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# DISPERSAL AND SURVIVAL OF JUVENILE GOLDEN EAGLES (*AQUILA CHRYSAETOS*) FROM FINNMARK, NORTHERN NORWAY

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ABSTRACT.—The Golden Eagle (*Aquila chrysaetos*) in Fennoscandia has a widespread breeding range. In Norway, it spans from 58° in the south to 71° north in Finnmark County, making it likely the northernmost breeding population of this species in the world. To gain knowledge about their dispersal and movement behavior, we tagged 25 nestling Golden Eagles in Finnmark with satellite transmitters at the age of 7–11 wk during 2002–2011. About half of the birds made preliminary dispersals of more than 10 km from the nest, before dispersing permanently. The median date of permanent dispersal was 21 October. The main dispersal direction was southerly into the forested and agricultural areas in Sweden, but some birds also moved to Finland, Russia, and the Norwegian coast. The maximum dispersal distance from the natal area was ca. 1500 km. There was a return movement in the spring, with movement rates of about 20–30 km/day. The pattern of southerly migration in the autumn and northerly return in the spring was repeated over consecutive years. The overall survival rate was estimated at 58% during the first year of life, and 50% were alive after 2 yr. However, the birds that were hatched in the interior had higher survival rates than those hatched on the northernmost outer islands, and they also dispersed earlier than those from the coast. Illegal killing of Golden Eagles in northern Sweden was cause of mortality.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *dispersal*; *migration*; *Norway*; *satellite tracking*.

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DISPERSIÓN Y SUPERVIVENCIA DE INDIVIDUOS JUVENILES DE *AQUILA CHRYSAETOS* EN FINNMARK, NORTE DE NORUEGA

RESUMEN.—*Aquila chrysaetos* tiene un área de distribución reproductora amplia en Fennoscandia. En Noruega, en el condado de Finnmark, abarca desde los 58° en el sur hasta los 71° en el norte, constituyendo la población reproductiva de esta especie más septentrional. Durante el periodo 2002–2011, marcamos en Finnmark 25 pollos de *A. chrysaetos* de 7–11 semanas de edad con transmisores satelitales para conocer su comportamiento de dispersión y movimientos. Cerca de la mitad de las aves realizó dispersiones preliminares a más de 10 km del nido, antes de dispersarse de forma permanente. La fecha mediana de dispersión permanente fue el 21 de octubre. La dirección principal de dispersión fue hacia el sur dentro de las áreas boscosas y agrícolas de Suecia, pero algunas aves también se trasladaron a Finlandia, Rusia y la costa de Noruega. La distancia máxima de dispersión desde el área natal fue de aproximadamente 1500 km. Hubo un movimiento de regreso durante la primavera, con tasas de movimientos de alrededor de 20–30 km/día. El patrón de migración hacia el sur en el otoño y el regreso hacia el norte en primavera se repitió entre años consecutivos. La tasa de supervivencia general se estimó en un 58% durante el primer año de vida, y un 50% de las aves estaban vivas después del segundo año. Sin embargo, las aves que eclosionaron en el interior del continente tuvieron tasas de supervivencia mayores que las de las aves que eclosionaron en las islas exteriores ubicadas más al norte, y también se dispersaron antes que las aves de la costa. Una causa de mortalidad de *A. chrysaetos* en el norte de Suecia fue la matanza ilegal.

[Traducción del equipo editorial]

The Golden Eagle (*Aquila chrysaetos*) breeds in all mountainous regions of Norway (Gjershaug et al. 1994) and is a protected species (Kålås et al. 2010). Recently, the species has come under pressure from farming interests due to its role as a predator on domestic lambs (Gjershaug and Nygård 2003). In addition, claims of heavy predation on semidomestic reindeer in Finnmark, especially during winter

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(Gjershaug and Nygård 2003, Johnsen et al. 2007), have made it important to learn more about the behavior and movements of Golden Eagles in this area. There is high mortality of Golden Eagles in the neighboring areas in northern Sweden from anthropogenic sources (Hjernquist 2011), suggesting that similar sources may also affect eagles in Norway, as the habitats and land-use forms are quite similar in these northern latitudes. The scant ringing recoveries indicate a general movement from north to south of juveniles from Norway (Fremming 1980), but little detail is known about their dispersal, migration routes, areas used during winter and other seasons, and the effects of age and sex on their movements.

Some Golden Eagle populations have relatively short juvenile dispersal distances (Watson 2010), whereas populations breeding at higher latitudes in North America have long-distance autumn migrations southward, followed by return movements in the following spring (McIntyre et al. 2008). The same was seen in juveniles tagged in central Sweden (Falkdalen and Nygård 2007). In this report, we examine the year-round movements of juvenile and subadult Golden Eagles from Finnmark in northern Norway over several seasons using satellite telemetry. Little is known of survival of and potential threats to this population of juvenile Golden Eagles, and one aim of our study was to understand these further. In other locations, poorly placed wind farms kill Golden Eagles in substantial numbers (Smallwood and Thelander 2008), and thus our study is both timely and important in the light of the rapid development of wind power in Sweden.

## Methods

We studied Golden Eagles during 2002–2011 in western Finnmark, northern Norway (69–71° N, 22.5–26° E; Fig. 1). We tagged 16 eagles as nestlings in the interior of the county and nine from nests on the coastal islands of West Finnmark. We entered the nests when the chicks were approximately 8.5 (7–11) wk of age. We took standard measurements (bill length and depth, wing length, tail length, length of rear talon, tarsus width, tarsus depth, and body mass) to aid in sex determination. This was performed later using discriminant analysis (Huberty 1994), yielding the canonical unstandardized discriminant function (DFA) of F = −39.511 + 0.981 * bill depth + 0.920 * tarsus width. Negative output values indicate males; positive indicate females. The DFA indicated that the tagged nestlings were 14 males and 11 females. The age of the birds at tagging was estimated using the length of the central rectrice. We used an average of 4.4 mm/day in our calculation, based on six nestlings that were measured twice with an interval of ca. 3.5 wk, (range 3.0–5.4 mm). Ellis (1979) found that rectrice growth averaged 4.7 mm/day ($n$ = 3, range 4.3–5.4), after emerging at about 20 d (estimated from Fig. 2 in Ellis 1979). We estimated the age of the birds at tagging as 20 d + the length of rectrice in mm/(4.4 mm/d). Accordingly, the age at dispersal was the estimated age at tagging plus the number of days elapsed until dispersal.

The birds were banded with aluminum rings and fitted with a satellite transmitter using the procedure described by Buehler et al. (1995), using Teflon ribbon harnesses. We used a loose fit to avoid wear on the skin during growth. The Teflon ribbon ends were secured across the upper part of the sternum with cotton thread, intended to degrade over time, so that the transmitter would eventually fall off. Eleven transmitters were Argos/GPS 70-g solar-powered, 11 were LC4 GPS 105-g battery-powered, and three were PPT 100 Argos weighing 100 g (Microwave Telemetry, Inc., Columbia, MD U.S.A.). All PTTs weighed 1.5–3% of the total body mass of a fully grown nestling.

The satellite tags of the PTT 100 type had a duty cycle of 6 hr on, 48 hr off, whereas the LC4 transmitters took one GPS location at 1200 H each day. The GPS/Argos transmitters were programmed to various schedules, varying from one location per hour to one every third hour during the summer months (May–July), to once a day during the darkest period of the year between 15 November to 15 February.

**Preliminary and Permanent Dispersal.** Argos classifies the signals received into different quality classes, mainly depending on the numbers of messages received during a satellite pass. Their estimation errors: LC3 < 250 m, LC2 250–500 m, LC1 500–1500 m, LC0 > 1500 m (CLS 2015). In addition, two classes with no precision estimates are provided; LCA, LCB, and LCZ class locations are rejected as invalid.

To draw the migration maps and to depict spatial distribution at different times of the year, the first position of each day was selected. For mapping purposes, some Doppler positions (the one of best quality) of the Argos satellites were used on dates where GPS positions were missing, and always in the case of PTT transmitters, which did not have GPS positioning. Locations of quality B and Z were not used. Only one position per day (the first one of each day of the highest quality) was used to draw the

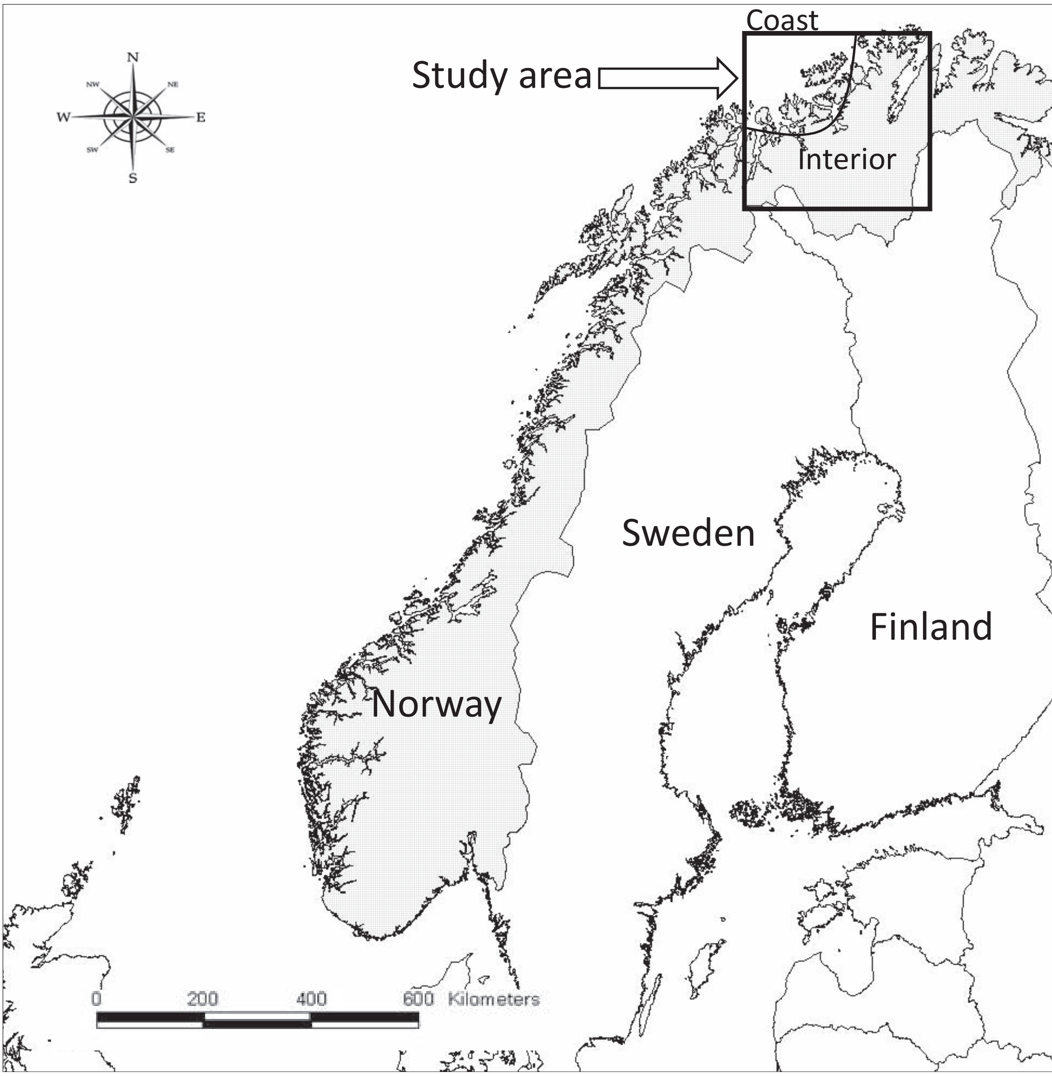


Figure 1. Golden Eagle study area in Finnmark, northern Norway, 69–71° N, 22.5–26° E, where 25 juvenile eagles were marked with satellite transmitters.

migration maps (for GPS positions: always the first). A visual inspection of the results led to the exclusion of some data points of classes LC0 and LCA that were obviously erroneous. A SAS algorithm developed by D.C. Douglas, U.S. Geological Survey, AK, (http://alaska.usgs.gov/science/biology/spatial/douglas.html) was rewritten into the SPSS command language to calculate distance between positions. Positions were subsequently imported into the SPSS v. 21.0 statistical program (SPSS Inc., Chicago, IL U.S.A.) for statistical analyses and graphs. Because the average nearest neighbor distance between 51 territories in western Finnmark was 12 km (median = 10 km, SD = 5 km; T. Nygård unpubl. data), we chose 10 km as an indicator distance for juvenile dispersal. We defined a preliminary excursion as a movement more than 10 km away from the nest site, but with a subsequent return closer than 5 km from the nest. We defined the date of permanent dispersal as the mean date between last date present <10 km from the nest and the first date >10 km away, with no subsequent return that season.

**Rates of Movement.** The rate of large-scale movements, "average speed" was calculated as the distance

Table 1. Duration of transmission from all the tagged young Golden Eagle nestlings in Finnmark, northern Norway 2002–2011, by year of tagging and transmitter type. Values in parentheses are based on sightings of live birds with defunct transmitters.

| Bird No. | Year of Tagging | Area of Tagging | Transmission Days | Transmission Years | Transmitter Type |
|---|---|---|---|---|---|
| 36364[a] | 2002 | Interior | 358(2353) | 0.98(6.44) | Argos/GPS 70 g |
| 36365 | 2002 | Interior | 96 | 0.26 | Argos/GPS 70 g |
| 41883 | 2003 | Interior | 420 | 1.15 | Argos/GPS 70 g |
| 41884 | 2003 | Interior | 1805 | 4.94 | Argos/GPS 70 g |
| 52453 | 2004 | Interior | 312 | 0.85 | Argos/GPS 70 g |
| 52456 | 2004 | Interior | 329 | 0.90 | Argos/GPS 70 g |
| 52457 | 2004 | Interior | 703 | 1.92 | Argos/GPS 70 g |
| 57357 | 2005 | Interior | 480 | 1.31 | Argos/GPS LC4 105 g |
| 57358 | 2005 | Interior | 138 | 0.38 | Argos/GPS LC4 105 g |
| 58970 | 2005 | Interior | 2324 | 6.36 | Argos/GPS 70 g |
| 58971 | 2005 | Interior | 56 | 0.15 | Argos PTT 100 95 g |
| 58972[a] | 2005 | Interior | 413(2425) | 1.13(6.64) | Argos PTT 100 95 g |
| 67120 | 2007 | Coast | 229 | 0.63 | Argos/GPS LC4 105 g |
| 67121 | 2007 | Coast | 160 | 0.44 | Argos/GPS LC4 105 g |
| 83228 | 2008 | Coast | 368 | 1.01 | Argos/GPS LC4 105 g |
| 83229 | 2008 | Coast | 221 | 0.61 | Argos/GPS LC4 105 g |
| 83230 | 2008 | Coast | 140 | 0.38 | Argos/GPS LC4 105 g |
| 95328 | 2009 | Coast | 19 | 0.05 | Argos/GPS LC4 105 g |
| 95329 | 2011 | Coast | 232 | 0.64 | Argos/GPS LC4 105 g |
| 152453 | 2006 | Interior | 120 | 0.33 | Argos/GPS 70 g |
| 152456 | 2006 | Interior | 2192 | 6.00 | Argos/GPS 70 g |
| 152457 | 2006 | Interior | 48 | 0.13 | Argos/GPS 70 g |
| 158971 | 2008 | Interior | 214 | 0.59 | Argos PTT 100 95 g |
| 183228 | 2011 | Coast | 149 | 0.41 | Argos/GPS LC4 105 g |
| 183229 | 2011 | Coast | 198 | 0.54 | Argos/GPS LC4 105 g |
| Mean | | | 629 | 1.72 | |

[a] Resighted alive.

moved between two consecutive points (the first GPS point each day), divided by the elapsed time (in fractions of a 24-hr period), expressed as km/d. The overall movement rate of subgroups of birds (by sex, or per month) per time unit was calculated as the mean of individual means. This measure is unrelated to instantaneous speed or flight velocity, but is a measure used to indicate the average rate at which birds move through the landscape at different times of the year. To obtain more detailed information on actual speed during a shorter time period, we used only the GPS positions, and calculated the speed as the distance moved between two consecutive GPS positions divided by the time elapsed. We excluded consecutive positions <1 km apart, to avoid those positions where the birds were at rest, but the dataset includes all seasons. We also analyzed the speed data directly measured by the transmitter sensors themselves.

**Survival.** The Kaplan–Meier method was used to model the survival (Kaplan and Meier 1958) from day of tagging. We recorded a terminal event if the bird was found dead, or if the signals indicated death even though the carcass was not retrieved (when the signals came from the same position over a length of time in an inaccessible location). When a signal was lost with no indication of death (i.e., no point cluster at last position), the bird was censored from the survival analysis, as in transmitter failure.

**Data Analysis.** To test differences between sexes concerning dates of dispersal, age at dispersal, and distance of travel, we used the Mann–Whitney *U*-test (Zar 1984). We used ANOVA to test for differences in dispersal dates between sexes for birds hatched in different locations. Data are reported as mean or medians ± SD, except where SE is used in the Kaplan–Meier results.

## RESULTS

Altogether, the performance and longevity of the transmitters varied greatly between birds, from 19 d

Table 2. Number of positions recorded and efficiency of the different transmitter types.

| Transmitter Type | No. of Transmitters | Measurement | Mean | Median | Min | Max | % of Days with GPS Position Received |
|---|---|---|---|---|---|---|---|
| Argos/GPS 70 g | 11 | No. of GPS positions | 1500 | 161 | 4 | 12586 | |
| | | No. of days | 781 | 346 | 48 | 2302 | 75.3 |
| LC4 105 g | 11 | No. of GPS positions | 184 | 193 | 7 | 352 | |
| | | No. of days | 211 | 198 | 19 | 480 | 98.7 |
| Argos PTT 95 g | 3 | No. of Argos positions | 795 | 577 | 255 | 1553 | |
| | | No. of days | 227 | 214 | 56 | 413 | 0 |

to more than 6 yr (Table 1). The number of positions and throughput rates also varied relative to transmitter type (Table 2). The bulk of the data derived from solar-powered Argos/GPS transmitters.

**Preliminary and Permanent Dispersal.** Dispersal occurred as a two-stage process for 13 eagles. (Table 3). The mean straight-line distance from the nest during these excursions was 45 km (median = 15 km, range = 10–167 km). Measured as continuous distance, using one (the first) position per day and summing these distances over all days until a return to the nest area, the total distance was of mean length 117 km (median = 56 km, range = 21–425 km). In addition, four birds made a second preliminary dispersal of mean straight-line distance 74 km (median = 18 km, range = 12–246 km), with mean continuous distance of 214 km (median 56 km, range = 32–772 km). Two birds made a third excursion before permanent dispersal, of straight-line distance 27 and 29 km from nest (total travelled distance of 73 and 84 km).

The median date for pre-dispersal excursions was 13 September (range 4 September–11 November, $n = 13$; Table 3). Nine birds never took a preliminary excursion >10 km, but departed permanently for their first winter migration. One male and one female probably died shortly after fledging close to the nest, but neither the birds nor their transmitters were found, so transmitter failure could not be ruled out. Remains of one male and its transmitter were found close to its natal nest. Two birds (a male and a female) performed preliminary excursions (>10 km), but both returned to their natal areas and died there. The male was found dead under a power line, and the female was found dead near a reindeer carcass, possibly killed in an intraspecific fight.

The median date of permanent dispersal was 21 October (range = 15 September– 7 January, $n = 21$; Table 3). Females ($n = 10$) tended to disperse permanently slightly earlier than males ($n = 11$); median dates were 17 October (females) vs. 26 October (males), but these did not differ significantly (Mann–Whitney $U$, $Z = -0.74$, $P = 0.46$, two-tailed; Table 3). Permanently dispersing juveniles hatched on the coastal islands ($n = 7$) dispersed later (median = 24 November, SD = 33 d) than those tagged in the interior ($n = 14$; median = 14 October, SD = 12 d; Mann–Whitney $U$, $Z = -3.21$, $P = 0.001$). An ANOVA

Table 3. Dispersal dates and maximum distance from natal site during winter for juvenile Golden Eagles from Finnmark, northern Norway, during their first year of life.

| Dispersal | Subgroup | Median Date (Min–Max) | Maximum Straight-line Distance (km) Median (Min–Max) | $n$ |
|---|---|---|---|---|
| Preliminary dispersal | All | 13 Sep (4 Sep–11 Nov) | 15 (10–167) | 13 |
| Permanent dispersal | Coastal | 24 Nov (26 Oct–7 Jan) | 155 (18–155) | 7 |
| | Inland | 14 Oct (15 Sep–1 Nov) | 460 (14–1484) | 14 |
| | Males | 26 Oct (7 Oct–7 Jan) | 270 (14–1484) | 11 |
| | Females | 17 Oct (15 Sep–3 Jan) | 383 (29–1053) | 10 |
| | All | 21 Oct (15 Sep–7 Jan) | 285 (14–1484) | 21 |


Figure 2. Seasonal distribution of juvenile Golden Eagles satellite-tagged in Finnmark 2002–2011 during (a) July–September, (b) October–December, (c) January–March, and (d) April–June. One position per day per bird is shown.

using sex and location (inner/outer) as fixed factors was significant for location ($P$ = 0.001), but not for sex, nor for the interaction of sex and location. The estimated median age at preliminary dispersal was 141 d (range = 133–205, $n$ = 8) for males and 133 d (range = 119–162, $n$ = 5) for females. The estimated median age at permanent dispersal was 177 d (range 151–253, $n$ = 11) for males, and 165 d (range

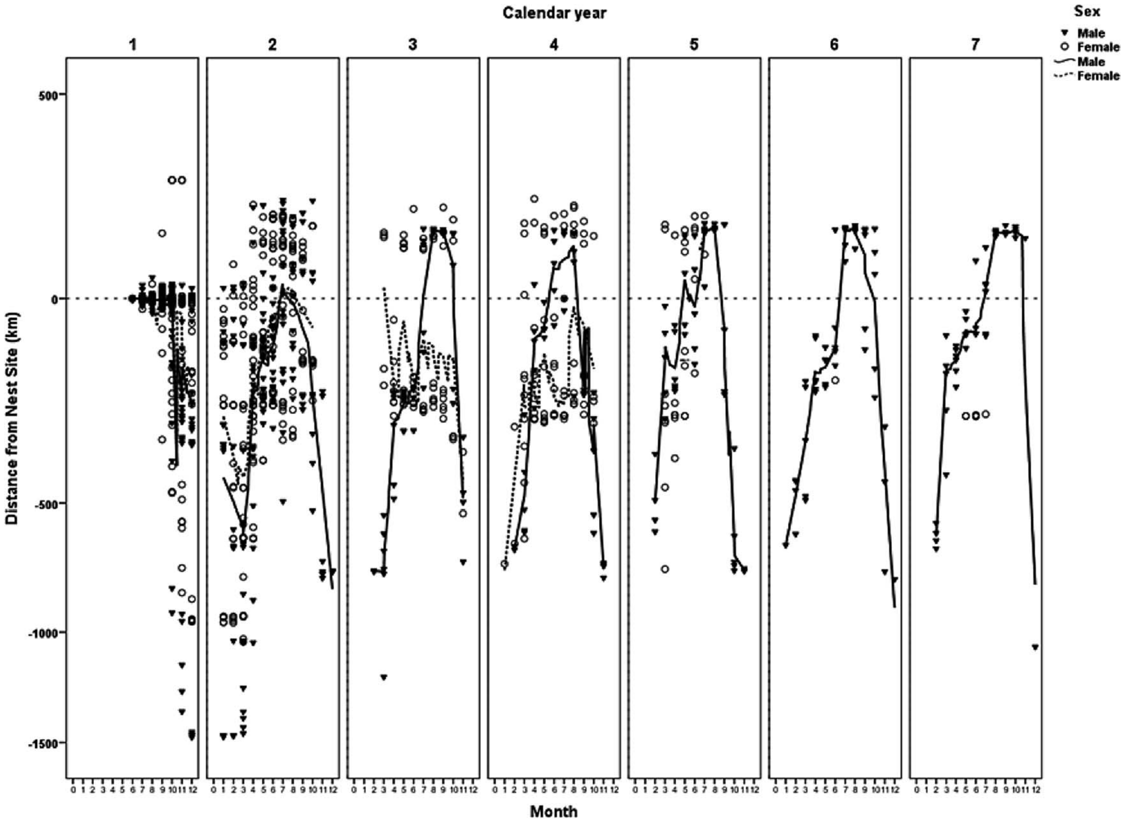


Figure 3. Distance from the natal nests of male and female Golden Eagles hatched in Finnmark, northern Norway, by calendar year and month. The average distance per bird by month and week are shown by symbols and overall averages by the trend lines (solid line = males, dotted = females). Negative values indicate that the position is south of a parallel drawn through the natal nest-site, positive values indicate north. Note: values denote the horizontal distance from the nest, not the distance from this parallel.

140–248, $n = 10$) for females. This means that they spent ca. 100 d in their natal areas after fledging before permanently dispersing, assuming a fledging age of 10 wk (Watson 2010).

**Dispersal Patterns.** After permanent dispersal, the general direction of movement was southerly, mainly south through Sweden, although birds visited all neighboring countries in the north including Sweden, Finland, and Russia. The overall pattern was for juvenile Golden Eagles to move out of their natal areas during autumn to winter in a more southerly location, with a return during spring (Fig. 2). This pattern was repeated in the following years during the subadult stage (Fig. 3). For those birds that did disperse, the median maximum distance from the natal sites during their first year of life was ca. 300 km (Table 3), generally to the south. When we excluded those birds whose transmitters did not yield signals into their second calendar year, the median maximum distance from the nest during their first year of life was 357 km ($n = 7$) for males, and 458 km for females ($n = 7$; Mann–Whitney $U$, $Z = 0.064$, $P = 0.949$). There were large variations; one male moved all the way down to the southernmost tip of Sweden (56° N), 1500 km, in its first winter. By contrast, one bird probably stayed in Finnmark during winter. Often the spring movement resulted in an "overshoot," i.e., travel to a position north of their natal area (Fig. 3).

On the return migration, the median nearest distance from the nest for males ($n = 12$ bird-years) was 10 km, and 88 km for females ($n = 14$ bird-years; Mann–Whitney $U$, $Z = -2.77$, $P = 0.005$). Notably, one male visited a spot only 100 m from its natal nest in its second calendar year, and another male was 2.6 km away in its fourth calendar year.

**Wintering Areas.** The eagles generally moved southward into central Sweden and even into Finland in the autumn, while a few birds moved into northwestern Russia and the northern coast of Norway (Fig. 2). Some birds, mainly those hatched in the coastal areas, stayed on the northern Norwegian coast for a prolonged time compared to the inland birds. One male used the same wintering area in central Sweden during five consecutive winters (male # 58970 tagged in 2005 in Karasjok municipality in Finnmark; Fig. 4). In its first winter, it wintered in Finland, then wandered into Russia during summer before ending up in central Sweden during late autumn. From 2006 through the winter of 2010–2011, he always used the same wintering area in the vicinity of the town of Östersund, Sweden.

**Rates of Movement.** Rates of movement were higher when the birds moved between their summering and wintering areas compared to when they were in their natal areas and in their wintering areas during their first year of life (Fig. 5). The average rates of movement were around 15 km/d (mean = 14.6, SD = 11.9) during the migration in their first autumn (November–December), and more than 20 km/d (mean = 21.3, SD = 20.4) during their first return migration during spring (March–May). Movement rates in their first wintering areas were generally less than 10 km/d (mean = 8.7, SD = 10.1). Late in their second summer, the movement rates again increased to more than 20 km/d (mean = 21.2, SD = 10.7). Movement data from their second autumn were scanty, as the number of birds from which we obtained data had declined from the initial 25 to five by October in their second year. There were small but insignificant differences in the rate of movement between sexes in most months, except in July in their second summer, when males moved more than females (Mann–Whitney $U$, $Z = -1.96$, $P = 0.05$). In January, there was a tendency for females to move more than males (Mann–Whitney $U$, $Z = -1.73$, $P = 0.083$). There may have been an overall tendency for males to move about more during their second summer than females (Fig. 5).

Virtually no movements were recorded during midnight hours (2200–0200 H), whereas the highest rates of movement were recorded during the day (0800–1600 H), with a peak 1200–1400 H (Fig. 6). This pattern was similar for all seasons.

The satellite transmitters also delivered data on instantaneous speed (speed as measured by the transmitter itself; Fig. 7). Speeds <3 km/hr were omitted to ensure that real movements were measured. The mean flight speed was 36 km/hr (max = 100 SD = 0.48, $n$ = 1344 readings). Transmitters of type LC4 did not deliver speed data. Transmitters from only nine birds gave good data on instantaneous speed. The distribution of speeds was normally distributed.

**Mortality and Survival.** In seven cases, we recorded a terminal event (carcass or remains found). In three additional cases, the signals indicated death, but the carcasses were not retrieved (Table 4). Death was also assumed in two more cases, when the transmitters were found under circumstances indicating illegal killing (functioning transmitters found, harnesses cut off with sharp object).

The overall survival during the first year of life was estimated at 0.58 ± 0.11, and 0.50 ± 0.12 were estimated to still be alive through the second year. For older year-classes, the small number of birds did not permit any reliable survival estimates.

First year survival differed notably between eagles from the coastal islands and those from the interior (Table 5). Only one of the birds from the outer coast ($n$ = 9) was proven to have survived through the first year, but only six were found dead. The fates of the remaining birds were unknown. Thus, estimated first year survival rate was 0.25 ± 0.15. The estimated survival rate for the birds from the interior ($n$ = 16) was 0.78 ± 0.11 during their first year of life and 0.67 ± 0.13 SE by the end of the second. Only four of the inland birds were actually found dead. Of the 11 birds where the cause of death was determined with reasonable certainty, three (27%) were due to human persecution, three (27%) were natural deaths away from the nest (possibly due to starvation), three (27%) were found dead near the nest (possibly due to starvation), one (9%) was found under a power line (electrocution), and one (9%) died probably as a result of a fight (Table 4). In addition, two transmitters indicated mortality, but from remote and inaccessible areas (Russia and Finland). Signals from ten birds were lost without any indication of cause. No tagged eagles were documented as breeders, but one female in her seventh calendar year was a suspected breeder based on the pattern of her locations; however, this was not confirmed in the field due to remoteness.

## DISCUSSION

**Transmission Efficiency.** The finding that battery-powered GPS transmitters (LC4s) had the highest transmission success clearly illustrated the limitation of solar-powered transmitters in areas of high latitude

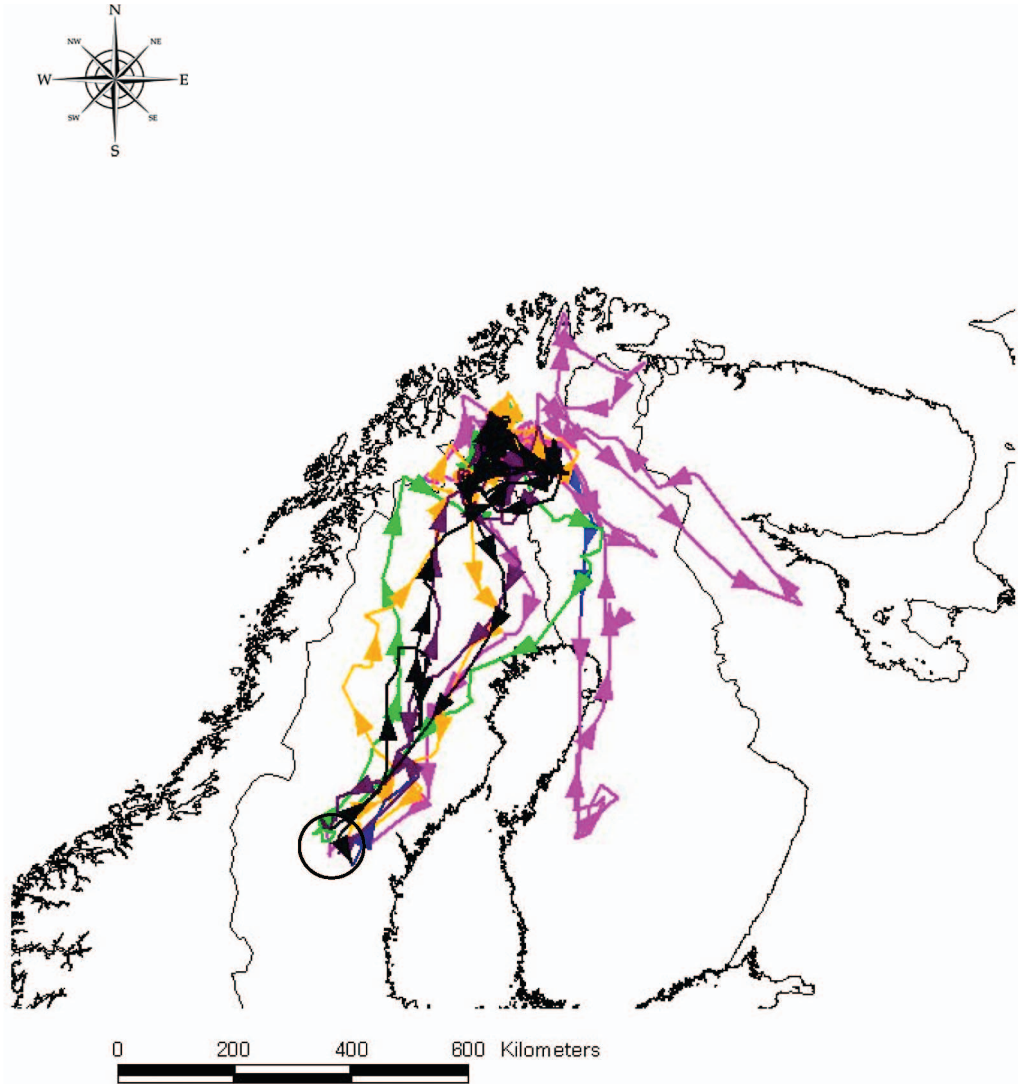


Figure 4. Use of same wintering area in central Sweden during five consecutive winters by male Golden Eagle 58970, tagged in 2005 in Finnmark as a nestling. In its first year of life, it spent the winter in Finland, and thereafter spent five winters in the vicinity of the town of Östersund in central Sweden. Different colors indicate migration routes in different years.

during winter (Table 2), as might be expected. Battery-powered transmitters are able to deliver accurate positions in the dark season of high latitudes, data that would be difficult to obtain otherwise. However, they have the limitation of producing only one location per day, and only three years of expected battery life. The proportion of days when the Argos/GPS solar-powered transmitters were able to transmit a GPS signal was highest during summer as expected, due to the long daylength in the high north. Some birds, however, migrated far enough south in winter to receive a minimal charge for their transmitters during the winter months. It must be added, however, that transmission rates of solar-powered transmitters have improved during recent years due to more efficient solar panels (Paul Howey, MTI, pers. comm.). For work in the high north, the sunlight condition is an important factor to consider when choosing transmitter type. The battery-driven 95-g Argos PTTs'

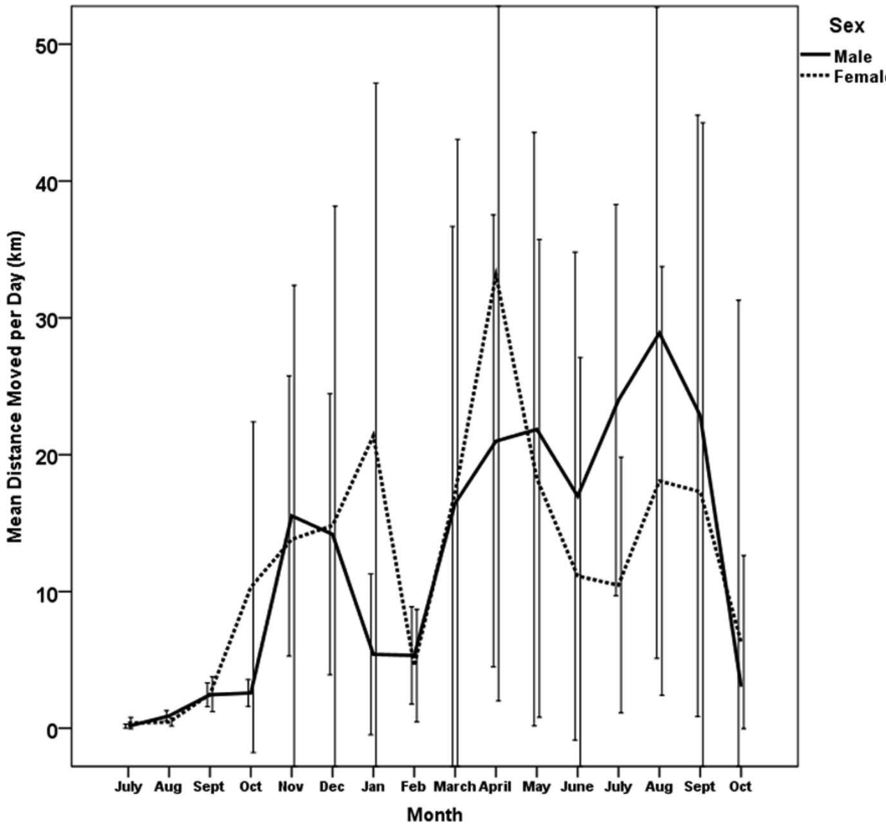


Figure 5. Mean rate of movement of Golden Eagles by month and sex as km/d per bird through their first and second calendar years. The sample size decreased from 25 in July in the first year to five in October the second year. The rate of movement was calculated as the distance between two consecutive positions at least one day apart, divided by the time elapsed. Monthly averages per bird were used to calculate overall averages. Solid line = males, broken line = females, error bars = 95% CI.

transmission rates dropped during February and March, which may be due to the relatively low ambient temperatures of this time of year that would lower the charge of the batteries. However, we note that the longevity and throughput rates in Tables 1 and 2 were to a large degree influenced by the fates of the birds, not just the quality of the transmitters.

**Dispersal Dates.** The early onset of winter at the high latitudes of Finnmark, involving bad weather and snowfall, may jeopardize the hunting success of young inexperienced eagles and their ability to provide food for themselves after their parents have ceased feeding them. Being capable of capturing their own prey during the very short daylight hours of winter probably requires learned skills. The preliminary dispersal patterns shown by most of the juvenile eagles that later dispersed permanently may be interpreted as a training and maturing experience. Perhaps they soon learn that capturing prey on their own is difficult, and therefore return to the area where food was once provided for them. When this does not happen, they presumably are forced to leave home permanently. This corresponds with the observations of juvenile Golden Eagles post-fledging behavior in Scotland (Walker 1987).

The permanent dispersal (around 21 October) after ca. 100 d post-fledging coincides with the typical time of the arrival of snow in Finnmark. This dispersal is later than was recorded in Alaska, where the dispersal date of 28 satellite-tagged juveniles was between 15 September and 5 October (McIntyre et al. 2008). This may be due to climatic reasons. In North Dakota, 28 radio-tagged juvenile Golden Eagles stayed within 5 km for about 100 d post-fledging, but dispersed up

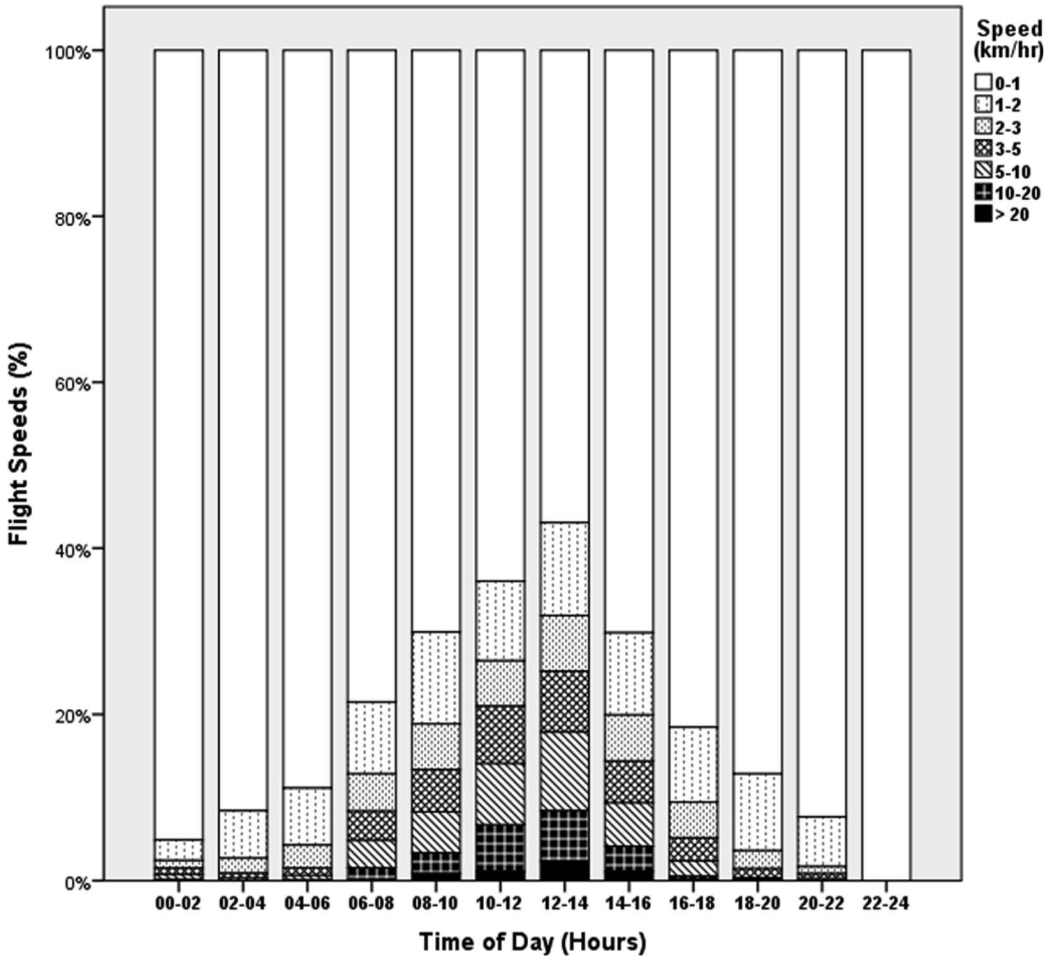


Figure 6. Flight speeds at different times of the day of satellite-tagged juvenile Golden Eagles, as calculated from position data delivered by the GPS transmitters and time elapsed between positions. Average values of all tagged individuals in all seasons.

to 15 km during the next 40 d (O'Toole et al. 1999). Our results were similar, except that the Finnmark birds took on very long flights once permanently dispersed. In the Negev Desert in Israel, two radio-tagged juveniles stayed for about 120 d within 4–5 km of the nest (Bahat 1992). Dispersal dates of 21 satellite-tagged juveniles in Scotland varied greatly, with dates of permanent dispersal ranging from August until March of the following year (Watson 2010). Presumably the environmental conditions in Scotland are favorable enough to permit some birds to stay, with little snow, and an abundance of rabbits, grouse, deer, and sheep for food.

The adult Golden Eagles in temperate latitudes are believed to be sedentary all year (Watson 2010). Little is known about the movements of adults in the northern boreal forest in Europe, although a recent study of satellite-tagged adults in northern Sweden has shown that even some adults may leave their territories, especially after failed breeding (Moss et al. 2014). Five of the juveniles that were tagged on the coast of Finnmark were found dead at varying distances in the same region within 7 mo after tagging. Whether they would have dispersed later and gone south if they had survived is unknown. So far, we have no proven wintering of juveniles in Finnmark for a full winter during their first year of life. However, data strongly suggest that at least one young female tagged in 2003 did so. The transmitter went silent by 1 November when she was still in

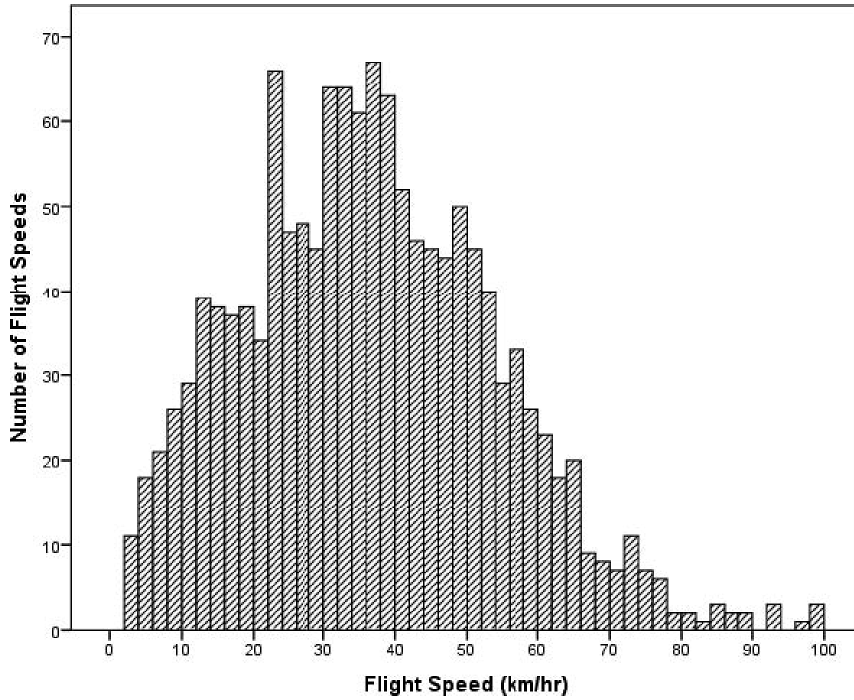


Figure 7. Flight speeds recorded for juvenile Golden Eagles in km/hr, as determined by the sensors in the satellite transmitters. Speeds less than 3 km/hr were omitted.

Finnmark, and reappeared in Finnmark again on 23 February the following year. We received signals from her for almost 5 yr, and she was never recorded south of 69° N.

**Dispersal Patterns and Wintering Areas.** Throughout northern and central Alaska, and in northern Canada, the entire population of Golden Eagles migrates south for the winter (Watson 2010), and the same is known from the populations breeding in Siberia in the northern taiga zone (Dementiev and Gladkov 1966). Our data indicate that migration to the south, especially into southern and central Sweden during winter, is the main pattern of juvenile Golden Eagles hatched in Finnmark. However, the juveniles we tagged in the northernmost coastal areas of Finnmark showed different behavior, with a tendency to stay well into the winter. This may be due to better feeding opportunities during winter compared to inland conditions, as seabirds are available, and hares (*Lepus timidus*) and Willow Ptarmigan (*Lagopus lagopus*) are abundant on the main islands due to the absence of foxes. The climate is also milder on the coast. Unfortunately, and surprisingly, they also had a high mortality during their first winter, so we have little information on the migratory behavior of these young birds. The majority of ringing of Golden Eagles in Norway has been done in the southern and central parts of Norway (Bakken et al. 2003); recoveries show that juvenile eagles move farther during their first years of life than older birds, with movements into Sweden (Fremming 1980) and Finland (Bakken et al. 2003). The pattern of ring recoveries is therefore consistent with that shown through satellite telemetry in our study. It is also consistent with Swedish ring recoveries, which show that most Golden Eagles ringed in northern Sweden migrate mainly to southern Sweden, but some move into southern Norway and southern Finland as well (Fransson and Petterson 2001). One might expect that Golden Eagles tagged in Finnmark would move in a more southeastern direction, as shown for birds ringed in Finland (Fremming 1980), as the Finnmark population and those breeding in northern Finland form a contiguous population. Although a few of the satellite-tagged birds in our study made excursions into Finland and even Russia, they did not progress further south into the

Table 4. Fates of Golden Eagles tagged with satellite transmitters as nestlings in Finnmark, northern Norway, 2002–2011. See Table 1 for longevity data and transmitter types.

| BIRD NO. | YEAR OF TAGGING | AREA OF TAGGING | FATE |
|---|---|---|---|
| 36364 | 2002 | Interior | Unknown; but observed on a carcass in Sweden in its seventh calendar year |
| 36365 | 2002 | Interior | Unknown; last signal from the Finnish side of Gulf of Bothnia in its first autumn |
| 41883 | 2003 | Interior | Unknown |
| 41884 | 2003 | Interior | Unknown |
| 52453 | 2004 | Interior | Probably dead; transmitter found in Swedish Lapland in its first winter with harness cut off |
| 52456 | 2004 | Interior | Probably dead; transmitter found in Swedish Lapland in its first winter with harness cut off |
| 52457 | 2004 | Interior | Remains and transmitter found in its second spring on the sewage dump in Gällivare, Swedish Lapland |
| 57357 | 2005 | Interior | Unknown; last signal from Finnish Lapland second autumn |
| 57358 | 2005 | Interior | Unknown; last signal from Pechenga, Russia, during first autumn, signals indicating death |
| 58970 | 2005 | Interior | Unknown; signal loss |
| 58971 | 2005 | Interior | Remains and transmitter found close to nest |
| 58972 | 2005 | Interior | Observed on carcass in south-central Sweden in February 2012 in its eighth calendar year |
| 67120 | 2007 | Coast | Found dead in a remote fjord in northern Norway |
| 67121 | 2007 | Coast | Found dead in Finnish Lapland |
| 83228 | 2008 | Coast | Unknown; last signal from Finnish Lapland |
| 83229 | 2008 | Coast | Found dead in a fjord in northern Norway |
| 83230 | 2008 | Coast | Unknown; last signal from Swedish Lapland |
| 95328 | 2009 | Coast | Probably dead close to nest |
| 95329 | 2011 | Coast | Unknown; signal loss |
| 152453 | 2006 | Interior | Unknown; signal loss |
| 152456 | 2006 | Interior | Unknown; signal loss |
| 152457 | 2006 | Interior | Probably dead, not far from nest |
| 158971 | 2008 | Interior | Last signals from Finnish Lapland, indicating death |
| 183228 | 2011 | Coast | Found dead under power line |
| 183229 | 2011 | Coast | Found dead at a reindeer carcass |

Baltic states and eastern Europe, as the birds tagged in Finland have.

Dispersal distance between the sexes did not differ during the first winter, although males showed a tendency to disperse later than females. In Alaska, no difference in departure dates was found regarding year, sex, or brood size in a migratory population of Golden Eagles from Denali National Park and

Table 5. Survival statistics of juvenile satellite-tagged Golden Eagles from Finnmark, northern Norway, based on Kaplan–Meier survival estimates.

| SUBGROUP | INTERVAL (YEARS OF LIFE) | NUMBER ENTERING INTERVAL | NUMBER WITHDRAWING | NUMBER OF TERMINAL EVENTS | PROPORTION SURVIVING AT END OF INTERVAL | S.E. |
|---|---|---|---|---|---|---|
| Overall | 0–1 | 25 | 7 | 9 | 0.58 | 0.11 |
| | 1–2 | 9 | 3 | 1 | 0.50 | 0.12 |
| Inland | 0–1 | 16 | 5 | 3 | 0.78 | 0.14 |
| | 1–2 | 8 | 2 | 1 | 0.67 | 0.14 |
| Coast | 0–1 | 9 | 2 | 6 | 0.25 | 0.15 |
| | 1–2 | 1 | 1 | 0 | 0.25 | 0.15 |

Preserve in Alaska (McIntyre and Collopy 2006). However, males migrated further south during their first autumn migration than females (McIntyre et al. 2008). In Spain, dispersing juvenile females tended to explore a larger area than males (Soutullo et al. 2006).

Finnmark has a very harsh winter climate; often the temperatures go down to −40°C in the interior, and the weather on the coast of the Barents Sea is often very stormy. It was therefore not surprising that most of the Finnmark birds left their natal areas and settled several degrees further south, where the winter climate is less fierce, and there is presumably more food available. The one male (#58972) that migrated all the way south to Skåne in southern Sweden came to an area that is normally snow-free during winter, and has a good population of prey species such as rabbits and pheasants, in addition to wintering ducks and geese. We believe that moving into such wildlife-rich areas for the winter has survival value for young, inexperienced Golden Eagles hatched in Finnmark. This means moving to partly wooded, partly farmed areas, where few breeding pairs of Golden Eagle are found (Svensson et al. 1999). This involves leapfrogging the taiga forest areas in northern Sweden where resident adult eagles may pose competition. A similar behavior was demonstrated for juvenile Golden Eagles from Alaska that leapfrogged over more sedentary populations in British Columbia and Alberta to spend the winter in a very wide range, from southwestern Canada to southeastern New Mexico ( McIntyre et al. 2008, McIntyre 2012). In contrast, satellite-tagged juveniles in Scotland stayed in the highlands after initial dispersal (Watson 2010). Perhaps the highlands are rich enough in food during winter to support both the adult breeding population and several cohorts of juveniles at the same time. The same seems to be the case in the Alps in central Europe (Haller 1994).

As all the solar-powered transmitters went silent during the darkest months of the winter, there were uncertainties regarding the birds' locations at that time, both regarding migration routes and maximum distance from their natal sites. The fact that some birds probably were killed by humans on their way south would also influence our interpretation of migration sites and maximum distances from natal sites, presumably biasing them low.

**Speed.** The readings provided by the GPS transmitters themselves indicated that the flight speed of the eagles can reach 100 km/hr, but most speeds ranged between 20 and 50 km/hr, with a peak at around 40 km/hr. Flap-gliding Golden Eagles studied by radar have a typical speed of ca. 54 km/hr (corrected for wind speed), with steeper glides at over 80 km/h (Bruderer and Boldt 2001). Juvenile Golden Eagles from Alaska moved at a speed of 16–73 km/hr during migration (McIntyre et al. 2008). Our estimated spring return speeds of 20–30 km/d) would bring the birds from central Sweden up to their natal areas in Finnmark, a distance of approximately 1000 km, in about a month. This seems reasonable, as spring arrives at the high latitudes in Finnmark considerably later than in central Sweden. The male we followed that wintered in the same area for consecutive seasons (Fig. 4), regularly took ca. 14 d to move from its wintering area to its summer quarters, a distance of >400 km, an average speed of ca 30 km/d. Three juvenile Golden Eagles in Spain averaged speeds (as measured by distance between locations/time elapsed) of 2–6 km/hr, which was similar to that of the birds from Finnmark. This, of course, was not actual speed through the air, but the rate at which the bird progressed through the terrain, including stops. The birds in Spain seemed to obtain maximum rates of movement a little later in the day than Finnmark birds, between 1200 and 1800 H, whereas we recorded maximum rates between 1100 and 1500 H, coinciding with the time when the sun is in its highest position and when the ground starts to heat up, creating favorable thermal conditions (thermal lift).

**Mortality and Survival.** The finding of two transmitters cut from the body of eagles in northern Sweden indicated that some illegal killing occurred. Three birds that were tagged at different locations in Finnmark in 2004 all headed south during autumn, but their signals were lost during the following winter. In spring 2005, we received signals from them in Swedish Lapland, and two of them became stationary during May. We retrieved both transmitters with their harnesses obviously cut with a sharp object. The third transmitter became stationary the following spring, and was found at the municipal garbage dump in Gällivare, a town in Swedish Lapland, with feathers scattered around it, bearing signs of having been chewed by a fox. We believe that the carcass was dumped there by humans, as similar incidents from this area were known. Of 225 Golden Eagle specimens where the cause of death was determined, 15 (7%) were attributed to illegal killing (Hjernquist 2011); the most important cause of death was collision with train or vehicle (49%).

One may, however, suspect that illegal killing is underrepresented, as carcasses may be destroyed or hidden to remove evidence of crime.

In two cases, birds wearing transmitters were identified at feeding stations in Sweden, both in their sixth year of life, without emitting signals. On one, the antenna was missing. These sightings illustrated that birds may be alive even when no signals are received.

Naïve and hungry birds may be easy victims to human persecution, as they often feed on carrion if live game is difficult for them to obtain (Watson 2010). Several birds (in addition to those whose transmitters were cut off) transmitted their last signal in Swedish Lapland, but their fates were unknown. In Sweden, an extensive program of making poison-free carcasses available for eagles in winter has been carried out since 1972 by "ÔRN-72" (a nongovernmental organization of eagle enthusiasts; Ahlgren 2004). The number of feeding stations for eagles in Sweden under this program has declined from 16 to 7 during 2003–2014 (Hedfeldt 2004, 2014). These feeding stations may have contributed to the survival of our tagged eagles, but it would only be speculative to estimate their importance. Observations from blinds near these carcasses have produced many sightings of ringed and tagged birds. This clearly indicates that survival estimates, especially of older age-classes, based only on telemetry data, should be considered with caution, as they may overestimate mortality, due to battery exhaustion or transmitter malfunction. The first year survival in our study (0.58 overall) seemed low, but McIntyre et al. (2006) estimated an even lower first-year survival in a similar study using satellite transmitters on Alaskan Golden Eagles. Their 1997 cohort had a survival of only 0.34 during the first 11 mo of life, and only 0.19 of the 1999 cohort. From a sample of ringed birds in the Rocky Mountains, U.S.A., it was estimated that 50% were dead by 2.5 yr of age, and 75% by the age of 5 yr (Harmata 2002), but the author did not provide any estimate of first-year survival.

The relatively high mortality of the juveniles hatched on the Finnmark coast that apparently tried to overwinter there parallels that in Alaska, where those birds who tried to winter there all died within 2 mo after completing their autumn migration (McIntyre et al. 2008). The high preadult mortality in our study may be compensated by high adult survival. Such data do not exist for any Fennoscandian population, but data from Germany, Scotland, and California all suggest annual adult survival rates between 0.91 and 0.98 (Watson 2010). However, the low survival rates of juveniles may be a limiting factor to the sustainability of this northern population of Golden Eagles, and the indications of illegal killings is an important concern. It also highlights that migrating species are vulnerable to negative influences along their migratory routes, which may include many different countries. Additionally, when comparing mortality sources and wintering areas between ring-tagged and satellite-tagged juvenile Golden Eagles from Alaska, McIntyre (2012) found differences that could be attributed to an effect of the extra burden of the transmitter (more deaths due to starvation and wintering ranges farther north). A study involving satellite-tagged adult Golden Eagles in Sweden showed indications of possible adverse effects of transmitters (high nesting failure; Moss et al. 2014). Our own data do not allow assessment of potential effects, due to few ring recoveries and lack of necropsies.

High mortality rates of Golden Eagles were documented in wind farm areas in California (Smallwood and Thelander 2008), and researchers have emphasized the risk of population declines of long-lived soaring raptors as a result of such added mortality (Hunt 2000, Carrete et al. 2009). Many governments, including those of Norway and Sweden, now encourage large-scale wind-power developments to reduce carbon emissions from energy production. In Norway, most existing and planned developments are in coastal areas, and such developments have been shown to kill relatively large numbers of White-tailed Eagles (*Haliaeetus albicilla*; Dahl et al. 2012). In Sweden, the wind-power industry is now moving inland, utilizing the wind resources of the mountains and hills of the interior (Energimyndigheten 2013), within the breeding range of Golden Eagles. We found that the migration routes of juvenile and subadult Golden Eagles from Finnmark cross these areas on both their southward and northward trips, and thus they may be exposed to increased risk of collision during migration. Golden Eagles and other soaring raptors use the thermal and orographic lifts generated by hills and ridges (Lanzone et al. 2012), which also are preferred development sites for wind farms in the interior, and this will increase the mortality risk of such species at such sites (Barrios and Rodriguez 2004). This factor, in addition to the high natural mortality and illegal killings, is of conservation concern for the Golden Eagles in Norway, especially given the very poor reproductive rate of the species in northern Fennoscandia recently (Ahlgren 2013, Knoff 2013).

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