Space use of adult Spanish Imperial Eagles *Aquila adalberti*

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Abstract. The ranges and space use of eight radio-tracked Spanish Imperial Eagles are described. The annual mean range was 25 146 ha during the breeding season (BS) and 20 557 ha in the non-breeding season (NBS). The eagles were found up to 35.9 km away from their nest during BS and nearly 62 km away during NBS. The maximum total distance covered in one day was 113.6 km, with males flying longer distances than females during BS. There was less overlap between ranges during BS, and the mean home range varied from 3881 ha in BS to 2085 ha in NBS. The areas where territorial behaviour (display flights, defence and/or aggression) was observed contained the nest-tree, the most frequently used perches, and the feeding ground nearest to the nest. Breeding home ranges were negatively correlated with densities of Rabbits *Oryctolagus cuniculus*. Breeding eagles whose home range had low rabbit densities travelled 16.2–28.9 km from their nest to reach distant, undefended feeding grounds with much higher rabbit densities. Our results suggest that home ranges varied with prey density and a bird's reproductive status. Larger breeding ranges are probably related to an increase in energy requirements, while habitat quality is probably a regulatory mechanism of space use. In terms of home range analysis methodology, our observations of eagle behaviour favour Cluster Analysis over Kernel, particularly for defining distant feeding grounds.

Key words: Spanish Imperial Eagle, *Aquila adalberti*, home range, spatial use, territorial behaviour

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INTRODUCTION

Home range is the fundamental measure of space used by animals (Hemson et al. 2005). For birds of prey, home range size is small if prey is abundant near the nest and is determined largely by the number of feeding places used and the distances between them (Newton 1979). The territory, or defended section of the home range, can be described in terms of two main factors: nesting requirements and food resources, with territory size varying in relation to the environment so as to maximize the fitness of the individual (Patterson 1980). Thus, territory size can be viewed in terms of two competing hypotheses: as a response to resource density (food availability), so that the territory contains enough food to satisfy energetic requirements (Schoener 1968, Gill & Wolf 1975); or as a response to defense costs, where the variation

in territory size occurs because more competitors are attracted to areas rich in resources, and such areas are, therefore, more costly to defend per unit area (Krebs 1971). The analysis of home range is based on the utilization density of the range, and is defined as the minimum area in which an animal has a given probability (for example of 95%) of being found (Worton 1995). Although data on breeding birds of prey tend to be centered on their active nest site, a more detailed estimate of their true use of space can be achieved with Cluster analysis (Kenward et al. 2001) and Kernel estimates (Hemson et al. 2005). The use of these methods is very common, yet evaluating and comparing area estimates with real data is difficult, since actual home range structure is unknown (Worton 1995).

The Spanish Imperial Eagle, a large-sized raptor, considered as one of the rarest and most

threatened birds of prey in the world (Birdlife International 2004), inhabits the south-western quadrant of the Iberian Peninsula and has a population estimated at around 200 breeding pairs (González et al. 2008). The breeding population is sedentary and monogamous (although see González et al. 2006a) and egg-laying takes place between March and April (Margalida et al. 2007b). Fledging takes place in June and July and, after around two months in the parental territory, the young begin to disperse (Margalida et al. 2007b). Although juvenile dispersal has been studied (González et al. 1989, Ferrer 1993, González et al. 2006b), information regarding range and territorial behaviour in breeding individuals is anecdotal and unquantified (Valverde 1960, Meyburg 1975, Ferrer 1993). In this sense, basic information regarding movements, feeding grounds and ranges of breeding eagles remains completely unknown. This knowledge is necessary to elaborate the management and protection plans needed to preserve the areas occupied by breeders, and is considered a priority in the Spanish Strategy for the recovery of the species (González 1996, MMA 2001).

In this paper we aim to describe 1) size and spatial structure of range, home-range, and territory of breeding Spanish Imperial Eagles, 2) variations due to season, gender and food resources and 3) to compare Cluster and Kernel area analysis methods with regards to actual home range structure, i.e., biologically significant behaviours.

MATERIAL AND METHODS

Study area

The study was carried out in the Central Spain (provinces of Madrid, Ávila and Toledo, 40°05'–41°23'N, 3°03'–5°30'W). Altitude in the area ranged from 350 to 2460 m and the climate is Mediterranean continental cold. The area contains a dense population of wild Rabbits and is dominated by smooth terrain with rolling plains, where Holm Oak *Quercus rotundifolia* predominates (MMA 2004), and provides the habitat most commonly occupied by the species (González et al. 1990, 2008).

Data collection

Eight Spanish Imperial Eagles (three males and five females) were trapped with nets in 1995 and 1996 (3 and 5, respectively). The individuals were

sexed, measured and aged according to the plumage age-class classification established for the species (see González 1991, Forsman 1999). All eagles fitted with tags have bred in the following years.

Birds were equipped with back-pack VHF radio-tags, model TW-5 from Biotrack Ltd., weighing 60 g with two AA batteries and maximum range of 60 km in flight and 12 km perched or at ground level (pers. observ.). Each eagle was tracked throughout the day at least once a week. Locations were simultaneously obtained by two people every 15 minutes with receivers and Yaggi 3 element antennas. Recorder positions were obtained with a GPS and eagles location registered in UTM coordinates, with accuracy ± 100 m. Only locations with a triangulation within 30° to 150° angles were used. In order to compare breeding ranges between years, we radio-tracked the same individual (M43) during the following breeding season (annually in 1995 and only breeding season in 1996).

Once the eagles were radio-located they were searched for with binoculars and telescopes and visual data were registered as follows: 1) display/threat flight: upward flapping flight followed by rapid descent with wings folded, often marked with vocalizations as described for this species (Mountfort 1958, Meyburg 1975) and 2) hunting flight: flapping flight chasing a prey item in the air, diving flapping flight in the air or from a perch towards the ground and lastly, approximation flight to a carcass (Valverde 1967, Meyburg 1975).

For every recorded eagle's hunting attempt the relative rabbit density of the area was estimated by surveying rabbit droppings in the location. During 1995, rabbit droppings were counted in 30 circles of 60 cm radius along a transect covering all habitats and topographical irregularities in a 1 x 1 km square area (Palomares 2001) centered around each hunting location. In 1996, the sampled area was reduced to 500 x 500 m and 21 circles (reducing the sampled area and increasing sampling stations per area). In cases where radio-locations had greater triangulation error than one grid cell ($n = 31$ hunting attempts), all grid cells were censused and that with the highest density was chosen as the foraged area. Cells which had been recently drenched by rain or upturned by agricultural practices were discarded. Data of circles on droppings heaps were discarded since they distort a cell's rabbit density.

Most hunting flights were observed in the territories or in the polygon adjacent to or bordering

it, and for this reason we designated this area as the proximate feeding ground (PFG). Additionally, some eagles were observed hunting in other areas, not immediate to territories, designated as distant feeding grounds (DFG).

Data were classified according to the reproductive behaviour of each individual as either 1) breeding season (BS) from the beginning of incubation until the beginning of dispersal (first day in which young eagles were not observed in the nest area); in case of brood failure the period ended when its loss was registered, or 2) non-breeding season (NBS) from the end of the post-fledging period until the pre-laying period (before egg-laying). For each individual the location farthest from the nest (maximum distance traveled) and overall daily movements (sum of distances between consecutive locations), were calculated per day. Since radio tracking was carried out during daylight hours, roosting places were clearly determined by the first and last perched location of each day.

We defined "range" as the total area covered by each eagle during each season (Wilson 1975), regardless of whether the area is used or not; "home range" as the area in which an animal normally lives, regardless of whether or not the area is defended as territory, and without reference to the home ranges of other animals (Odum & Kuenzler 1955, Wilson 1975, McFarland 1987), commonly referred to as the minimum area in which an animal has a given probability (for example of 95%) of being found (Worton 1995); and "territory" as the area defended against conspecifics and heterospecifics (Wilson 1975, Newton 1979). Ranges were obtained using the outer most locations and forming the exterior concave and the exterior convex polygons. Since concave polygons appear to better adjust to the actual range than convex polygons (see Marzullf et al. 1997), we defined ranges with the area obtained by concave polygons but give the values of convex polygons for comparison purposes with other studies.

Home range estimates obtained with Cluster and Kernel analyses (calculated at 95%) were compared with visual data on territorial and feeding behaviour. Cluster analysis, which highlights the discontinuity of the used area and eliminates outliers (Kenward 1992, Kenward et al. 2001), was calculated with Ranges V (Kenward & Hodder 1996) and Kernel contour estimates, which may include areas not covered by the radio-tracked individual (Kenward et al. 2001), were made with an extension of Animal Movement in Arcview GIS (Hooge

& Wichenlaub 1997). Locations that produce the greatest discontinuity in size of the total area were excluded from the analysis by the Utilization Distribution Curve (Kenward 1992), in all areas this occurred with 5% of locations. Kernels were fixed and least squares cross validation method was not used. Previous information about the behaviour of this species suggests that they spend a great deal of time in the nest during the breeding season (Meyburg 1975, Margalida et al. 2007a) and certainly both Cluster and Kernel analysis resulted in a unique and very small home range around the nest during this period. Therefore, all nest locations during BS were excluded from home range analysis to allow for comparison with the non-breeding season. Range overlap was studied only between radio-marked eagles (with only one individual marked per territorial pair in all cases), regardless of gender or whether or not they occupied adjacent territories. The study site included 18 additional territorial pairs (own data), but none of them were radio-tagged and thus, their ranges were unknown and could not be included in range overlap analysis.

To avoid autocorrelation between locations these must be spaced in time so that an individual can travel from one edge of its home range to the other (Swihart & Slade 1985). In our study, this interval was established by eagle M43, who traveled the greatest distance from its nest. Thus we used locations taken 30 minutes apart; using shorter time intervals when there was no data at that interval. Regardless of the time interval, all hunting attempts and territorial behavioural data were used since these events were infrequently registered (0.5 and 0.4 daily observations, respectively).

Statistical analyses

To analyze maximum distance traveled and daily movement, the data on all individuals were used, except for the bird F3U because it was not paired. Maximum distance data were $\log(x+1)$ transformed to obtain a normal distribution. Individuals as the sample units were analyzed with a nested ANOVA for differences in the maximum distance between gender and seasons, with similar transformation and analysis performed on movement data. Rabbit dropping data were analyzed per year comparing PFG between individuals and, in cases where eagles had DFG, comparing DFG versus PFG within each eagle's range. Mean values of rabbit dropping counts were compared using Mann-Whitney U-tests. Relative

rabbit densities were rank ordered and correlated with ranges and home ranges by the Kendall Tau test. Second year data for M43 was recorded solely during the breeding period, so only the complete year-round data of 1995 was used in the annual analyses. Comparison of M43's two year BS data was made possible by using values of droppings/m². Eagle F1V was excluded from rabbit abundance analysis, since no hunting attempts were registered. The statistical significance was set at $p < 0.05$. Values are presented as means $\pm$ SD.

RESULTS

More than 14000 eagle radio locations were obtained in 336 days of study, with at least 40 eagle locations per days (from radio tracking data and visual observations). In order to avoid autocorrelation between data, we used only 7889 locations in the analysis (every 30 min, Table 1).

Range

Most eagles had larger ranges during the breeding (BS) than non-breeding season (NBS) (between 23% and 76% greater, Fig. 1 and 2), but differences were not significant (Wilcoxon test $z = 1.2$, $p = 0.225$, $n = 5$). Mean range areas during the BS were 25146 ha (range: 2377–61787 ha, $n = 5$) and 20557 ha during the NBS (range: 1898–61513 ha, $n = 7$). The male M43, tracked during two consecutive breeding seasons, used similar ranges, both in shape and location (28008 and 30018 ha, respectively; Table 1) with a 75% overlap. The unpaired female F3U, with 116844 ha, had an area noticeably greater than the paired birds.

Percent overlap between ranges varied between individuals and seasons. An overlap between individuals may be related to range size: i.e., F1C's area, which was very large (61787 ha), was overlapped in a very small percentage (2.67%) by eagle F45, yet F45's area (which was very small, 2475 ha) was overlapped extensively by eagle F1C, by 65.94% (Table 2). Total mean range overlap was higher in the NBS (47.6%) than in the BS (37.5%; Table 2, Fig. 1 and 2) although the differences were not statistically significant (Wilcoxon test $z = 0.4$, $p = 0.686$, $n = 5$). Overall, small-sized ranges overlapped extensively in both seasons and to a greater degree (more than 70% of their area) than in the case of large ranges (large ranges had less than 12% of their range overlapped).

Fig. 1. Ranges and home ranges of Spanish Imperial Eagles obtained from concave and Cluster analyses, respectively, during the breeding season. Stars within the polygons indicate the nest and dots indicate hunting attempts.

Distance from a roosting site to the nest varied with the season: while during the BS all birds spent the night less than 1 km from the nest, except two days when the birds F1C and F40 remained 11.5 and 35.8 km away, respectively, in the NBS this distance increased to 1 to 3 km away from the nest.

The average distance from the nest covered by eagles was 8.24 ± 6.07 km (range 2.6–17.8 km, $n = 5$) during the BS and 9.14 ± 8.19 km (range 2.6–27.3 km, $n = 7$) during the NBS. Maximum distance from the nest was 35.9 km in the BS and 61.5 km in the NBS. The longest movement in a day was 113.6 km and 90.7 km, for the BS and NBS, respectively. Differences in distances from the nest were not a direct result of either sex or season but rather of a combination of these two factors (nested ANOVA $F_{5,256} = 11.6$, $p = 0.0001$; Fig. 3), where males were significantly farther away from the nest than females (males: 13.4 ± 1.8 km vs females: 5.4 ± 1.9 km) only during the BS.

Fig. 2. Ranges and home ranges of Spanish Imperial Eagles obtained from concave and Cluster analyses, respectively, during the non-breeding season. Stars within the polygons indicate the nest and dots indicate hunting attempts.

Table 1. Descriptive variables and key results obtained during the study of eight radio-tracked Spanish Imperial Eagles. F — female, M — male, BS — breeding season, NBS — non-breeding season, N — No of locations. Distance from nest and daily movements — in km.

	First/Last Location	Season	Days	N	Range (ha)		Home range (ha)		Distance from nest (range)	Daily movement (range)
					Concave	Convex	Kernel	Cluster		
F40	30.01/30.12.95	BS	14	426	2377	4075	518	688	2.6 (0.0–11.5)	6.8 (0.0–23.6)
		NBS	39	784	25421	33 412	1676	1989	5.9 (2.6–24.2)	20.4 (1.0–58.7)
F45	02.02/28.12.95	BS	29	817	2475	2475	1542	1273	3.4 (0.4–5.4)	19.8 (0.8–47.0)
		NBS	21	466	1898	2050	206	607	2.6 (0.9–4.4)	13.0 (2.9–27.8)
F1C	03.04/26.12.96	BS	33	939	61787	80894	8960	8027	8.4 (2–35.9)	33.9 (8.3–68.7)
		NBS	12	291	28393	37648	1327	1612	7.9 (1.5–25.3)	28.3 (2.8–64.9)
F1V	01.09/1.12.96	NBS	21	229	8692	13792	2151	2325	6.5 (0.2–27.9)	16.3 (9.4–25.9)
M43-95	04.02/29.12.95	BS	38	941	28008	34975	13919	5304	17.8 (1.8–32.3)	56.1 (5.0–113.6)
		NBS	26	495	10504	11612	3 995	3325	6.4 (1.5–16.3)	27.7 (0.5–90.7)
M43-96	05.05/2.10.96	BS	26	773	30018	36954	9203	2044	-	-
M3X	16.02/21.12.96	BS	38	1054	31083	35453	3401	4115	9.0 (0.8–18.2)	38.6 (3.4–75.8)
		NBS	16	342	7478	9699	2217	645	7.4 (4.5–17.6)	20.5 (7.1–50.1)
M15	12.10/29.12.96	NBS	9	184	61513	144042	5751	4092	27.3 (15.3–61.5)	29.6 (1.6–82.9)
F3U	29.02/06.04.96	-	14	148	116844	197720	30806	81217	-	48.4 (14.7–116.3)

Fig. 3. Influence of the interaction between sex and season on the Spanish Imperial Eagles' maximum distance (km) from the nest.

This relationship also holds for movements, with males moving significantly more than females only during the BS (males: 47.3 ± 2.9 km vs females: 23.5 ± 1.9 , nested ANOVA $F_{5, 256} = 11.2$, $p = 0.0001$).

Home range

Home ranges obtained with Kernel estimates were located in positions similar to those obtained through Cluster analyses and had similar size (BS: Wilcoxon test $z = 0.674$, $p = 0.50$; NBS: $z = 0.676$, $p = 0.498$). Nonetheless, greater spatial detail is obtained for low-intensity-use areas by Cluster analyses. Outside the main nucleus, Cluster

analysis localizes up to 10 micronuclei while Kernel estimates represent an extensive area including areas not in use or does not localize any area at all.

Spanish Imperial Eagles had larger home ranges during the BS than during the NBS, but the differences were not significant (Wilcoxon test $z = 1.4$, $p = 0.138$, $n = 5$). Mean home ranges established by Cluster analyses were 3881 ha (range 688–8027, $n = 5$) in the BS and 2085 ha (range 607–4092, $n = 7$) in the NBS, covering a very small percentage of each season's range, only 15% of the BS range and 10% of the NBS range, although one bird, F45, did have a greater percentage of its breeding range covered by the home range (up to 51%). Mean home ranges obtained using Kernel estimates, with isolines at 95%, were 5668 ha (range 518–13919, $n = 5$) in the BS and 2474 ha (range 206–5751, $n = 7$) in the NBS and represent 23% and 12% of the range, respectively.

Display/threat flights were registered in both seasons and for both genders, with most of these flights (94.2%, in Cluster and 92.0% in Kernel, $n = 137$) being observed within the polygons/isolines that contained the nest-tree. The remainders of these flights were observed in the calculated home ranges. The total area of the recorded display/threat flights (e.g., the eagles' territory), was situated in all cases at the edge of the range, with the nest-tree at one corner. DFG were relatively distant from the territories (median = 21.4 km, IQR = 6.34; Fig. 1 and 2) and, in these areas, no display, defense or threat flights were ever

Table 2. Range overlap (percentage) between different Spanish Imperial Eagles and their overlap with all individuals together during the breeding season (BS) and non breeding season (NBS).

BS								
	F1C	M43	F45	F40	M3X	Global range overlap		
F1C		3.05	2.67	2.67	0.67	6.06		
M43-95	6.65		0	1.17	0.06	7.47		
F45	65.94	0		0	23.23	91.07		
F40	68.62	13.76	0		0	79.97		
M3X	1.32	0.05	1.86	0		3.13		
NBS								
	F1C	M43	F45	F40	M3X	M15	F1V	Global range overlap
F1C		0.0	0.82	60.11	0.0	0.0	2.04	61.39
M43-95	0.0		0.0	0.0	0.0	0.0	3.79	3.79
F45	12.38	0.0		96.36	0.0	0.0	0.0	99.73
F40	67.13	0.0	7.19		0.0	0.0	0.95	73.07
M3X	0.0	0.0	0.0	0.0		0.0	0.0	0.0
M15	0.0	0.0	0.0	0.0	0.0		0.0	0.0
F1V	6.69	4.61	0.0	2.8	0.0	0.0		11.32

Table 3. Mean $\pm$ s.d. of rabbit dropping counts in Spanish Imperial Eagles' proximate (PFG) and distant feeding grounds (DFG). * — differences between areas significant at $p < 0.05$ (Mann-Whitney U-test), N — number of hunting locations of each eagle where rabbit density was surveyed.

1995									
	N	Mean $\pm$ SD	M43 PFG	M43 DFG			F40 PFG	F45 PFG	
M43 PFG	9	2.7 $\pm$ 3.1		0.004*			0.0001*	0.0001*	
M43 DFG	7	15.1 $\pm$ 11.0					0.787	0.095	
F40 PFG	23	14.6 $\pm$ 7.5						0.0001*	
F45 PFG	30	7.9 $\pm$ 2.9							
1996									
	N	Mean $\pm$ SD	M43 DFG	F1C PFG	F1C DFG	M3X PFG	M3X DFG	M15	F3U
M43 PFG	6	2.8 $\pm$ 3.3	0.005*	0.509	0.020*	0.005*	0.002*	0.087	0.121
M43 DFG	10	39.8 $\pm$ 17.3		0.0001*	0.128	0.039*	0.790	0.322	0.062
F1C PFG	10	1.7 $\pm$ 2.2			0.011*	0.0001*	0.0001*	0.065	0.026*
F1C DFG	3	60.1 $\pm$ 13.4				0.012*	0.307	0.157	0.014*
M3X PFG	44	24.8 $\pm$ 21.1					0.041*	0.601	0.382
M3X DFG	8	47.1 $\pm$ 32.5						0.601	0.046*
M15	4	30.6 $\pm$ 22.2							0.610
F3U	8	19.3 $\pm$ 20.0							

observed. Spatial overlap between eagles was observed in DFG while none was registered within PFG (Fig. 1 and 2).

Cluster areas contained 88.2% of display/threat flights and 63.6% of hunting attempts, while Kernel contours covered 82.7% and 51.5%, respectively. Although both methods seem to closely reflect home ranges, it is in distant feeding grounds that Cluster areas adjust much better to the shape and form of eagle usage, characterized by small sized areas (between 200 and 800 ha) scattered in space (between 1 to 6 km apart).

Hunting grounds

Highest rabbit densities were registered in DFG, being statistically different from PFG, for all eagles and in all cases (Mann-Whitney U-test, Table 3). In 1995, the number of rabbit droppings in PFGs of eagles F40 and F45 were significantly greater than in the PFG of M43, but not with respect to its DFG. While in 1996, the number of rabbit droppings in PFGs of eagles F1C, M43 and M3X, where all significantly smaller than in all DFGs. DFG are used most intensively from July to September, when chicks are fledging. Rabbit dropping values were below 5 droppings/m² in PFG for all eagles when they used DFG. Birds that only used a PFG always had values above 5 droppings/m² in their hunting ground. Annual variations in rabbit densities can only be compared for bird M43's BS hunting grounds in 1995 and 1996, where they showed no significant variations.

Breeding home range sizes were significantly negatively correlated with rabbit densities at breeding seasons' PFG (Kendall Tau = -0.9, $p = 0.028$, $n = 5$), with highest rabbit densities found in the smaller home ranges. There was no correlation between PFG rabbit densities and NBS home range size ($p = 0.583$), or with range size in either season (BS, $p = 0.100$; NBS, $p = 0.583$).

DISCUSSION

These are the first quantified results obtained on the area use and territorial behaviour of breeding Spanish Imperial Eagles. Our data suggest that this species shows territorial behaviour and well defined home ranges, with range size varying greatly between pairs. Range use was marked by directional flights that were most frequently started from the nest or nearby perches and could transverse great distances (up to 61 km from their nest); considerably superior to those observed in other large eagles as the Golden Eagle *Aquila chrysaetos* (Marzluff et al. 1997, McGrady et al. 2002). Thus, sighting adult individuals outside known breeding areas does not imply the existence of new territorial pairs.

It has been suggested in other studies that displacement flights serve as an exploratory surveillance of the home range (Collopy & Edwards 1989, Marzluff et al. 1997, McGrady et al. 2002), possibly being related to prey search. Yet, Spanish

Imperial Eagles' largest distances from the nest were registered for males during the breeding season, which concurs more with their role as food providers during this period (Margalida et al. 2007a). Results for this species in Doñana (Valverde 1960, Ferrer 1993) have already suggested that large displacements were a result of flights to hunting grounds, located up to 20 km away from their nest. However, in our study we have also found that some of these flights are probably caused by human disturbance (see González et al. 2006c); with female F40 roosting 24 km from its nest during the incubation phase due to human hunting activities directly under its nest, thus causing the subsequent breeding failure. In another female (F1C), disturbances caused by human activities also resulted in the bird roosting 35 km from its nest.

Display flights were performed throughout the year and by both sexes. The abundance of their main prey item (the rabbit, see Delibes 1978, Sánchez et al. 2008) throughout the year coincides with the hypothesis that suggests that territoriality appears when conditions are favorable in terms of food availability and predictability (Schoener 1968). This results in large overlaps between ranges yet none within home ranges, similar to what has been observed in other eagles (Marzluff et al. 1997).

Home ranges were very small compared to the ranges, yet they are of great importance for eagles, as this area includes their nest, where they carry out reproductive activities and where they obtain their food. As in other raptors (Collopy & Edwards 1989, Marzluff et al. 1997), their fixation to an area would be related to mating. In this sense, the only non-mated eagle studied (F3U) clearly showed a different spatial structure, with a scattered home range, a significantly larger range and with no territorial behaviour.

In raptor species, home range varies with food availability (Marquiss & Newton 1981, Selås & Rafoss 1999). In our study, the size of the home range varied according to 1) prey density in the home ranges and 2) reproductive status of the bird with larger areas during the breeding season probably resulting from an increase in demand of prey items. There is a negative association between home range size and rabbit density, with small home ranges corresponding to areas with the greatest rabbit densities. Rabbit abundance creates an increase in territorial tensions in eagles, at least during the breeding season, since we observed that an increase in rabbit densities resulted in a decrease in home range size and an increase in range overlap. On the other hand,

displays in hunting areas close to the nest are probably due to the proximity of these hunting terrains to the nesting sites. Also, abundant rabbit densities explain why eagles only utilize proximate feeding grounds. The use of distant feeding grounds could be a result of rabbit densities below 5 droppings/m², and thus function as backup feeding grounds for deficient proximate feeding grounds. Meanwhile, the energetic cost of large displacements to distant feeding grounds is compensated for by benefits in prey abundance in those areas.

We observed that Spanish Imperial Eagles showed no territorial behaviour in distant feeding grounds, even though other eagles were regularly present (pers. obs.). These results support the hypothesis that birds defend permanent territories where food is predictable and abundant whereas where food is very seasonal individuals do not defend any fixed areas (Schoener 1968). Also, these areas, unlike proximate feeding grounds, could serve as communal hunting grounds (see Marzluff et al. 1997). Additionally, they are most frequently utilized during the fledgling dependence period (Alonso et al. 1987, González 1991), thereby reducing the energetic cost of food transport and supply to the young, since fledglings chase the parents for food. In situations of rabbit abundance there appears to be an increase in tolerance between eagles, and thus an increase in carrying capacity, which can be interpreted as an indicator of habitat quality. Territorial behaviour in eagles would be tied to the existence of an available food source (rabbits), following the model that proposes that feeding territories are defended at "intermediate" resource densities (proximate feeding grounds in our case) but not when resource densities are insufficient to satisfy energetic requirements (Brown 1964, Schoener 1968, MacFarland 1987). Super-abundance models suggest that when there is a high density of resources there is no need to defend the area since an individual can obtain the necessary energy without needing to exclude other individuals, which would correspond to eagle behaviour in distant feeding grounds.

With respect to area analysis methods, we found that with a small sample size (< 30 locations), the area analysis based on exclusion of outliers did not adequately quantify eagle home ranges, underestimating areas of sporadic use yet important to breeding success. This is the case of distant feeding grounds, since more than 75% of eagle locations were less than 3 km from the nest.

In addition, the home range estimate which best described areas of biological importance for eagles, were those obtained with multinuclear polygons (Cluster analysis) over Kernel estimates. To define some specific areas, such as distant feeding grounds, home range analysis should be performed excluding nest and nest-adjacent locations. Analysis which simply reduce percentage of location, exclude outliers or outline an arbitrary perimeter around the nest, will significantly under evaluate the spatial requirements of the species.

In conclusion, there is great variability in breeding Spanish Imperial Eagle home range size and structure. This appears to be determined by its main prey abundance (the rabbit), thus stressing the importance of habitat quality to this population and its spatial distribution. In this sense, a high quality habitat indicator for Spanish Imperial Eagles could be rabbit densities above which eagles use only the proximate feeding grounds (5 droppings/m²). Conservation measures for the species must not solely be based on territory protection, but also on the appropriate management of distant feeding grounds of reproductive populations.

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STRESZCZENIE

[Arealy osobnicze i wykorzystanie terenu przez orła iberyjskiego]

Badania prowadzono w środkowej Hiszpanii, na obszarach o wysokim zagęszczeniu królików stanowiących podstawę pokarmu orła iberyjskiego. W 1995 i 1996 schwytano w sumie 8 orłów (3 samce i 5 samic), które po oznaczeniu płci, dokonaniu pomiarów i określeniu wieku zostały wyposażone w nadajniki o masie 60 g (VHF model TW-5). Każdy z osobników był śledzony w ciągu całego dnia przynajmniej raz na tydzień. Lokalizację każdego ptaka określano z dokładnością do 100 m. Po każdym zarejestrowanym ataku orła określano zagęszczenie królików w miejscu polowania. W 1995 odchody królików liczono w 30 okręgach o promieniu 60 cm położonych wzdłuż transektów w różnych środowiskach w obrębie kwadratów 1x1 km, których środek był miejscem polowania. W 1996 liczbę powierzchni zmniejszono do 21 okręgów w kwadracie 500 x 500m.

Podczas 336 dni badań dokonano ponad 14000 lokalizacji. By uniknąć autokorelacji, do analiz użyto 7889 z nich. Średnia wielkość arealu sięgała w okresie lęgowym 25146 ha, orły oddalały się od gniazd w tym okresie na odległość do 35.9 km (Tab. 1, Fig. 1). Poza okresem lęgowym ptaki penetrowały obszar o powierzchni średnio 20557 ha i spotykano je do niemal 62 km od stanowisk lęgowych (Tab. 1, Fig. 2). Arealy poszczególnych osobników w różnym stopniu zachodziły na siebie (Tab. 2, Fig. 1, 2). Samce w okresie lęgowym pokonywały większe odległości niż samice; maksymalny dystans pokonywany w tym czasie w ciągu dnia przekraczał 113 km (Tab. 1, Fig. 3). Rozległość terytorium orłów w okresie lęgowym była negatywnie skorelowana z zagęszczeniami królików (Tab. 3). Osobniki z terenów o niskiej dostępności ofiar pokonywały 16–29 km do odległych, niebronionych żerowisk, zasobnych w zdobycz. Wyniki uzyskane podczas badań wskazują, że wielkość terytorium zależy od zagęszczenia potencjalnych ofiar oraz statusu reprodukcyjnego poszczególnych osobników.

W pracy porównano także dwie metody oceny wielkości arealów osobniczych (Cluster Analysis oraz Kernel) prezentując wyniki uzyskane obema metodami analiz (Tab. 1). Stwierdzono, że pierwsza z nich w badaniach sprawdziła się lepiej, szczególnie przy określaniu terenów odległych żerowisk.