Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*

MIGUEL FERRER
Estación Biológica de Doñana CSIC, Avda. Maria Luisa, Pabellón del Perú, E-41013 Sevilla, Spain

The dispersal behaviour of 30 radio-tagged young Spanish Imperial Eagles *Aquila adalberti* was studied in southwestern Spain in 1986–1990. The dispersal process involved first departure from the natal population, exploratory movements, temporary settlements and returns to the natal population. The dispersal process lasted for the whole of the immature period studied, and behaviour was radically different from that displayed by territorial adults. Movements between temporary settling areas and the natal population occurred continually throughout the dispersal period. Return to the natal population could be used by the young to explore the possibilities for pair formation where a vacancy may have occurred in the breeding population.

Dispersal is one of the most important, yet least known, phenomena in population biology (Gadgil 1971) and may affect many aspects of the ecology and behaviour of a species (Horn 1983). Until now, most dispersal studies of birds have been done using ringed or wing-marked individuals. Most available information is from isolated observations of individuals (Greenwood *et al.* 1978, Dhondt 1979, Weise & Meyer 1979, Fleischer *et al.* 1984, Nilsson & Smith 1985, Matthysen & Schmidt 1987, Drilling & Thompson 1988, Moore & Dolbeer 1989). Few dispersal studies have been carried out using radio-transmitters, which allow prolonged observation of individuals and give better information on changes in behaviour (Beske 1978, Belthoff & Ritchison 1989).

Most studies of non-migratory birds suggest that immature birds, once they have dispersed, do not return to the area of their birth (Beske 1978, Marquiss & Newton 1981, Newton & Marquiss 1983, Newton 1986, Korpimäki *et al.* 1987, Korpimäki & Lagerström 1988, Belthoff & Ritchinson 1989). Subsequent movements have not been detected, and the young have been assumed to remain in the same area until they reach sexual maturity.

Juvenile dispersal of Spanish Imperial Eagles *Aquila adalberti* was studied using wing-tagged birds (González *et al.* 1989). These authors distinguished two different dispersal strategies; most young dispersed to areas where they settled for periods longer than a year, while a few did not disperse but stayed in the natal population until they reached maturity.

This paper reports on a study of dispersal behaviour in Spanish Imperial Eagles in southwest Spain, with information on the behaviour during the first 22 months of life. Observations are compared with reported dispersal behaviour of other birds.

MATERIAL AND METHODS

The study was carried out in the Doñana National Park (37°N, 6°30′W), southwestern Spain, during the years 1986 to 1990 inclusive. During the first 3 years, successive young were marked with long-life (5 years) solar radio-transmitters, and, during the last 2 years, only the survivors of previous years were observed. In total, 30 nestlings were equipped with transmitters (Wildlife Materials, model HPSB 1400 3XA) fixed on the back of the chicks by a harness (Kenward 1987). Among the 30 nestlings, 14 were male and 16 female; eight were marked in 1986, eight in 1987 and 14 in 1988. The sex was determined according to the forearm length (Ferrer & De le Court 1992). Of the 30 nestlings, 14 were alive for at least 6 months, 10 for at least 1 year and seven for at least 2 years.

Three teams were used to track the young. One was located in a 35-m tower in the middle of the Doñana National Park and recorded the direction of every young bird every half-hour for the first 2 months after fledging and at least once a day during the remainder of the study. The second team carried out searches, by light aircraft, of all individuals within a circle of 300-km radius, centred on the natal population. Two flights per week were made during September, October and November, and two flights per month during the rest of the year, totalling 256 flying hours. Initial searches used a non-directional antenna, usually fixed below the aircraft. When individuals were detected, their position was determined by triangulation with a directional antenna and the compass of the aircraft. The third team made observations from a vehicle equipped with a non-directional antenna with a magnetic base fixed to the roof; triangulation was done using a directional antenna when a radio-tagged eagle was detected.

This last team also made direct observations of individuals when possible. Usually, once a bird was detected away from the natal population, follow-up was carried out over two complete days. During these days, counts of rabbits *Oryctolagus cuniculus* were performed at sunset in the area used by the young eagles during the day. These counts were made by foot along a 3-km transect, counting all the rabbits inside a 25-m strip at both sides. During the study, the three teams sought at least two contacts per week for each individual bird. A total of 2106 contacts of 30 radio-tagged young eagles outside the natal population were obtained. I consider as the first departure the first time that a young eagle moved away from the natal population, leaving the Doñana area, and when the place of contact was more than 20 km away from the natal nest.

In order to analyse dispersal behaviour, two kinds of distance measures were used: the distance from the natal nest and the distance between successive roosting-sites. Using these two variables, I considered three different activities for dispersing young: (1) exploratory movements, when the distance between roosting-sites was greater than 10 km and distance from the natal nest was more than 20 km, (2) temporary settlements, when the distance between roosting-sites was less than 10 km and distance from the natal nest was over 20 km, and (3) returns to the natal population, when distance from the natal nest was less than 20 km. Range size was measured by a digital planimeter on 1:25,000 aerial photographs and 1:50,000 charts.

RESULTS

First departure from the natal population occurred on average at the age of 137 days (range 116–162 days, n = 17). The age at the first departure did not show any relationship with sex (Table 1). On nine occasions, the direction of departure was towards the Huelva Mountains (between 330° and 15°) and 12 times it was towards the Sierra of Cádiz (between 118° and 180°). The average distance between successive roosting-sites at departure was 77 km (range 45–115 km, n = 13). In one case the total distance flown in a departure was 145 km.

Figures 1 and 2 show the frequency distribution for the two kinds of distances used, distance between successive roosting-sites and distance from natal nest (separately for males and females), of 600 radio-contacts of young selected at random.

Exploratory movements

The average distance between roosting-sites during an exploratory flight was 46 km per day (range 11–114 km, n = 20). Every zone subsequently used as a temporary settling area had been previously visited by the young during exploratory movements (Fig. 3). The total distance flown during an exploratory movement was, on average, 101 km (range 45–173 km, n = 11). No significant differences in distances

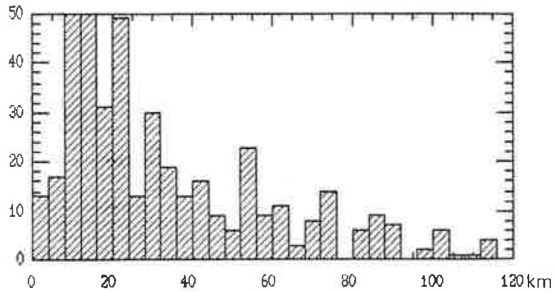

Figure 1. Frequency distribution of distances between successive roosting-sites of 600 radio-contacts of young Spanish Imperial Eagles selected at random.

between roosting-sites during exploratory flights were found between sexes (Table 1).

On average, time devoted to exploratory movements represented 16.2% of the total time that birds were observed during the study period. No significant differences were found between sexes (Table 1).

Temporary settlements

Temporary settling areas were inside the accumulated ranges during the exploratory movements (Fig. 3). Ten settling areas were detected in the mountain area of Huelva and 11 in Cádiz (Fig. 4). The first temporary settlement occurred on average at 163.9 days of age, an average of 27.5 days after the first departure from the natal population. No significant differences were found between sexes (Table 1). Each zone was used intensively for a variable but short period, and each individual used between three and eight different areas in turn. The same settling areas were selected by different individuals (Table 2).

Rabbit densities in the temporary settling areas varied between 3.3 and 5.6 rabbits per ha (Table 2). In general, these were areas of pasture with low cover. All areas lacked breeding pairs of medium to large eagles.

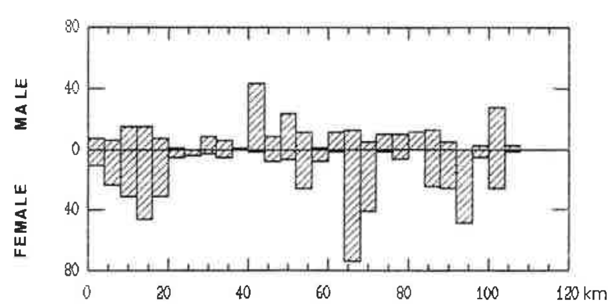

Figure 2. Frequency distribution of distances from the natal nest of 600 radio-contacts of young male and female Spanish Imperial Eagles.

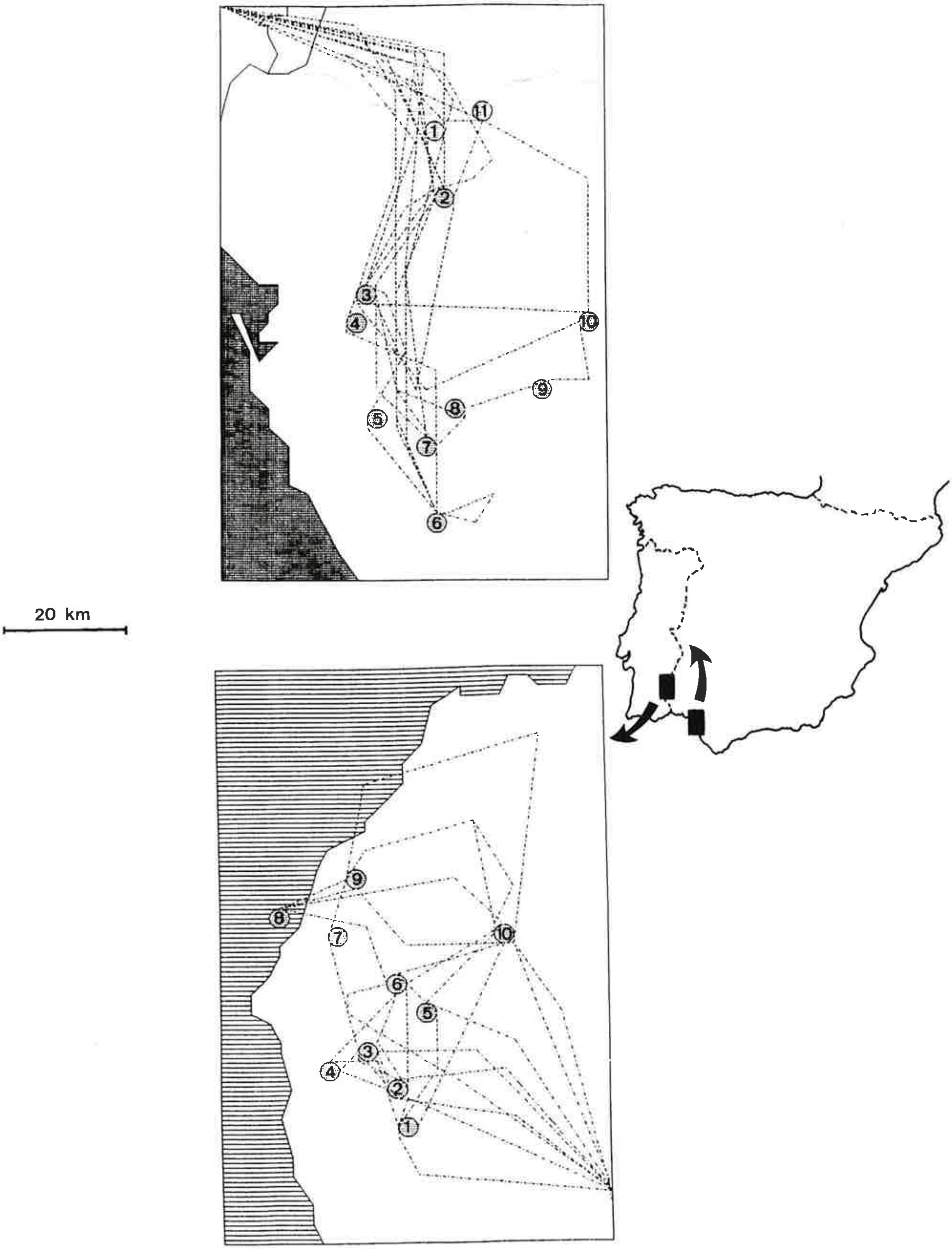

Figure 3. Exploratory movements of immature Spanish Imperial Eagles in the dispersal area from Cádiz (top) and Huelva (bottom). Discontinuous lines indicate exploratory flights. The circles represent temporary settling areas C1–11 (top) and H1–10 (bottom).

Table 1. *Differences between sexes during the dispersal process in the Spanish Imperial Eagle*

Activity	Sex	Average	*n*	d.f.	*F*	*P*
First departure (age, days)	Male	134.1	11	1,19	1.516	0.233
	Female	140.2	10			
Exploratory flights (distance between successive roosts, km)	Male	41.3	8	1,18	2.273	0.149
	Female	48.6	12			
Exploratory flights (percent of days)	Male	15.8	8	1,16	0.783	0.701
	Female	16.4	10			
Temporary settlements (distance from natal nest, km)	Male	68.1	8	1,18	8.436	0.009
	Female	79.9	12			
Temporary settlements (length of stay, days)	Male	11.9	6	1,13	0.008	0.931
	Female	12.0	9			
Age at first temporary settlements (days)	Male	160.1	6	1,8	1.100	0.324
	Female	169.5	4			
Temporary settlements (percent of days)	Male	52.5	8	1,16	0.417	0.975
	Female	54.7	10			
Age at first return (days)	Male	150.3	6	1,12	0.067	0.803
	Female	154.4	7			
Length of returns (days)	Male	2.65	4	1,11	1.099	0.317
	Female	4.05	9			
Returns (percent of days)	Male	29.5	8	1,16	0.741	0.747
	Female	30.6	10			

Table 2. *Occurrences of utilization of different settling areas by young Spanish Imperial Eagles in Cadiz and Huelva and rabbit densities in Cádiz*

	Temporary settling areas in Cádiz											
Eagle no.	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	NP[1]
855	2	1	4	1	1	2						10
860	1		3				1		1			7
847		1	1				1			1		4
872			3	1	1	3	1	1			1	9
876			1									3
890			1									2
888	1	1										2
887			1	2		2						5
Total	4	3	14	4	2	7	3	1	1	1	1	42
Rabbit density (rabbits/ha)	3.8	5.0	5.6	3.6	3.3	5.2	4.6	3.4	3.5	4.3	3.6	

	Temporary settling areas in Huelva										
Eagle no.	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	NP
846	1		2							1	3
874	1			1							2
883		2	1		1						5
878	2			2				1	1		8
393	1	2	1				1		1		5
882	1				2	2					4
Total	6	4	4	3	3	2	1	1	2	1	27

[1] NP = returns to natal population.

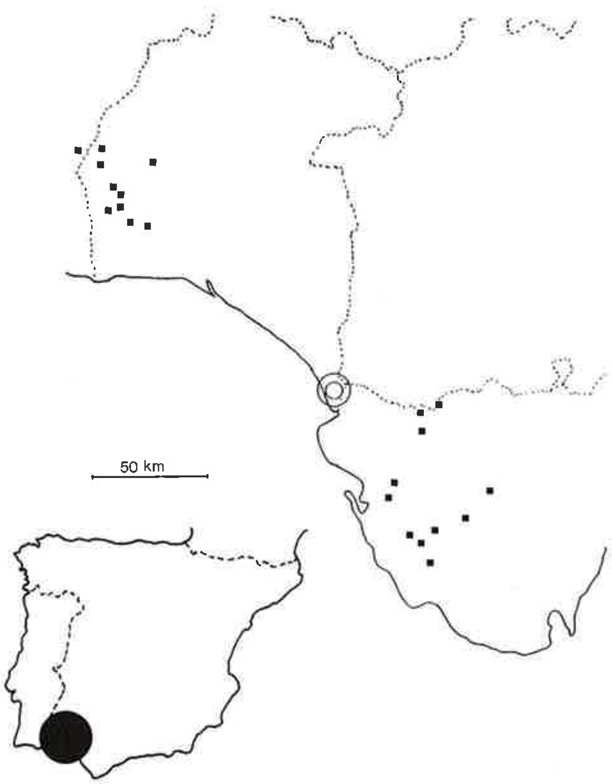

Figure 4. Temporary settling areas (solid squares) used by dispersing immature Spanish Imperial Eagles and the natal population (large circle) of Doñana National Park.

Significant differences were found between the sexes in average distance from the natal nest during temporary settlements; females used the more distant zones more frequently (Table 1). The accumulated home range during a stay in each temporary settling area was on average 433 ha (range 260–731 ha, n = 12). This area was less than the area used by a pair of adults in Doñana National Park (919 ha, M. Ferrer, unpubl.).

The average length of stay in these temporary settling areas was 12 days (Table 1), and there were no significant differences between sexes (Table 1) nor between different areas ($F_{13,21} = 0.24$, $P = 0.994$). There were significant differences in the number of times that a zone was selected by young eagles (for areas in Cádiz $\chi^2_4 = 38.8$, $P < 0.001$; for areas in Huelva $\chi^2_3 = 8.4$, $P = 0.037$; Table 2), and this was correlated with the rabbit density in the zone (for areas in Cádiz $r_{10} = 0.748$, $P = 0.008$; Table 2).

The temporary settling areas were used during every year of the study. The home ranges of different young in the same zone were similar, with exactly the same perches and roosting-sites as used by other Spanish Imperial Eagles. Time devoted to temporary settlements represented on average 53.6% of total activity. Again, no differences between sexes were detected (Table 1).

Returns to the natal population

Immature birds returned to the natal population frequently throughout the whole period of dispersal (Fig. 2, Table 3).

Table 3. *The percentage of days (mean ± s.e.) devoted to returns to the natal population, exploratory flights and temporary settlements, and variations in accumulated range size, in relation to age of immature Spanish Imperial Eagles*

Age (days)	n	Natal returns (%)	Exploratory flights (%)	Temporary settlements (%)	Range size (km²)
130–160	21	37 ± 6.1	58 ± 5.3	5 ± 2.6	532 ± 41.9
161–190	16	19 ± 6.9	22 ± 6.7	59 ± 8.5	2437 ± 122.8
191–220	14	15 ± 6.9	18 ± 6.7	67 ± 8.3	2884 ± 57.8
221–250	12	47 ± 10.2	12 ± 3.0	41 ± 9.6	2912 ± 68.1
251–280	10	54 ± 9.9	9 ± 3.1	37 ± 8.2	2933 ± 112.8
281–310	8	15 ± 2.5	10 ± 2.6	75 ± 3.1	2933 ± 123.2
311–340	7	25 ± 4.5	7 ± 2.6	68 ± 4.7	2933 ± 91.3
341–370	7	17 ± 3.8	11 ± 3.1	72 ± 5.5	3027 ± 142.4
371–400	7	15 ± 3.6	6 ± 2.7	79 ± 4.0	3027 ± 137.9
401–430	7	9 ± 1.2	6 ± 1.0	85 ± 1.2	3027 ± 137.9
431–460	7	7 ± 1.2	6 ± 1.6	87 ± 1.9	3027 ± 137.9
461–490	7	10 ± 1.5	5 ± 1.3	85 ± 2.4	3027 ± 137.9
491–520	7	10 ± 1.3	5 ± 1.2	85 ± 1.9	3027 ± 137.9
521–550	7	31 ± 8.9	4 ± 1.3	65 ± 9.0	3027 ± 137.9
551–580	7	62 ± 11.4	4 ± 1.4	34 ± 11.6	3027 ± 137.9
581–630	7	69 ± 4.8	6 ± 1.6	25 ± 4.4	3027 ± 137.9
631–660	7	63 ± 5.5	3 ± 1.0	34 ± 5.9	3027 ± 137.9
F		6.89	12.18	14.45	54.16
d.f.		16,141	16,141	16,141	16,141
P		<0.001	<0.001	<0.001	<0.001

The first return occurred on average 17.23 days after first departure (range 1–84 days, $n = 13$), and it happened on average at 152 days old (range 130–212 days, $n = 13$). No differences were found between sexes in the age at the first return (Table 1). Thereafter, returns were frequent and had not ceased by the end of the study period (Table 3), representing 30.2% of the time that birds were tracked. The mean length of stay in the natal population was 3.61 days (range 1–15 days, $n = 13$). There were no significant differences in the length of return by males and females (Table 1).

During these returns, behaviour of the young was similar to that observed during the predispersal period (Ferrer 1992), with numerous interactions with breeding pairs that attacked them on each occasion ($n = 34$). The time that the young spent in the natal population during a return was significantly shorter than the length of the stay in temporary settlement areas ($t = 9.84$, $n = 28$, $P < 0.001$). However, the frequency with which immature birds selected the natal population was significantly higher than the frequency of choosing temporary settling areas (for areas in Cádiz $\chi^2_1 = 194.4$, $P < 0.001$; for areas in Huelva $\chi^2_1 = 107.4$, $P < 0.001$; Table 2).

Changes in dispersal behaviour

The proportion of days on which exploratory flights were recorded changed from 58% between 130 and 160 days of age to 9% at 251–280 days of age (Table 3). From 100 days after leaving the natal population, birds occupied temporary settlement areas for about 67% of the time. Increase in the time devoted to settlement and decrease in exploratory behaviour were both significant (Table 3). Nevertheless, no trend was recorded towards a longer stay in any particular settlement area as the age of the individual increased ($F_{8,23} = 0.351$, $P = 0.934$).

The accumulated range size increased exponentially until 60 days after the departure from the natal population, becoming stabilized after 100–120 days (Table 3).

Returns to the natal population developed differently. Although immatures continued to return to Doñana regularly, the frequency of returns was greatest during November and December. Nevertheless, there was no significant variation in the length of stay in the natal population with age of the young, at least until observations ceased ($F_{10,44} = 0.855$, $P = 0.580$).

DISCUSSION

All young studied dispersed out of the natal area. Thus, we have not detected non-dispersal of young as proposed by other authors (González *et al.* 1989). Such exploratory movements have been described in other birds (Beske 1978). In Spanish Imperial Eagles, the decrease of exploratory flights after the fourth month of dispersal, and the stabilization by then of the accumulated home range, seems to show that by this time the young have already acquired a sufficient knowledge of the dispersal area.

Sex differences in the average distance from the natal nest during temporary settlements could be interpreted as a consequence of female-biased dispersal. Nevertheless, the time that both sexes spent in the natal population was equal. Philopatric behaviour seems, therefore, to be equal for males and females.

Returns to the natal population could be interpreted in two ways. First, the natal population could be used as another area of temporary settlement, in which the average stay is shorter due to expulsion by territorial adults. A high prey density in this area could justify a higher frequency of visits. An alternative possibility, though not incompatible with the first, would be that frequent returns could be used by the young to explore the possibility of pair formation with a territorial bird that had lost its mate. Pairs with immature members are frequent in long-lived raptors (Newton 1979, Steenhof *et al.* 1983), including the Spanish Imperial Eagle (Ferrer & Calderón 1990). In a situation with high adult mortality, an immature eagle may have an opportunity for establishment in the reproductive population (Steenhof *et al.* 1983, Ferrer & Calderón 1990). One way to detect the existence of vacancies is to check the breeding population frequently. The trend towards higher return rates in November and December could be interpreted in this way because November and December are the time of nest-building (Calderón *et al.* 1987).

The dispersal behaviour found in the population of Spanish Imperial Eagles of the Doñana National Park differs from that described for other diurnal (Newton & Marquiss 1983) and nocturnal birds of prey (Belthoff & Ritchinson 1989). In the Spanish Imperial Eagle, the dispersal process lasted the whole of the immature period studied, characterized by behaviour radically different from that of territorial adults. Alternation between temporary settling areas and returns to the natal population occurred throughout the dispersal period. This difference could be due to the immature period of the Spanish Imperial Eagle being longer than that of other species studied (Newton & Marquiss 1983, Belthoff & Ritchinson 1989). A shorter period of immaturity may determine a faster definitive settlement.

On the other hand, differences detected in the dispersal process could be an effect of the method employed in different studies. The fact that my results are different from those obtained by other authors who have studied the same population with wing-tags (González *et al.* 1989) suggests that the utilization of isolated point observations instead of continuous monitoring to study dispersal can provide biased information.

I am indebted to L. Garcia, R. Cadenas, C. Vila, M. de la Riva and J. J. Negro for help in the field. I am grateful for the comments provided by Dr P. J. Jones. This study was supported by DGICYT, project number PB87-0405.

REFERENCES

Belthoff, J.R. & Ritchison, G. 1989. Natal dispersal of Eastern Screech Owls. Condor 91: 254–265.

Beske, A.E. 1978. Harrier radio-tagging techniques and local and migratory movements of radio-tagged juvenile Harriers. Unpubl. MS thesis, University of Wisconsin, Stevens Point.

Calderón, J., Castroviejo, J., Garcia, L. & Ferrer, M. 1987. El Aguila Imperial Ibérica *Aquila adalberti* en Doñana: algunos aspectos de su reproducción. Alytes 5: 47–72.

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.

Ferrer, M. 1992. Natal dispersal in relation to nutritional conditions in Spanish Imperial Eagles. Ornis Scand. 23: 104–107.

Ferrer, M. & Calderón, J. 1990. The Spanish Imperial Eagle *Aquila adalberti* in Doñana National Park: a study of population dynamics. Biol. Conserv. 51: 151–161.

Ferrer, M. & De le Court, C. 1992. Sex determination in the Spanish Imperial Eagle. J. Field Ornithol. 63: 359–364.

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.

Gadgil, M. 1971. Dispersal: population consequences and evolution. Ecology 52: 253–261.

González, L.M., Heredia, B., González, J.L. & Alonso, J.C. 1989. Juvenile dispersal of Spanish Imperial Eagles. J. Field Ornithol. 60: 369–379.

Greenwood, P.J., Harvey, P.H. & Perrins, C. 1978. The role of dispersal in the Great Tit *Parus major*: the causes, consequences and heritability of natal dispersal. J. Anim. Ecol. 48: 123–142.

Horn, H.S. 1983. Some theories about dispersal. *In* Swingland, R. & Greenwood, P.J. (eds) The Ecology of Animal Movement: 54–59. Oxford: Oxford University Press.

Kenward, R.E. 1987. Wildlife Radio Tagging. London: Academic Press.

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.

Korpimäki, E., Lagerström, M. & Saurola, P. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus.* Ornis Scand. 18: 1–4.

Marquiss, M. & Newton, I. 1981. A radio-tracking study of the ranging behaviour and dispersion of European Sparrowhawks *Accipiter nisus.* J. Anim. Ecol. 51: 111–133.

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

Moore, W.S. & Dolbeer, R.A. 1989. The use of banding recovery data to estimate dispersal rates and gene flow in avian species: case studies in the Red-winged Blackbird and Common Grackle. Condor 91: 242–253.

Newton, I. 1979. Population Ecology of Raptors. Berkhamsted: T. & A. D. Poyser.

Newton, I. 1986. The Sparrowhawk. Calton: T. & A. D. Poyser.

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

Nilsson, J. & Smith, H.G. 1985. Early fledgling mortality and the timing of juvenile dispersal in the Marsh Tit *Parus palustris.* Ornis Scand. 16: 293–298.

Steenhof, K., Kochert, M.N. & Doremus, J.H. 1983. Nesting of subadult Golden Eagles in southwestern Idaho. Auk 100: 743–746.

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

Submitted 18 November 1991; revision accepted 14 June 1992