Home range requirements in Bonelli's eagle (*Aquila fasciata*): prey abundance or trophic stability?

Beatriz Martínez-Miranzo[1] · Eva Banda[1,2] · José I. Aguirre[1]

Abstract

Prey abundance is one of the limiting factors for establishment a home range. In particular, biomass abundance could act as a key element for generalist top predators, with wide prey type spectrum, for establishing their home ranges. We studied if biomass abundance may act as a limiting factor for the establishment of home range in a generalist top predator, Bonelli's eagle (*Aquila fasciata*). We used GPS satellite data on breeding individuals over a 10-year period to deepen into home range behaviour. To quantify biomass abundance, we performed surveys at different periods of the year cycle for potential prey inside the home ranges and outside them. We checked if differences in biomass were identified between home ranges and potential adjacent areas. Also, annual and seasonal variation in biomass abundance may be recorded. Variations in biomass abundance among home range were detected but no annual or seasonal variation within home range was identified. Differences in biomass abundance were identified between each of the home range and their potential adjacent areas. Although biomass abundance is lower inside the home range, it remains stable throughout the year while strong fluctuations in biomass abundance were detected outside them. Our results show that Bonelli's eagle may establish their home range based on permanent biomass stability (*Trophic Stability Hypothesis*) rather than great seasonal but unpredictable abundances. This approach may have strong implications for management conservation programs of territorial top generalist predators.

Keywords Bonelli's eagle · Home range establishment · Trophic behaviour · Biomass availability · Prey survey · Spatial ecology

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 and Pleguezuelos 2000, Benson, Chamberlain and Leopold 2005, Lourenço et al. 2015). Individuals tend to establish a minimum home range size with adequate prey abundance for survival (Benson et al. 2005). But in times of food scarcity, *optimal foraging theory* predicts that animals show a broader spectrum of prey compared with those in the periods of great prey abundance (MacArthur and Pianka 1966, Perry and Pianka 1997). In this context, scarcity of profitable prey may influence home range size or maintenance and indirectly in home range behaviour (Lourenço et al. 2015).

In generalist top predators, where prey type is not a limiting factor and the trophic spectrum is larger, the total amount of biomass available provided by all potential prey plays a key role (Fargallo et al. 2009, Lourenço et al. 2105). Even more when the abundance of profitable prey is scarce, they select more accessible and easier to detect prey types (Ontiveros et al. 2005 and Palma et al. 2006). Previous studies have used prey abundance as an index to assess the availability of food within a home range (Ontiveros and Pleguezuelos 2000, Ontiveros, Pleguezuelos and Caro 2005). However, the total

✉ Beatriz Martínez-Miranzo
   bmartinez@ucm.es

1   Department of Biodiversity, Ecology and Evolution, Faculty of Biology, Complutense University of Madrid, José Antonio Novais 12, 28040 Madrid, Spain

2   ENARA Educación Ambiental, Las Rozas, 28090 Madrid, XI, Spain

amount of available biomass to be consumed would be more realistic approach than particular prey abundance (Lourenço et al. 2015).

In addition, prey abundance can be influenced by seasonal variations on the prey biological cycle and habitat characteristics (Korpimäki and Krebs 1996, Millon et al. 2008, White 2008). This may be determinant for home range size and maintenance over time, especially in environments under marked seasonality. This is the case of Mediterranean ecosystems, where the limited prey abundance 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 on 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 prey as rabbits (Ontiveros et al. 2005, Moleón et al. 2012) makes it a great model to understand the underlying processes relating home range structure under extreme seasonal environments.

Based on long-term monitoring programmes of breeding individuals, that maintain their home ranges' size and shape over the years (Martínez-Miranzo et al. 2016a), we tested whether a Western European population with a wide trophic spectrum (Moleón et al. 2009, Resano-Mayor et al. 2015) establish their home ranges based on biomass abundance or otherwise seek for stable biomass abundance to be consumed over time.

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

Material and methods

Study species and study area

Bonelli's eagle is a large raptor distributed almost exclusively in the 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 abundance (Ontiveros 2016). Such trophic plasticity 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 47,719 km^2 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 large farming areas, mostly of dry cereals (wheat and barley), olive trees and vineyards (70%) filled of Mediterranean scrub (16%) and coniferous forests (10%). Crags, cliffs and steppes are also present in this area (1%) (Sampietro et al. 1998) (see Martínez-Miranzo et al. 2016a and Martínez-Miranzo et al. 2016b for further details about the study area).

Home range behaviour

For this study, we selected 6 breeding home range distributed throughout the Aragón region (Fig. 1). The eagles were trapped by a radio-controlled bow-net trap during winter (October–February) between 2007 and 2014; 6 breeding individuals (3 males and 3 females), one for each home range, were ringed with a metal ring and were equipped with a 45-g Argos/GPS Platform Transmitter Terminal (PTT) 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 (range: 1.6–2.4-kg personal data), (Kenward 2001). PTTs were programmed to work between 6:00 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. Locations between 6:00 and 21:00 were used during summer.

With the collected data (about 48,000 locations), we estimated the breeders' home range using Fixed Kernel methods, isopleths 95% (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).

In addition, home ranges under study were selected based on the presence of different habitat types, covering a wide variety of habitats, from coniferous forests to steppe areas and upland crops, through rocky and difference scrub types.

Survey methodology

To identify relationships between home range behaviour and food abundance, specific survey methodology to record
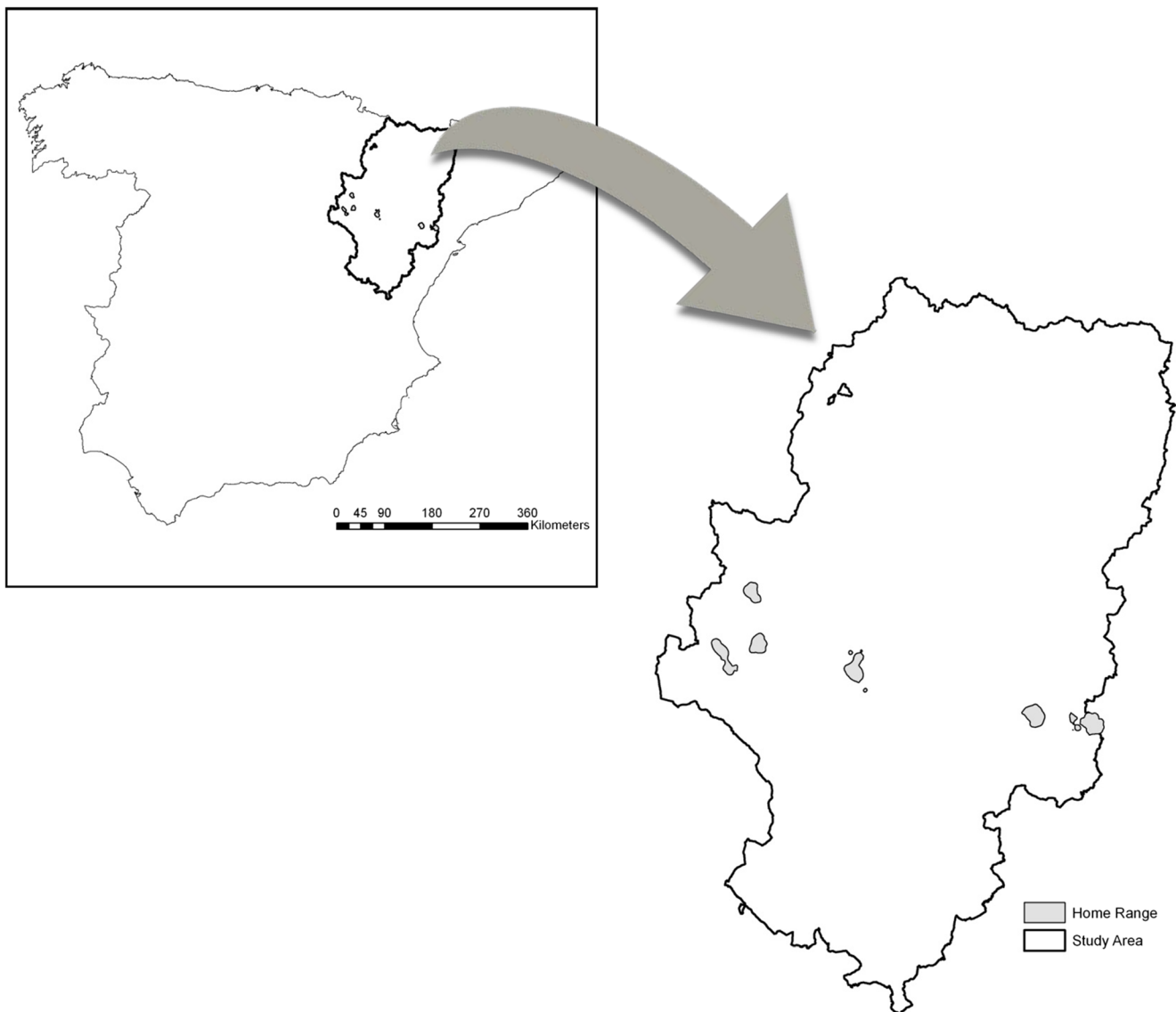
Fig. 1 Map showing the Aragon Region on NE of Spain and the location of home ranges of Bonelli´s eagle included in this study

potential preys was designed. Pigeons (including *Columba sp.*, *Streptopelia* sp.) (27%), rabbits (*Oryctolagus cuniculus*) (22%), red-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).

In this population, the eagles maintain the shape and size of the home range over the years (Martínez-Miranzo et al. 2016a). Such circumstance allowed to perform stripe transect on foot during two consecutive years (2013 and 2014). All eagles were also tracked during the surveys.

We established two survey 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 centroid of the home range 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 did not use by the individuals according with GPS data (see Martínez-Miranzo et al. 2016a for more details). All buffers were calculated using the "Buffer analysis" tool in ArcGIS 9.3.

We divided both areas in a 1 × 1-km grid and randomly chose 20 grids per settlement area (ten in HR and ten in PB) (Fig. 2). In every grid, the survey transects 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
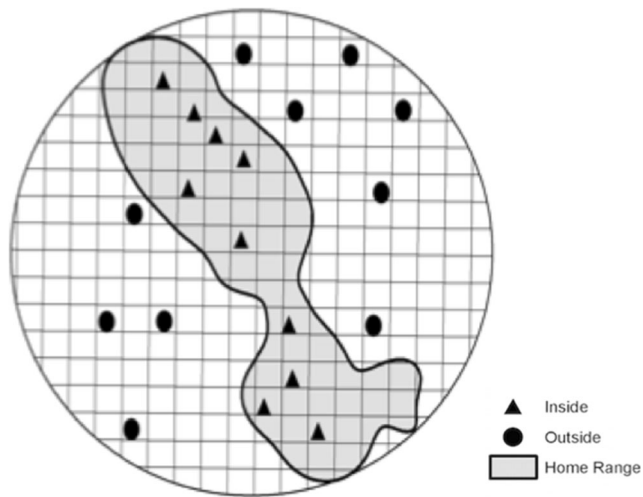
Fig. 2 Example of survey methodology. A grid (UTM 1X1 Km) was overlaid in order to randomize survey transects. Grey area shows the home range and white area shows the buffer corresponding to the potential area outside the home range. Triangles represent the randomly UTM itineraries performed inside the home range and circle outside it

25 m (Tellería 1986). The duration of each itinerary was approximately 1 h at a constant speed of 2.5 km/h. The surveys were conducted in the early morning hours and late afternoon (Palomares 2001, Moleón et al. 2012). We always avoided the midday hours, with more sun exposure and lower potential prey activity. In addition, we avoid weather conditions that compromise the survey, particularly rain or wind. 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 abundance, we repeated exactly the same itineraries during three different periods related to the biological cycle of prey and predators. Only one visit per itinerary was doing in each period. Winter survey 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 abundance is lower and human hunting activities are in progress so may cause difference in prey abundance. Spring survey, in March, is related to the Eagle's breeding season (Br). In general, breeder's movements are restricted, normally the female spend the most part of the day incubate. Also, prey abundance at this time is important for breeding (Ontiveros 2016). Summer survey was carried out in June, synchronised with post-fledging dependence period (Pfdp), were parents continue to feed their fledglings near nesting areas until the juveniles leave the home range 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 and index of biomass/distance unit or Kilometric Biomass Index (KBI onwards).

Data analysis

We determined general abundance of the different prey types. After that, 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 analysed our data using zero-inflated hurdle regression model with binomial distribution (Cragg 1971). General models were constructed using KBI as dependent variable. Settlement areas, with two levels (HR or BD), year and period were used as covariates in different models. All the residual's distributions were checked to validate the use of the different models (Potts and Elith 2006). All analyses were performed using R software (3.2.2).

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

In order to determine the distribution of biomass abundance in the home range, we constructed a model where KBI was used as dependent variable and settlement areas (HR/BD) 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 abundance. To test for annual variation, we used KBI as a dependent variable and year and settlement areas at two levels (HR/BD) 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 settlement area 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 abundance

A total of 1050 km were surveyed and 2042 prey records were obtained during 2013–2014. Rabbits (160 records) were the least recorded type of prey and pigeons (1065 records) were the most recorded. Red-legged Partridges (526 records) and corvids (291 records) were prey type with medium abundances.

Biomass distribution

Significant differences between total biomass abundance and home range were found ($Z_{1, 6} = 3.032$, $p = 0.024$). That is, each home range has a different abundance of biomass. We did not find any correlation between KBI and home range size ($R^2 = 0.25$ and $p = 0.179$), indicating that KBI does not influence home range size.

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

A total of 6 models were built (Tables 1 and 2). Biomass abundance distribution is explained by the settlement areas (HR or PB). Also biomass abundance is influenced by seasonal variation, particularly NBr period. 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 home ranges. Therefore, we found an irregular biomass abundance in PB and large fluctuations over the year (range 1188–232 g/km), while biomass abundance in HR is regular and similar in all home ranges (range 678–285 g/km) (Fig. 3)

Temporal variation

We did not find significant differences in biomass abundance 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 analysed seasonal biomass abundance between HR and PB, we found significant differences ($Z_{1,6} = 2.740$, $p = 0.006$) (Table 1) and low biomass abundance in NBr period too. Therefore, there is no difference in biomass abundance over the years. However, there is a seasonal variation influenced by the non-breeding season (where biomass available is low) in settlement areas, HR and PB.

Discussion

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

The study of home range behaviour has 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

Fig. 3 Mean biomass abundance (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
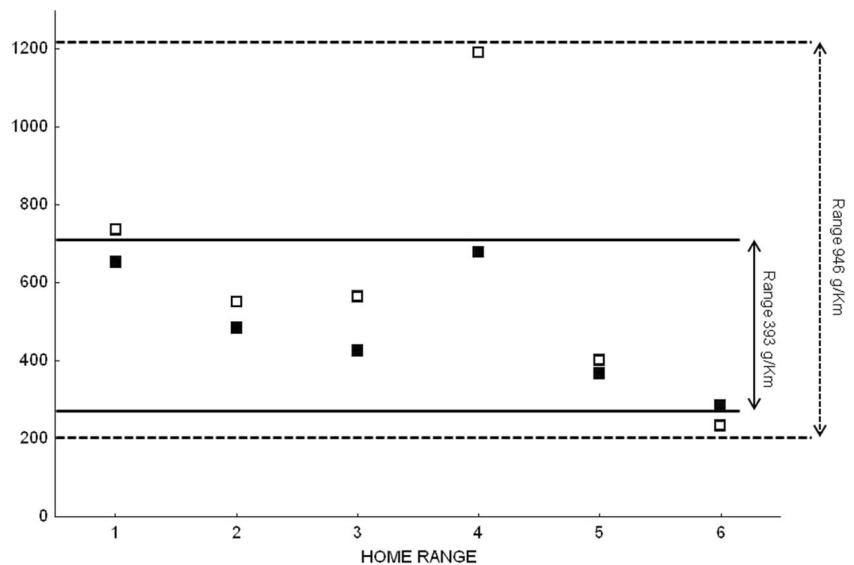
Table 1 Mean KBI values (g/km) by period in potential boundaries areas (PB) and inside the six home range (HR) in the settlement areas (SA) under study. The total size of each home range (HR size) is shown in km². Total mean values represent pooled mean data for each home range during all study years not accounting for period (see Fig. 3)

SA (HRSize)	Side	NBr period	Br period	Pfd period	Total mean values
SA1 (63.5)	PB	688.20	311.08	1130.39	735.56
	HR	756.43	395.25	767.93	652.75
SA2 (61.9)	PB	414.56	745.77	544.47	552.23
	HR	564.08	568.72	342.64	483.27
SA3 (50.1)	PB	556.70	460.44	656.32	563.42
	HR	376.21	382.79	525.99	425.21
SA4 (43.3)	PB	1685.28	1107.40	751.73	1188.76
	HR	1062.79	607.98	348.53	678.60
SA5 (68.5)	PB	535.81	557.90	153.5	400.32
	HR	572.34	137.45	328.17	369.16
SA6 (75.1)	PB	401.469	139.04	98.75	232.03
	HR	448.27	254.98	164.89	285.09

selection (Martínez-Miranzo et al. 2016a, Martínez-Miranzo et al. 2016b). But, the main limiting factor when establishing home ranges is food abundance (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. 2016). For territorial species, it is important to know how food abundance, 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 1998, Moleón et al. 2012, Palma et al. 2006) or by direct survey of prey (Ontiveros et al. 2005). Usually, they have been performed only during the breeding season (Ontiveros and Pleguezuelos 2000). When the abundance of profitable prey is scarce, 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 abundance is a more

realistic approach to explain home range structure in relation to food availability in a top generalist predator.

The *optimal foraging theory* predicts that animal choose the most economically advantageous foraging pattern, such as the most abundance food per time unit (Emlen 1966, MacArthur and Pianka 1966). The animals try to obtain the higher benefit (energy) under the lowest foraging cost, so that they can maximise fitness. Under this approach, territorial species use the smallest possible home range 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. They establish their home ranges based on greater profitable prey abundances that allow them to maximise their fitness. However, top generalist predators, particularly our model species Bonelli's eagle, follow a strategy that we called the *Trophic Stability Hypothesis*. According to which, when profitable prey is scarce, regular biomass stability available over the entire year cycle is more important than relatively high but unpredictable abundances of each prey species over the same period. In particular fluctuating conditions, like Mediterranean environments, predators adjust their home range 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 abundance within the home range. Although there is a decrease in total biomass abundance 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).

Table 2 Ranking of the models used to explain prey availability using KBI (kilometric abundance index) and year, period (periods related to the biological cycle of the Bonelli's eagle), home range (home range ID) and settlement areas (SA) at two levels (inside home range or boundary areas, outside home range) under study us covariates. Akaike's information criterion (AIC), difference between model and minimum AIC values (ΔAIC_c) and AIC weights (ω_i). Models separated by less than 2 ΔAIC_c points are considered equally probable

	Hypothesised model	AIC_c	ΔAIC_c	ω_i
KBI	Year + period + home range + SA	6520.461	0	0.551
	Period + home range + SA	6521.420	0.959	0.341
	Year + period + home range	6523.714	3.253	0.108
	Year + home range + SA	6561.965	41.504	< 0.0001
	Year + period + SA	6563.632	43.171	< 0.0001
	Period + SA	6565.174	44.713	< 0.0001

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 optimisation 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 abundance inside home ranges differs only by 393 g/km while outside the home ranges its variation is three times bigger (see Fig. 3). This suggests the *Trophic Stability Hypothesis* and opens a new approach to conservation of top predator raptors. This new approach should be considered in conservation programmes 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 favour not only the establishment but the maintenance of home range 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.

References

Aebischer NJ, Potts GR, Rehfisch M (1999) Using ringing data to study the effect of hunting on bird populations. Ringing Migr 19(S1):67–81

Alcántara M, Ferreiro E, Gardiazábal A (2003) El Águila-azor Perdicera en Aragón. Naturaleza Aragonesa 10:41–47

Arroyo B, Beja P (2002) Impact of hunting management practices on biodiversity. Report WP2 to REGHAB project. European Commission, Brussels. Available at http://digital.csic.es/bitstream/10261/8260/1/WP2-repportf.pdf

Benson JF, Chamberlain MJ, Leopold BD (2005) Regulation of space use in a solitary felid: population density or prey availability? Anim Behav 71:685–693

Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol Lett 11:637–650

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352

Burnham KP, Anderson DR (1998) Model selection and inference. A practical information-theoretic approach, Springer, New York, NY, 353 pp

Carrascal LM, Seoane J (2009) Factors affecting large-scale distribution of the Bonelli's eagle (Aquila fasciata) in Spain. Ecol Res 24:565–573

Carrete M, Sánchez-Zapata JA, Tella JL, Gil-Sánchez JM, Moleón M (2006) Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. Oikos. 112:680–690

Campioni L, Delgado MM, Lourenço R, Bastianelli G, Fernández N, Penteriani V (2013) Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. Oecologia 172:371–385

Cragg JG (1971) Some statistical models for limited dependent variables with application to the demand for durable goods. Econometrica 39:829–844

Cramp S, Simmons KEL (1980) The birds of the western Palearctic Volume II. Oxford University Press, Oxford, New York, 695 p

Fargallo JA, Martínez-Padilla J, Viñuela J, Blanco G, Torre I, Vergara P, De Neve L (2009) Kestrel–prey dynamic in a Mediterranean region: the effect of generalist predation and climatic factors. PLoS One 4:e4311

Fitzner RE, Rogers LE, Uresk DW (1977) Techniques useful for determining raptor prey species abundance. J Raptor Res 11:67–71

Gálvez-Bravo L (2011) Conejo – Oryctolagus cuniculus. In: Salvador A, Cassinello J (eds) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid Available from http://www.vertebradosibericos.org/

Garcelon DK (1985) Mounting backpack telemetry packages on Bald Eagles. Institute for Wildlife Studies, Arcata

Kenward RE (2001) A manual for wildlife radio tagging. Academic Press, London

Korpimäki E, Krebs CJ (1996) Predation and population cycles of small mammals. BioScience. 46:754–764

López-López P, García-Ripollés C, Aguilar J, García-López F, Verdejo J (2006) Modelling breeding habitat preferences of Bonelli's eagle (Hieraaetus fasciatus) in relation to topography, disturbance, climate and land use at different spatial scales. J Ornithol 147:97–106

Lourenço R, Delgado MM, Campioni L, Korpimäki E, Penteriani V (2015) Evaluating the influence of diet-related variables on breeding performance and home range behaviour of a top predator. Popul Ecol 57:625–636

MacArthur RH, Pianka ER (1966) On Optimal Use of a Patchy Environment. The American Naturalist 100(916):603–609

Martínez JA, Calvo JF, Martínez JE, Zuberogoitia I, Zabala J, Redpath SM (2008) Breeding performance, age effects and territory occupancy in a Bonelli's Eagle Hieraaetus fasciatus population. Ibis 150:223–233

Martínez-Miranzo B, Banda E, Gardiazábal A, Ferreiro E, Aguirre JI (2016a) Differential spatial use and spatial fidelity by breeders in Bonelli's eagle (Aquila fasciata). J Ornithol 157:971–979

Martínez-Miranzo B, Banda E, Aguirre JI (2016b) Multiscale analysis of habitat selection by Bonelli's eagle (Aquila fasciata) in NE Spain. Eur J Wildl Res 62:673–679

Maynard Smith J (1974) Models in ecology. Cambridge University Press, Cambridge

Millon A, Bretagnolle V (2008) Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. Oikos. 117:1500–1510

Moleón M, Sánchez-Zapata JA, Gil-Sánchez JM, Ballesteros-Duperón E, Barea-Azcón JM, Virgós E (2012) Predator–prey relationships in a Mediterranean vertebrate system: Bonelli's eagles, rabbits and partridges. Oecologia 168:679–689

Ontiveros D, Pleguezuelos JM (2000) Influence of prey densities in the distribution and breeding success of Bonelli's eagle (Hieraaetus fasciatus): management implications. Biol Conserv 93:19–25

Ontiveros D, Pleguezuelos JM, Caro J (2005) Prey density, prey detectability and food habits: the case of Bonelli's eagle and the conservation measures. Biol Conserv 123:19–25

Ontiveros D (2016) Águila perdicera – Hieraaetus fasciatus. In: Enciclopedia Virtual de los Vertebrados Españoles. Salvador A, Morales, MB (eds) Museo Nacional de Ciencias Naturales, Madrid (n.d.) Available from http://www.vertebradosibericos.org/

Palma L, Beja P, Pais M, Da Fonseca LC (2006) Why do raptors take domestic prey? The case of Bonelli's eagles and pigeons. J Appl Ecol 43(6):1075–1086

Palomares F (2001) Comparison of three methods to estimate rabbit abundance in a Mediterranean environment. Wildl Soc Bull 29(2):578–585

Perry G, Pianka ER (1997) Animal foraging: past, present and future. Trends in Ecology & Evolution 12(9):360–364

Potts JM, Elith J (2006) Comparing species abundance models. Ecol Model 199:153–163

Resano-Mayor J, Real J, Moleón M, Sánchez-Zapata JA, Palma L, Hernández-Matías A (2016) Diet–demography relationships in a long-lived predator: from territories to populations. Oikos. 125: 262–270

Real J (1998) El Águila Perdicera (Hieraaetus fasciatus) en Cataluña. Status, Ecologia trófica, Biología reproductora y demografia. PhD Thesis. University of Barcelona. Spain.

Real J, Mañosa S, Codina J (1998) Post-nestling dependence period in the Bonelli's eagle Hieraaetus fasciatus. Ornis Fenn 75:129–137

Sampietro FJ, Pelayo E, Hernández F, Cabrera M, Guiral J (1998) Aves de Aragón. Atlas de especies nidificantes, Diputación General de Aragón Ibercaja, Zaragoza

Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085

Swihard RK, Slade NA (1985) Testing for independence of observations in animal movements. Ecology 66:1176–1184

Tellería JL (1986) Manual para el censo de los vertebrados terrestres. Raíces, Madrid

Van Moorter B, Rolandsen C, Basille M, Gaillard JM (2016) Movement is the glue connecting home ranges and habitat selection. J Anim Ecol 85:21–31

Wilson EO (1975) Sociobiology: the New Synthesis. Belknap Press, Cambridge, Massachusetts

White TCR (2008) The role of food, weather and climate in limiting the abundance of animals. Biol Rev 83:227–248