence or absence of other species (like Golden Eagle or Griffon Vulture in the case of Aragón) that could compete for nesting sites and hunting areas may determine the selection of each individual territory (Martínez et al. 1994; Ontiveros and Pleguezuelos 2000; Gil-Sánchez et al. 2004). Individual performance (i.e. ability to find food or territorial defence, Ontiveros et al. 2005) also plays a major role in such a selection process. Man-built infrastructure like roads, and major infrastructure such as wind farms and high-speed railroad lines can also determine the size and shape of territories. In addition, all of the above can show variation related to the period of the year (Bosch et al. 2009).

We found differences in home range size as well as other spatial parameters in relation to the period of the year. Börger et al. (2008) noted that one of the factors influencing the establishment of territories is the physical and physiological state of the individual. In our study, females showed smaller sizes in their spatial parameters during the reproduction period. They decreased their activity due to the presence of eggs or chicks in the nest (Arroyo et al. 1995), restricting their movements and focusing on reproduction, remaining closer to the nest and making shorter flights in the search for food (Bosch et al. 2009), which is a common behaviour in other raptors (Marzluff et al. 1997; Haworth et al. 2006). However, no differences were found in males. This could indicate that, despite the fact that they also decrease their activity during the breeding season, they are still more active than females. The male's role is usually restricted to the custody of the nest and food supply (Newton 1979). In relation to food supply, Ontiveros and Pleguezuelos (2000) described how successful breeding of the species is not related to the abundance of their main prey, rabbits and pigeons (Martínez et al. 1994; Gil-Sánchez et al. 2004), but more so to the presence or detectability of alternative prey (Ontiveros et al. 2005). In our case, it is likely that males require the use of the entire home range to find food to feed the females and chicks. Thus, home range does not shrink in the breeding season and does not vary from the rest of the annual cycle.

There were no interannual variations for the same individual. Individuals also showed great fidelity to their home range over consecutive years. Home range fidelity is not a frequently evaluated topic in birds of prey. In contrast to the results described by Pérez-García et al. (2012) for Bonelli's Eagle in Valencia and Tarragona, which showed only a 30 % overlap, our results show a greater overlap, of about 76.18 % (Table 2), similar to that described in other species of raptor such as the Spanish Imperial Eagle (75 %, Fernández et al. 2009) and fidelity in the Golden Eagle (60 %, Marzluff et al. 1997). As for home range size, the degree of overlap could be determined by the availability of food resources and suitable nesting areas. The high degree of overlap in core areas could indicate that the availability of food is not a limiting factor for home ranges in Aragón. The high trophic plasticity described by Ontiveros and Pleguezuelos (2000) for Bonelli's Eagle enables them to establish a specific territory size and to maintain it over time in order to obtain all necessary resources. On the other hand, in Aragón, it does not seem to influence partner replacement after the death of one individual, or reproductive success in maintaining the territory (*unpublished authors data*). Although females have a lower degree of overlap in the core area in the breeding season, this is related to decreased activity by the female in the period associated with breeding.

However, fidelity to nesting areas is low (Table 2). Several raptors have different nests within their territories that they may occupy in different years (Newton 1979). In Aragón, nest competition with Griffon Vultures is quite strong. Starting their breeding season early, vultures occupy Bonelli's Eagle platforms before they begin reproduction. In addition, breeding failure or the death of one of the breeders could lead to a change in the nest in subsequent years (Ontiveros and Pleguezuelos 2000). Alternative nests also help mitigate the presence of ectoparasites (Ontiveros et al. 2008).

Our results provide compelling information with very important implications for conservation management. An essential measure is the conservation and protection of the home range, but some conservation programs only protect known nesting areas (Ontiveros 2016). In addition, many conservation programs have recommended buffer protection. This is usually designated as a 5 km circle around nest areas because there

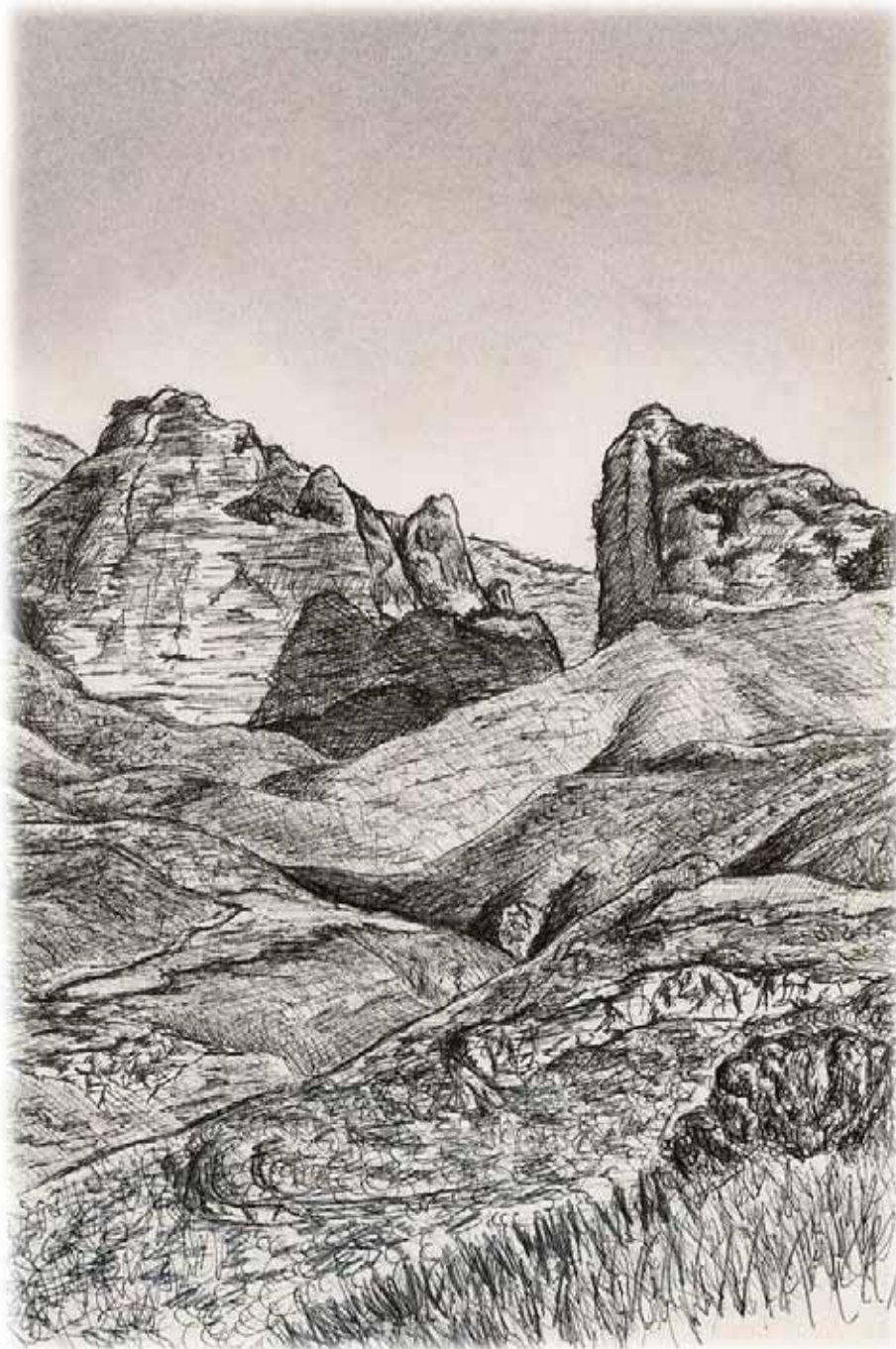
is insufficient information about spatial-temporal variations of individuals. In Aragón, the breeding Bonelli's Eagles showed strong individual variations in home range size and shape as well as in core and nesting areas. Therefore, establishing identical protection areas for all individuals is an inadequate measure that does not guarantee full protection because it may leave important areas unprotected or may waste resources on protecting areas that are not used by individuals.

Moreover, our results show that Bonelli's Eagle not only maintains home range sizes and core areas between years, but they also have a high degree of home range fidelity. We believe it is indispensable to extend certain protection measures to the total home range size, including correction of power lines, which are responsible for the highest number of deaths. We consider that the minimum area of protection must include not only the nesting areas but also all other areas chiefly used for hunting and roosting. We propose these areas to be limited by the K75 areas. Furthermore, some conservation measures such as restricting climbing, hunting and other outdoor activities should be carried out throughout the year, becoming more restrictive during the breeding season when individuals, especially females, are more vulnerable to human disturbance.

The fidelity to home range implies that conservation actions like correcting power lines or restricting infrastructure would have a lasting impact over time. Other factors such as habitat preference and food availability may determine fidelity to home ranges for this species and should also be addressed in the future. In addition, sound habitat management may assure the long-term persistence of this species in Aragón, Spain and therefore, in Europe.



Chapter 2: Multiscale analysis of habitat selection by Bonelli's Eagle (*Aquila fasciata*) in NE Spain



This chapter is based on the manuscript: **Martínez-Miranzo B**, Banda EI, Aguirre JI. Multiscale analysis of habitat selection by Bonelli's Eagle (*Aquila fasciata*) in NE Spain. European Journal of Wildlife Research 2016 62: 673-679. doi:10.1007/s10344-016-1041-x

Multiscale analysis of habitat selection by Bonelli's Eagle (*Aquila fasciata*) in NE Spain

Introduction

Spatial and temporal scales in ecology have been included in scientific research for decades (Wiens 1989; Levin 1992). In the field of conservation biology, and more specifically in habitat selection studies, the selection of an appropriate scale is very important. Ecological patterns that determine habitat selection may act differently depending on both the spatial scale and temporal scale (Wiens 1989; Levin 1992; Rico et al. 2001). Moreover, multiscale approaches may reveal patterns that are not perceived at a single scale (Levin 1992) and may be determinant in species conservation (Ontiveros et al. 2004).

The use of new tools allows a non-arbitrary scale selection based on biological criteria for the species. The implementation of Geographic Information Systems (GIS), GPS-tracking data and ecological data have been selected in these types of multiscale habitat selection studies, especially land cover databases (Balbontín 2005). One of the most popular land cover databases in Europe is CORINE. Despite the fact that CORINE is a systematically constructed land cover database covering a large area, it has been shown that this type of land cover data may be insufficient at a detailed scale (Heikkinen et al. 2014). For this reason, it is important to explore particular habitat structures, especially at a local scale where these features may change more rapidly (Wiens 1989). In addition, comparisons should be made with the available digital land cover information.

Similar to habitat structure, climate and resource availability can influence habitat selection as well (Ontiveros and Pleguezuelos 2000; Ontiveros et al. 2005; López-López et al. 2006). Territorial species establish their home range based on resource availability, for example, the availability of nesting areas (López-López et al. 2006) and prey (Ontiveros and Pleguezuelos 2000). However, this resource availability

may vary over the years or over particular periods in a single season. Recording food availability and its distribution throughout the home range can help to understand occurrence patterns of individuals at a particular place (regional scale) or the establishment of their territories (home range scale), but also their particular use of resources within the home range (local scale).

This is the case of Bonelli's Eagle (*Aquila fasciata*), a territorial raptor that is distributed throughout the western Palearctic, but mainly restricted to the Mediterranean region (Hagemaijer and Blair 1997; Ontiveros 2016). In the last several years, it has suffered a general decline in its populations (Birdlife International 2015), but most severely in the Western area of the Iberian Peninsula (Ontiveros 2016). Changes in land use by humans and a decrease in potential prey availability have played an important role in their decline (Ontiveros 2016).

Studies about habitat selection by Bonelli's Eagle are key to gaining knowledge about the spatial ecology of this species. Muñoz et al. (2005) and Carrascal and Seoane (2009) indicated the factors affecting the distribution of this species at a large-scale using geographic, climatic, landscape and human variables. On the other hand, Carrete et al. (2002) and López-López et al. (2006), explored habitat preference factors at a local scale also using these types of variables. Balbontín (2005) used the same approach to study juvenile dispersal. To our knowledge, this is the first study that uses precisely-defined home ranges (Martínez- Miranzo et. al. 2016a) of 14 adult individuals of different sexes at different spatial and temporal scales.

The aim of this study is to evaluate habitat selection by Bonelli's Eagle at different spatial and temporal scales and whether factors like habitat structure and prey availability determine long-term habitat selection. According with that, the results of this study may have important repercussions in the knowledge about the spatial ecology of this Eagle, helping to establish appropriate conservation policies.

Methods

Study area

The study was conducted in the Aragón Region, Northeast Spain. The altitude in the area ranges from 130 to 1200 m above sea level. Land cover consists mainly of coniferous forests and large areas of Mediterranean scrub filled with cultivation areas, mostly of dry cereals, fruit trees and Mediterranean crops (olive trees and vineyards). Craggs, cliffs and other unproductive areas like steppes are also present in this area (Sampietro et al. 1998).

Data collection

From 2004 to 2013, 14 adult breeders of Bonelli's Eagles (8 males, 6 females) were trapped in Aragón using radio-controlled bow-net traps. All individuals were ringed with a metal ring and were equipped with a 45-g Argos/GPS PTTs device (Microwave Telemetry, MD, USA). Transmitters were powered with solar panels and fixed to birds as backpacks with a Teflon harness with a central ventral rupture point (Garcelon 1985). The weight of the transmitters only represents 2.25% of total body weight (Kenward 2001). PTTs were programmed to work between 6:00 h. and 21:00 h. and collect one location per hour. To avoid bias towards roosting areas, consecutively repeated locations in the early morning and late evening of inactive Eagles were excluded because they were considered to be non-independent (Swihard and Slade 1985; Seaman and Powell 1996; Kenward 2001). A total number of 59 482 locations from the fourteen individuals were obtained.

Multi-scale and temporal habitat selection

The size and shape of the home range between years is maintained by Bonelli's Eagles in this area, but there are variations in the use within the home range depending on the period of year (Martínez-Miranzo et al. 2016a). The analysis of habitat selection was conducted at three different temporal scales and spatial levels of detail according to Johnson (1980) (Regional Scale, included all Aragón Geographical Region; Study Area scale, included all space with valid location obtained by GPS; and Home Range scale, within each territory calculating from GPS data ; RS, SA, HR, hereafter).

| H. TYPE | CLC 2006 | % | CLC 2000 | % |
|---------------------|------------------------------|-------|-------------------|-------|
| Scrub | | | Coniferous scrub | 5.13 |
| | Transitional woodland shrub | 3.67 | Dense scrub | 19.32 |
| | Sclerophyllous vegetation | 12.15 | Open scrub | 35.62 |
| | | | Mixed scrub | 0.07 |
| | | | Hardwood Scrub | 1.04 |
| | Broad-leaved forest | 2.47 | Evergreen forest | 3.19 |
| Forest | Coniferous forest | 7.44 | Coniferus forest | 33.65 |
| | Mixed forest | 0.29 | Riparian forest | 0.74 |
| Grassland | Natural grassland | 0.99 | Natural grassland | 1.24 |
| | Non-irrigated arable land | 40.97 | Non-considered | |
| | Permanently irrigated land | 9.34 | Non-considered | |
| | Rice fields | 0.52 | Non-considered | |
| Crops | Annual crops | 0.00 | Non-considered | |
| | Complex cultivation | 7.63 | Non-considered | |
| | Crops and natural vegetation | 8.01 | Non-considered | |
| | Vineyards | 1.37 | Non-considered | |
| Fruit Crops | Fruit trees | 1.05 | Non-considered | |
| | Olive groves | 1.09 | Non-considered | |
| | Urban Continuous | 0.31 | Non-considered | |
| | Urban Discontinuous | 0.14 | Non-considered | |
| | Industrial area | 0.25 | Non-considered | |
| Urban | Human networks | 0.04 | Non-considered | |
| | Mineral extraction | 0.12 | Non-considered | |
| | Dump sites | 0.02 | Non-considered | |
| | Construction sites | 0.15 | Non-considered | |
| | Ocio area | 0.02 | Non-considered | |
| Water | Inland waters | 0.29 | Non-considered | |
| | Water bodies | 0.37 | Non-considered | |
| Bare rock | Bare rock | 0.09 | Non-considered | |
| | Sparsely vegetated areas | 1.13 | Non-considered | |
| Unproductive | Burnt areas | 0.03 | Non-considered | |
| | Dunes and sand plains | 0.05 | Non-considered | |

Table 1. Habitat type composition (H. Type). Percentage of diferent habitat categories extracted from CLC depend on the scale : CLC 2006 (Regional scale and Study area scale) and CLC 2000 (Home range scale).

For the temporal variations in habitat selection we divided the year into three periods related to the biological cycle of the species (Arroyo et al. 1995). Period 1 was defined as the non-breeding season (NBr), from September 1 to February 14, when breeding individuals are less tied to their nesting area and made distant movements (Ontiveros 2016). In period 2, or the breeding season (Br) (from February 15 to June 14), both parents invest in clutches but females spend most of the time at the nest, and in general parents' movements are restricted (Ontiveros 2016). During period 3, or post-fledging dependence period (Pfd), between June 15 to August 31, parents continue to feed fledglings near nesting areas until the juveniles leave the territories where they were born and disperse (Real et al. 1998).

The different habitat types were extracted following habitat structure criteria from previous Bonelli's Eagle preferences (Ontiveros 2016) from categories in CORINE Land Cover (European Environment Agency 2007) depending on the scale used for the analysis (CLC 2006 for regional and study area scale and CLC 2000 for home range scale). We were unable to use the same CLC data for all the analysis because the detail level of CLC 2006 is lower than later versions of CLC 2000 (Table 1). In order to establish more precise habitat structure preferences at a home range scale the 3 highly selected categories for study area scales (Forest, Scrub and Grassland) were redefined more precisely into 9 new categories following CLC 2000 (i.e study area: scrub was redefined at a home range scale into dense scrub, open scrub, coniferous scrub and hardwood scrub) (Table 1). The number of categories were restricted according to data analysis used (Aebischer et al. 1993).

To test for random habitat selection by breeders at a RS we performed Chi square analysis in Statistica 8.0 software (StatSoft, 2007). Using Random Point Generation in ArcGis 9.3 software (ESRI 1999-2009), we generated the same number of random points as GPS locations in all Aragón Region area and tested the frequency difference between the two data sets. ANOVA analysis in Statistica 8.0 software was selected to test the temporal variation at this scale.

To perform habitat selection analysis at the SA level, we built a Minimum convex polygon (MCP 100%) defined as the maximum area used by individuals

(Kenward 2001). MCP was calculated with all valid locations including outermost locations. Individual home range was estimated using Hawth's tools (Beyer 2004) and Fixed Kernel methods, 95% isopleths (Worton 1989) with a default smoothing factor=1 (Fernández et al. 2009; Bosch et al. 2009; Martínez-Miranzo et al. 2016a) in ArcGIS 9.3 software. Home range sizes were constructed using only diurnal locations.

Compositional Analysis described by Aebischer et al. (1993) was selected to study habitat selection at SA and HR levels. This analysis utilizes a MANOVA test to compare the proportion of habitat available to habitat used and shows a rank of habitat types in order of use. In the cases where the habitat value is zero (not available or no use), we used the value 0.01 as recommended in Aebischer et al. (1993).

We conducted vegetation templates within the study area to find differences in habitat structure at an HR scale between CLC 2000 and actual composition. Following the method described by Prodon and Lebreton (1981), we recorded the vegetation structure along 140 randomly selected transect (2.5Km approx. each). In total, 1033 vegetation templates were made at the beginning and end of each itinerary and each time there was contact with any potential prey. Line transects were performed on foot during two consecutive years during the three annual periods previously described. We visually estimated grass cover (the percent of vegetation below 0.5m in height), scrub cover (the percent of vegetation between 0.5m and 2m in height) and tree cover (the percent of vegetation above 2m in height).

Only scrub cover was selected for the analysis because scrubland has a positive effect on the frequency of species occurrence (Carrascal and Seoane 2009) and is one of the most selected habitat types at this scale. With the percent of vegetation structure calculated in each transect, we created two categories in relation to the principal type of scrub cover in CLC 2000. Values between 0% and 40% were selected because they best fit the values recorded by CLC 2000. Open scrub was assigned to percent between 0%-40% and dense scrub to percent between 40% and 100%. We compared whether there were differences between scrub cover in CLC 2000 and the actual scrub cover. In addition, we checked for the possible difference between periods and years.

Prey availability

To record prey availability at different habitat types, we selected the main prey groups for this species in Aragón. Pigeons (including *Columba* sp. and *Streptopelia* sp.) (27 %), Lagomorphs (including *Oryctolagus cuniculus* and *Lepus europaeus*) (22%), partridges (*Alectoris rufa*) (11%) and corvids (*Corvus* sp.) (7%) (Alcántara et al. 2003) represent up to 67 % of Bonelli's Eagle diet in Aragón. Direct censuses on foot were performed (Tellería 1986). A total of 140 random transect (2.5 Km aprox. each) were performed during two consecutive years in the three annual periods described above in the study area. A total of 1,050 km were censused and 753 contacts of prey were obtained. The very low presence of rabbit and partridge in the study area was insufficient for analysis. For each itinerary, the total number of available prey was recorded and corrected by the total length of each transect obtaining an index of prey/length unit (KAI, kilometric abundance index) (Tellería 1986).

We compared prey availability with scrub habitat type. This type of habitat may influence the presence and detectability of prey by the Eagles. To overcome the large number of no prey presence in the transect Generalized Linear Models (GLZ) analysis in Statistica 8.3 software with Poisson distribution and logit transformation was performed. Prey type was used as a dependent variable and the presence of clear and dense scrub were the categorical explanatory variables. For all statistical tests, probability values less than 0.05 were considered significant.

Results

Habitat selection

At the regional scale, habitat selection by Bonelli's Eagle showed a strong tendency towards scrub and forest, which represent 76.5 % of the total habitat selection. Results differed significantly from random ($\chi^2 = 68874.42$, $p < 0.001$). No differences between periods were found at this scale.

Compositional analysis at the study area scale showed that Eagles do not use the habitat randomly. We found significant differences in habitat-use among three periods of the year (see Table 2). According to the ranking matrix, forest and scrub

habitat were the most used while agricultural areas like fruit trees and crops were less selected. Nevertheless, we detected differences in selection order between periods (Table 2). Forest was selected more than scrub outside of the breeding season while during the breeding season scrub and rock were the most chosen habitats. In addition, urban areas were significantly more preferred during the breeding season.

We also found significant values at a home range scale (Table 2). Compositional analysis showed that coniferous forest and dense scrub were the most selected and evergreen and riparian forests were the least preferred habitats. Differences in use between periods were also found. Dense scrub is more selected during the breeding season and post-fledging dependence period while coniferous forest was the most preferred during the non-breeding season.

We found significant differences between scrub cover in different periods ($F_{(2,631)} = 7.6649$; $p < 0.001$). The scrub cover values were higher during the breeding season and lower during the nonbreeding season. No differences were found between actual scrub cover categories and CORINE categories ($F_{(1,631)} = 0.00063$; $p = 0.979$). The scrub cover values did not change between years.

Prey availability

GLZ models showed significant differences between pigeon abundance and habitat structure. Higher abundances of pigeons were found in dense scrub (Wald $X^2(1) = 17.563$, $p < 0.001$). On the other hand, when we compared corvids abundance and habitat structure, they showed higher abundances in clear scrub (Wald $X^2(1) = 5.6962$, $p = 0.017$).

| Scale | Period | Wilk's λ | P | Ranked habitat types |
|-------|--------|------------------|--------|---|
| SA | NBr | 0.1046 | 0.0090 | FOR>SCR>ROC>GRA>WAT>URB>UNP>FRU>CRO |
| | Br | 0.0937 | 0.0020 | SCR> ROC>FOR>URB>GRA>WAT>UNP>FRU>CRO |
| | Pfd | 0.0547 | 0.0010 | FOR>SCR>WAT>ROC>GRA>URB>UNP>FRU>CRO |
| HR | NBr | 0.3324 | 0.0355 | CON.F>CON.S>GRA>DEN.S>OPE.S>MIX.S>HAR.S>RIP.F>EVE.F |
| | Br | 0.2893 | 0.0171 | DEN.S>GRA>CON.F>MIX.S>CON.S>OPE.S>RIP.F>EVE.F>HAR.S |
| | Pfd | 0.2857 | 0.0160 | DEN.S>MIX.S>CON.S>GRA>CON.F>OPE.S>HAR.S>RIP.F>EVE.F |

Table 2. Ranked matrix of habitat type selection for all individuals (n = 14). For Study Area scale (SA) habitat types, Forest (FOR), Scrub (SCR), Bare rock (ROC), Grassland (GRA), Water (WAT), Urban (URB), Unproductive (UNP), Crop fruit (FRU) and Crops (CRO). For Home range scale (HR) habitat types, Coniferous forest (CON.F), Coniferous scrub (CON. S), Grassland (GRA), Dense scrub (DEN. S), Open scrub (OPE.S), Mixed scrub (MIX.S), Hardwood Scrub (HAR. S), Riparian forest (RIP.F) and Evergreen forest (EVE.F).

Discussion

This study shows the importance of a multiscale approach to identify habitat selection by Bonelli's Eagle. Our results show that while, at a regional scale, individuals select heterogeneous habitat with crops areas, scrub areas and coniferous forest, at a smaller scale habitat structure within the home range plays a key role in habitat selection. Increased use of scrubland and coniferous forest, as with other areas with human presence, has been detected. Selection seems to be conditioned by the presence of potential prey and personal experience of each individual. Such selection varies depending on the season and the needs of individuals at each particular moment of the season.

The integration of modern tracking tools and classical census methods provides large amounts of high quality data. This allowed us to implement the method described by Aebischer et al. (1993), avoiding its main problems (i.e., inappropriate level of sampling and sample size, non-independence of proportions and arbitrary

definition of habitat availability). It also allowed us to establish sampling periods synchronized with the biological cycle of the species.

Similarly, studies involving comparisons over time can reveal differences in habitat use related to the needs of each species at a particular time during the annual cycle (e.g. breeding season in raptors). For this reason it is important to consider seasonal variability in the use of space and should be linked to the availability of resources and the importance of a heterogeneous and changing habitat within a study area. Therefore, long-term studies of endangered species are also important because conservation policy implementation in large areas is often based on very short-term studies (Wiens 1989).

At a regional scale, we found a non-random selection of habitat types. In line with other studies (Carrascal and Seoane 2009, Ontiveros 2016), Bonelli's Eagle in the Aragón region selected heterogeneous landscapes with scrub and forest, dotted with cliffs (important for nest site selection by this raptor) (López-López et al. 2003). Prey detectability seems to be the main factor driving the selection of this type of habitat (Ontiveros et al. 2005). Nevertheless, crops and other fruit fields were not selected by individuals (Carrete et al. 2002). Despite the fact that this species can tolerate human presence (Muñoz et al. 2005), high-intensity human activities such as agricultural practices or heavy vehicle traffic in the area may exceed the Eagles tolerance threshold, regardless of higher prey abundance (pigeons, partridges and rabbits in fruit crops and edge habitats) (authors' unpublished data). Furthermore, no temporal variation was found at this scale. This variation is difficult to detect at a large scale and even at others levels.

At the study area scale, Eagles showed a differing habitat selection among seasonal periods. Rocks were selected by individuals during the breeding season. The Bonelli's Eagle is a Mediterranean raptor that nests in cliffs at moderate altitudes, and therefore a positive selection for this habitat is expected during this period. Scrub was also more selected during this period. The presence of chicks during the breeding season demands provision of high amounts of food by the breeders. Scrub is the preferred habitat for the main prey species of Bonelli's Eagle (rabbits and partridges) (Gil-Sánchez et al. 2000; Carrete et al. 2002). Therefore, individuals spend more time in

these areas hunting. Forests (principally coniferous forests) are more selected during the rest of the periods. Although they do not visit the nest area frequently, they spend a lot of time in forest habitat during the rest of the year, primarily for roosting and defending their home range.

Urban areas (small rural villages and open industrial areas) were primarily selected during the breeding season over other habitats. The scarce abundance of prey for these Eagles (rabbits and partridges) in their original habitats and the plasticity of this species to adjust their diet can condition such selection (Ontiveros and Pleguezuelos 2000). Under conditions of prey shortage, Bonelli's Eagles can hunt rock pigeons (*Columbia livia*) and common woodpigeons (*Columba palumbus*). Pigeons concentrate mainly in urban habitats (Palma et al. 2006) and therefore Eagles use these high-density areas to hunt more efficiently. In fact, there is an important percent of this type of prey in the Bonelli's Eagle diet in Aragón (Alcántara et al. 2003).

Individuals' experience, especially in raptors with large home ranges, is important to optimize resource exploitation. At the home range scale, we found that dense scrub is more selected than open scrub. In contrast to other studies (Balbontín 2005; López-López et al. 2006) breeders in Aragón preferred this type of scrub although prey detectability is lower. In spite of the fact that the main prey such as rabbits and partridges are very common in areas with clear Mediterranean scrub, alternative prey such as pigeons (which makes up 26.7 % of the diet in Aragón (Alcántara et al. 2003)) are also associated with coniferous forest and transition areas with dense scrub. The shortage of main prey in the study area along with the personal experience of the individuals and the knowledge of their home range can lead individuals to spend more time looking for alternative prey such as pigeons in these areas of dense scrub despite their lower detectability.

In conclusion, long-term multiscale habitat selection studies can reveal aspects that are undetected at a single scale or that might need some time to be revealed due to changes during the year mainly driven by differential resource availability. In addition, the use of new tracking technology can show more precise results in certain areas and can address more precise conservation concerns. In our study area, we confirmed that in spite of the fact that individuals follow a general pattern for

establishing home range, prey availability is very important to determining that home range. The home range use by individuals is closely related to the period of the year. Therefore, it is very important to implement conservation measures not only at a large scale but also at a short time scale, keeping in mind variation throughout the year. Habitat structure and the adaptation of the species to habitat changes should be considered. For example, the use of urban areas by Bonelli's Eagles during the breeding season is not usually included in conservation programs. In the same way, conservation policies addressing temporal variation could be considered, for example, regulating climbing activities during the breeding season and managing forest areas during the non-breeding season.

Chapter 3: Home range requirements in a generalist top predator: prey abundance or trophic stability?



This chapter is based on the manuscript: **Martínez-Miranzo B**, Banda EI, Aguirre JI. Home range requirements in a generalistic top predator: prey abundance or trophic stability? Population ecology *under review*

Home range requirements in a generalist top predator: prey abundance or trophic stability?

Introduction

Understanding the underlying mechanisms by which species establish their home ranges is an issue that has been approached in studies about home range behaviour (Burt 1943; Börger et al. 2008; Van Moorter et al. 2016). Theory predicts that individuals establish their home range based on the need for minimal resources to survive and reproduce (Maynard Smith 1974; Wilson 1975). One of the commonly accepted limiting factors in the establishment of home ranges is food availability, especially in top predators (Ontiveros & Pleguezuelos 2000; Benson, Chamberlain & Leopold 2005; Lourenço et al. 2015). Individuals establish a minimum territory size with adequate prey availability for survival, thus optimal foraging (Benson et al. 2005). If prey abundance is scarce it may involve territory size or maintenance and indirectly in home range behavior (Lourenço et al. 2015).

Top predators select a specific prey types and prefer more profitable prey (Sih & Christensen 2001). In generalist top predators, where prey type is not a limiting factor, the total amount of biomass available from all potential prey plays a key role (Fargallo et al. 2009; Lourenço et al. 2015). Previous studies have used prey abundance as an index to assess the availability of food within a home range (Ontiveros & Pleguezuelos 2000; Ontiveros, Pleguezuelos & Cano 2005). However, not particular prey abundance but the total amount of available biomass to be consumed would be more realistic approach (Lourenço et al. 2015).

In addition, prey abundance can be influenced by temporal variations on the prey biological cycle and habitat characteristics (Korpimäki & Krebs 1996; Millon et al. 2008; White 2008). This may be determinant for territory size and maintenance over time, especially in environments under marked seasonality. This is the case of Mediterranean ecosystems, where the limited prey availability at certain times of the

year may influence home range behaviour or even survival of these territorial species (Fargallo et al. 2009).

In this study, we examined the effect of available biomass in the home range behaviour of Bonelli's Eagle (*Aquila fasciata*), a long-lived Mediterranean territorial raptor. They are able to maintain home range size and shape over the years (Martínez-Miranzo et al. 2016a). In addition, the trophic plasticity acquired by this species in particular areas of its distribution (mainly due to the absence of potential preys as rabbits (Ontiveros et al. 2005; Moleón et al. 2012a) makes it a great model to understand the underlying processes relating home range structure under extreme seasonal environments.

Based on long-term monitoring programs of breeding individuals, that maintain their home ranges' size and shape over the years (Martínez-Miranzo et al. 2016a), we tested whether Western European populations with a wide trophic spectrum (Resano-Mayor et al. 2015) establish their home ranges based on biomass abundance or otherwise seek for stable biomass availability to be consumed over time.

We assume that for generalist top predators, the best approach would be the one involving total available biomass to be consumed. In particular we tested whether there is a difference in the biomass availability inside and outside the home ranges. In addition we checked whether there is a temporal variation in the total biomass availability which can be extreme in ecosystems with a strong seasonality such the Mediterranean ones.

Methods

Study Species and study area

Bonelli's Eagle is a large raptor distributed almost exclusively in the European Mediterranean region and south-east of Asia (Cramp and Simmons, 1980). It is considered a territorial raptor and a generalist predator that can adapt its diet to prey availability (Ontiveros 2016). Such adaptation allows this species to establish their home range in a wide range of ecosystems from desert to forested areas with patchy

crops and Mediterranean scrub (López-López et al. 2006; Carrascal and Seoane 2009, Martínez-Miranzo et al. 2016b).

From 2004 to 2014, we monitored a population of Bonelli's Eagle in Aragón (Northeast of Spain), over a 47719 km² area which holds less than 30 Bonelli's Eagle breeding pairs representing 4 % of the entire Spanish population. The altitude in the area ranges from 130 to 1200 m.a.s.l. Land cover consists mainly of coniferous forests and large areas of Mediterranean scrub filled with farming areas, mostly of dry cereals, olive trees and vineyards. Crags, cliffs and steppes are also present in this area (Sampietro et al. 1998), see Martínez-Miranzo et al. 2016a and Martínez-Miranzo et al. 2016b for further details about the study area.



Fig 1. Home range distribution around the study area.

Home range behaviour

For this study we selected 6 breeding areas distributed throughout the Aragón region (Fig. 1) based on the presence of diverse habitat, covering a wide variety of habitats, from coniferous forests to steppe areas and upland crops, through rocky and diverse scrub types. In addition all breeding areas were selected based on the previous knowledge of the home range behaviour of the breeding pair.

We trapped 6 individuals (3 males and 3 females), in 6 territories, using radio-controlled bow-net traps. All individuals were ringed with a metal ring and were equipped with a 45-g Argos/GPS PTTs device (Microwave Telemetry, MD, USA). Transmitters were powered with solar panels and fixed to birds as backpacks with a Teflon harness with a central ventral rupture point (Garcelon 1985). The weight of the transmitters only represents 2.25% of total body weight (Kenward 2001). PTTs were programmed to work between 6:00 h. and 21:00 h. and collect one location per hour. To avoid bias towards roosting areas, consecutively repeated locations in the early morning and late evening of inactive Eagles were excluded because they were considered to be non-independent (Swihard and Slade 1985; Seaman and Powell 1996; Kenward 2001). Particularly, locations before 8:00 and after 18:00 were rejected during winter and all locations were kept during summer.

With the collected data (about 48000 locations), we estimated the breeders home range using Fixed Kernel methods (see Martínez-Miranzo et al. 2016a for more details). In spite that home range size differs between individuals, the size and shape of the home range between years remains constant for each individual over the years in this area (Martínez-Miranzo et al 2016). Nevertheless, there are variations in the use within the home range depending on the period of year (Martínez-Miranzo et al. 2016b).

Census methodology

To identify relationships between home range behaviour and food availability, specific census methodology to record potential preys was designed. Pigeons (including *Columba* sp. and *Streptopelia* sp.) (27%), rabbits (*Oryctolagus cuniculus*)

(22%), led-legged partridges (*Alectoris rufa*) (11%) and corvids (*Pica pica*, *Corvus monedula* and *Corvus frugilegus*) (7%) represent up to 67% of Bonelli's Eagle diet in Aragón (Alcántara et al. 2003). We selected these prey types as representatives of potential prey for this raptor and recorded their abundance by stripe transects to provide an index of prey abundance (Fitzner et al. 1977).

During two consecutive years (2013 and 2014) stripe transect on foot were performed. We established 2 census areas, one within the home range (HR onwards) and another one outside it but within the potential boundaries (PB onwards) of a circular buffer established with a central point in the territory and a maximum radius determined by the outermost point of the established home range (Fig 2). Those areas were to be potentially occupied by breeders but they were never used (see Martínez-Miranzo et al. 2016a for more details). Kernel polygon, isopleths 95% (Martínez-Miranzo et al. 2016a) was considered as home range. To calculate the area outside the home range a buffer was calculated using the "Buffer analysis" tool in ArcGIS 9.3.

We divided the study area in a 1x1 km grid and randomly chose 20 grids per settlement area (ten within home range and ten outside it) (Fig. 2). In every grid the census transect followed paths, field edges and open landscape where no significant differences on the detectability of the prey with other areas within the grid were detected (see Martínez-Miranzo et al. 2016b for further details). Since the surveys were conducted simultaneously for the 4 prey types, bandwidth was established at 25m (Tellería 1986). The duration of each itinerary was approximately one hour at a constant speed of 2.5 km / h. The censuses were conducted in the early morning hours and late afternoon (Moleón et al. 2012; Palomares 2001). We always avoided the midday hours, with more sun exposure and lower potential prey activity. All transects were conducted with sunlight to adjust to the phenology of a diurnal predator, such as the Bonelli's Eagle.

In order to identify temporal variations in prey availability, we repeated exactly the same itineraries during three different periods related to the biological cycle of prey and predators. Winter census was carried out in November, related with non-breeding season of the Eagle (NBr) when breeding individuals are less tied to their

nesting area and perform distant movements (Ontiveros 2016). In this period, prey availability is lower and human hunting activities are in progress so may caused difference in prey availability. Spring census, in March, is related to the Eagle's breeding season (Br). In general breeder's movements are restricted and prey availability at this time is important for breeding (Ontiveros 2016). Summer census was carried out in June, synchronized with post-fledging dependence period (Pfdp), were parents continue to feed their fledglings near nesting areas until the juveniles leave the territories where they were born and disperse (Real et al. 1998). In the summer period prey populations increase (Gálvez-Bravo 2011) and human hunting activities start.

To determine relative prey abundance, a Kilometric Abundance Index (KAI) is usually recommended (Telleria 1986). For top predators biomass rather than prey abundance is important in the diet (Lourenço et al. 2015). For that reason, an index based on prey biomass was calculated. We assigned a relative prey biomass contribution adapting the method designed by Real (1998). We assigned a relative biomass of 900 g per rabbit, 420 g per red-legged partridge, 400 g per pigeon and 642.5 g per corvid (included the biomass average between all corvids species were accounted). For each transect, the total number of available prey biomass contributing was recorded and corrected by the total length of each transect obtaining an index of biomass/distance unit or Kilometric Biomass Index (KBI onwards).

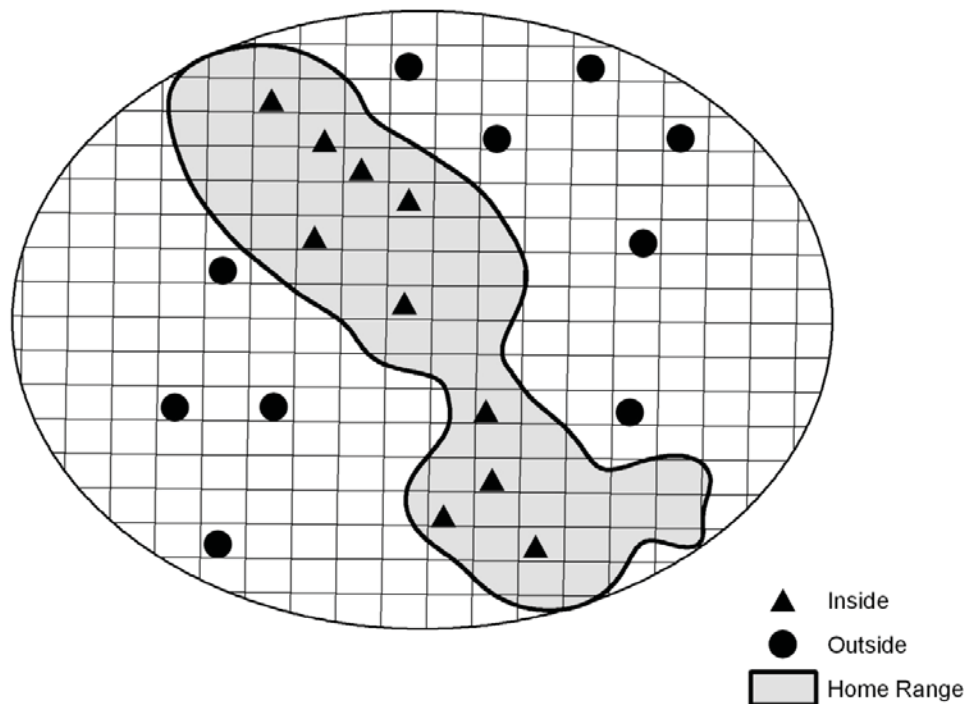


Fig 2. Example of census methodology. Grey area shows the home range and white area shows the buffer corresponding to the potential area outside the home range. A grid (UTM 1X1 Km) was overlaid in order to randomize census transects. Triangles represent the randomly UTM itineraries performed inside the home range and circle outside it.

Data analysis

First we determined general availability of the different prey types.

We examined the distribution of KBI to give the proper treatment to our data. Due to the limited presence of some potential prey data obtained for this study with a lot of absences over transects (Zero inflated) we analyzed our data using zero-inflated hurdle regression model with binomial distribution (Cragg 1971). General models were constructed using KBI as dependent variable. Home ranges, with two levels (inside (in) or outside (out)), year and period were used as covariates in different models. All the residuals distributions were checked to validate the use of the different models (Potts & Elith 2006). All analyses were performed using R software (3.2.2).

We checked if there was a difference in the biomass availability between territories using KBI as the response variable and home range as explanatory variable. Also, we constructed a Linear Regression to test if home range size influences KBI.

In order to determine distribution of biomass availability in the territories we built a model where KBI was used as response variable and home range (in/out) as explanatory variable. In addition, a series of *post hoc* Tukey's tests were performed to identify particular relations between biomass distribution and home ranges.

We also examined if any temporal variation pattern could be identified concerning biomass availability. To test for annual variation, we used KBI as a dependent variable and year and side as explanatory variables in different models. Also, we tested for any seasonal variation in KBI. We constructed different models using KBI as dependent variable and period and side as covariates.

Models were evaluated following Akaike Information Criteria (AIC) (Burnham and Anderson 1998) and were fitted one by one and ordered according to their decreasing AIC values. We used AIC weights (ω_i) to generate weighted model-averaged parameter estimates.

Results

Prey availability

A total of 1050 km were censused and 2042 prey contacts were obtained during two consecutive years. Rabbits (160 contacts) were the less recorded type of prey and pigeons (1065 contacts) were the most recorded. Red-legged Partridges (526 contacts) and corvids (291 contacts) were prey type with medium abundances.

Biomass distribution

Significant differences between total biomass availability and home range were found ($Z_{1,5} = 3.032$, $p = 0.024$). That is, each home range has a different availability of biomass. We did not find any correlation between KBI and home range size ($R^2 = 0.25$ and $P = 0.179$), indicating that home range size does not influence KBI.

Also, we found significant differences in biomass availability distribution ($Z_{1,6} = 3.173$, $p = 0.001$) between home range and potential boundaries areas. It was higher outside the home range (PB) than inside (HR) (Fig. 3).

A Total of 6 models were built. The best model to explain biomass variation was $KBI \sim \text{Period} + \text{Home range} + \text{Side}$ (Table 2). So, biomass availability distribution is explained by home range, and the situation (HR or PB). Also seasonal variation, particularly NBr period, influence biomass availability.

After the *post hoc* analyses we found a variation in KBI of potential boundaries areas between home range 4, 6 and the rest. On the other hand, a stable KBI was found for all real home ranges. So, there is an irregular biomass availability outside the home range and show large fluctuation (range 1188-232 g/Km) while biomass availability inside is regular and similar in all home range (range 678-285 g/Km) (Fig. 3)

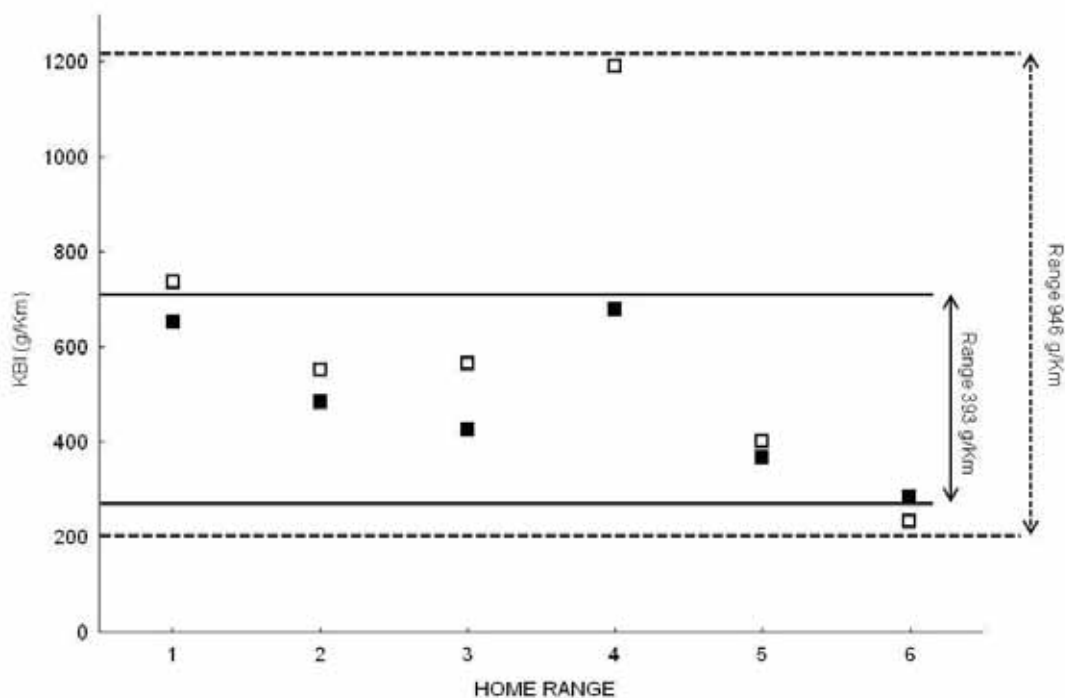


Fig 3. Mean biomass availability (using KBI g/Km). Solid squares represent KBI inside the home range and open squares outside of it for the six Home Ranges under study (Note that KBI variation outside territories is three times bigger than inside).

Temporal variation

We did not find significant differences in biomass availability between years ($Z_{1,6} = -1.536$, $p = 0.125$). Neither did we find interaction between year and period. In general, regarding temporal variations among periods, we found significant differences between NBr and the other periods (Br and Pfdp) ($Z_{2,6} = 2.950$, $p = 0.003$). When we analyzed seasonal biomass availability between real home range and potential boundaries areas we found significant differences ($Z_{1,6} = 2.740$, $p = 0.006$) (Table 1) and low biomass availability in NBr period too. Therefore there is no difference in biomass availability over the years. However, there is a seasonal variation influenced by the non-breeding season (where biomass available is low) inside and outside the home range.

| HR id (HRSize) | Side | NBr Period | Br Period | Pfd Period | Total Mean Values |
|---------------------------|-------------|-----------------------|----------------------|-----------------------|------------------------------|
| HR1 (63.5) | Outside | 688.20 | 311.08 | 1130.39 | 735.56 |
| | Inside | 756.43 | 395.25 | 767.93 | 652.75 |
| HR2 (61.9) | Outside | 414.56 | 745.77 | 544.47 | 552.23 |
| | Inside | 564.08 | 568.72 | 342.64 | 483.27 |
| HR3 (50.1) | Outside | 556.70 | 460.44 | 656.32 | 563.42 |
| | Inside | 376.21 | 382.79 | 525.99 | 425.21 |
| HR4 (43.3) | Outside | 1685.28 | 1107.40 | 751.73 | 1188.76 |
| | Inside | 1062.79 | 607.98 | 348.53 | 678.60 |
| HR5 (68.5) | Outside | 535.81 | 557.90 | 153.5 | 400.32 |
| | Inside | 572.34 | 137.45 | 328.17 | 369.16 |
| HR6 (75.1) | Outside | 401.469 | 139.04 | 98.75 | 232.03 |
| | Inside | 448.27 | 254.98 | 164.89 | 285.09 |

Table 1. Mean KBI values (g/Km) by Period outside and inside the six home range (HR id) under study. The total size of each home range (HR size) is shown in Km². Total Mean Values represent pooled mean data for each home range during all study years not accounting for period (See figure 3).

| | Hypothesized model | AIC | ΔAIC | ω_i |
|------------|-----------------------------------|------------|-------------------------------|------------------------------|
| KBI | Year + Period + Home range + Side | 6520.461 | 0 | 0.551 |
| | Period + Home range + Side | 6521.420 | 0.959 | 0.341 |
| | Year + Period + Home range | 6523.714 | 3.253 | 0.108 |
| | Year + Home range + Side | 6561.965 | 41.504 | < 0.0001 |
| | Year + Period + Side | 6563.632 | 43.171 | < 0.0001 |
| | Period + Side | 6565.174 | 44.713 | < 0.0001 |

Table 2. Ranking of the models used to explain prey availability using KBI. Akaike's information criterion (AIC), difference between model and minimum AIC values (Δ AIC), and AIC weights (ω_i). Models separated by less than 2 Δ AIC points are considered equally probable.

Discussion

This study shows that home range structure is more strongly influenced by continuous biomass availability than a relatively high but unpredictable abundance. Biomass availability outside the home range was irregular and higher over the year. However, biomass availability was regular and predictable inside the home range over the year but lower than inside. In addition larger territories do not show higher biomass availability, which confirms our hypothesis of the importance of continuous biomass availability when establishing and maintaining a home range.

The study of home range behaviour have been issued under different approaches: landscape characteristics (Carrascal and Seoane 2009), species interactions (Carrete et al. 2006), human interference, breeding performance (Martínez et al. 2008) even individual characteristics based on the space use or habitat selection (Martínez-Miranzo et al. 2016a; Martínez-Miranzo et al. 2016b). But, the main limiting factor when establishing home ranges is food availability (Ontiveros and Pleguezuelos 2000; Benson et al. 2005; Lourenço et al. 2015). Such trait is strictly related to the reproductive success and demographic parameters, the number of

individuals or breeding pair in a particular population (Resano-Mayor et al. 2015). For territorial species it is important to know how food availability, period of the year cycle or even foraging behaviour may alter that home range structure (Martinez-Miranzo et al. 2016b). Prey abundance and prey availability were used either through indirect counts, pellet or remains (Real 1987; Moleón et al. 2012; Palma et al. 2006) or by direct census of prey (Ontiveros et al. 2005). Usually they have been performed only during the breeding season (Ontiveros and Pleguezuelos 2000). For a generalist predator, which is not restricted to a single type of prey, it is more important the total amount of biomass than the type of prey (Lourenço et al. 2015). Our results suggest that biomass availability is a more realistic approach to explain home range structure in relation to food availability in a top generalist predator.

Abundance Theory predicts that individuals use the smallest home range possible in order to acquire the necessary resources for reproduction and survival (Burt 1943; Benson et al. 2005). This approach may be suitable for specialist predators. However, top generalist predators, particularly our model species Bonelli's Eagle, follow a strategy that we called the *Trophic Stability Hypothesis*. According to which, is more important regular biomass stability available over the entire year cycle than relatively high but unpredictable abundances of each prey species over the same period. In particular fluctuating conditions, like Mediterranean environments, predators adjust their territory based on biomass stability rather than on high prey abundances (Fargallo et al. 2009).

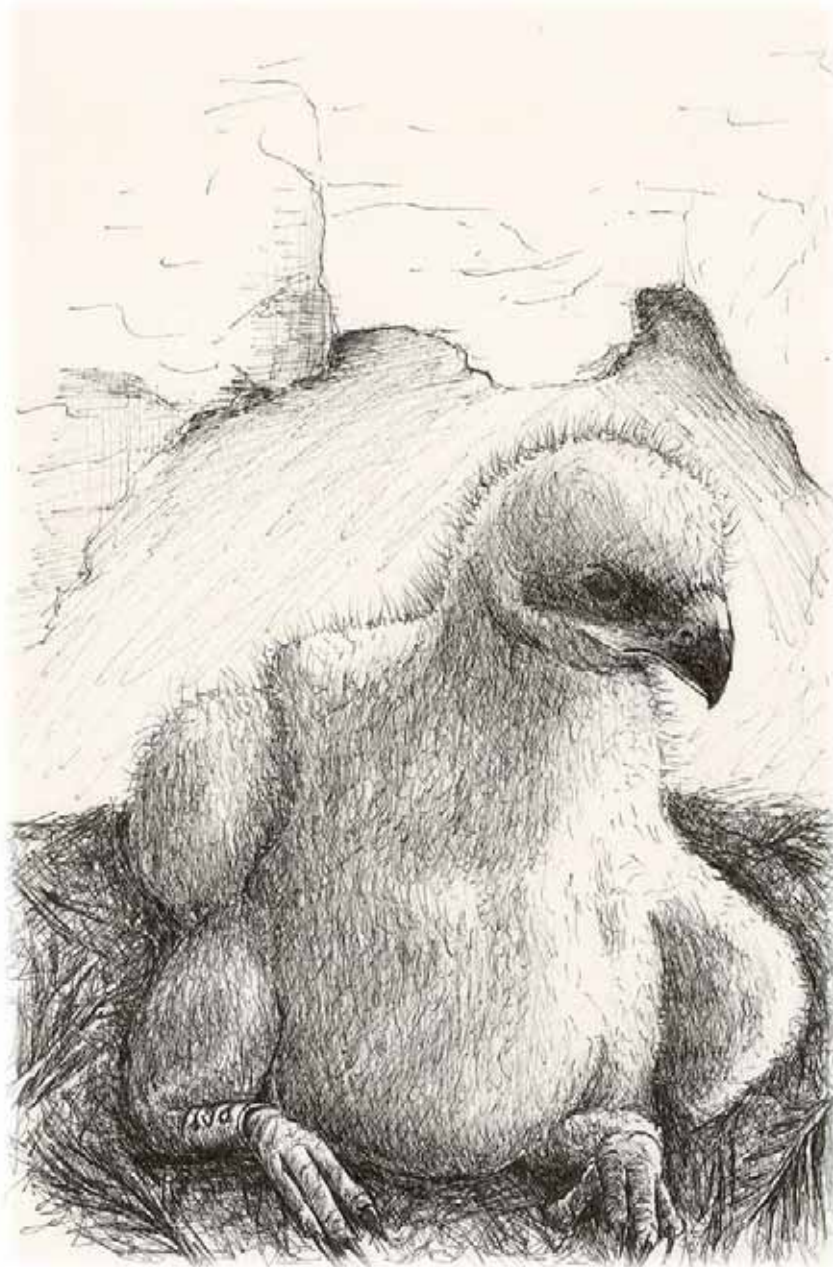
Once an individual has found an optimal home range that ensures trophic stability, this is maintained over the years (Martinez-Miranzo et al. 2016a). Although there is a differential use in the home range marked by the breeding season (Martinez-Miranzo et al. 2016b) such differences are not reflected in the biomass availability within the territories. Although there is a decrease in total biomass availability during Non-breeding season (NBr), such decrease can be linked to biological cycles of prey species (Millon et al. 2008) and human hunting activities to which these populations are subjected during the summer months (Aebischer et al. 1999 ; Arroyo and Beja 2002).

Our results show that almost all individuals have the same threshold trophic availability. However to acquire it, home range sizes differ for each individual. Individual experience, individual quality or home range structure seems to be the most realistic explanation for this result (Martinez-Miranzo et al. 2016b). Individual knowledge of their own home range helps effort optimization when searching for food resources and increases fitness (Campioni et al. 2013). Individual experience also plays an important role in obtaining food, especially in Mediterranean areas with abundant scrubland and forest where the detectability of prey is low (Martinez-Miranzo et al. 2016b)

On the other hand, larger home ranges do not guarantee higher prey abundances, but provide an equivalent minimum biomass stability level for all individuals to enable them to perform. As shown in our results, trophic availability inside home ranges, differ only by 393 g/Km while outside the home ranges its variation is three times bigger (see Fig 3). This confirms the *Trophic Stability Hypothesis* and opens a new approach to conservation of top predator raptors. This new approach should be considered in conservation programs of endangered territorial generalist top predators, such as the Bonelli's Eagle in the Northeastern area of the Iberian Peninsula. Helping maintaining constant biomass stability throughout the year, will favor not only the establishment but the maintenance of territories over time. Our results show that conservation actions should focus on Non Breeding period, regulating prey populations and restricting human activities such as hunting that have a negative impact on the population dynamics of prey species (Aebischer et al. 1999; Arroyo and Beja 2002). In addition long term studies allow us to improve the knowledge about home range structure and maintenance and provide conservation management tools.



Chapter 4: Mismatch between spatial distribution and breeding success reveals sink population dynamics in an endangered raptor species



This chapter is based on the manuscript: **Martínez-Miranzo B**, Banda EI, Gardiazábal A, Ferreiro E, Seoane J, Aguirre JI. Mismatch between spatial distribution and breeding success reveals sinks population in an endangered raptor species

Mismatch between spatial distribution and breeding success reveals sink population dynamics in an endangered raptor species

Introduction

Species distribution patterns are fundamental topics of ecology studies (Krebs 1978; Channel and Lomolino 2000). Classical approaches are related to the identification of biotic and abiotic traits and patterns and can be applied to conservation biology (Guisan and Zimmermann 2000; Pearce and Ferrier 2001). However, few studies identify the relationships between these factors and breeding success (Carrascal and Seoane 2009). By such an approach, it is possible to reveal the population dynamics of the species of interest.

When considering endangered species, factors influencing the distribution patterns are crucial for conservation management (Channel and Lomolino 2000; Whitfield 2005). Understanding the occurrence of species might help to mitigate population decline. However, on some occasions, identifying such factors is insufficient to control population decline. In this context, the inclusion of ecological processes might be key. Pulliam (1988) presented a successful framework in ecology based on what is currently known as the source-sink model. In a metapopulation dynamic, the source population includes those that reproduce successfully, are self-supporting and contribute with dispersant individuals. A sink population suffers from an unbalanced local mortality and depends on immigration from source populations to survive. Identifying source-sink dynamics in fragmented metapopulations could probably be used to explain population declines (Murphy 2001).

Bonelli's Eagle (*Aquila fasciata*) is a long-lived territorial raptor. The species is distributed in the western Palearctic and mainly restricted to the Mediterranean Region (Cramp and Simmons 1980). The Bonelli's Eagle population has suffered a general decline in recent decades. The population on the Iberian Peninsula supports

70% of the total European population (Birdlife International, 2015). Large-scale studies reveal a metapopulational dynamics in Spain (Muñoz et al. 2005; Hernández-Matías et al. 2013), where two different populations have been identified. The southern and southeast populations remain stable, whereas the northern population remains low due to less favourable conditions (Hernández-Matías et al. 2013). Due to the metapopulational dynamics on the Iberian Peninsula (Muñoz et al. 2005), the approaches for overall conservation of this species should be reviewed.

Although many studies have addressed the local distribution patterns, habitat selection or breeding success of Bonelli's Eagle (Rico et al. 2001, Carrete et al. 2002; López-López et al. 2006). However, these studies have not addressed the internal dynamics of the population at this scale. Therefore, joining demographic processes and occurrence of the species might help to understand the dynamics of the population. Nevertheless, Carrascal and Seoane (2009) related density, productivity and population trends but at a larger scale (Iberian Peninsula), rather than at the population level, which is more suitable for management and conservation applications.

The main aims of this work are to provide an integrated approach to habitat quality focused on breeding success, which will ultimately determine the viability of the population. First, we identify how different abiotic and biotic variables might affect the distribution and the potential occurrence areas of the model species. Then, we identified which of these variables condition the breeding success. Finally, we analyze the relationship between potentially good areas and breeding success. By this method, we will create an integrated approach to population dynamics that can help species conservation projects at the local level. Also, we will provide information to contribute to conservation plans for the entire distribution area. This type of research can also be useful for other endangered species that are suffering similar conservation problems.

Methods

Study area

Aragón is a Mediterranean Region in the northeast of Spain. Aragón shows great thermal amplitude. Temperatures fluctuate between -10 and 35°C. Total annual precipitation is 800 mm in most of the region, although it can reach up to 2,000 mm per year in high mountain areas and be as low as 300 mm per year in the lower areas of the region.

Our study area includes different habitat types in a relatively small area (47,719 km²). These include mountainous areas (maximum altitude of 3,404 m), desert areas in the centre of the region, river depressions (such as the Ebro valley) and heterogeneous areas dominated by Mediterranean forest. In these areas, great forest formations (pine or oak) and Mediterranean scrub alternate with crops and fruit trees (e.g., vineyards and olive trees) (Fig 1.).

Data on species distribution and breeding success

From 2004, a monitoring program of Bonelli's Eagle was carried out in Aragón (D326/ 2011). The presence of all breeding pairs in the Aragón Region has been recorded. A total of 32 breeding pairs were identified in this period. Of those, 21 were equipped with GPS satellite telemetry and their home range determined (Martínez-Miranzo et al. 2016a). Of the remaining 11, the nesting area and the approximate breeding area were also estimated. We based these estimations on previous home range size data and observations of the breeding couples, and also take into account the topography around the nesting zone. These works are included in Bonelli's Eagle Management Program of Aragón Government (D386/2011). To homogenize the actual distribution of Bonelli's Eagle in Aragón, we divided the entire area using a 10 x 10 km UTM grid. Cells in which a Bonelli's Eagle home range was present were assigned a value of 1, whereas empty cells were assigned as zero.

Breeding data were also monitored. We monitoring the breeding success of Bonelli's Eagles in this region (32 home ranges between 2004 and 2016). Over the entire study, the number of chicks produced, the number of years with reproductive

activity, and replacement in the breeding pairs were recorded for each territory. All data on breeding monitoring were provided by Bioma TBC and authorized by the Aragón Government.

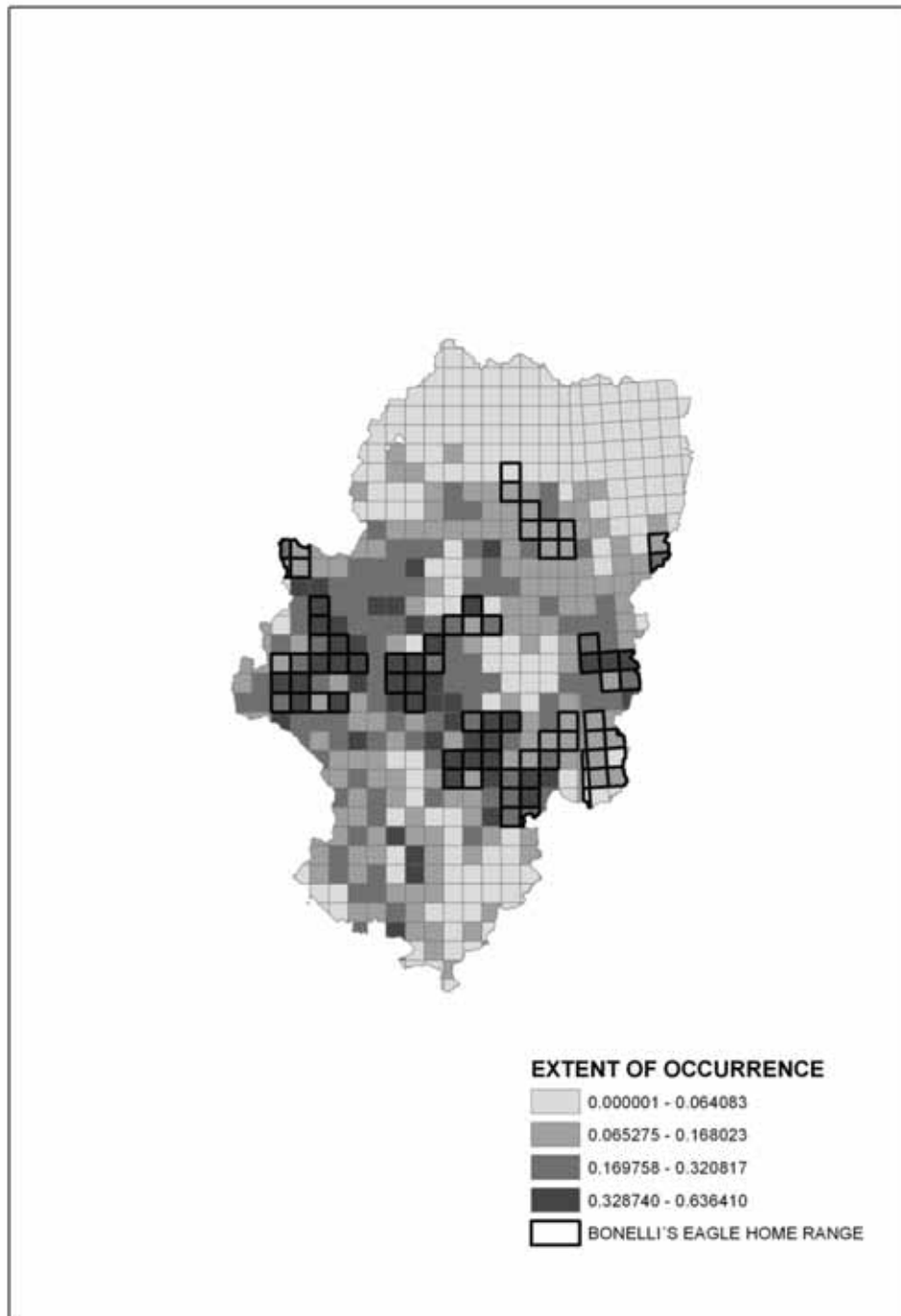


Fig. 1 A map of the occurrence of Bonelli's Eagles. Cells with bold borders represented the Eagles' home ranges.

Variable selection

Based on previous studies (see Martínez-Miranzo et al. 2016a,b for more details) we considered the following variables, measured in each of the UTM 10 × 10 grid cells: i) *Climate variables*: The mean annual temperature and precipitation for each grid were calculated using ArcGis 9.3, and the climate variables were obtained from Worldclim (Worldclim 1.4). ii) *Habitat variables*: The total percentage of forest and scrub and land use variables were extracted from CORINE Land Cover 2006 (European Environmental Agency, 2006). Because land use categories are over detailed for a 10 x 10 km UTM grid scale, they were grouped as follows: forest (including broad-leaved forest, coniferous forest and mixed forest) and scrub percentage (including transitional woodland shrub and sclerophyllous vegetation). The percentage of each variable was calculated for each grid. iii) *Biological variables*: The presence of Golden Eagles and total of biomass availability (Chapter 3). The Golden Eagle is considered a principal competitor of Bonelli's Eagles (Carrete et al., 2002). We only considered confirmed the presence of Golden Eagles for each 10 x 10 Km cell. We calculated the total prey biomass as a contribution to the diet of Bonelli's Eagle (Chapter 3.). As a total of biomass availability, we only considered rabbit (*Oryctolagus cuniculus*) and partridge (*Alectoris rufa*) because we only have data for these two prey for the whole study area. Even so, they represent the main prey for this species (Real 1987; Alcántara et al. 2003). Data from rabbit and partridge censuses during this period were obtained by Finland Transect, following Telleria (1986). The censuses were adapted to each species. For rabbit, censuses by car were performed. The censuses were carried out during twilight hours at a constant speed of 20 km/h and 30 km of length per transect. Partridge censuses were done by line transect on foot (Telleria 1986). A total of five transects of approximately 3 km were performed between sunrise and midday. For each transect, the total number of available prey biomass was recorded and corrected by the total length of each transect. We obtained an index of biomass/distance unit (Chapter 3). The censuses were performed in areas that encompass different proportions of the 10 × 10 Km UTM grid. Because the entire study area was not surveyed, we performed a spatial approximation using the Kriging method in ArcGis 9.3 (Oliver and Webster 2007). Kriging is based on regionalized variable theory. It

provides an optimal interpolation estimate for a given coordinate location, as well as a variance estimate for the interpolation value. Using the knowledge about the underlying spatial relationships in our data, we obtained interpolating values for total biomass available for the entire study area. All biological variables were provided by the Government's Environment Department of Aragón.

Data analyses

To determine the distribution patterns, breeding success and the relationship between the presence of the species and the reproductive success of the Bonelli's Eagle in Aragón, we constructed different models using Generalized Additive Models (GAM) and General Linear Models (GLM) in R software.

First, we performed a preliminary GAM to explore the effects of our variables, potentially curvilinear. This helped us to improve our final model, eliminating variables that do not provide useful information and suggesting relationships forms between response and explanatory variables that were later modelled by GLM (for instance, a U-shaped relationship suggested by GAM could be modelled with second-order polynomials in GLM). We prefer building final models with GLM because this type of model is more easily interpreted (for example, through tables of coefficients) and carried to GIS software. We built a GLM (logistic regression) with species occurrence as the response variable (using 10 × 10 Km grid, presence = 1 and absence = 0) and climatic, habitat and biological traits as explanatory variables. After an exploratory analysis, the temperature was eliminated from the model because it showed a strong correlation with precipitation. Due to the importance of correlation in species distribution models and the true purpose for which the model was constructed, we decided not to take into account other aspects, such as spatial autocorrelation (Legendre 2003). Also, the relative contribution of each variable to the derived factors was calculated. To evaluate the predictive capacity of the model, we used AUC using pROC package in R software (Robin et al. 2011).

Secondly, we performed a GLM (Poisson regression) for breeding success. We used the total number of chicks born in each home range as the response variable ('breeding index'). The same climatic, habitat and biological traits as in the previous

model were used as explanatory variables. We included in the model a factor taking into account whether there was a replacement of one of the members of the breeding pairs ('change'), and the number of monitoring years for each home range as an offset.

Finally, we looked at the relationship between the species distribution and its breeding success. We constructed a linear regression using the breeding index as a response variable. As an explanatory variable, we used the values of the predictions for each UTM 10×10 obtained from the initial distribution model. As the home range occupies several cells within the UTM 10×10 grids, we selected the cell with the highest value within each home range. We performed *a posteriori* analysis, including 'change' as a predictor and its interaction to verify the relation within the model.

Results

Species distribution

Previous exploratory analysis showed a high correlation between the climatic variables. Precipitation was included in the model due to its limiting effect under strong Mediterranean conditions, such as those found in the study area (Ontiveros, 2016).

The GAM model showed that percentage of forest is not informative and, therefore, could be excluded from the GLM model. Only percentage of Scrub was included in the GLM model as habitat variable (Table 1). The presence of Golden Eagle, biomass and precipitation are the variables that best explain the Bonelli's Eagle occurrence in this model. Contrary to the results expected, Golden Eagle presence is positively related to Bonelli's Eagle occurrence. The habitat requirements for the two species might overlap at this large scale. About the other biotic variable, biomass availability reveals a range for Bonelli's Eagle occurrence. The Eagles prefer areas with a threshold of biomass that varies between 800 and 1,000 g/km. The Eagles least select areas with biomass lower than 800 g/km or higher than 1000g/km. The presence of Bonelli's Eagle is negatively related to precipitation. An increase in the probability of

rain implies a decrease in the presence of the Eagle. In general, the occurrence of this population explains 57% of the variance by biotic variables and 43% by abiotic variables (Table 1). The AUC of this model was 0.739 revealing a good discriminatory power.

Breeding success

GLM showed that the percentage of scrub and the replacement of one of the breeders are important in breeding success, explaining around 30% of the breeding success (Table 1). The percentage of scrub is negatively related with breeding success. The number of chicks decreases as the percentage of scrub increases. In the case of replacement of any of the breeders, the analysis shows a negative relationship with the number of chicks produced. In particular, the change of one of the breeders implies a 68% decrease in the number of chicks. Biological variables, such as the presence of competitors (e.g., Golden Eagle) or the amount of available biomass do not seem to be a determinant in the reproductive success of this population.

Relationship between species distribution & breeding success

The regression showed an interaction between probability of occurrence and replacement of any of the breeders ($P = 0.01$) (Table 1), meaning that territories in high-quality areas (those with high occurrence probability) had low predictive success for breeding pairs in which a member was replaced; for the rest there was no relation between breeding success and occurrence probability (Fig. 2).

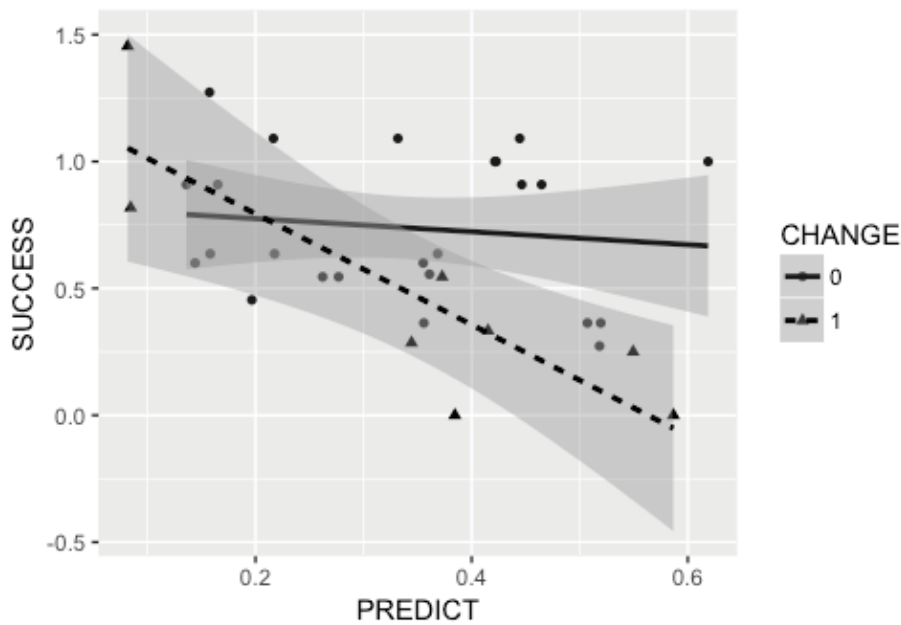


Fig. 2 The relation between breeding success (Success) and occurrence probability (Predict) for territories having (dashed line) or not having (continuous line) a replacement of either of the breeding pair during the study period.

Distribution Model ($D^2=0.20$)

| Variables | Golden Eagle | Biomass | P.Scrub | Precipitation |
|-----------|--------------|---------|---------|---------------|
| Estimate | 18.188* | 2.905* | 29.881 | 32.783* |

Breeding Model ($D^2=0.41$)

| Variables | P.Scrub | Precipitation | Change |
|-----------|---------|---------------|--------|
| Estimate | -0.01* | -0.003 | -1.08* |

Distribution & Breeding Model ($D^2=0.35$)

| Variables | P. Occurrence | Change | Occurrence : Change |
|-----------|---------------|--------|---------------------|
| Estimate | -0.256 | 0.405 | -1.93* |

Table 1. Variables included in each model. The significant variables ($P < 0.05$) are represented with *. Deviance explained by the model (D^2).

Discussion

This study shows the importance of population dynamics in conservation biology. We related the distribution patterns of an endangered species with its breeding success. In our region, the distribution of Bonelli's Eagle is mediated by precipitation, prey biomass availability and the presence of other competitors. On the other hand, its breeding success is related to the habitat structure, mainly to the percentage of scrub, precipitation and other important factors in a long life territorial species, such as the replacement of any of the members of the breeding pair. In our study, the relationship between distribution and breeding success is negatively correlated. In this case, high-quality places show low reproductive success, because of the high rate of replacement of one of the members of the breeding pair. Because of this, we detected a sink dynamics within the study population that should be taken into account when developing conservation measures aimed at this species.

In general, to determine species distribution patterns, abiotic variables, mainly climate and habitat, have been applied (Krebs 1978; Channel and Lomolino 2000; Guisan and Zimmermann 2000). Such patterns are usually employed at very large scales (Graf 2005), masking the situation at a population level. However, in many of these models, the use of biotic variables is not included. This is possibly because they are more difficult to obtain at different scales. However, they might play an important role in the distribution of territorial species. In our study region, the distribution pattern of Bonelli's Eagle is more related to biotic variables than to abiotic ones.

Because Bonelli's Eagle is a territorial species, prey biomass availability plays a great influence in their distribution patterns. Species that can maintain their territories over the years (Martinez-Miranzo et al. 2016a) establish their territories based on certain characteristics. Such factors can be related to the habitat structure (Martinez-Miranzo et al. 2016b) that allows them to satisfy some biological needs (i.e., appropriate sites to establish their nests). However, this can also be related to other types of resources, such as the trophic resources. There are studies showing that generalist top predators establish their home range based on average prey biomass

availability, a threshold which remains stable throughout the year (Lourenço et al. 2015; see chapter 3). Our results show that the distribution of Bonelli's Eagle in Aragón includes a prey biomass availability threshold. Occurrence areas offered a not very high but presumably stable biomass availability over the entire year. Eagles probably select these zones rather than areas of higher but unstable prey density (see Chapter 3). These areas also include middle latitudes, where they also find suitable places for nesting and Mediterranean forest habitats preferred by this species (Muñoz et al. 2005; Carrascal and Seoane, 2009).

The Mediterranean habitat provides a suitable setting for many other raptors, such as the Golden Eagle, which might be a direct competitor of the Bonelli's Eagle. Our results show a positive relationship between the distributions of the two species. This might be because of habitat requirements and because the prey species are similar for both raptors and match at the study scale (Carrete et al. 2006). During this study, it has not been possible to verify actual competition between the two species in this region.

The Bonelli's Eagle is distributed along a thermophilic climate gradient (Carrascal and Seoane 2009). In other studies addressing the Bonelli's Eagle, precipitation plays an important role in the presence of the Eagle (López-López et al. 2006; Real et al. 2013). Our results also show precipitation as a determinant factor in the Eagle's presence. The Eagles do not select areas with a high percentage of annual precipitation. This might be due to the thermophilic character of the species (Ontiveros 2016), whose breeding season is determined by climatic conditions (Arroyo et al. 1995) and whose reproductive success is negatively related to precipitation (Real et al. 2013).

Our study shows a relationship between breeding success and precipitation; areas with higher precipitation levels produce fewer chicks. The breeding season of the Bonelli's Eagle extends from March to June; when chicks leave the nest and begin the dependence period (Real et al. 1998). This time is crucial for the reproductive success of breeding pairs. High precipitation areas, might involve to lose the lay and, therefore, a decrease of breeding success (Balbontín and Ferrer 2005).

Habitat structure, specifically the percentage of scrubland, also seems to be negatively related to breeding success. Territories with a high percentage of scrub

produce lower numbers of chicks over time. The microstructure of the habitat plays a very important role in the establishment of home range at small-scales (Martínez-Miranzo et al. 2016b). Bonelli's Eagle in Aragón selects areas with certain scrub coverage. This scrubland usually constitutes the habitat of potential prey for the Eagle, such as Led-legged partridges and pigeons (Ontiveros and Pleguezuelos 2000). However, the denser shrub coverage is more difficult for hunting, especially during the period of chick rearing. The low degree of prey detectability in this habitat (Ontiveros et al. 2005) implies a high degree of home range knowledge by the breeders, who will efficiently exploit the resources available according to the experience of each individual. So, breeding success will be influenced not only by abiotic factors but also by intrinsic factors, such as experience within the breeding pair (Ontiveros and Pleguezuelos 2003).

For long-lived species, such as Bonelli's Eagle, these intrinsic factors might be determinants of breeding success and might even determine whether a couple is reproducing or not (Balbontin et al. 2003). These species are monogamous and territorial; individuals that are typically monogamous over their life once they have established a territory, although it has been proven that, as in many other species, extra-pair copulations can occur. Our results suggest that the replacement of one of the breeders reduces the breeding success by 68%. The replacement will be accomplished by another individual, possibly young or immature under dispersion (Balbontín et al. 2003). The new individual, if sub-adult, will not be able to reproduce during the first year after the new pair is established, or possibly more than two years until the individual becomes sexually mature and that pair start breeding (Ontiveros 2016). This might jeopardize the viability of the population (Balbontín et al. 2003), with a low number of effective breeding pairs and serious conservation problems.

Accordingly, it might be interesting to use different approaches in populations and species with conservation problems. In general, conservation programs are focused on habitat conservation or management actions. However, very few of these programs identify the actual population dynamics (Furrer and Pasenelli 2016). The population of Bonelli's Eagle in Aragón might follow a sink dynamic. When we relate the distribution of the species and its breeding success, the sites that are assumed to

be favourable and are selected by the species to establish their home range are associated with low reproductive success. This low breeding success is due to the loss of population members; 40% of the study population died during the study period. These deaths are caused by unnatural factors, mainly electrocution, collision with power lines, poisoning or direct persecution (Hernandez-Matías et al. 2015). These individuals are replaced by young, immature Eagles who are unable to maintain the reproduction rate. Thus, we are facing a sink population scenario with a continuous decrease in population numbers.

Under this situation, management conservation measurements should be reviewed (Albert et al. 1990; Nichols and Williams 2006). In Aragón, a recovery plan for the Bonelli's Eagle was approved in 2011 (D 386/2011). In this plan, the main actions are related to the monitoring of the population, the habitat management and conservation or the recovery of rabbit populations. These measures should be complementary to the reduction of the loss of effective populations. Our results demonstrate that changing a breeding pair greatly reduces breeding success. Thus, conservation efforts should focus on reducing electrocutions and others factor responsible for deaths. This could be achieved by making agreements with the electricity companies and actions related to territory custody with local population awareness campaigns. The region of Aragón has managed a project (LIFE04 NAT/ES/000034) aimed at the correction of power lines in the Pyrenees area. This project succeeded in increasing the number of breeding pairs in the area. The extension of these measures to the entire study area would likely increase the number of breeding pairs in the region. Also, it would reduce the loss of individuals, coming from other Iberian populations.

Therefore, we suggest a conservation strategy that is carried out on two scales. First, identifying the problems at the population level. Local sink population can play a role in population network, supporting viable metapopulations (Furrer and Pasinelli 2016). Second, we might adjust the strategy of the species conservation at the level of the metapopulation that has already been raised on other occasions (Carrascal and Seoane 2009; Hernandez-Matías et al. 2013). Also, this type of approach provides tools

that can be used in the conservation of other endangered species with this sink dynamic.

General Discussion

The population of Bonelli's Eagle in Aragón shows uncertain population viability. To be a territorial top generalist predator in the Northeastern distribution limit of the Iberian Peninsula has implications in the behavior of the species derived from the ecological characteristics of the region. Despite each home range having a particular shape and size, breeders show considerable home range fidelity. Therefore, for the establishment and maintenance of home range in a particular place by individuals, different factors must combine. These factors might be related to individual condition (sex or personal experience) or environmental factors involving the landscape. In the study population, habitat structure plays a key role in the establishment and maintenance of home range. However, at a broader scale, habitat requirements are uniform (Mediterranean forest interspersed with Mediterranean scrub, crops and medium cliffs) but at fine scale habitat microstructure determines home range behavior. The individuals of this population select dense Mediterranean scrub inside the home range and urban areas (mainly small rural villages and open industrial areas), depending on the season. This habitat type seems to be related to the presence of other resources, such as prey availability. The trophic spectrum of Bonelli's Eagle in Aragón is determined by the low rabbit density. This means that partridges, pigeons and corvids are often selected as prey. Transitional areas with Mediterranean scrub are suitable for prey species. When trophic requirements are larger (e.g., during the breeding season), individuals select urbanized areas because flocks of pigeons are numerous and easy to obtain. Thus, prey availability seems to contribute to the home range behavior of this population. As Bonelli's Eagle is a generalist predator, for our analyses, we used total biomass rather than prey availability. Related to trophic resources, continuous and predictable biomass availability during the year determines the establishment and maintenance of home range.

Although habitat structure and prey availability contribute to the home range behavior of the studied Bonelli's Eagles, they are not decisive. Other factors associated with breeding success also influence in population viability. Our data

reveals an ecological sink dynamic. Breeding pairs that establish their territories within more suitable areas (by climate, habitat characteristic and resource availability) show a low breeding success. This low success is determined by the breeder's disappearance from the population, mainly by the non-natural death of the individuals. These underlying patterns have direct consequences for the conservation of Bonelli's Eagle in this region. These findings improve our knowledge of the spatial ecology of the Bonelli's Eagle and will likely be useful when planning future conservation approaches.

Conservation Managements and Future Research.

Here, we propose a series of guidelines to be considered when developing future conservation programs for Bonelli's Eagles and similar endangered species.

Because Bonelli's Eagles maintain home range sizes and core areas over multiple years and have a high degree of home range fidelity, we believe it will be useful to extend protection measures to the total home range size. This might include correction of power lines, which are responsible for the highest number of deaths. The fidelity to home range implies that conservation actions like correcting power lines or restricting infrastructure would have a lasting impact over time. Also, we consider that the minimum area of protection must include a combination of nesting hunting, roosting and areas. Furthermore, some conservation measures, such as restricting climbing, hunting and other outdoor activities, should be carried out throughout the year, becoming more restrictive during the breeding season when individuals, especially females, are more vulnerable to human disturbance. Because of the high degree of home range fidelity, it will be interesting to check if the home range is maintained when one of the breeding pair is replaced. By monitoring new individuals that replace others breeders in a known home range, we will be able to determine whether the same shape and size of the home range are maintained between different individuals. Such approaches will allow us to infer the importance of individual characteristics and habitat quality in the establishment and maintenance of home range behaviour.

Regarding habitat selection, long-term multiscale studies can reveal aspects that are undetected at a single scale or that might need some time to be revealed due to changes during the year, mainly driven by differential resource availability. In our study population, we confirmed that it is necessary to know the habitat structure inside the home range. The home range used by individuals is closely related to the period of the year. Therefore, it is important to implement conservation measures at different scales, spatial and temporal, keeping in mind variation throughout the year. Habitat structure and the adaptation of the species to habitat changes should be

considered. For example, the use of urban areas by Bonelli's Eagles during the breeding season is not usually included in conservation programs, nor is managing forest areas. Such managements can be performed during the non-breeding season. It would be interesting to check how the spatial structure is changing and how this change can affect the use of the home range.

According to our results, we suggest reviewing the trophic resource approach thoroughly. The trophic stability hypothesis opens a new approach to conservation of top predator raptors. This new approach should be considered in conservation programs of endangered territorial generalist top predators, such as the Bonelli's Eagle in the north-eastern area of the Iberian Peninsula. Maintaining a constant biomass stability throughout the year will favour the establishment and maintenance of territories over time. Our results show that conservation actions should focus on the non-breeding period, including regulating prey populations and restricting human activities that have a negative impact on the population dynamics of prey species (e.g., hunting). Nevertheless, we are planning to extend the census of prey availability to more home ranges, and selecting those in different habitat types. This will allow us to test our trophic stability hypothesis in the entire population. Also, it would be interesting to compare this issue with other Bonelli's Eagle populations in Spain with limited food resources.

Based on the diet of Bonelli's Eagle in Aragón, it will be necessary to improve our knowledge about the trophic spectrum in a particular population. As we have mentioned throughout this study, the Bonelli's Eagle is a top generalist predator that adapt its diet to prey availability. It would be interesting to check the actual trophic spectrum of the Bonelli's Eagle in Aragón. For this purpose, studies are being carried out. We have placed cameras in the nests of the home range where the prey censuses were performed. We want to test whether what the Eagles eat is in line with the actual prey availability.

In conservation biology, a multivariate approach for modelling distribution, habitat selection and resource selection will be useful to connect different methodologies. Accordingly, it might be interesting to use different approaches in populations of species with conservation issues. In general, conservation programs are

focused on habitat conservation or management actions. However, few of these programs identify the actual population dynamics. The population of Bonelli's Eagle in Aragón might follow a sink population dynamic. Under this situation, management conservation measurements should be reviewed. In Aragón, a recovery plan for the Bonelli's Eagle was approved in 2011 (D 386/2011). In this plan, the main actions are related to the monitoring of the population, the habitat management and conservation or the recovery of rabbit populations. These measures should be complementary to the reduction of the loss of effective populations. Our results demonstrate that changing a breeding pair greatly reduces breeding success. Efforts in conservation plans should focus on reducing deaths, especially electrocution.

Under the population dynamics framework, it should be interesting to establish the genetic relationships between individuals. This would allow us to determine the genetic viability of the population. With genetic data over ten years from breeders and their progeny, we intend to determine the degree of kinship of the Aragonese population and establish a relationship with the rest of Spanish population. Thus, we can verify the true gene flow in the metapopulational dynamics of this species.

Also, we would like to explore other factors that might be affecting breeding success, such as the presence of contaminants or the effect of bioaccumulation on reproductive success.

In conclusion, based on our finding, we propose that a general conservation strategy is necessary to protect the Bonelli's Eagle in Aragón.



Conclusions

- I. Breeders of Bonelli's Eagle in Aragón show high home range fidelity. However, they show less fidelity to the nesting areas within the same territory determined by each breeding pair.
- II. Home range behaviour of individuals in this population is influenced by seasonality and the sex of individuals.
- III. The use of different spatial and temporal scales reveals differences in habitat selection among the individuals of this population.
- IV. The habitat structure plays an important role in the establishment and maintenance of the territories.
- V. The use of space of individuals inside the territories depends on the habitat structure and the ecological requirements of the species during the different periods of the year.
- VI. The continuous and predictable trophic availability over the year contributes to the establishment and fidelity to the territory in the study population.
- VII. Bonelli's Eagle in Aragón seems to follow ecological sink dynamics within the Iberian population. Breeding pairs that establish their territories in presumably more suitable areas for the presence of the species, due to their favourable ecological characteristics, show a low breeding success. This is conditioned mainly by the high replacement rate of individuals due to death or emigration of either member of the breeding pair.
- VIII. For endangered species conservation, we recommend long-term monitoring studies of the different aspects related to the management of the species. It is desirable to use several scales, both temporal and spatial, which might reveal underlying problems and provide specific patterns of management. Also, the use of integrative approaches can reveal population dynamics not previously identified.



Outreach

In the context of this study, other aspects related to Bonelli's Eagle biology have been discussed. Considering the importance of the transference of information between academic world and the administrations as well as the transmission of information with the general public, the actions that have been carried out related to this study are detailed below.

Research studies

- **Buendía, L. 2015. Bonelli's Eagle (*Aquila fasciata*): Patterns in nest parental care in Aragón. Degree Thesis co supervised by Martínez-Miranzo, B. & Aguirre, J.I.**

In order to implement adequate management strategies, the understanding of basic biology of the species involved is a plays a key role. In this study, we analyze parental care of Bonelli's Eagle in Aragón. Specifically, the differences in reproductive behaviour between sexes. We explored The parental behaviour in the nest reproductive success and duration of incubation in the study population.

Camera traps were set up near five nests between February to June over two consecutive years (three cameras in 2014, and two cameras in 2015). A total of 43157 photographs were obtained, of which only 8,039 were analyzed.

Female Eagles stayed 81.5% of total occupation time inside the nest. Male and female parental behaviour in the nest follow patterns in which male stays inside the nest without taking care of the chicks while female feeds and looks after them. After analyzing reproductive success and incubation time we found that incubation lasts longer than in the average Spanish nests (1.2 to 1.17) and incubation lasted for 10 more days.

- **Buendía, L. 2015. Interaction between mesopredators and top predators: Fox (*Vulpes vulpes*) and Bonelli's Eagle (*Aquila fasciata*) in the NE of Spain. Final Presentation in the Research initiation of Biology Degree. Co supervised by Martínez-Miranzo, B. & Aguirre, J.I.**

There is an interaction between top predators and mesopredators. The first can control the populations of the second directly or indirectly if they perceive them as competition. We analyze if fox abundance varies between (1) Bonelli's Eagle breeding or non-breeding season, (2) the situation within the Bonelli's Eagle home range or (3) the abundance of its potential prey.

Censuses of potential prey and presence of fox have been performed in 6 home ranges of Bonelli's Eagle. With the data obtained, the Kilometric Abundance Index (KAI) for fox presence and the Kilometric Biomass Index (KAIBIO) for the potential prey were calculated.

Our result shows that the abundance of the fox is greater during the breeding season within the Eagles' home range than outside of them. Previous studies have shown that Bonelli's Eagle in Aragón select for biomass stability within its home range. Mesopredator may not be displaced by the top predator if the resources are abundant or if the trophic spectrum is different because we only found a correlation between fox abundance and rabbit latrines or pigeons' biomass.

- **Martínez- Miranzo, B. 2013. Home range characterization in breeders of Bonelli's Eagle in Aragón. Master Thesis supervised by Aguirre, J.I. & Banda, E. I.**

Bonelli's Eagle (*Aquila fasciata*) has suffered a general decline since the 1980s and is included in the Spanish Catalog of Endangered Species, therefore, studies that provide results that can be applied directly to the conservation of the species are very necessary. A study was carried out in the Aragón Region. We characterize the home range of 17 breeders in different periods of the annual cycle over 7 years, based on accurate data obtained by GPS satellite telemetry.

In this population, there are individual variations in size and use of the home range. Although no annual variations have been found. There is a decrease in the use of the home range by females in the breeding season. Ultimately these results can be applied for a more efficient management of this species in the Aragón Region.

Technical support

- **Feeding of Bonelli's Eagle in Aragón during the breeding season. Reports presented in the Provincial Delegation belong to Recovery Plan of the Bonelli's Eagle (R363/2011).**

Since 2014, camera traps have been installed in 5 nests of the species in the Region. The objective is to check the real composition of the diet during the breeding season, relating these observations to the results of the prey censuses carried out in different home range.

During the two years a total of 50,000 photographs have been obtained. In total, 28% of partridges, 22% of pigeons, 9% of birds, 9% of lizards, 6% of rabbits and 26% unidentified have been reported. These results corroborate the low presence of the rabbit in the diet and the increase of the pigeons in their habitual diet, as a substitute for the rabbit. In addition, the presence of lizards has been revealed in a very high percentage (10% of the total in the diet) that until now had not been detected by other methods such as the study of pellets (1% of the identified remains). In addition, the placement of this type of infrastructure has not caused any disturbance in the breeding success and a much more precise monitoring of the breeding performance has taken place by the photographs obtained.

- **Technical sessions for the Government of Aragón and Nature Protection officers belong to Recovery Plan of the Bonelli's Eagle (R363/2011).**

In order to make public the results of the research carried out in this study, annual technical sessions have been held with Nature Protection officers

and other members of the administration. This is intended to encourage the exchange of information between both to improve the Recovery Plan of the species.

- **Initial workshop in the framework of LIFE BONELLI (LIFE12 NAT/ES/000701).**

In the initial meeting belong to LIFE BONELLI, 5 lectures and 20 oral communication were held to discuss and analyze the status of the Bonelli's Eagle populations in the Western Mediterranean, their threats and the results of the conservation measures carried out.

Conference communications

- **VII Ornithology Meeting UCM, 2016. Spatial ecology of Bonelli's Eagle in Aragón. Complutense University of Madrid.**
- **X Conference of the European Ornithologists' Union, 2015. Prey abundance or biomass availability? The case of Bonelli's Eagle *Aquila fasciata* in Aragón (NE Spain). Martínez-Miranzo, B.; Banda, E. & Aguirre, J.I.**
- **XXII Conference of Spanish Ornithology, 2014. Multiscale analysis of habitat selection by the Bonelli's Eagle (*Aquila fasciata*) in Aragón: adapting to changes. Martínez-Miranzo, B.; Banda, E. & Aguirre, J.I.**
- **VI Ornithology Meeting UCM, 2013. Monitoring of endangered species: applications to conservation. The case of Bonelli's Eagle in Aragón. Complutense University of Madrid.**
- **IX Conference of the European Ornithologists' Union, 2013. Differential spatial use and spatial fidelity by breeders of Bonelli's Eagle. Autores: Martínez- Miranzo, B.; Banda, E.; Ferreiro, E.; Gardiazábal, A. & Aguirre, J.I.**
- **XXI Spanish Conference & V Iberian of Ornithology, 2012. Home range behaviour in breeders of Bonelli's Eagle (*Aquila fasciata*) in Aragón. Autores: Martínez- Miranzo, B.; Banda, E.; Ferreiro, E.; Gardiazábal, A. & Aguirre, J.**

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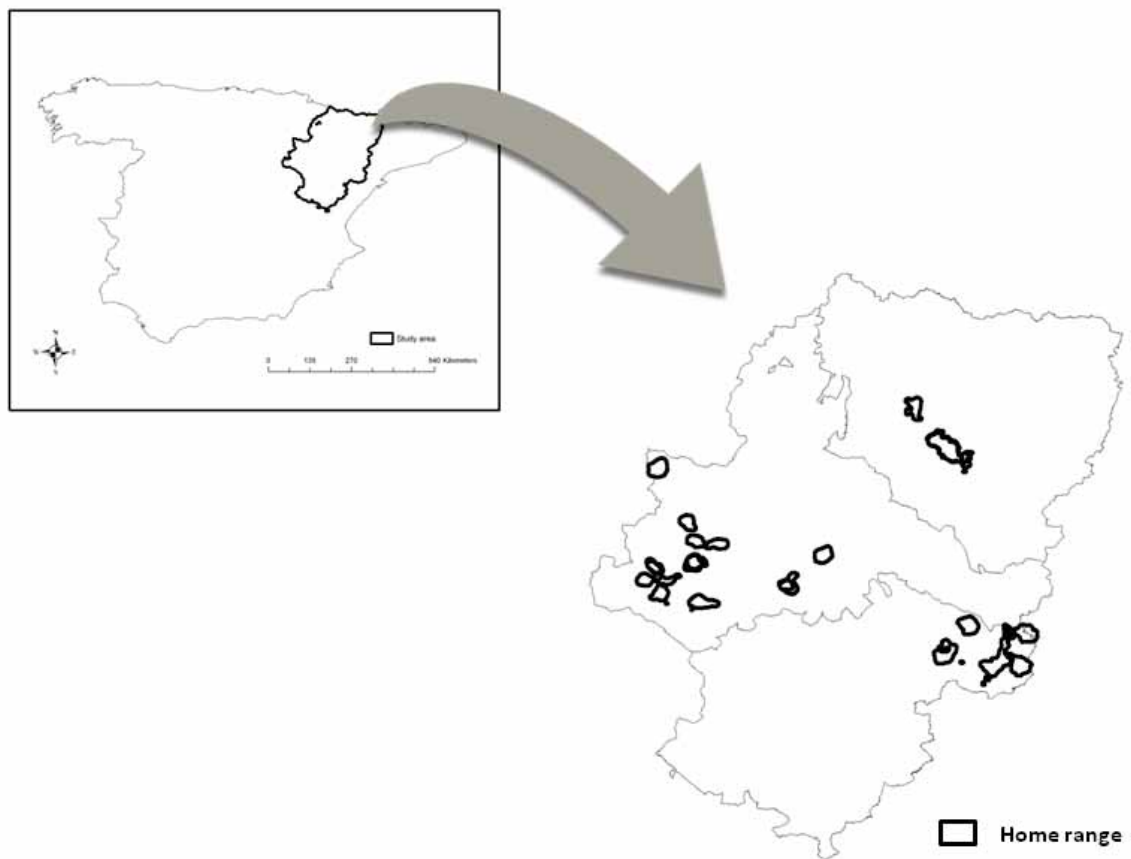
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Supplementary Material

Supplementary figure 1

Home range distribution in the study area



Supplementary table 1

Example of data output by ARGOS. Headlines include: Date of each coordinate, Time, Latitude and Longitude in Decimal Degree, Speed (Km/h), Course (indicates the transmitter position, and therefore the orientation of the Eagle, in the range of 360 degrees) and the Altitude in meters. Note: Precise coordinates have not been included in the table for security reasons (safety for the endangered species).

| Date | Time | Latitude(N) | Longitude(W) | Speed | Course | Altitude(m) |
|------------|-------|-------------|--------------|-------|--------|-------------|
| 2011-02-02 | 10:00 | | | 0 | 205 | 748 |
| 2011-02-02 | 11:00 | | | 0 | 52 | 742 |
| 2011-02-02 | 12:00 | | | 0 | 332 | 694 |
| 2011-02-02 | 13:00 | | | 0 | 247 | 706 |
| 2011-02-02 | 14:00 | | | 0 | 160 | 840 |
| 2011-02-02 | 15:00 | | | 0 | 336 | 836 |
| 2011-02-02 | 16:00 | | | 0 | 143 | 854 |
| 2011-02-02 | 17:00 | | | 0 | 122 | 851 |
| 2011-02-04 | 10:00 | | | 0 | 248 | 843 |
| 2011-02-04 | 11:00 | | | 0 | 186 | 845 |
| 2011-02-04 | 12:00 | | | 0 | 175 | 623 |
| 2011-02-04 | 13:00 | | | 0 | 308 | 624 |
| 2011-02-04 | 14:00 | | | 0 | 318 | 623 |
| 2011-02-04 | 15:00 | | | 34 | 111 | 750 |
| 2011-02-04 | 16:00 | | | 37 | 182 | 943 |
| 2011-02-04 | 17:00 | | | 0 | 154 | 924 |
| 2011-02-04 | 20:00 | | | 0 | 0 | ZD fix |
| 2011-02-04 | 21:00 | | | 0 | 0 | ZD fix |
| 2011-02-05 | 06:00 | | | 0 | 0 | ZD fix |
| 2011-02-05 | 07:00 | | | 0 | 102 | 849 |
| 2011-02-05 | 08:00 | | | 0 | 112 | 802 |
| 2011-02-05 | 09:00 | | | 0 | 284 | 785 |
| 2011-02-05 | 10:00 | | | 0 | 8 | 632 |
| 2011-02-05 | 11:00 | | | 71 | 353 | 649 |
| 2011-02-05 | 12:00 | | | 0 | 246 | 645 |
| 2011-02-05 | 13:00 | | | 0 | 197 | 719 |
| 2011-02-05 | 14:00 | | | 0 | 191 | 727 |
| 2011-02-07 | 13:00 | | | 0 | 145 | 615 |
| 2011-02-07 | 14:00 | | | 0 | 267 | 861 |
| 2011-02-07 | 15:00 | | | 26 | 14 | 967 |
| 2011-02-07 | 16:00 | | | 34 | 234 | 706 |
| 2011-02-07 | 17:00 | | | 0 | 77 | 727 |
| 2011-02-07 | 18:00 | | | 0 | 211 | 545 |
| 2011-02-07 | 19:00 | | | 0 | 195 | 555 |
| 2011-02-07 | 20:00 | | | 0 | 293 | 554 |
| 2011-02-07 | 21:00 | | | 0 | 197 | 554 |
| 2011-02-08 | 06:00 | | | 0 | 59 | 561 |
| 2011-02-08 | 07:00 | | | 0 | 25 | 561 |
| 2011-02-08 | 08:00 | | | 0 | 18 | 563 |
| 2011-02-08 | 12:00 | | | 0 | 83 | 587 |

Chapter 1: Differential spatial use and spatial fidelity by breeders in Bonelli's Eagle (*Aquila fasciata*).

Supplementary table 2

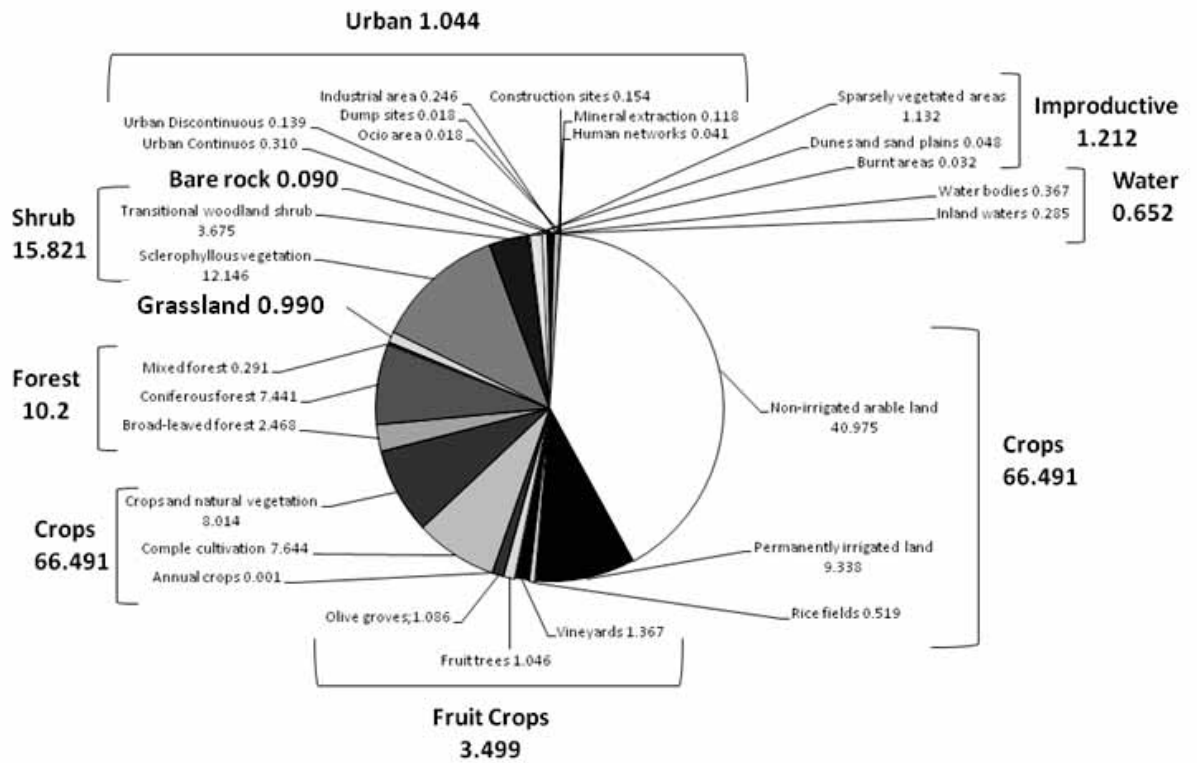
Localtion number for each individual (ID) male (1) and female (2) during three periods of the annual cycle. Non- breeding (1), Breeding (2) and chicks dependence period (3).

| | | 2004 | 2004 | 2005 | 2005 | 2005 | 2006 | 2006 | 2006 | 2007 | 2007 | 2007 | 2008 | 2008 | 2008 | 2009 | 2009 | 2009 | 2010 | 2010 | 2010 | 2011 | 2011 | 2011 | General total | |
|---------------|----|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|---------------|-------|
| Sex | ID | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | | | |
| 1 | 12 | | | | 367 | 80 | | | | | | | | | | | | | | | | | | | 447 | |
| 1 | 9 | | | | 315 | 297 | 447 | 318 | 271 | 373 | 296 | 269 | 631 | 438 | 312 | 220 | | | | | | | | | | 4187 |
| 1 | 15 | | | | | | | | | | | 208 | 536 | 456 | 505 | 539 | 432 | 422 | 168 | | | | | | | 3266 |
| 1 | 13 | | | | | | | | | | | | | | | 84 | 477 | 522 | 605 | 318 | 590 | 697 | 505 | | | 3798 |
| 1 | 1 | | | | 142 | 47 | | | | 167 | 126 | 276 | 445 | 355 | 344 | 335 | 231 | 392 | 457 | 317 | 379 | 503 | 322 | | | 4838 |
| 1 | 10 | | | | | | | | | 189 | | | | | | | | | | | | | | | | 189 |
| 1 | 16 | | | | | | | | | | | | | | | | | | 831 | 549 | 740 | 989 | 690 | | | 3799 |
| 1 | 14 | | 37 | 658 | 530 | 383 | 841 | 597 | 239 | | | | | | | | | | | | | | | | | 3285 |
| 1 | 3 | | | | | | | | | | | | | | | | | 327 | 815 | 722 | 437 | 700 | 129 | | | 3130 |
| 1 | 4 | | | 39 | 639 | 403 | 156 | | | | | | | | | | | | | | | | | | | 1237 |
| Total 1 | | 0 | 76 | 1297 | 1757 | 963 | 1288 | 915 | 510 | 729 | 422 | 753 | 1612 | 1249 | 1161 | 1178 | 1467 | 2151 | 2783 | 1621 | 2409 | 2318 | 1517 | | | 28176 |
| 2 | 8 | | | | | | | | | | | 173 | 200 | 484 | 505 | 262 | 546 | 438 | 224 | 324 | 494 | 77 | | | | 3727 |
| 2 | 2 | | | | | | | | | | | 40 | 476 | 731 | 285 | 482 | 673 | 331 | 441 | 700 | 465 | 538 | | | | 5162 |
| 2 | 5 | 268 | 160 | 175 | 356 | 253 | 278 | 161 | 135 | 288 | 133 | 157 | 176 | 461 | 145 | | | | | | | | | | | 3146 |
| 2 | 7 | | | | | | | | | | | 94 | 135 | 414 | 568 | 318 | 275 | 637 | 28 | | | | | | | 2469 |
| 2 | 11 | | | | | | | | | | | | | | | | | | | | 92 | 969 | 614 | | | 1675 |
| 2 | 6 | | | | | | | | | | | | | | | | | 205 | 373 | 636 | 502 | 570 | | | | 2376 |
| 2 | 17 | | | | | | | | | | | | | | | | | | | | 66 | 571 | 632 | | | 1269 |
| Total 2 | | 268 | 160 | 175 | 356 | 253 | 278 | 161 | 135 | 288 | 133 | 424 | 551 | 1835 | 1949 | 885 | 1303 | 1748 | 788 | 1138 | 1988 | 2674 | 2354 | | | 19824 |
| General total | | 268 | 236 | 1472 | 2113 | 1216 | 1566 | 1076 | 645 | 1017 | 555 | 1177 | 2163 | 3084 | 3110 | 2043 | 2770 | 3899 | 3571 | 2759 | 4397 | 4992 | 3671 | | | 48000 |

Chapter 2: Multiscale analysis of habitat selection by Bonelli's Eagle (*Aquila fasciata*) in NE Spain

Supplementary figure 2

Habitat type (%) composition of the study area.



Chapter 3: Home range requirements in a generalist top predator: prey abundance o trophic stability?

Supplementary table 3.

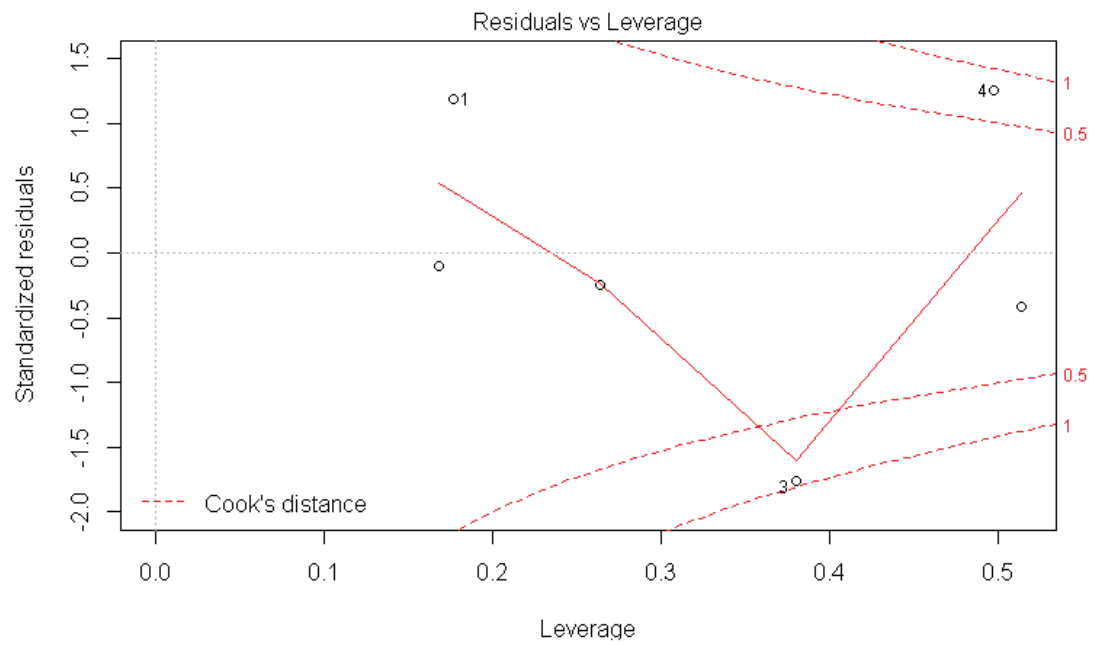
Census templates for prey availability.

| CENSUS TEMPLATE | | | | | | | | | | | | | |
|-----------------|----|---------------------------------|---|------------------|-------------------|-----------|----------------|-------|-----------------|-------------------------|----------|------|--|
| Home range ID: | | Grid ID: | | | Date: | | Observer Name: | | | | | | |
| Start time: | | Final time: | | | Distance: | | | | | | | | |
| TIME OBS. | WP | COORDINATE (DECIMAL DEGREE) | | N° OF LATRINE | N° OF INDIVIDUALS | | | | HABITAT CODE | VEGETATION TEMPLATE (%) | | | |
| | | X | Y | | rabbit | partridge | pigeon | cavid | | < 0,5m | 0,5 - 2m | > 2m | |
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**NOTE: ONLY ONE PAPER PER ITINERARY
OBSERVATION:**

Supplementary figure 3

Cook Distance and Residuals vs. Leverage of the general model.



Chapter 4: Mismatch between spatial distribution and breeding success reveals sinks population in an endangered raptor species.

Supplementary figure 4

Variables effects in different models: distribution model (A) and breeding model (B)

