JUVENILE DISPERSAL OF SPANISH IMPERIAL EAGLES

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Abstract.—Postfledging dispersal of juvenile Spanish Imperial Eagles (Aquila adalberti) was studied from 51 records of recoveries, sightings, and contacts with banded, and wing or radio-tagged birds. When they become independent young eagles leave their natal areas, travelling up to 350 km. Dispersal can be divided into three phases (1) exploratory flights with return to the natal area, (2) long distance trips away from the natal area during which some birds establish temporary territories in areas of apparent food abundance, and (3) return to the vicinity of the natal area. During dispersal the young suffered high mortality, which is attributed to the risks of dispersion "per se" and the lack of familiarity with the new areas they explore. The distance between natal areas and recoveries first increased and then decreased with age, the birds tending to return to the areas where they were born, a fact probably related to marked philopatry in this species. However, there is evidence of at least one individual breeding in an area different from its place of birth, which suggests that there is some genetic exchange among the different sub-populations.

DISPERSIÓN DE LOS JÓVENES DE AQUILA ADALBERTI

Resumen.—En base a 51 registros de avistamientos, contactos de individuos anillados o con radiotransmisores y recapturó de aves se estudias el patrón de dispersión de jóvenes de *Aquila adalberti*. Cuando los jóvenes se independizan, dejan sus áreas natales y viajan distancias hasta de 350 km. El patrón de dispersión se puede dividir en tres fases. Jóvenes: (1) vuelos exploratorios con regreso a su área natal, (2) largos vuelos fuera del área natal en donde las aves establecen territorios temporeros en lugares con aparente abundancia de alimento y (3) regreso a la vecindad del área natal. Durante la dispersión los jóvenes sufren una alta mortalidad, atribuida a los riesgos de la dispersión per se y a la falta de familiaridad con las áreas que exploran. Las distancias entre las áreas natales y lugares de recuperación de jóvenes, aumenta y luego disminuye con la edad de las aves. Hay una tendencia a regresar a los lugares natales, probablemente debido a la marcada filopatría en la especie. Sin embargo, hay evidencia de al menos un individuo, que se reprodujo en un área diferente a la que nació, lo que sugiere un cierto intercambio genético entre diferentes sub-poblaciones.

The most frequent definition of dispersal is "permanent movement an individual makes from its birth site to the place where it reproduces or would have reproduced if it had survived and found a mate" (Howard 1960). The definition refers explicitly to the movement of prereproductive individuals. Greenwood and Harvey (1982) suggested that dispersal from the site or group of birth to that of first reproduction or potential reproduction should be labelled natal dispersal. Subsequent movement between sites or groups should be labelled breeding dispersal. Juvenile dispersal refers only to the movements of individuals once they become independent from their parents.

In most birds of prey, juveniles are more likely to perform longer dispersal movements than adults (Brown and Amadon 1968, Newton

1979). Reasons for juvenile dispersal include: age of the individual, limited food availability in the natal area, previous or genetic experience, intrasexual competition, and territorial disputes (Adamcik and Keith 1978, Houston 1978, Newton and Marquiss 1983, Snow 1968, and Stewart 1977). Many of these individuals return to their natal area to breed (Newton 1979, Newton and Marquiss 1983).

Adult Spanish Imperial Eagles (Aquila adalberti) remain on their breeding territories throughout the year (González 1989, Valverde 1960), whereas juveniles leave their natal area once the post-fledging period has ended (Alonso et al. 1987, González et al. 1985). The characteristics of their movements at this stage are unknown (Bernis 1966, Valverde 1960). In this paper we describe these juvenile dispersal movements and discuss them in relation to the age of the individuals.

METHODS

Data are from: recoveries of banded individuals found dead, sightings of wing-tagged individuals, and radio contacts of ten young eagles radio-tagged in 1984 (Alonso et al. 1987, González et al. 1985). The data represent 51 band recoveries and contacts where place of birth, age, and locality of observation or banding recovery were known.

From 1984 to 1986, 46 young Spanish Imperial Eagles in southwestern Spain were fitted with plastic wing color-markers. Markers were fitted around the leading edge of the humerus and secured at the pointed ends between the tertiaries and scapulars with a pop rivet (Kochert 1972). Tags were 750×350 mm. and weighed 8 g. They were made of Saflag (Safety Flag Co. of America, Pawtucket, Rhode Island).

Eagles were color-marked individually each year. Each was fitted with two colored markers; one indicated the place of origin (Guadarrama, Extremadura or Doñana, in central, western and south of Spain respectively) and the other the year in which the individual was marked (1984, 1985, or 1986). Both tags were provided with individual symbols indicating the exact nest.

Ten young were marked individually with radio-transmitters at Doñana National Park. The telemetry equipment consisted of solar-powered transmitters, LA 12 DS receivers, and three-element hand-held yagi antennas, all from AVM-Instruments Co., Livermore, California. The transmitter packages weighed 75–80 g, approximately 2–2.5% of the body weight of the bird, and had an estimated average lifetime of 3 y. The packages were attached to the eagles with a back-pack harness. No abnormal behavior associated with the harnesses or transmitter packages was observed. Reception ranges were about 5–8 km when the bird was perched on a tree, and 20–30 km when the bird was flying. Once the young started to fly long distances, they were tracked from vehicles and a Dornier aircraft.

All marked and unmarked individuals received aluminum leg-bands. Chicks were tagged at approximately 75% their normal fledging age to allow sufficient size and feather development for adequate marker reten-

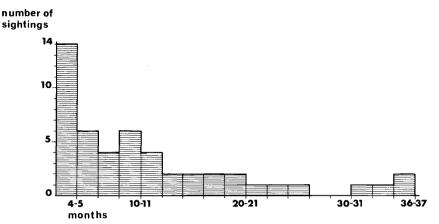


FIGURE 1. Band recoveries and wing-radio marker sightings of young Spanish Imperial Eagles in relation to age.

tion. We published announcements in technical publications and sent circulars to universities, ornithological societies and environmental agencies, requesting information on sightings of color-marked birds. Not all observations of marked birds gave us complete information; in those cases where nest of origin could not be identified, we considered the centroid of all nests marked that year within the place of origin, following Steenhof et al. (1984).

Observations and radio-contacts of individuals which had not yet completed the post-fledging period (age 4 mo, approximately) were not considered. we also did not consider two chicks marked in 1984, whose post-fledging period and dispersal had been abnormal due to the accidental death of their parents (González et al. 1986).

The age of young individuals was determined to the nearest month. As the majority of the birds hatched in late April or the beginning of May, we assigned "age one" to June 1st.

RESULTS

Tag loss observed between tagging and dispersal from the natal area was 4% (n = 46), similar to that observed in Golden Eagles (*Aquila chrysaetos*) (Kochert et al. 1983). There is a regular decrease in the number of sightings and recoveries with time (Fig. 1).

We obtained information from 9 banding recoveries, 29 sightings of wing-markers and 13 radio-contacts (Table 1). To evaluate the effectiveness of wing-marking, we calculated wing-marked sighting rates (number of sightings/number of marked birds). The rate was 43.4% (n = 46), similar to the one obtained with Golden Eagles (33.2%, n = 256) (Kochert et al. 1983) and much larger than that of Bald Eagles (*Haliaeetus leucocephalus*) (4.4%, n = 56) (Gerrard et al. 1978). Sighting rates for Spanish Imperial Eagles far exceed band recovery rates (5.5%, n = 109)

(Fernández-Cruz and Asensio 1982) showing the high profitability of wing-marking in relation to banding in eagle post-fledging dispersal studies.

Once the young completed the postfledging period in September (Alonso et al. 1987, González et al. 1985) they left the natal area. Two of the radio-marked individuals undertook long distance flights, while the other six made exploratory flights of considerable length, sometimes returning to the natal area within the same day (Table 1). These pre-dispersal movements lasted 1–7 d, extended 20–135 km, and took different directions. Two individuals tagged in Doñana were observed in the Gibraltar area. In all these flights, the young went alone and did not depend on their parents. Final dispersion from the area took place between 1 Sep. and 3 Oct., at ages of 123–156 d (Table 1). The birds set out in different directions: one went NE, two E, and two SE. It was not possible to determine the direction followed by the other three young.

From our data, we could not determine that the young birds cross to Africa over the Gibraltar Straits, even though individuals have been observed there (Table 1). However, the crossing of the Straits does seem to happen. Between 1967 and 1974, at least four individuals did follow this route (Bensusan, in litt.) and other similar cases have been published (Bernis 1980, Cortés et al. 1980, Evans and Lathbury 1973, Pineau and Giraud-Audine 1978). Furthermore, a bird banded in Doñana in 1982 was recovered dead in Aim Jorra (Morocco) in 1984 (Bergier 1987; Calderón et al. 1988).

According to the distance between the place of birth and the place of recovery or sighting, the juvenile dispersal could be divided in to three different phases (Fig. 2, see also Table 1). The first phase lasts approximately 3 mo (4–6 mo of age) and is characterized by short movements ($\bar{\mathbf{x}} = 45.8$; km; n = 18; SD = 45.1), and exploratory flights of the young returning usually to the natal area. This phase is coincident with the predispersive phase that has been described in other bird studies (Baker 1978, Lawn 1984).

The second phase lasts approximately 9 mo (7–15 mo of age) and includes juvenile dispersal. The young travel longer distances ($\bar{\mathbf{x}} = 162.4$ km; n = 16; SD = 121.0) than in the first phase, the difference being significant ($\mathbf{F}_{75,77} = 7.1$; P < 0.01). However, some individuals stay in the vicinity of the natal area and thus a gradation in the dispersal behavior of this species appears to exist, between the long distance flights and the short trips within the natal area.

The third and last phase takes place after the 16th mo of age and is marked by the existence of recoveries near the natal area ($\bar{x} = 41.9 \text{ km}$; n = 15; SD = 64.9). The mean distance is significantly smaller ($F_{15,14} = 3.47$; P < 0.01) than that of the second phase. During this third phase, the birds that have undergone dispersal and travelled long distances return to the natal area.

The individuals marked in Doñana performed the longest trips. Dispersal does not follow a preferred direction (G = 2.3; P > 0.05, Table

Table 1. Band recoveries, wing marker sightings, and radio tracking sightings of young Spanish Imperial Eagles with reference of distance in km, orientation and age in years (a) and months (m), from hatching site to recovery site. Symbols are (EURING code): 1—ringed as pull.; †—shot or killed by man; ‡—killed by electrocution; RT—radio tracking sighting; A—wing-mark sightings.

Type of return	Dates	Origin and location	Dis-	Com- pass direc- tion from natal site	Age (yr:mo)
		— _ 	tance	Site	(91 . 1110)
1 ‡	10.06.77 00.04.78	Toledo Cenicientos, Madrid (Fernandez-Cruz, 1982)	70	NE	10m.
1 †	13.06.80 26.10.81	Madrid Villanueva de los Infantes, Ciudad Real	230	SSE	1a.2m.
1 ‡	22.05.76 00.06.83	Toledo Malpartida de Plasencia, Caceres	80	wsw	6a.11m.
1 †	.06.80 23.05.83	Toledo Ventas con Peña Aguilera, Toledo	2	_	3a.1m.
1 ‡	.05.87 16.10.87	Madrid Villamantilla, Madrid	20	ESE	6m.
1 ‡	.05.86 24.04.88	Caceres Torrejon el Rubio, Caceres	105	NE	1a.10m.
1	.05.85 25.11.85	Caceres Quismondo, Toledo	130	ENE	7m.
1	.05.84	Doñana, Huelva			
RT	15.09.84	Sanlucar, Cadiz	35	SE	5m.
A	22.09.84	Tarifa, Cadiz	115	SE	5m.
RT †	24.09.84 25.10.84	Tarifa, Cadiz Puerto Real, Cadiz	135 40	SE SE	5m. 6m.
		· · · · · · · · · · · · · · · · · · ·	40	SE	om.
1 RT	.05.84 01.09.84	Doñana, Huelva Doñana, Huelva	20	SSW	5m.
RT	02.09.84	Villamanrique de la Condesa, Sevilla	25	E	5m.
1	.05.84	Doñana, Huelva		_	2111
RT	21.09.84	Villamanrique de la Condesa, Sevilla	30	NE	5m.
1 RT	.05.84	Doñana, Huelva	40	NE	5m.
A	19.09.84 21.09.84	Villamanrique de la Condesa, Sevilla Tarifa, Cadiz	130	SE	5m.
RT	25.09.84	Villamanrique de la Condesa, Sevilla	40	NE	5m.
RT	06.02.85	Alcala de los Gazules, Cadiz	80	SE	9m.
RT	27.03.85	Alcala de los Gazules	80	SE	11m.
RT	16.04.85	Alcala de los Gazules	80	SE	12m.
1	.05.84	Doñana, Huelva			
RT	16.04.85	Setenil, Malaga	120	\mathbf{E}	12m.
1	.05.84	Doñana, Huelva		~	_
RT	24.09.84	Tarifa, Cadiz	130	SE	5m.
1 D.T.	.05.84	Doñana, Huelva	10	er.	6
RT	10.11.84	Doñana	12	SE	6m.
1 A	.05.84 15.12.84	Doñana, Huelva Doñana	5	E	8m.

TABLE 1. Continued.

		TABLE 1. Continued.		10	
				Com- pass	
				direc-	
				tion	
Type				from	
of	ъ.		Dis-	natal	Age
return	Dates	Origin and location	tance	site	(yr : mo)
1	.05.84	Doñana, Huelva	_		
Α	03.04.87	Doñana	2	_	2a.11m.
1	.05.84	Doñana, Huelva	440		
Α	00.03.86	Cazalla, Sevilla	110	NNE	1a.11m.
1	.05.84	Doñana, Huelva		CCTAZ	1 1
A	21.08.85	Doñana	4	SSW	1a.4m.
1	.05.84	Doñana, Huelva	12	wsw	1a.9m.
A	26.01.86	Doñana	12	WOW	14.9111.
1 A	.05.84 03.04.87	Doñana, Huelva Doñana	1		2a.11m.
A	00.12.87	Doñana Doñana	1	_	3a.7m.
1	.05.85	Doñana, Huelva	•		<i>3</i> 4. 7 111.
A	00.12.85	Villamanrique, Ciudad Real	325	NE	8m.
A	00.01.86	Viso del Marques, Ciudad Real	305	NE	9m.
Α	00.02.86	Villamanrique /	325	NE	10m.
A	20.04.86	Amedina, Ciudad Real	340	NE	12m.
Α	29.04.86	Villamanrique	325	NE	12m.
1	.05.85	Doñana			
A	07.03.86	Doñana	4	N	10m.
1	.05.85	Doñana, Huelva			
A A	12.11.86	Doñana Doñana	3	NE NE	1a.6m. 1a.7m.
A	23.11.86 00.01.87	Doñana Doñana	10	NE NE	1a./m. 1a.9m.
‡	00.07.87	Vejer de la Frontera, Cadiz	110	SSE	2a.3m.
i	.05.85	Doñana, Huelva			
À	00.12.87	Doñana	1		2a.7m.
1	.05.85	Madrid			
A	28.08.85	El Tiemblo, Avila	25	W	4m.
Α	23.08.86	Navas del Marques, Avila	35	NNW	1a.4m.
1	.05.85	Madrid			
Α	27.03.86	Alia, Caceres	125	sw	11m.
1	.05.86	Badajoz			
Α	20.08.86	Villar del Rey	8	NNE	4m.
1	.05.86	Badajoz			
A	20.08.86	Villar del Rey	8	NWE	4m.
1	.05.86	Badajoz			
A	20.10.86	Villar del Rey	1		6m.
1	.05.86	Caceres	10	N.T	1
A	20.08.86	Aldea del Cano	12	N	4m.
1	.05.86	Caceres	20	SW	10m.
A 1	00.02.87	San Vicente de Alcantara	20	D ##	TOIII.
1 A	.05.86 06.01.87	Badajoz Cheles, Badajoz	95	ssw	8m.
A	11.08.87	Cheles	115	SSW	15m.

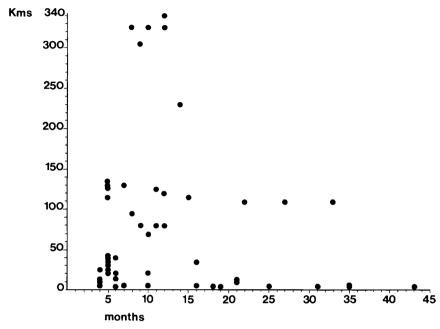


FIGURE 2. Variation of the recovery distance in kms in relation to age, in months of young Spanish Imperial Eagles, ringed as nestlings. Black dots represent sightings and recoveries.

1). After dispersal has taken place, some individuals settle down in temporary territories. This behavior was observed in three young (Fig. 3): the first had been radio-tagged in Doñana in 1984, and was found 80 km away from the natal area from February to April 1985. The second was wing-tagged in Extremadura in 1986 and was observed from January to August 1987 in an area along the Spanish-Portuguese border, 95–115 km from its place of birth. The third individual was wing-tagged in Doñana in 1985 and regularly seen in the plains of La Mancha (Ciudad Real) from December 1985 to April 1986, the distance from the natal area was 350 km. The existence of temporary territories has been mentioned for other birds of prey (Beske 1982, Gargett 1975, Gerrard et al. 1978, Newton 1979, Picozzi and Weir 1976), with the suggestion that this behavior can help birds become familiar with new areas where they could breed subsequently (Baker 1978).

DISCUSSION

The pattern of juvenile dispersal in Spanish Imperial Eagles is similar to the pattern described for other eagles of similar size, such as the Golden Eagle (*Aquila chrysaetos*) and Wedge-tailed Eagle (*A. audax*) (Ridpath and Brooker 1986, Steenhof et al. 1984). We think that the decrease in

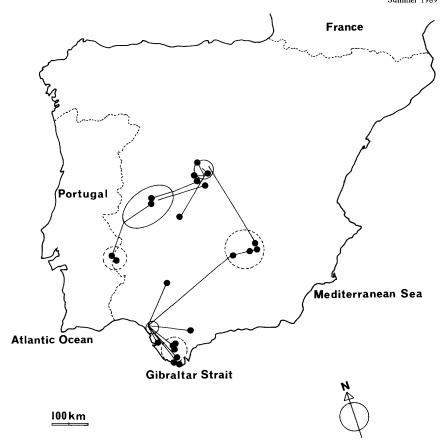


FIGURE 3. Sightings and recovery locations of young Spanish Imperial Eagles that moved >20 km, from the marking location. Areas into open lines have been used to mark the location of the temporary territories established by some young, and in continuous line to mark the location of the marking study areas.

the number of band recoveries and sightings observed in relation to age of the bird could be related to the high rate of juvenile mortality in the first months of the dispersal process, due mainly to movement of the young away from the natal area (González 1989; see also Farner 1945, Greenwood and Harvey 1982).

Additionally, a small percentage of the decrease in the frequency of contacts or recoveries of wing-marked eagles with time may have been caused by wearing of the plastic material and consequent loss of the marker. However, we have been unable to quantify such wear and thus to correct figures for such effect. The longest lifetime of a wing-marker in this study was 4 yr 2 mo, within the range for other species (average 2–3 yr, exceptionally up to 10 yr, Kochert et al. 1983). In general in-

dividual wing-markers have proved to be of great help in studying the dispersal of young Spanish Imperial Eagles. As has already been shown for other birds of prey (see review in Young and Kochert 1987).

There is evidence that points to territorial behavior as the main cause for juvenile dispersal (Newton 1979). The fact that young from Doñana, the area with the highest breeding density, disperse furthest, is in accordance with this hypothesis and agrees with the results described for other species (Myers and Krebs 1971, Watson and Moss 1970). In the Spanish Imperial Eagle young that dispersed suffered higher mortality rates than those that remained in the natal area (González 1989). The probability of survival of these individuals is shorted by the costs and risks of dispersion "per se" and the lack of familiarity with the new areas they explore (Greewood and Harvey 1976, Jenkins et al. 1963, Krebs 1971). However, the dispersal pattern of Figure 3 suggests that at least some of the young were successful in finding areas of high food availability. In these areas the young settled for several months, exploiting the extraordinary abundance of rabbits (*Oryctolagus cuniculus*) (ICONA 1983), which is the main prey of this species (González 1989).

The decrease in the mean dispersal distance after the bird is 8 mo old is surely related to philopatry, which is common among birds of prey (Newton 1975, 1979, Osterlof 1977). Long distance dispersal must facilitate genetic exchange (Greenwood and Harvey 1976, 1982). In the Spanish Imperial Eagle juvenile birds may reach areas where other breeding populations exist and sometimes remain there to breed, as evidenced by an adult bird found breeding in an area different from its place of birth. This suggests that there must exist some genetic exchange among the various breeding groups of the Spanish Imperial Eagle population in Spain, though the magnitude of this interchange is still unknown.

ACKNOWLEDGMENTS

We are indebted especially to F. Hiraldo for his encouragement and support and to J. Garzon, M. Caballero, T. Gullick, J. Diaz, A. Mugica, F. Palacios, J. J. Hernandez, L. Diaz-Ambrona, J. Guzman, J. Jimenez, A. Sanchez, J. M. Salinas, J. Marcos, M. Alvarez, J. Alonso and the staff of National Park of Doñana, Estacion Biologica de Doñana, Unidad de Zoologia Aplicada, Museo Nacional de Ciencias Naturales, Direccion Gral. Medio Ambiente Extremadura, for the valuable field assistance provided. We thank also C. Aikin for help in the translation of the text. This study was a cooperative project of ICONA and CSIC, with financial support from ICONA and DGICYT project No. 9261.

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- Received 13 Jul. 1988; accepted 25 Feb. 1989.