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Dispersal of Golden Eagles *Aquila chrysaetos* during their first year of life

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Capsule The area explored increased throughout the year and tended to be much larger for females than males.
Aims To explore how the process of juvenile dispersal unfolds spatially and temporally, and compare the size of the areas explored by the two sexes.
Methods Thirteen chicks were captured between June 2002 and July 2004, tagged with satellite transmitters, and subsequently tracked using the ARGOS system.
Results In both sexes the total area explored increased with time. The average (± sd) size of the area explored in the whole year was 3713 km^2 (± 2586) in males and 10 652 km^2 (± 7451) in females. Both the monthly increase in the total area explored (individuals' averages ranging from 22 to 2526 km^2) and the overlap between areas used consecutively (about 25%) remained relatively constant throughout the year. Conversely, the size of the area used within a month, and the distance between consecutive areas, increased towards the end of the year; 87.5% of the individuals survived to their first year of life.
Conclusions While females are prominent dispersers and show a more eager exploratory behaviour, males remain within a more restricted area closer to the natal nest, and make more regular use of it. Differences in the total area explored might be linked to differences in food requirements, but other factors are also likely to be involved.

In large raptors, the fate of progeny after leaving the nest can have a larger effect on population trends than the production of offspring (Newton 1979, Real & Mañosa 1997, Whitfield *et al.* 2004). The mortality rate among non-breeding birds is normally considerably higher than in adults, at least 50% higher in pre-adult raptors (Newton 1979). The post-fledging period is thus of particular importance for the conservation of species with delayed breeding (Ferrer 1993a, 1993b, 1993c, 2001, Balbontín & Ferrer 2002), such as the Golden Eagle *Aquila chrysaetos*. However, because of the difficulties in obtaining sufficient and reliable information during this phase, little is known about the post-fledging period for most avian species, including the Golden Eagle (Watson 1997).

Dispersal studies of birds have traditionally used ringed or wing-marked individuals to reconstruct the birds' movements, and more recently have followed individuals using VHF radiotelemetry (Ferrer 1993a, Kenward 2001, Kenward *et al.* 2001). The development of lightweight satellite telemetry in the last decade has allowed the study of both migratory and dispersal movements of medium to large birds using satellite transmitters, or PTTs (Fuller *et al.* 1995, Kenward 2001, McGrady *et al.* 2003). Since 2002 we have been using this technology to monitor the movements of Golden Eagles in Spain.

The Golden Eagle is a long-lived monogamous raptor with a wide global distribution (Cramp & Simmons 1980). Pairs remain in the same area throughout the year. First breeding typically takes place when individuals are four to five years old (Brown & Amadon 1968). Where suitable habitat is available and continuous, nesting areas are spatially distributed at regular intervals (Urios 1986, Watson 1997). Usually two eggs are laid with an interval of three to four days between them, and incubation takes 43 to 45 days. Pairs usually have two or three alternative nest locations (Beecham & Kochert 1975). Golden Eagles show a prolonged

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period of parental care, with chicks leaving the nest some 60 to 80 days after hatching (Watson 1997). In Spain, the species is mostly distributed across the main mountain systems, covering an area of about 250 000 km^2. Population size is estimated to be stable or slightly increasing. Although not globally endangered, they are categorized as rare in the Red Data Book of the Vertebrates of Spain (Blanco & González 1992).

The life of Golden Eagles between the age of six months and adulthood is still essentially a mystery (Watson 1997). With the exception of some radio-telemetry studies (Haller 1994, Grant & McGrady 1999, O'Toole *et al.* 1999), no systematic study of birds' movements during this stage has been conducted. Here we present the results of tracking the movements of 13 juvenile Golden Eagles during their first year of life using satellite telemetry. We explore how the process of dispersal unfolds spatially, and compare the size of the areas explored by the two sexes during this period. Numerous studies have shown differences between sexes in juvenile dispersal (Dhondt 1979, Fleischer *et al.* 1984, Greenwood *et a1.* 1979, Greenwood 1980, Newton & Marquiss 1983, Drilling & Thompson 1988, Korpimäki *et al.* 1988). In raptors it is more usual for the female to travel further; this has been interpreted as a behavioural mechanism to decrease the likelihood of inbreeding (Greenwood *et al.* 1979, Greenwood 1980), or as a result of differences between sexes with regard to competition for the acquisition of a territory (Moore & Ali 1984) or food requirements (Newton 1979).

STUDY AREA AND METHODS

Between June 2002 and July 2004, we captured 13 nestling Golden Eagles in the Communities of Valencia, Murcia and Cataluña, eastern Spain (Fig. 1). Chicks were removed from the nest, weighed, measured, tagged with satellite transmitters (PTTs), and then replaced in their nests. Blood samples were taken for gender determination. PTTs were fixed to the

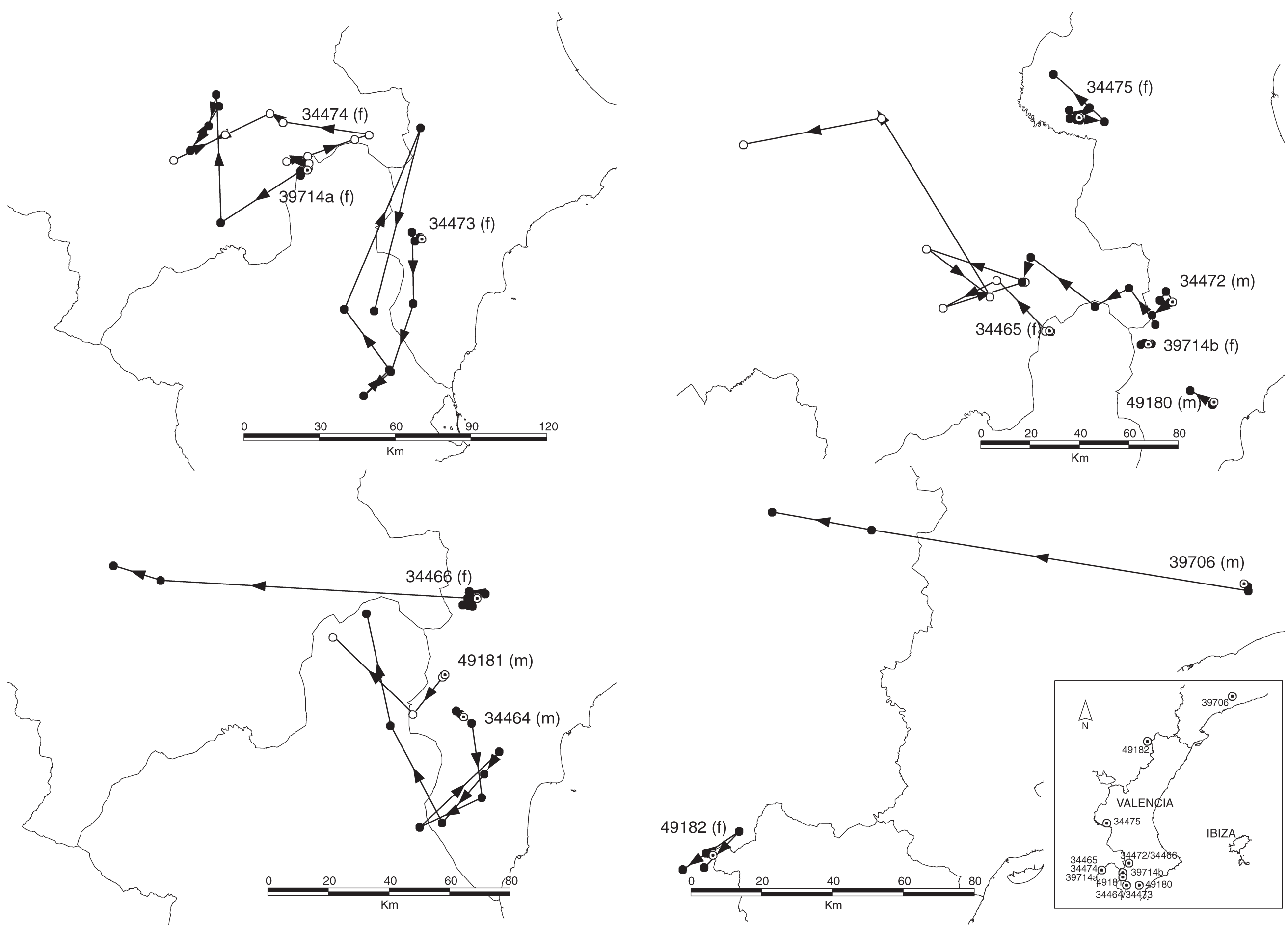


Figure 1. Progressive dispersal from the nest of 13 Golden Eagles in eastern Spain. ●, Centroid of the locations recorded each month; ⊙, nest location (f, female; m, male). Directions of movement are indicated by arrows. The inset shows the nest locations of all 13 birds.

birds' back using a breakaway Teflon harness. Three types of PTTs, all manufactured by Microwave Telemetry, were used: four 45-g PTT-100, five 50-g Solar PTT-100 (one was recovered in the field and re-used), and three 70-g Argos/GPS Solar PTT-100. Transmitters fixed in 2002 were programmed to an 8-hours-on/120-hours-off schedule; all others were programmed to a 16-hours-on/56-hours-off schedule. Small VHF radio transmitters (8 g) with an eight-month battery life expectancy were attached to the 45-g and 50-g PTTs. These were for use in case of accidents, making it possible to locate the injured animals. The full transmitter equipment never exceeded 2.5% of the juveniles' body mass (1.81 ± 0.29%, n = 13); this is well below the 5% relative weight suggested by Caccamise & Hedin (1985) and the 3% suggested by Kenward (2001) to minimize the effects of an additional mass on birds' movements.

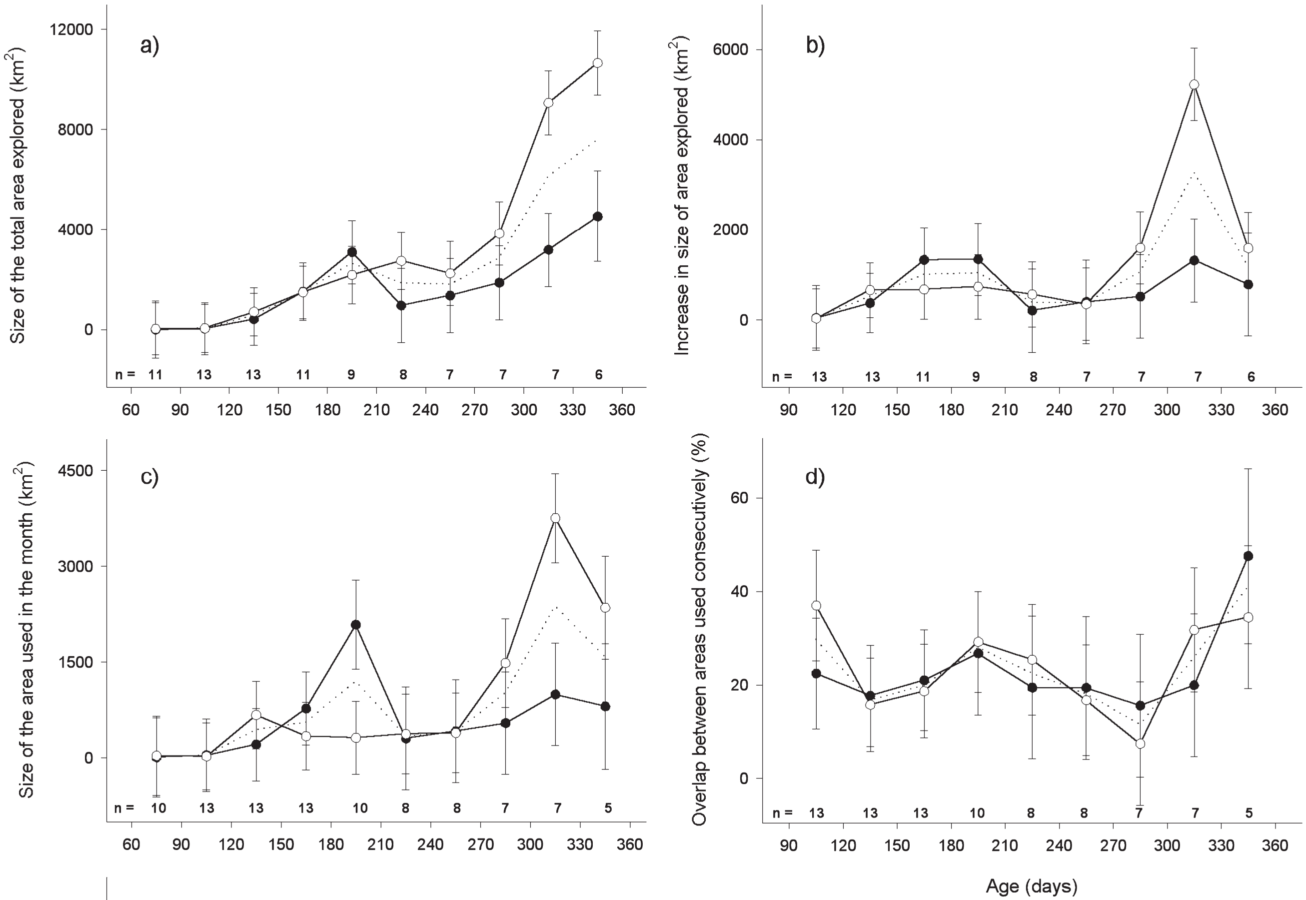
Before marking we visited several locations where nests had been located and monitored since the beginning of the breeding season, to determine brood size and to choose which nestlings to tag. Nests selected were those more easily monitored from a distance that minimized disturbance and the chance of premature fledging, but also allowed an accurate estimation of chick age. Nestlings were tagged when they were about 50 days old. At that age, chicks have almost attained adult size but the risk of early fledging is limited (Watson 1997). The age was estimated from plumage traits using a telescope (Torres *et al.* 1981), and corroborated with the date of hatching when this was known. For gender determination we used the PCR-based method described by Griffiths *et al.* (1998) and Fridolfsson & Ellegren (1999). For computational purposes all individuals were treated as if tagging had occurred when they were 50 days old.

The reception of the locations was managed by ARGOS, a satellite-based location and data collection system (Kenward 2001). The PTTs send ultra-high-frequency signals to a network of satellites that relay the messages to the ARGOS centres for data processing and location. As the accuracy of the satellite locations varies depending on several factors (Fancy *et al.* 1989, Keating *et al.* 1991, Kenward 2001, Vincent *et al.* 2002), the system provides seven Location Classes (LCs) that reflect the nominal accuracy of a given location. LCs 3, 2 and 1, the most reliable location classes, were used in this study (for these LCs, nominal accuracies are estimated to be within 150, 350 and 1000 m, respectively; Hays *et al.* 2001, Vincent e*t al.* 2002). Locations belonging to lower quality LCs (0, A, B and Z) were used only when they were consistent with the movements of juveniles suggested by the other LCs in terms of distance covered and time elapsed between locations. Thus, locations corresponding to movements in which the birds covered unrealistically long distances in a very short period of time were excluded (Hays *et al.* 2001). These constituted about 30% of the locations provided by ARGOS. Although we gathered information on birds' positions between June 2002 and 30 October 2004, here we only analyse locations corresponding to individuals' first year of life.

In order to investigate how the process of dispersal unfolds, we divided the first year of life into 30-day 'months', starting when the individuals were 60 days old. We then calculated the size of the minimum convex polygon including all the locations recorded for each month (MCP_M) and their centroids, the overlap with the polygon calculated for the previous month (O_{MCP}), the distance between consecutive centroids (D_C), the size of the minimum convex polygon including all the locations recorded until then (MCP_{Ac}), and the increase in the size of MCP_{Ac} compared to that calculated for the previous month (ΔMCP_{Ac}). Data were analysed using ArcView 3.2. We used the Animal Movement SA v 2.04 extension (Hooge & Eichenlaub 1997) to calculate the polygons and the distance between consecutive centroids, and the Xtools extension to calculate centroids and the size of polygons. Overlap between consecutive months was calculated using the Geoprocessing extension. We used STATISTICA 6.0 to conduct repeated-measures ANOVAs (with months as within-subject factors) to test for differences in these variables between both months and sexes, as well as between sexes within the same month (i.e. interactions). We conducted Spearman's correlation analyses to test for temporal trends in those variables for which significant differences between months were observed. Finally, for individuals for which data for the entire first year of life were available, we also calculated the minimum convex polygon including all the locations recorded in the year (MCP_T); that is, a measure of the total area covered by birds during their first year of life. Between-sex differences in MCP_T were analysed with the Mann–Whitney test. Except for repeated-measures ANOVAs, all statistical analyses were conducted using SPSS 11.5.

RESULTS

Most individuals showed a progressive increase in distance from the natal area throughout the year (Fig. 1). As expected, the total area explored (MCP_{Ac})



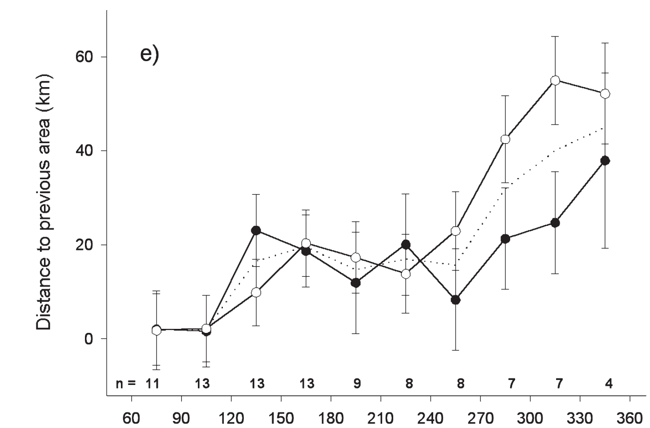


Figure 2. Dispersal of 13 Golden Eagles during their first year of life. (a) Size of the minimum convex polygon including all locations recorded (MCP_{Ac}); (b) monthly increase in size of MCP_{Ac} (ΔMCP_{Ac}); (c) size of the minimum convex polygon including all locations recorded in a given month (MCP_M); (d) overlap with the polygon calculated for the previous month (O_{MCP}); (e) distance between centroids of consecutive monthly polygons (D_C). Mean (± se) monthly values for males (●) and females (○) are indicated. Dotted line indicates the overall mean.

increased with time ($F_{9,27}$ = 3.98, P = 0.003; Fig. 2a), and although the area explored by females increased more sharply in the last months of the year, no statistical differences were observed between sexes ($F_{1,3}$ = 0.08, P = 0.80; Table 1). Except for a marked increase in March, the monthly increase (ΔMCP_{Ac}) was, however, relatively constant during the year ($F_{7,28}$ = 1.71, P = 0.35; Fig. 2b) and similar in both sexes ($F_{1,4}$ = 1.72, P = 0.26; Table 1). Though the average size of the areas used within a month (MCP_M) increased towards the end of the year, these differences were not statistically significant either ($F_{9,18}$ = 1.30, P = 0.30; Fig. 2c). MCP_M was also similar in both sexes ($F_{1,2}$ = 0.31, P = 0.63; Table 1). The overlap between areas used consecutively (O_{MCP}) was similar in both sexes ($F_{1,3}$ = 3.60, P = 0.15; Fig. 2d, Table 1) and remained relatively constant throughout the year ($F_{8,24}$ = 0.96, P = 0.49). Conversely, the distance between consecutive areas (D_C) increased steadily with time ($F_{9,18}$ = 5.73, P < 0.001; Fig. 2e; Spearman's rho = 0.69, n = 92, P < 0.0001; Table 1), though it was also similar in both sexes ($F_{1,2}$ = 0.26, P = 0.66). In all cases, between-sex

Table 1. Data for 13 Golden Eagles monitored during their first year of life with satellite telemetry.

PTT number	Date tagged	End of transmission	Sex	Weight (g)	MCP_T (km^2)	ΔMCP_{Ac} (km^2)	Overlap (%)
34464	11/06/02	–	M	2925	6694	742 ± 240	27.2 ± 7.7
34465	12/06/02	25/06/03	F	3400	16 690	1854 ± 1019	15.3 ± 6.6
34466	10/06/02	03/05/04	F	4025	3492	383 ± 340	27.4 ± 11.9
34472	10/06/02	15/04/03	M	3400	2371	291 ± 156	22.5 ± 7.7
34473	11/06/02	30/09/03	F	3860	17 466	1939 ± 1066	20.1 ± 7.3
34474	12/06/02	25/09/03	F	3525	4959	551 ± 200	17.1 ± 5.2
34475	27/05/02	13/08/03	M	2900	2074	258 ± 161	31.7 ± 7.5
39706	07/07/04	–	M	2360	–	743 ± 613	4.8 ± 3.2
39714a	09/06/03	03/01/04	F	3315	–	1195 ± 837	25.0 ± 15.7
39714b	09/06/04	–	F	3300	–	22 ± 0	60.3 ± 8.5
49180	08/06/04	–	M	3310	–	195 ± 194	13.3 ± 6.8
49181	09/06/04	–	M	3000	–	2526 ± 1262	9.3 ± 8.1
49182	22/06/04	–	F	3940	–	835 ± 762	36.9 ± 31.6

Date of end of transmission is given if before 30 October 2004 (the end of this study). Sex: M, male; F, female. MCP_T, size of the total area explored in the first year of life; ΔMCP_{Ac}, mean (± se) monthly increase of area. 'Overlap' is average (± se) percentage of overlap between areas used consecutively.

differences within the same month (i.e. interactions) were not significant ($P > 0.48$). Finally, although the total area explored by females throughout the year tended to be considerably larger than the area explored by males, the difference was not statistically significant (mean area ± sd for males: 3713 ± 2586 km^2, females: 10 652 ± 7451 km^2; $z = 1.41$, $n = 7$, $P = 0.16$). In all cases, lack of statistical differences is hardly conclusive, as in the last months of the year, when between-sex differences seem to be larger, sample size is smaller. Furthermore, this lack probably reflects the large variability of the data, which in turn probably reflects large differences between individuals in their behaviour not associated with sex.

Only one bird was confirmed dead during its first year of life, but the cause of death was not determined. Therefore, excluding the five birds marked in 2004 (which were about six months old at the end of this study), 87.5% of the individuals we monitored survived to their first year of life.

DISCUSSION

We present the results of the first study of juvenile dispersal in Golden Eagles using satellite technology. Compared to conventional radiotracking and sightings or recovery studies, the use of PTTs overrides the problem of not being able to detect long-distance dispersers (Grant & McGrady 1999, O'Toole *et al.* 1999, Cadahía *et al.* 2005). Furthermore, it allows detailed tracking of individual positions several times in a day. Satellite telemetry with conventional PTTs (i.e. non-GPS) is, however, less accurate than conventional VHF radiotracking (Keating *et al.* 1991) and thus unsuitable for studies that demand very precise knowledge of individuals' locations (McGrady *et al.* 2003). However, in species such as the Golden Eagle, with individuals moving several kilometres in one day, this is not an important limitation for the monitoring of juvenile dispersal.

Irrespective of sex, large differences in individuals' dispersal behaviour were observed. For most birds we observed a progressive increase in distance from the nest and an increase in the total area explored over the course of the year. In general, the area explored by females tended to be much larger than that covered by males. However, while in males both the size of the area used during a month and the monthly rate of increase of the area explored remained unchanged throughout most of the year, for female eagles both the area used and the proportion of land that was previously unexplored increased with time. Furthermore, while in both sexes the distance between the midpoints of successive monthly locations increased for most of the first year, in females those distances tended to be larger and to increase for longer. Therefore, it seems likely that the observation that females tended to explore larger areas than males was to a large degree a consequence of females moving progressively further away from previously used areas and the natal nest-site. Thus, while the total area explored by males increased approximately linearly, in females it increased almost exponentially. Nevertheless, in both sexes the amount of overlap between areas used in consecutive months remained largely unchanged throughout the year (about 25%).

Differential dispersal has been described in numerous species of birds (Greenwood 1980, Newton & Marquiss 1983, Drilling & Thompson 1988, but see Matthysen & Schmidt 1987, Newton *et al.* 1989). In a few species males have been found to move further than females (Greenwood 1980), which has led some authors to suggest that this irregular dispersal pattern is a deliberate mechanism designed to diminish the likelihood of interbreeding between siblings (Dhondt 1979, Greenwood *et al.* 1979, Weise & Meyer 1979, Greenwood 1980). However, this does not seem to be the reason for differences in dispersal in Golden Eagles. As male and female ranges overlap considerably, it seems unlikely that differential dispersal would have any effect in reducing the likelihood of breeding between relatives. It has also been suggested that in territorial birds differential dispersal may result from stronger competition for a territory between members of one sex than the other (Moore & Ali 1984). However, while in Golden Eagles dispersal differences between the sexes developed during the first year of dispersal, we did not find immature eagles settling 'definitively' in an area during that period (though males do seem to remain within a more restricted area than females, closer to the natal nest). It has been found that other birds of prey that are dimorphic in terms of size, such as Sparrowhawk *Accipiter nisus* (Newton & Marquiss 1983), exhibit sex-related differences in dispersal, whilst in monomorphic species such as Red Kite *Milvus milvus* (Newton *et al.* 1989) no such differences exist. This suggests that rather than representing a mechanism in itself, the differences in dispersal we observed most likely reflect differences in habitat selection, prey distribution and energy expenditure in flight, resulting from size differences.

In general, the total area explored during the first year of life in Spain is similar to the 2000–15 000 km^2 reported by Haller (1994) in Switzerland. These areas are larger than the 2000–4000 km^2 reported for subadults of two or more years, which in turn are exceptionally large compared to the 75–191 km^2 reported for adults (Haller 1982, 1994). This suggests the existence of two distinct phases during juvenile dispersal, with an early 'dispersive' phase probably characterized by more frequent long-range exploratory movements (Watson 1997).

Although very little is known about pre-adult mortality in Golden Eagles (Watson 1997), the 12.5% annual juvenile mortality that we observed is in line with the 16% reported by Hunt (2002) for the species in California. Both Hunt (2002) and Whitfield *et al.* (2004), studying Golden Eagles in Britain, estimate 21% annual juvenile mortality after the first year of life. Compared to rates for the other two large eagles nesting in Spain, this is close to the 15–29% reported by Cadahía *et al.* (2005) for Bonelli's Eagle *Hieraaetus fasciatus* but well below the 59% estimated by Real & Mañosa (1997) for the same species, and the 65–70% reported by Ferrer (2001) for the endangered Spanish Imperial Eagle *Aquila adalberti*.

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REFERENCES

Balbontín, J. & Ferrer, M. 2002. Plasma chemistry reference values in free-living Bonelli's eagle *Hieraaetus fasciatus* nestlings. *J. Raptor Res.* **36:** 231–235.

Beecham, J.J. & Kochert, M. 1975. Breeding biology of the Golden Eagle in southwestern Idaho. *Wilson Bull.* **87:** 506–513.

Blanco, J.C. & González, J.L. 1992. *Libro Rojo de los Vertebrados de España*. ICONA, Madrid.

Brown, L.H. & Amadon, D. 1968. *Eagles, Hawks, and Falcons of the World*. McGraw-Hill, New York.

Caccamise, D.F. & Hedin, R.S. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bull.* **97:** 306–318.

Cadahía, L., Urios, V. & Negro, J.J. 2005. Survival and movements of satellite tracked Bonelli's Eagles during their first winter. *Ibis* **147:** 415–419.

Cramp, S. & Simmons, K.E.L. 1980. *The Birds of the Western Palearctic*, Vol. 2. Oxford University Press, Oxford.

Dhondt, A.A. 1979. Summer dispersal and survival of juvenile great tits in southern Sweden. *Oecologia* **42:** 139–157.

Drilling, N.E. & Thompson, C.F. 1988. Natal and breeding dispersal in house wrens *Troglodytes aedon*. *Auk* **105:** 480–491.

Fancy, S.G., Pank, K.R., Whitten, K.R. & Regelin, W.L. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. *Can. J. Zool.* **67:** 644–650.

Ferrer, M. 1993a. Juvenile dispersal behaviour and natal philopatry of a long - lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* **135:** 132–138.

Ferrer, M. 1993b. Ontogeny of dispersal distances in young Spanish Imperial Eagles. *Behav. Ecol. Sociobiol.* **32:** 259–263.

Ferrer, M. 1993c. Reduction in hunting success and settlement strategies in young Spanish Imperial Eagles. *Anim. Behav.* **45:** 406–408.

Ferrer, M. 2001. *The Spanish Imperial Eagle*. Lynx edicions, Barcelona.

Fleischer, R.C., Lowther, P.E. & Johnston, R.F. 1984. Natal dispersal in house sparrows: possible causes and consequences. *J. Field Ornithol.* **55:** 444–456.

Fridolfsson, A.K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30:** 116–121.

Fuller, M.R., Seegar, W.S. & Howey, P.W. 1995. The use of satellite systems for the study of bird migration. *Israel J. Zool.* **41:** 243–252.

Grant, J.R. & McGrady, M.J. 1999. Dispersal of golden eagles *Aquila chrysaetos* in Scotland. *Ring. Migr.* **19:** 169–174.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28:** 1140–1162.

Greenwood, P.J., Harvey, P.H. & Perrins, C. 1979. The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. *J. Anim. Ecol.* **48:** 123–142.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7:** 1071–1075.

Haller, H. 1982. Raumorganisation und Dynamik einer Population des Steinadlers *Aquila chrysaetos* in den Zentralalpen. *Ornithol. Beobacht.* **79:** 163–211.

Haller, H. 1994. Der Steinadler *Aquila chrysaetos* als Brutvogel im schweizerischen Alpenvorland: Ausbreitungstendenzen und ihre populations - ökologischen Grundlagen. *Ornithol. Beobacht.* **91:** 237–254.

Hays, G.C., Åkesson, S., Godley, B.J. Luschi, P. & Santidrian, P. 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Anim. Behav.* **61:** 1035–1040.

Hooge, P.N. & Eichenlaub, B. 1997. *Animal Movement Extension to Arcview*, Version 1.1. Alaska Science Center - Biological Science Office, US Geological Survey, Anchorage.

Hunt, W.G. 2002. *Golden Eagles in a Perilous Landscape: Predicting the Effects of Mitigation for Wind Turbine Blade-strike Mortality*. Consultant Report 500-02-043F to California Energy Commission, Sacramento, California [available from http://www.energy.ca.gov/reports/2002-11-04_500-02-043F.PDF].

Keating, K.A., Brewster, W.G. & Key, C.H. 1991. Satellite telemetry: performance of animal-tracking systems. *J. Wildl. Manage.* **55:** 160–171.

Kenward, R.E. 2001. *A Manual for Wildlife Radio Tagging*. Academic Press, London.

Kenward, R.E., Rushton, S.P., Perrins, C.M., Macdonald, D.W. & South, A.B. 2001. From marking to modelling: dispersal study techniques for land vertebrates. In Bullock, J.M., Kenward, R.E. & Hails, R.S. (eds) *Dispersal Ecology*: 50–71. Blackwell, Oxford.

Korpimäki, E. & Lagerström, M. 1988. Survival and natal dispersal of fledglings of Tengmalm's owl in relation to fluctuating food conditions and hatching date. *J. Anim. Ecol.* **57:** 433–441.

Matthysen, E. & Schmidt, K. 1987. Natal dispersal in the nuthatch. *Ornis Scand.* **18:** 313–316.

McGrady, M.J., Ueta, M., Potapov, E.R., Utekhina, I., Masterov, V., Ladyguine, A., Zykov, V., Cibor, J., Fuller, N. & Seegar, W.S. 2003. Movements by juvenile and immature Steller's Sea Eagles *Haliaeetus pelagicus* tracked by satellite. *Ibis* **145:** 318–328.

Moore, J. & Ali, R. 1984. Are dispersal and inbreeding avoidance related? *Anim. Behav.* **32:** 94–112.

Newton, I. 1979. *Population Ecology of Raptors*. T&AD Poyser, Berkhamsted.

Newton, I. & Marquiss, M. 1983. Dispersal of sparrowhawks between birthplace and breeding place. *J. Anim. Ecol.* **52:** 463–477.

Newton, I., Davies, P.E. & Davis, J.E. 1989. Age of first breeding, dispersal and survival of Red Kites *Milvus milvus* in Wales. *Ibis* **131:** 16–21.

O'Toole, L.T., Kennedy, P.L., Knight, R.L. & McEwen, L.C. 1999. Postfledging behavior of golden eagles. *Wilson Bull.* **111:** 472–477.

Real, J. & Mañosa, S. 1997. Demography and conservation of western European Bonelli's eagle *Hieraaetus fasciatus* populations. *Biol. Conserv.* **79:** 59–66.

Torres, J.A., Jordano, P. & León, A. 1981. *Aves de presa diurnas de la provincia de Córdoba*. Publicaciones del Monte de Piedad y Caja de Ahorros de Córdoba, Madrid.

Urios, V. 1986. Biología, requerimientos ecológicos y relaciones interespecíficas del águila real *Aquila chysaetos homeyeri* Severtrov, 1888 y del águila perdicera *Hieraaetus fasciatus fasciatus* Viellot, 1822 (Accipitriformes, Accipitridae) en la Provincia de Valencia. BSc Thesis, University of Valencia.

Vincent, C., McConnel, B.J., Fedak, M.A. & Ridoux, V. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. *Mar. Mammal Sci.* **18:** 301–322.

Watson, J. 1997. *The Golden Eagle*. T&AD Poyser. London.

Weise, C.M. & Meyer, J.R. 1979. Juvenile dispersal and development of site-fidelity in the black-capped chickadee. *Auk* **96:** 40–55.

Whitfield, D.P., Fielding, A.H., Mcleod, D.R.A. & Haworth, P.F. 2004. Modelling the efects of persecution on the population dynamics of golden eagles in Scotland. *Biol. Conserv.* **119:** 319–333.

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