Post-fledging behaviour in Golden Eagles *Aquila chrysaetos*: onset of juvenile dispersal and progressive distancing from the nest

ALVARO SOUTULLO,[1]* VICENTE URIOS,[1] MIGUEL FERRER[2] & SANTIAGO G. PEÑARRUBIA[1]

[1] *Estación Biológica Terra Natura (CIBIO – Fundación Terra Natura), Universidad de Alicante, Apdo. correos 99, Alicante E-03080, Spain*

[2] *Departamento de Conservación de la Biodiversidad, Estación Biológica de Doñana, Consejo Superior de Investigaciones Cientificas, Avda. de María Luisa s/n, Pabellón del Perú, Sevilla 41013, Spain*

Thirteen juvenile Golden Eagles *Aquila chrysaetos* were tracked during their first year of life using satellite telemetry. Distances to the nest attained during that period and the age at the onset of juvenile dispersal were explored. The performance of nine different criteria to determine that age was analysed. In general, after a brief period of restricted movements around the nest, the average distance to the nest increased with time. Maximum distances to the nest ranged between 57.7 and 184.3 km, and were considerably greater in females (mean ± sd, 138.5 ± 44.5 km) than in males (70.5 ± 14.0 km). No sex difference was observed in the age at which that distance was attained (males: 329 ± 32 days, females: 312 ± 20 days). The onset of juvenile dispersal took place around the fifth month of life (September in Spain). Eight of the nine criteria provided similar results, suggesting that in Spain dispersal starts when birds are between 140 and 180 days old, and that the post-nestling period lasts between 60 and 120 days. For future studies, to determine the age at which the onset of juvenile dispersal occurs, we recommend the use of either the first day on which individuals were located beyond the mean distance between nests of different pairs (10 km in our study area), or the date of the record midway between the first and the last location recorded during the month in which the maximum variability in the distance to the nest was observed.

Dispersal is one of the most important yet least understood phenomena in population biology, ecology and evolution (Gadgil 1971, Wiens 2001). It plays a key role in many aspects of the ecology and behaviour of species, and is therefore tightly linked to species persistence, evolution and conservation (Gadgil 1971, Johnson & Gaines 1990, Clobert *et al.* 2001). Knowledge of the distance moved by animals during dispersal is therefore fundamental to our understanding of many ecological and evolutionary processes, as well as to the design of successful conservation strategies (e.g. Paradis *et al.* 1998).

Dispersal is often defined as 'the permanent movement an animal 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). However, as this definition only refers to the movements undertaken by pre-reproductive individuals, Greenwood and Harvey (1982) have suggested that such movements should rather be termed 'natal dispersal'. They differentiate them from the subsequent movements that adults undertake between reproductive areas, a process they call 'breeding dispersal'. In this context, the movements undertaken by juveniles once they become independent from their parents are often denominated 'juvenile dispersal' (e.g. González *et al.* 1989, Ferrer 2001, Kenward *et al.* 2001).

As in many large raptors, juvenile dispersal in the Golden Eagle *Aquila chrysaetos* is characterized by an initial wandering and exploratory phase after becoming independent (González *et al.* 1989, Walls & Kenward 1995, Watson 1997), in which the birds' behaviour is to a large degree determined by the search for food (Ferrer 1993a, 2001, Watson 1997). The life of the Golden Eagle from its first winter to

*Corresponding author.
Email: a.soutullo@gmail.com

its first breeding is, however, still largely a mystery (Walker 1987, Watson 1997). Most of what we currently know about this period is based on the study of a handful of radiotagged individuals (e.g. Bahat 1992, Haller 1994, 1996, Grant & McGrady 1999, O'Toole *et al.* 1999, Soutullo *et al.* 2006a, 2006b) and a few studies of ringed or wing-marked individuals (e.g. Fremming 1980, Steenhof *et al.* 1984, Watson 1997). However, as information derived from ringing recoveries gives only a single record of movement, it cannot reveal much about the nature of dispersal in individual birds, and how movements may change across several years before breeding commences (Watson 1997).

The aim of this paper is to provide some of the first information regarding the pattern of distancing from the natal area during the first months of juvenile dispersal. In particular, we investigate the age at which the onset of juvenile dispersal takes place and, hence, the length of the post-nestling period. With this in mind, we explore the value of alternative metrics to determine the age at which the onset of dispersal occurs.

STUDY AREA AND METHODS

We used satellite telemetry to collect information on the locations of 13 nestlings (seven females and six males) from a resident population of Golden Eagles in eastern Spain (Communities of Valencia, Murcia and Catalonia). Individuals were captured between June 2002 and October 2004, while still in the nest, at an age of *c.* 50 days old, and tagged with platform transmitter terminals (PTTs) that send signals to satellites that retransmit them to ARGOS centres for processing and estimation of the PTT position. For computational purposes all individuals were treated as if tagging had occurred when they were exactly 50 days old.

PTTs were fixed to the birds' backs using a breakaway Teflon harness. Three types of PTTs, all manufactured by Microwave Telemetry, were used: four 45-g PTT-100s, five 50-g Solar PTT-100s (one was recovered in the field and re-used) and three 70-g Argos/GPS Solar PTT-100s. Transmitters fixed in 2002 were programmed to an 8-h on/120-h off schedule; all others were programmed to a 16-h on/56-h off schedule. The full transmitter equipment never exceeded 2.5% of the juvenile's body mass (1.81%, sd = ±0.29, n = 13), which is below the 3% suggested by Kenward (2001) to minimize the effects of additional mass on a bird's movements.

Of a total of 2913 locations supplied by the ARGOS system, only 1960 (67%) were used for the analyses. These included locations in location classes (LCs) 3, 2 and 1 (with nominal accuracies estimated to be within 150, 350 and 1000 m, respectively; but see Hays *et al.* 2001; Vincent *et al.* 2002). Locations belonging to lower quality LCs (0, A and B) were only used when they were consistent with the juveniles' movements in terms of distance covered and time elapsed between locations (see Soutullo *et al.* 2006a). Thus, locations corresponding to movements in which the birds covered unrealistically long distances for the time elapsed were excluded (Hays *et al.* 2001). Soutullo *et al.* (2006b) provide more details on individuals studied and the tagging and tracking techniques.

In order to investigate how far Golden Eagles disperse from their natal area and how that changes with age, we divided the first year of life into 30-day-long periods ('months'), starting when birds were 60 days old, and calculated the distance from the nest to each recorded location: the 'distance to the nest' (D). For each individual 'monthly' (30-day period) averages of D (D_m) were also calculated. We conducted a Kruskal–Wallis test to evaluate between-'month' differences in D_m, and used the Games–Howell multiple comparisons test for unequal variances (Zar 1999) to conduct all two-'months' comparisons of D. Between-sex differences in D_m were evaluated with the Mann–Whitney test. For individuals for which data for the entire first year of life were available we also calculated the annual maximum distance to the nest (D_{Max}) and determined the age at which it was attained. Between-sex differences in D_{Max} and the age at which it was attained were evaluated with the Mann–Whitney test. As six of the individuals were siblings from three different nests, and hence their movements might not be independent, we checked how the results of all the analyses changed after removing one of the chicks of each pair. Chicks removed were chosen at random. Both results are provided.

The onset of juvenile dispersal is usually more or less arbitrarily defined on the basis of some estimation of the typical size of the territory of adults (e.g. Ferrer 1993a, 1993b, 2001, Walls & Kenward 1995; see also Kenward *et al.* 2001). However, juvenile dispersal is characterized by an initial wandering and exploratory phase that contrasts with the restricted pre-dispersal movements. Such contrast is likely to be identifiable as a period of increased variability in the distance to the nest, and hence could be used to

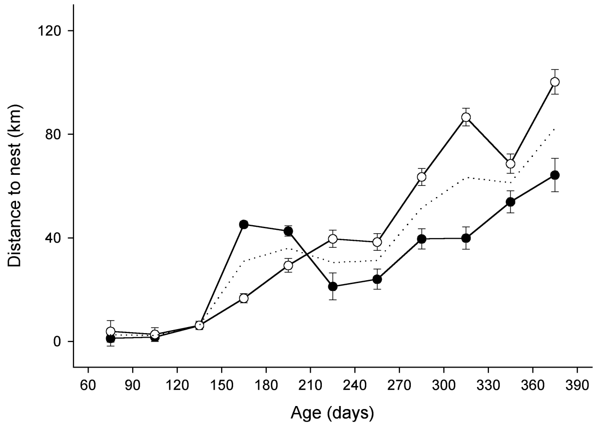

Figure 1. Progressive distancing from the nest of 13 juvenile Golden Eagles during their first year of life. 'Monthly' means (± se) are shown for both males (black dots) and females (white dots). The dotted line indicates the overall mean.

Table 1. Mean (± se) distance between individual's locations and the natal nest (*D*) during the first year of life of 13 Golden Eagles. Four homogeneous groups (*P*-values of the Games–Howell test > 0.05) are identified based on the similarity of the 'monthly' means of *D*. Groups probably reflect different stages in Golden Eagles' ontogeny.

Age (days)	Distance (km)	Group 1	Group 2	Group 3	Group 4
60–90	2.5 ± 2.6	xxx			
90–120	2.2 ± 1.6	xxx			
120–150	6.2 ± 1.0		xxx		
150–180	31.0 ± 1.1			xxx	
180–210	36.0 ± 1.7			xxx	
210–240	30.4 ± 3.1			xxx	
240–270	31.2 ± 2.5			xxx	
270–300	51.6 ± 2.5				xxx
300–330	63.3 ± 2.7				xxx
330–360	61.3 ± 2.8				xxx
360–390	82.3 ± 4.0				

identify the onset of juvenile dispersal. Four criteria based on this idea are explored here. First, for each 30-day period we calculated the coefficient of variation of D (D_{CV}) and used the date of the record midway between the first and the last location recorded during the period in which D_{CV} was maximum to determine the age at which the onset of juvenile dispersal took place (A_O). We then calculated the moving average and variance for three, five and ten consecutive observations (moving one record forward each time) to calculate the corresponding D_{CV} and determine A_O as described above.

Five criteria often used to determine the onset of dispersal were also used for comparison – the first day the individual was located at a distance from the nest that is larger than: (1) half of the mean distance between different pairs' nests (roughly the radius of a circular natal home range with its centre in the nest; see McLeod *et al.* 2002), 5 km in our study area (Urios 1986, Sánchez-Zapata *et al.* 2000); (2) the minimum distance between different pairs' nests, 10 km in our study area (Urios 1986, Sánchez-Zapata *et al.* 2000) – to avoid confusing early exploratory movements with the actual onset of the dispersal, we also considered the first day the individual was located beyond 5 and 10 km but not less than those distances in the following two records, as suggested by Walls and Kenward (1995); and (3) the first day the individual was located more than 20 km from the nest, as used for other eagles in Spain (e.g. Arroyo *et al.* 1992, Ferrer 1993a, 1993b, 2001, Real *et al.* 1998, Cadahía *et al.* 2005). Note that given the duty cycle of tags, the mean number of days between consecutive locations ranged between 0.18 (sd = ±0.51) and 6.70 (sd = ±11.08) days.

To compare the values of A_O obtained using these criteria we conducted a one-way ANOVA, and used the Games–Howell test (Zar 1999) to compute all two-criteria comparisons. Statistical analyses were conducted using SPSS version 11.5. Distance data are presented as means ± sd.

RESULTS

In general, after a brief period of restricted movements around the nest, the average distance to the nest increased with time, although differences between males and females were observed (Fig. 1). Between-sex differences were, however, not statistically significant (males $Z = 1.01$, $n = 101$, $P = 0.31$; females $Z = 0.42$, $n = 71$, $P = 0.68$). Differences in 'monthly' averages (males $\chi^2 = 66.8$, $df = 10$, $P < 0.0001$; females $\chi^2 = 43.8$, $df = 10$, $P < 0.0001$) probably reflect different stages in the Golden Eagles' post-fledging period (Table 1). Annual maximum distances to the nest (D_{Max}) ranged between 57.7 and 184.3 km, and were considerably larger (males $Z = 1.77$, $n = 7$, $P = 0.077$; females $Z = 1.55$, $n = 4$, $P = 0.33$) in females (138.5 ± 44.5 km) than in males (70.8 ± 14.0 km). No sex difference was observed in the age at which D_{Max} was attained (males 329 ± 32 days, females 312 ± 20 days; $Z = 1.06$, $n = 7$, $P = 0.29$ and $Z = 0.78$, $n = 4$, $P = 0.44$, respectively).

Table 2. Estimated age (in days) at the onset of juvenile dispersal of 13 Golden Eagles from Spain, according to nine different criteria (see text for details). Platform transmitter terminal numbers are used to identify individuals.

	34464	34465	34466	34472	34473	34474	34475	39706	39714a	39714b	49180	49181	49182	mean	sd	median	CV
> 5 km	64	79	55	103	106	111	75	103	81	92	153	129	134	99	28.5	103	29%
> 5 km in 3 consecutive locations	143	153	165	208	157	168	204	114	81	–	153	129	148	152	34.9	153	23%
> 10 km	154	153	118	145	132	127	167	114	81	–	167	144	148	138	24.7	145	18%
> 10 km in 3 consecutive locations	154	153	270	249	178	184	274	114	128	–	167	144	148	180	54.5	161	30%
> 20 km	154	169	270	255	178	184	284	132	128	–	168	144	148	185	54.4	169	30%
'Monthly' D_{CV}	75.5	153	128	114	157	137	140	103	107	–	163	137	167.5	132	27.6	137	21%
D_{CV} of 3 consecutive locations	70	116	255	244	168	127	300	110	139	145	166	144	118	162	65.9	144	41%
D_{CV} of 5 consecutive locations	143	122	249	244	162	137	300	114	123	145	166	144	118	167	59.2	144	36%
D_{CV} of 10 consecutive locations	125	145.5	244	182	157	108.5	263	108.5	120.5	166	165	144	173	162	47.4	157	29%

The onset of juvenile dispersal took place around the fifth month of life. Significant differences in the (log-transformed) age at the onset of juvenile dispersal estimated using the criteria described above were observed ($F_{8,103} = 5.52$, $P < 0.0001$). This results from the value for A_O estimated using the 5-km criterion being significantly less than that estimated otherwise (Table 2). All other criteria provided similar results ($P > 0.05$). In terms of consistency, A_O estimated for different individuals using the 10-km criterion (the first day individuals were located beyond the mean distance between different pairs' nests), and the maximum 'monthly' D_{CV} criterion showed the lowest variability. Conversely, the values estimated on the basis of the D_{CV} calculated using the moving average of three and five consecutive observations showed the greatest variability.

DISCUSSION

Juvenile dispersal in the Golden Eagle is characterized by an initial exploratory and nomadic phase followed by a return to the vicinity of the natal area (Watson 1997). Here we monitored the dispersal of 13 Golden Eagles during their first year of life. After restricted pre-dispersal movements around the natal nest, juvenile dispersal began at the fifth month of life. In general, the distance to the nest was significantly shorter between July and August than afterwards. Such differences are likely to reflect different stages in Golden Eagles' ontogeny: the post-nestling or post-fledging dependence period (from the first flight to the onset of dispersal) and the initial stages of juvenile dispersal. After independence, females moved away from the nest throughout the whole year. Conversely, males showed a more rapid increase in distance to the nest soon after independence, and only a slight increase thereafter. Yet, in both sexes annual maximum distance to the nest was attained towards the end of the first year of life, although females dispersed much further from the nest than males. This is in line with our previous observation (Soutullo *et al.* 2005) that whereas in both sexes the total area explored continues to increase for most of the first year, in females not only is the total area explored considerably larger but the rate of increase accelerates towards the end of the first year. In general, the maximum distances to the nest we report here match those reported for the species in southwest Idaho, where 78% of the individuals remained within 100 km of the nesting area (Steenhof *et al.* 1984), and in Scotland, where maximum distances to the nest oscillated between 100 and 150 km (Watson 1997, Grant & McGrady 1999). They are considerably shorter, however, than those reported for the species in Switzerland (up to 1000 km; Haller 1994) and Norway (up to 800 km; Fremming 1980). These differences may be a consequence of the greater extent of continuously suitable habitat in these countries (Watson 1997).

By contrast, the fact that distances to the nest attained in September differ significantly from those attained in the rest of the year highlights the transitional stage in these birds' ontogeny that takes place around September: independence from parents and the onset of dispersal. This interpretation is reinforced by the fact that the age at the onset of dispersal estimated using the different criteria overlaps significantly, strongly suggesting that in Spain it takes place when individuals are about 140–180 days old (i.e. around September). This figure is in line with the age reported for the species in England (Walker 1987) and the USA (O'Toole *et al.* 1999). However, it is considerably less than the 240 days reported by Bahat (1992) for the Golden Eagle in Israel. These differences may reflect environmental differences between Spain and England (and to a lesser degree North Dakota, USA), and the Negev desert in Israel, with chicks remaining longer in their natal area when the chances of ending up in habitats of poor quality are higher (e.g. Ferrer 1992, Watson 1997). Alternatively, they may reflect differences in the way the onset is determined.

In Golden Eagles, the first flight takes place when the birds are between 60 and 80 days old (Walker 1987, Watson 1997, O'Toole *et al.* 1999), and in Spain the onset of juvenile dispersal occurs when they are about 140–180 days old. Thus, in our study area the post-nestling period is restricted to an interval of 60–120 days in between (i.e. July to mid September).

All the criteria we used to determine the onset of dispersal are based on some knowledge of the species' biology. However, they rely on different and largely independent aspects of the birds' behaviour: patterns of post-fledging movements and the adult's territory size. For the latter, a provision to distinguish between early exploratory movements and true independence was also introduced. Given the low frequency with which locations are obtained (1–7 days on average), it is arguable whether it is advisable to use this kind of provision with satellite telemetry data. Regardless, all but one of the criteria provided remarkably similar estimates of the age at which the onset of juvenile dispersal takes place. Hence, in principle they are all usable to estimate the age at which Golden Eagles become independent. However, as the internal consistency of the first day individuals were located beyond the mean distance between different pairs' nests, and the record midway between the first and the last location recorded during the 'month' in which the maximum variability in the distance to the nest was observed seem to be slightly superior, we recommend their use in future studies. This is because despite sex, individual and year-to-year (e.g. due to body condition or food availability) differences in the age at which Eagles become independent, in the same region all chicks are expected to abandon the natal home range within a few weeks (usually less than 2 months; Walker 1987, Ferrer 1992, Grant & McGrady 1999). Hence, a criterion that suggests that some individuals begin their juvenile dispersal when they are around 70 days old, but that some others do not disperse until they are 300 days old, seems much less reliable than one that suggests that Eagles leave the natal area when they are between 80 and 160 days old (see Table 2). Regardless, the criterion of maximum 'monthly' variability has the advantage that it can be used even in the absence of detailed knowledge of the spatial distribution of nests and territories. As distance between nests may vary widely throughout the species' geographical range, and knowledge is often incomplete, the maximum variability criterion might sometimes be the only reliable option available. Moreover, we argue that it would always be better than using an arbitrary value extrapolated from other areas without a clear understanding of why such a value was used, and has the advantage of being computed easily from the data gathered. The question remains as to how it would fare for other species or in situations where the onset of dispersal may not be defined simply.

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