



Movements of juvenile Bonelli's Eagles *Aquila fasciata* during dispersal

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Capsule Juvenile non-breeding males and females explored surrounding areas, returned to breeding areas, and settled in temporary settlement areas.

Aims To describe movement patterns of juvenile Bonelli's Eagles during the transient phase of dispersal.

Methods Radiotelemetry data from 16 individuals were studied.

Results Six main temporary settlement areas were located. No sex differences were found in the time to first departure from natal areas, time to the first temporary settlement, or time of the first return to natal areas. Juvenile eagles did not settle in temporary settlement areas until they were, on average, 245 days old. In general, males and females did not differ in their movement patterns during the early part of the dispersal period. However, after approximately 500 days males spent 60.8% of their time exploring surrounding areas, probably with the aim of searching for vacant territories or mates, whereas females of the same age devoted 26.7% of their time to exploration.

Conclusion Movements and use of sites during the transient phase of dispersal are complex. They have important implications for the conservation of this endangered species.

MANY VERTEBRATES ARE CHARACTERIZED BY HAVING DEFERRED MATURATION RESULTING IN A RELATIVELY LONG NON-REPRODUCTIVE STAGE EARLY IN THEIR LIFE. THERE HAVE BEEN FEW STUDIES OF MOVEMENT PATTERNS DURING THIS PERIOD (FERRER 1993A, WALLS ET AL. 2005). THE TRANSIENT PHASE OF DISPERSAL IS THE PERIOD WHEN INDIVIDUALS SEARCH FOR OR MOVE TO A NEW SITE FROM THEIR NATAL SITE (CLOBERT ET AL. 2001, WIENS 2001). LITTLE EMPIRICAL INFORMATION EXISTS ABOUT THIS PERIOD FOR MOST ANIMAL SPECIES (MARSH & JONES 1988, WENNERGREN ET AL. 1995, ZOLLNER & LIMA 1999, MCDONALD & JOHNSON 2001). HOWEVER, SUCH INFORMATION IS CRUCIAL FOR UNDERSTANDING THE PROXIMATE MECHANISMS INVOLVED IN THE EVOLUTION OF NATAL DISPERSAL (GREENWOOD 1980, JOHNSON & GAINES 1990, PUSEY & WOLF 1996). INFERENCES ABOUT MOVEMENTS BASED ON SINGLE-LOCATION STUDIES ARE NECESSARILY LIMITED (BENNETTS ET AL. 2001). ONLY METHODS SUCH AS RADIOTELEMETRY, WHICH PROVIDE KNOWLEDGE OF THE STATUS OF AN ANIMAL AT ANY GIVEN TIME, ARE ADEQUATE FOR DESCRIBING BEHAVIOUR EXHIBITED BY INDIVIDUALS DURING THIS PHASE OF DISPERSAL.

BONELLI'S EAGLES *AQUILA FASCIATA* ARE LONG-LIVED WITH A

MAXIMUM LIFE SPAN OF 20 YEARS IN CAPTIVITY (NEWTON 1979). JUVENILE BONELLI'S EAGLES HAVE BEEN STUDIED DURING THE POST-FLEDGING DEPENDENCE PERIOD BY MORVAN & DOBCHIES (1990), REAL ET AL. (1998), MINGUEZ ET AL. (2001) AND BALBONTÍN & FERRER (2005). CADAHÍA ET AL. (2005) PROVIDED INFORMATION ON THE MOVEMENTS OF SEVEN SATELLITE-TRACKED BONELLI'S EAGLES IN EASTERN SPAIN DURING THEIR FIRST WINTER. HOWEVER, THE MOVEMENTS OF JUVENILE BONELLI'S EAGLES DURING THE FULL DISPERSAL PERIOD HAVE NOT BEEN DESCRIBED.

STUDIES OF THE MOVEMENT PATTERNS OF BIRDS OF PREY, SUCH AS COMMON BUZZARDS *BUTEO BUTEO*, HAVE SHOWN THAT NOT ALL BIRDS LEAVE THEIR NATAL AREAS DURING THEIR FIRST YEAR OF LIFE AND THE BIRDS THAT DO LEAVE FREQUENTLY RETURN WHILE THEY ARE STILL IMMATURE (WALLS & KENWARD 1995). IN THIS SPECIES, AN INCREASE IN DISTANCE FROM THE NATAL NEST WAS ASSOCIATED WITH A DECREASE IN RANGE SIZE AND WITH EARLIER DISPERSAL (WALLS ET AL. 1999). SIMILARLY, DISPERSAL DISTANCE WAS GREATER FOR SPANISH IMPERIAL EAGLES *AQUILA ADALBERTI* WITH BETTER NUTRITIONAL STATUS (FERRER 1993B). OTHER FACTORS, SUCH AS WEATHER, CAN ALSO INFLUENCE DISPERSAL. FOR INSTANCE, GOOD WEATHER CONDITIONS WERE SUGGESTED TO FACILITATE THE ONSET OF DISPERSAL IN COMMON BUZZARDS (WALLS ET AL. 2005), AND

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WIND DIRECTION MAY ALSO DETERMINE THE DISPERSAL DIRECTION IN BOTH SPANISH IMPERIAL EAGLES AND COMMON BUZZARDS (FERRER 1993C, WALLS ET AL. 2005). MOVEMENT PATTERNS IN NEW WORLD BIRDS OF PREY HAVE BEEN STUDIED FOR MIGRATORY AND SEDENTARY SPECIES, INCLUDING THE PRAIRIE FALCON *FALCO MEXICANUS* (STEENHOF ET AL. 2005), FERRUGINOUS HAWK *BUTEO REGALIS* (SCHUECK ET AL. 1998, WATSON 2003) AND OTHERS (STEENHOF ET AL. 1984, MABIE ET AL. 1994, RESTANI 2000, DYKSTRA ET AL. 2004, LAING ET AL. 2005). IT HAS BEEN SHOWN THAT INTER-ANNUAL VARIATION IN STAPLE PREY DID NOT AFFECT DISPERSAL DISTANCE IN GOLDEN EAGLES *AQUILA CHRYSAETOS* (STEENHOF ET AL. 1984) AND NO RELATIONSHIP WAS FOUND BETWEEN DISTANCE TRAVELLED AND PREVALENCE OR INTENSITY OF HEMATOZOAN INFECTIONS IN SHARP-SHINNED HAWKS *ACCIPITER STRIATUS* (SMITH ET AL. 2004).

THE MAIN OBJECTIVE OF OUR STUDY WAS TO DESCRIBE THE MOVEMENT PATTERNS OF 16 RADIOTRACKED JUVENILE BONELLI'S EAGLES. WE DESCRIBE MOVEMENT BEHAVIOUR FROM THE PERIOD OF PARENTAL INDEPENDENCE (MEAN 148 ± 15.9 SD DAYS OF AGE, RANGE 121-169 DAYS, $N = 16$) TO A MEAN AGE OF 531.7 ± 205.7 DAYS (RANGE 240-681 DAYS). NATAL DISPERSAL IS FEMALE-BIASED IN MOST BIRDS (GREENWOOD 1980, NEWTON 2003) THUS WE ALSO INVESTIGATED THE EFFECT OF GENDER ON MOVEMENT BEHAVIOUR AND DESCRIBE MOVEMENT WITH RESPECT TO FERRER'S (1993A) CRITERIA ON MOVEMENT PATTERNS OF A RELATED MEDITERRANEAN EAGLE SPECIES, THE SPANISH IMPERIAL EAGLE. WE ALSO STUDIED THE ONTOGENY OF MOVEMENT BEHAVIOUR.

METHODS

Geographical area

WE STUDIED A BREEDING POPULATION OF BONELLI'S EAGLE IN THE PROVINCE OF CÁDIZ, SOUTHERN SPAIN ($5^{\circ}32'W$, $36^{\circ}41'N$), LOCATED IN THE CORDILLERAS BÉTICAS, WHICH IS THE MAIN MOUNTAIN SYSTEM OF THE REGION AND IS COMPOSED OF THE SIERRAS PENIBÉTICAS IN THE SOUTH NEAR THE MEDITERRANEAN, AND THE SIERRAS SUB-BÉTICAS FURTHER NORTH. ALTITUDE RANGES FROM 80 TO 3482 M ASL, AND THE CLIMATE IS SUB-ARID MEDITERRANEAN (RIVAS-MARTINEZ 1986) WITH AN ANNUAL RAINFALL RANGING FROM 200 TO 1500 MM. AS IN OTHER EAGLE SPECIES, THE BEHAVIOUR AND HABITAT USE OF BREEDING BONELLI'S EAGLES DIFFER FROM THE JUVENILES. BREEDERS DEFEND YEAR-ROUND TERRITORIES IN MOUNTAINOUS AREAS, WHERE CLIFFS ARE AVAILABLE FOR NESTING. IN CONTRAST, ONCE JUVENILES DISPERSE FROM THE BREEDING AREAS THEY SPEND MOST OF THEIR TIME OUTSIDE THESE AREAS (I.E. OUTSIDE MOUNTAINOUS HABITATS), MOSTLY AT LOWER ALTITUDES, IN MORE HUMAN-DISTURBED HABITATS

WHERE NON-IRRIGATED CROPS (MAINLY WHEAT) ARE THE DOMINANT HABITAT TYPE, BUT WITH IRRIGATED CROPS (MAINLY BEETROOT, COTTON AND RICE), PASTURE, SCRUBLAND, BUILT-UP AREAS AND FOREST AS LESS FREQUENT HABITAT TYPES (BALBONTÍN 2005).

Data collection

WE VISITED BREEDING TERRITORIES TO MARK YOUNG AT A TIME WHEN NESTLINGS WERE 47-53 DAYS OLD, APPROXIMATELY TEN DAYS BEFORE FLEDGING. MEAN (\pm SD) HATCHING DATE WAS 17 MARCH (\pm 18 DAYS). YOUNG WERE RINGED AND EQUIPPED WITH TRANSMITTERS WEIGHING 30-35 G, REPRESENTING 2-3% OF TOTAL BODY WEIGHT AT THE TIME OF MARKING (MEAN \pm SD BODY WEIGHT FOR MALES 1637 ± 175 G, FEMALES 2065 ± 135 G). THE RADIOTAGS WERE PROVIDED BY BIOTRACK (WAREHAM, UK) AND WERE FIXED ON THE BACKS OF THE EAGLES WITH A HARNESS SECURED WITH TEFLON-COATED RIBBON (KENWARD 1987). RADIOTAGS WERE FIXED SECURELY TO AVOID PREMATURE DETACHMENT BECAUSE OUR MAIN AIM WAS TO STUDY EAGLE MOVEMENTS DURING THE PERIOD ENCOMPASSING THE TRANSIENT PHASE OF DISPERSAL (LASTING AROUND THREE YEARS). HOWEVER, IN SOME CASES THE MATERIALS EMPLOYED LASTED LESS THAN THREE YEARS OR DETERIORATED EARLIER THAN EXPECTED. RADIOTAGGING HAS BEEN SHOWN TO HAVE NO DETECTABLE ADVERSE EFFECTS ON PRE-DISPERSAL BEHAVIOUR (TYACK ET AL. 1988), DISPERSAL MOVEMENTS (WALLS & KENWARD 1995) OR SURVIVAL (KENWARD ET AL. 2000).

WE USED THE CELLULAR FRACTION OF A BLOOD SAMPLE TO SEX THE YOUNG. WE COLLECTED 2 ML OF BLOOD FROM THE BRACHIAL VEIN OF THE WING OF NESTLINGS. ALL BLOOD SAMPLES WERE TAKEN BETWEEN 11:00 AND 15:00 HOURS AND STORED IN LITHIUM-HEPARIN TUBES. FOR THIS ANALYSIS, PRIMERS 2945E, CFR AND 3224R WERE USED FOLLOWING ELLEGREN (1996).

Radiotelemetry

WE MONITORED RADIOTAGGED YOUNG FOR FIVE DAYS PER WEEK FROM THE DATE THE FIRST YOUNG BIRD WAS MARKED IN APRIL 1998 UNTIL SEPTEMBER 2000. THE DATE AT WHICH YOUNG EAGLES DEPART FROM THE TERRITORY OF THEIR PARENTS (INDEPENDENCE DATE) WAS DETERMINED WHEN OFFSPRING WERE TRIANGULATED AS BEING OVER 3.5 KM FROM THE NEST (HALF THE NEAREST NEIGHBOUR DISTANCE, NND) ON TWO SUCCESSIVE RADIO CONTACTS OBTAINED ON DIFFERENT DAYS (BALBONTÍN ET AL. 2003, PENTERIANI ET AL. 2003, SOUTULLO ET AL. 2006). AFTER INDEPENDENCE, WE PROSPECTED FOR RADIO SIGNALS FROM UNIFORMLY DISTRIBUTED OBSERVATIONAL POINTS SITUATED AT A CERTAIN HEIGHT IN ORDER TO IMPROVE

THE DISTANCE AT WHICH TEMPORARILY LOST SIGNALS COULD BE DETECTED. THIS ALLOWED US TO DETECT SIGNALS AT AN AVERAGE DISTANCE OF 40 KM (RANGE 0-80 KM).

IN TOTAL, WE WORKED 590 DAYS IN THE FIELD, PROSPECTING AN AREA OF ABOUT 16 000 KM² EVERY WEEK. EACH YOUNG EAGLE WAS LOCATED AT LEAST THREE TIMES EVERY MONTH BY SHORT-DISTANCE TRIANGULATION (2 KM) WITH 100 M TRACKING RESOLUTION, USING A STABO RECEIVER PROVIDED BY GFT (STABO ELEKTRONIK GMBH, GERMANY) AND A THREE-ELEMENT YAGI ANTENNA. WE ARE CONFIDENT OF OUR RESULTS BECAUSE AS WELL AS HIGH-ACCURACY LOCATIONS (100 M), WE ALSO HAVE LOWER QUALITY RADIO-LOCATIONS (>500 M) OBTAINED BY TRIANGULATION, AND MANY OBSERVATIONS OF SINGLE DIRECTIONS OF TAGGED INDIVIDUALS OBTAINED FROM POINTS AT HIGH ALTITUDE (E.G. GEODESIC POINTS AT ELEVATED POSITIONS SUCH AS MOUNTAIN TOPS) WHICH GIVE AN IDEA OF THE DAY-TO-DAY MOVEMENTS OF EAGLES. THE LATTER INFORMATION IS NOT PRESENTED HERE, BUT IT WAS USEFUL TO DOUBLE-CHECK THAT THE MOVEMENT BEHAVIOUR OF JUVENILES PRESENTED HERE AGREES WITH BEHAVIOUR OBSERVED IN THE FIELD USING ALL AVAILABLE INFORMATION. WE USED POSITIONAL FIXES TAKEN AT LEAST 24 HOURS APART TO ENSURE INDEPENDENCE OF THE RADIOTRACKING DATA.

WE USED THE UTILIZATION DISTRIBUTION (UD) CURVE (KENWARD & HODDER 1996) TO DEFINE 'CORE AREAS' FOR EACH RADIOTAGGED EAGLE. CORE AREAS WERE DEFINED BY EXCLUDING THE PERCENTAGE OF FIXES THAT PROVOKED A DISCONTINUITY IN THE CUMULATIVE HOME RANGE SIZE, USING THE HARMONIC MEAN AS A MEASUREMENT OF THE FOCAL SITE (DIXON & CHAPMAN 1980). WE CONSIDERED 'TEMPORARY SETTLEMENT AREAS' TO BE THOSE AREAS THAT WERE MOST INTENSIVELY USED BY THE YOUNG EAGLES. BECAUSE CORE AREAS FROM DIFFERENT EAGLES COULD OVERLAP, WE DEFINED 'TEMPORARY SETTLEMENT AREAS' BY JOINING TOGETHER THE OUTERMOST FIXES OF COINCIDING CORE AREAS TO OBTAIN A FINAL POLYGON. DURING TEMPORARY SETTLEMENTS JUVENILE EAGLES OCCUPIED THESE AREAS WHICH WERE, IN TERMS OF PREY ABUNDANCE AND HABITAT FEATURES, HIGHER QUALITY HABITAT PATCHES (MAÑOSA ET AL. 1998, FERRER & HARTE 1997, BALBONTÍN 2005).

BONELLI'S EAGLES SHOWED THE SAME THREE TYPES OF MOVEMENT BEHAVIOUR DESCRIBED FOR JUVENILE SPANISH IMPERIAL EAGLES: EXPLORATORY MOVEMENTS, NATAL RETURNS AND TEMPORARY SETTLEMENTS (FERRER 1993A). WE CALCULATED THE DISTANCE BETWEEN ROOSTING SITES (*DROOST*) AND THE DISTANCE TO THE NATAL NEST (*DNATAL*) FOR EACH RADIO CONTACT FROM EACH RADIOTAGGED EAGLE. DISTANCE BETWEEN ROOSTING SITES WAS DEFINED AS THE DISTANCE BETWEEN TWO SUCCESSIVE RADIO CONTACTS OBTAINED IN THE EARLY MORNING OR AT DUSK ON DIFFERENT DAYS, IN ORDER TO BE SURE THAT THE RADIO-LOCATED EAGLE HAD SPENT THE NIGHT AT A GIVEN

LOCATION. THEREFORE, FOLLOWING FERRER'S (1993A) CRITERIA, ALL RADIO CONTACTS WERE CLASSIFIED ACCORDING TO THE DISTANCE TO NATAL AREAS AND TO THE DISTANCE BETWEEN ROOSTING SITES AS FOLLOWS: (1) 'EXPLORATORY MOVEMENTS', WHEN THE DISTANCE BETWEEN ROOSTING SITES WAS GREATER THAN 10 KM AND THE DISTANCE FROM THE NATAL NEST WAS GREATER THAN 20 KM; (2) 'TEMPORARY SETTLEMENTS', WHEN THE DISTANCE BETWEEN ROOSTING SITES WAS LESS THAN 10 KM AND THE DISTANCE FROM THE NATAL NEST WAS OVER 20 KM; AND (3) 'NATAL RETURNS', WHEN RADIO CONTACTS WERE INSIDE A POLYGON USED TO DEFINE THE BREEDING AREAS (FERRER 1993A). TIME DEVOTED TO PERFORMING EXPLORATORY FLIGHTS, TEMPORARY SETTLEMENTS AND NATAL RETURNS WAS DEFINED AS THE PERCENTAGE OF RADIO CONTACTS CLASSIFIED ON A PARTICULAR TYPE OF MOVEMENT PATTERN FROM THE TOTAL OF RADIO CONTACTS OBTAINED FOR EACH INDIVIDUAL. WE USED RANGES V SOFTWARE (KENWARD & HODDER 1996) AND ANIMAL MOVEMENT ANALYSIS, AN EXTENSION FOR ARCVIEW (HOOGE & EICHENLAUB 1997), TO ANALYSE SPATIAL AND HOME RANGE DATA.

Statistical analysis

IN TOTAL, 16 YOUNG BIRDS (SEVEN MALES AND NINE FEMALES) WERE RADIOTRACKED (TABLE 1). WE USED LINEAR MIXED EFFECTS (LME) MODELS TO INVESTIGATE THE EFFECT OF AGE AND SEX ON RANGING BEHAVIOUR (E.G. TIME DEDICATED TO PERFORM EXPLORATORY FLIGHTS, TEMPORARY SETTLEMENTS AND NATAL RETURNS). THE KEY FEATURE OF LONGITUDINAL DATA IS THAT INDIVIDUALS ARE MEASURED REPEATEDLY THROUGH TIME, AND LME MODELS ARE PARTICULARLY USEFUL WHEN THERE IS TEMPORAL PSEUDO-REPLICATION (REPEATED MEASUREMENT). WE USED LME MODELS USING THE LME PROCEDURE OF S-PLUS 2000 (MATHSOFT 1999) TO INVESTIGATE THE EFFECTS OF AGE AND SEX ON THE TIME DEDICATED TO PERFORM EXPLORATORY FLIGHTS, TEMPORARY SETTLEMENTS AND NATAL RETURNS.

WE USED A BINOMIAL ERROR DISTRIBUTION WITH A LOGIT LINK FUNCTION TO MODEL EXPLORATORY FLIGHTS (NUMBER OF FIXES CLASSIFIED AS EXPLORATORY FLIGHTS/TOTAL NUMBER OF FIXES), TEMPORARY SETTLEMENTS (NUMBER OF FIXES CLASSIFIED AS TEMPORARY SETTLEMENTS/TOTAL NUMBER OF FIXES) AND NATAL RETURNS (NUMBER OF FIXES CLASSIFIED AS NATAL RETURNS/TOTAL NUMBER OF FIXES) AS RESPONSE VARIABLES. AGE WAS DEFINED AS A CATEGORICAL VARIABLE HAVING NINE LEVELS (FROM PARENTAL INDEPENDENCE TO 200 DAYS, 201-260, 261-320, 321-380, 381-440, 441-500, 501-560, 561-620, 621-680 DAYS).

BIRD IDENTITY WAS INTRODUCED AS A RANDOM FACTOR WITH THE AIM OF ESTIMATING THE VARIATION ASSOCIATED WITH THIS VARIABLE AND TO CONTROL FOR TEMPORAL PSEUDO-REPLICA-

Table 1. Summary of radio locations, time monitored and causes of signal loss for 16 juvenile Bonelli's Eagles radiotagged in southern Spain.

| ID | Year | Sex | Independence date | Date signal lost | Time monitored (days) | Number of fixes | Cause of signal loss |
|-----|------|-----|-------------------|-------------------|-----------------------|-----------------|-------------------------|
| 520 | 1998 | F | 15 September | 2 February 2000 | 505 | 33 | Recruited in natal area |
| 540 | 1998 | M | 15 September | 5 March 1999 | 171 | 7 | Harness breaking |
| 560 | 1998 | M | 1 August | 10 December 1999 | 496 | 31 | Unknown |
| 600 | 1998 | M | 30 August | 16 August 2000 | 717 | 42 | End of study |
| 640 | 1999 | F | 3 August | 15 September 2000 | 409 | 43 | End of study |
| 660 | 1999 | F | 10 August | 28 September 2000 | 415 | 39 | End of study |
| 680 | 1998 | F | 21 July | 12 November 1999 | 114 | 12 | Unknown |
| 700 | 1999 | M | 28 August | 18 July 2000 | 325 | 44 | End study |
| 760 | 1998 | F | 30 August | 1 February 2000 | 520 | 33 | Recruited in natal area |
| 780 | 1998 | F | 24 August | 14 August 2000 | 721 | 39 | End of study |
| 803 | 1998 | F | 26 July | 24 January 1999 | 182 | 14 | Unknown |
| 840 | 1998 | M | 17 August | 22 February 1999 | 189 | 6 | Harness breaking |
| 863 | 1998 | M | 23 August | 6 January 2000 | 501 | 30 | Death |
| 882 | 1999 | F | 5 August | 25 January 2000 | 173 | 11 | Death |
| 903 | 1999 | F | 2 October | 28 February 1999 | 149 | 4 | Harness breaking |
| 960 | 1998 | M | 24 August | 28 February 2000 | 553 | 38 | End of study |

ATION. WE ALSO USED LME MODELS TO ASSESS THE EFFECTS OF AGE AND SEX ON THE DISTANCE BETWEEN TWO CONSECUTIVE ROOSTING SITES (*DROOST*) AND THE DISTANCE TO THE NATAL NEST (*DNEST*) AS RESPONSE VARIABLES. THESE VARIABLES WERE NORMALIZED AFTER SQUARE ROOT TRANSFORMATIONS ALLOWING THE SPECIFICATION OF A NORMAL ERROR DISTRIBUTION WITH AN IDENTITY LINK FUNCTION IN THE LME MODELS.

THE STATISTICAL SIGNIFICANCE OF EACH FIXED-EFFECT (AGE AND SEX) AND POSSIBLE TWO-WAY INTERACTIONS BETWEEN THEM WERE TESTED IN TURN USING A BACKWARD STEPWISE PROCEDURE TO SELECT THE MOST PARSIMONIOUS MODEL. THEREFORE, WE FIRST INCLUDED FIRST-ORDER MAIN FIXED EFFECTS AND THEIR POSSIBLE INTERACTIONS IN A SATURATED MODEL; WE THEN REDUCED IT BY ELIMINATING NON-SIGNIFICANT TERMS FROM THE FIXED STRUCTURES (CRAWLEY 2002). IN THE CASE THAT THE INTERACTION BETWEEN AGE AND SEX WAS SIGNIFICANT, THE MAIN FIXED EFFECT WAS RETAINED IN THE MODELS. MODELS WITH DIFFERENT FIXED STRUCTURES WERE COMPARED USING AN *F*-TEST AND AKAIKE'S INFORMATION CRITERION (*AIC*) FOR THOSE RESPONSE VARIABLES WITH BINOMIALLY DISTRIBUTED ERROR TERMS AND LIKELIHOOD RATIO TEST (*LRT*) FOR THOSE VARIABLES WITH A NORMAL ERROR DISTRIBUTION (CRAWLEY 2002). THE FINAL MODEL WAS CONSIDERED TO HAVE BEEN REACHED WHEN ALL VARIABLES RETAINED IN THE MODEL HAD A SIGNIFICANT EFFECT AT $P < 0.05$.

WE USED NON-PARAMETRIC STATISTICS (MANN-WHITNEY *U*-TEST) TO TEST FOR GENDER DIFFERENCES IN THE AGE AT WHICH PARENTAL INDEPENDENCE AND THE AGE AT WHICH THE FIRST SETTLEMENT OR FIRST NATAL RETURN OCCURRED (SOKAL & ROHLF 1998). ALL TESTS WERE TWO-TAILED AND STATISTICAL SIGNIFICANCE WAS SET AT $P < 0.05$. MEANS ARE GIVEN WITH ± 1 SD.

RESULTS

Ontogeny of movement behaviour

THE JUVENILE EAGLES' FIRST DEPARTURE FROM THE NATAL AREA OCCURRED AT 148 ± 15.9 DAYS OF AGE (MEAN DATE 7 AUGUST, RANGE 121-169 DAYS OF AGE, $N = 16$). THERE WAS NO GENDER DIFFERENCE IN THE AGE AT WHICH YOUNG EAGLES FIRST DEPARTED FROM THE NATAL AREA ($U = 19$, $N_1 = 9$, $N_2 = 7$, $P = 0.18$; AGE AT FIRST DEPARTURE, MALES = 150.8 ± 11.9 DAYS OF AGE, FEMALES = 142.9 ± 17.3 DAYS OF AGE). THE MINIMAL ADEQUATE LME MODEL FOR DISTANCE BETWEEN TWO SUCCESSIVE ROOST SPOTS WAS STATISTICALLY SIGNIFICANT (*LRT* = 7.80, DIFFERENCE IN *DF* = 3, $P = 0.05$). IN GENERAL, SEX DID NOT AFFECT THE DISTANCE EAGLES MOVED BETWEEN TWO SUCCESSIVE ROOSTS SPOTS. MEAN (\pm SD) DISTANCE BETWEEN TWO SUCCESSIVE ROOST SPOTS WAS 16.9 ± 19.0 KM (RANGE 0.2-113.1 KM) FOR MALES AND 16.9 ± 22.1 KM (RANGE 0-137.1 KM) FOR FEMALES. HOWEVER, THE REDUCED LME MODEL RETAINED A SIGNIFICANT INTERACTION BETWEEN AGE AND SEX. MALES MOVED FURTHER BETWEEN ROOST SITES THAN FEMALES, BUT ONLY WHEN THEY WERE OLDER THAN 501 DAYS (I.E. ABOUT SEPTEMBER IN THE SECOND CALENDAR YEAR; *DROOST*, MEAN \pm SD FOR MALES = 36.6 ± 33.9 KM, FEMALES = 7.3 ± 8.5 KM) (TABLE 2, FIG. 1A). THERE WAS CONSIDERABLE BETWEEN-INDIVIDUAL VARIATION IN DISTANCE BETWEEN TWO SUCCESSIVE ROOST SPOTS, WITH BIRD IDENTITY ACCOUNTING FOR 23.9% OF THE TOTAL VARIANCE.

AN LME MODEL FOR DISTANCE TO THE NATAL NEST SHOWED NO EFFECT OF AGE, SEX OR AN INTERACTION BETWEEN AGE AND SEX (FULL MODEL VERSUS NULL MODEL, *LRT* = 1.54, DIFFERENCE IN *DF* = 3, $P = 0.67$) (FIG. 1B). AVERAGE (\pm SD) DISTANCE FROM THE NATAL NEST WAS 47.9 ± 13.3 KM (RANGE 0.6-

Table 2. Linear mixed effects models (LME) of distance between two successive roosting spots (droost) as response variables.

| Random effects | | | | | |
|---------------------|----------|-------------|-------|-------|---------|
| | sd | 95% CI | | | |
| Individual identity | 0.970 | 0.496–1.896 | | | |
| Residual | 1.729 | 1.474–2.027 | | | |
| Fixed effects | | | | | |
| | Estimate | se | df | F | P |
| Intercept | 1.643 | 1.598 | 1, 68 | 132.6 | <0.0001 |
| Age | 0.396 | 0.244 | 1, 68 | 2.54 | 0.11 |
| Sex | 1.901 | 0.968 | 1, 14 | 0.43 | 0.52 |
| Age × Sex | −0.333 | 0.151 | 1, 68 | 4.86 | 0.03 |

Full models built with age, sex and interaction between age and sex as explanatory variables.

88.0 KM) FOR MALES AND 48.8 ± 17.8 KM (RANGE 0.6–99.4 KM) FOR FEMALES. THERE WAS CONSIDERABLE BETWEEN-INDIVIDUAL VARIATION IN DISTANCE TO THE NATAL NEST, WITH BIRD IDENTITY ACCOUNTING FOR 46.7% OF THE TOTAL VARIANCE.

Exploratory flights

TAKING INTO ACCOUNT ONLY THOSE RADIO CONTACTS CLASSIFIED AS EXPLORATORY FLIGHTS, THE MEAN DISTANCE BETWEEN TWO

SUCCESSIVE ROOST SPOTS WAS 32.3 ± 22.3 KM, AND MEAN DISTANCE TO THE NATAL NEST WAS 47.5 ± 17.1 KM. THE FINAL LME MODEL EXPLAINED A SIGNIFICANT PART OF THE VARIATION IN THE PERCENTAGE OF TIME EAGLES DEDICATED TO PERFORMING EXPLORATORY FLIGHTS ($LRT = 27.1$, DIFFERENCE IN $DF = 3$, $P < 0.0001$). THIS WAS DUE TO THE SIGNIFICANT INTERACTION BETWEEN AGE AND SEX IN EXPLAINING THE PERCENTAGE OF TIME JUVENILE EAGLES DEDICATED TO EXPLORING SURROUNDING AREAS (TABLE 3). SPECIFICALLY, MALES DEDICATED MORE TIME TO PERFORMING EXPLORATORY FLIGHTS THAN FEMALES, BUT ONLY WHEN THEY WERE OLDER THAN 501 DAYS (I.E. ABOUT SEPTEMBER, DURING THEIR SECOND CALENDAR YEAR, MEAN \pm SD, MALES = $60.8 \pm 42.6\%$, FEMALES = $26.7 \pm 32.0\%$, FIG. 2A). THERE WAS CONSIDERABLE BETWEEN-INDIVIDUAL VARIATION IN EXPLORATORY FLIGHTS, WITH BIRD IDENTITY ACCOUNTING FOR 40.0% OF THE TOTAL VARIANCE.

Temporary settlements

FIRST TEMPORARY SETTLEMENTS OCCURRED WHEN JUVENILES WERE 245.6 ± 86.0 DAYS OLD (I.E. ABOUT NOVEMBER OR DECEMBER IN THE FIRST CALENDAR YEAR). THERE WERE NO GENDER DIFFERENCES IN THE AGE AT WHICH JUVENILES FIRST SETTLED IN TEMPORARY SETTLEMENT AREAS (U -TEST = 27, $P = 0.63$, $N_1 = 7$, $N_2 = 9$, MALES = 231.4 ± 71.1 DAYS, FEMALES = 257.9 ± 98.7 DAYS). TAKING INTO ACCOUNT ONLY THOSE RADIO CONTACTS CLASSIFIED AS TEMPORARY SETTLEMENTS, AVERAGE DISTANCE TO THE NATAL NEST WAS 49.3 ± 10.2 KM

Table 3. Linear mixed effects models (LME) of exploratory flights (ES), temporary settlements (TS) and natal returns (NR) as response variables.

| | ES | | TS | | NR | |
|---------------------|----------|-----------|-------|-----------|---------|-----------|
| | sd | 95% CI | sd | 95% CI | sd | 95% CI |
| Individual identity | 1.76 | 0.95–3.27 | 0.68 | 0.24–1.88 | 0.17 | 0.02–1.13 |
| Residual | 2.16 | 1.83–2.56 | 1.97 | 1.68–2.31 | 0.90 | 0.77–1.04 |
| Fixed effects | | | | | | |
| | Estimate | se | df | F | P | |
| ES | | | | | | |
| Intercept | −2.607 | 1.909 | 1, 69 | 42.1 | <0.0001 | |
| Age | 0.740 | 0.336 | 1, 69 | 1.20 | 0.27 | |
| Sex | 3.532 | 1.171 | 1, 14 | 2.30 | 0.15 | |
| Age × Sex | −0.557 | 0.210 | 1, 69 | 7.01 | 0.01 | |
| TS | | | | | | |
| Intercept | 1.620 | 0.489 | 1, 70 | 52.1 | <0.0001 | |
| Age | 0.152 | 0.086 | 1, 70 | 3.08 | 0.08 | |
| NR | | | | | | |
| Intercept | −0.060 | 0.197 | 1, 70 | 13.8 | 0.0001 | |
| Age | 0.101 | 0.037 | 1, 70 | 7.23 | 0.008 | |

Full models incorporated age, sex and interaction between age and sex as explanatory variables. Standard deviations (sd) of random effects were estimated in a model without covariates.

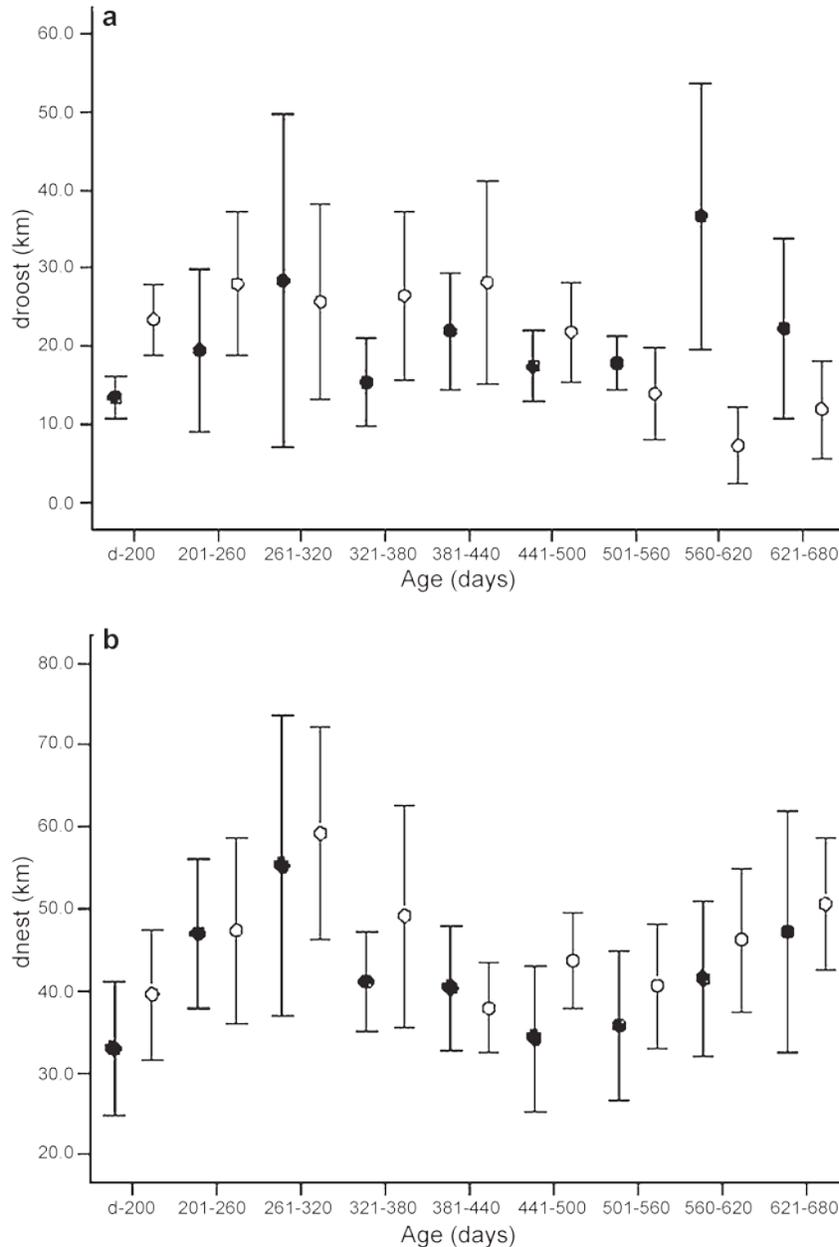


Figure 1. (a) Ontogeny of distances between two successive roost spots (droost, mean \pm se in km) and (b) distance to natal nests (dnest, mean \pm se in km) for juvenile Bonelli's Eagles. First age-class included individuals from the age at first departure from natal territories (range 121–169 days, $n = 16$) to the age of 200 days. Filled circles and bold bars are males; open circles and grey bars are females.

AND AVERAGE DISTANCE BETWEEN TWO SUCCESSIVE ROOST SPOTS WAS 3.48 ± 2.67 KM. THE FINAL LME MODEL INDICATED THAT ONLY AGE HAD AN EFFECT ON THE TIME EAGLES SPENT IN TEMPORARY SETTLEMENT AREAS (LRT = 2.79, DIFFERENCE IN DF = 1, $P = 0.09$). THERE WAS NO DIFFERENCE BETWEEN MALES AND FEMALES IN THE PERCENTAGE OF TIME JUVENILE EAGLES DEDICATED TO STAYING IN TEMPORARY SETTLEMENT AREAS, AND AGE ONLY SLIGHTLY AFFECTED THE TIME EAGLES DEDICATED TO THIS ACTIVITY (TABLE 3, FIG. 2B).

THERE WAS SOME BETWEEN-INDIVIDUAL VARIATION IN TEMPORARY SETTLEMENT, WITH BIRD IDENTITY ACCOUNTING FOR 10.7% OF THE TOTAL VARIANCE.

JUVENILE EAGLES USED BETWEEN ONE AND THREE DIFFERENT SETTLEMENT AREAS (MODE = 1). THE MEAN SIZE OF CORE AREAS WAS 1294.5 ± 649.7 HA ($N = 13$ ESTIMATED CORE AREAS). TEMPORARY SETTLEMENT AREAS WERE ON AVERAGE 11.0 ± 7.8 KM² (RANGE 1.3–21.6 KM²). IN OUR STUDY AREA WE DETECTED SIX SETTLEMENT AREAS, FOUR IN CÁDIZ PROVINCE

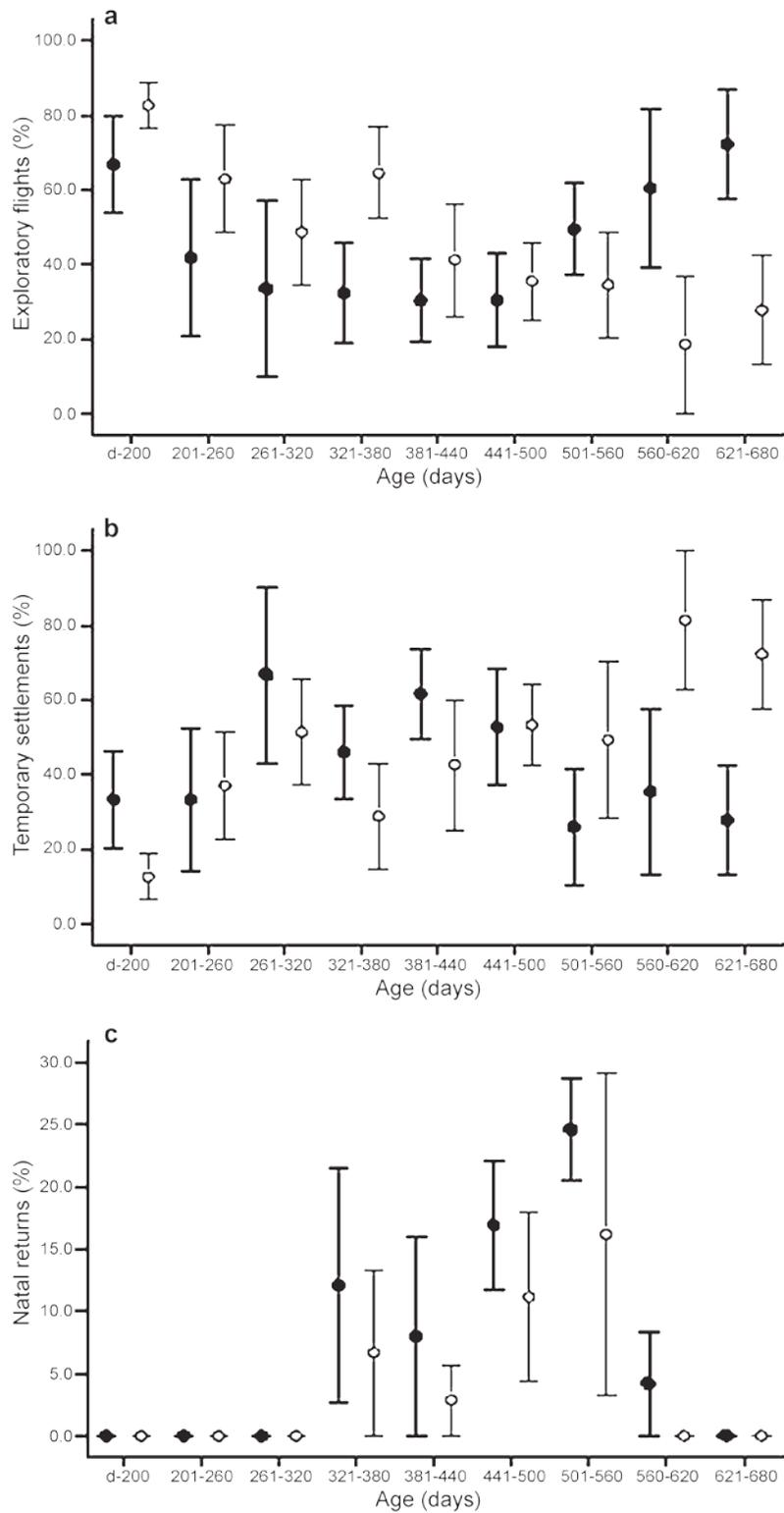


Figure 2. Percentage of time dedicated to (a) exploratory flights, (b) temporary settlements and (c) natal returns (mean \pm se) for different age-classes. First age-class included individuals from the age at first departure from natal territories (range 121–169 days, $n = 16$) to the age of 200 days. Filled circles and bold bars are males; open circles and grey bars are females.

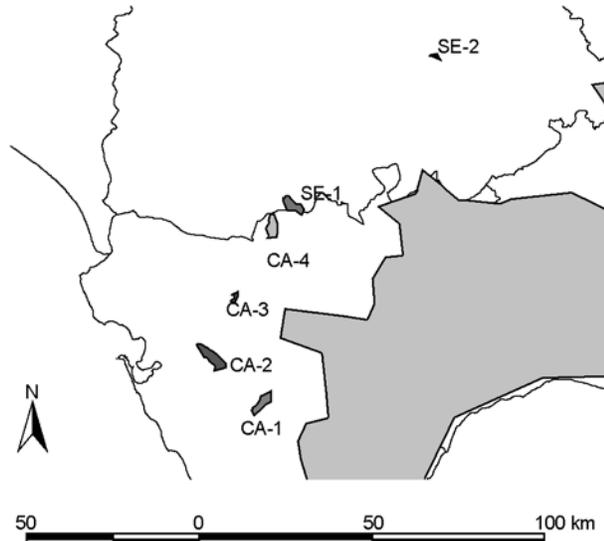


Figure 3. Locations of the six temporary settlement areas used by juvenile Bonelli's Eagles in southern Spain: four in Cádiz Province (CA-1 to CA-4) and two in Seville Province (SE-1 and SE-2).

AND TWO IN SEVILLE PROVINCE (FIG. 3). JUVENILE EAGLES USED TEMPORARY SETTLEMENT AREAS DIFFERENTLY. SPECIFICALLY, THE AREAS CA-3 AND SE-1 WERE USED BY ONLY ONE RADIO-TAGGED JUVENILE EAGLE (A DIFFERENT ONE IN EACH AREA), SE-2 WAS USED BY TWO JUVENILE EAGLES AND CA-1, CA-2, CA-4 WERE EACH USED BY FIVE RADIOTAGGED JUVENILE EAGLES. OTHER NON-TAGGED JUVENILE BONELLI'S EAGLES AS WELL AS JUVENILES BELONGING TO OTHER LARGE EAGLE SPECIES (SPANISH IMPERIAL EAGLES, GOLDEN EAGLES) WERE OBSERVED FREQUENTLY IN THESE AREAS.

Natal returns

AN LME MODEL INDICATED A SIGNIFICANT EFFECT OF AGE ON THE PERCENTAGE OF TIME DEDICATED TO RETURNING TO NATAL AREAS ($LRT = 151.7$, DIFFERENCE IN $DF = 1$, $P < 0.0001$). FIRST NATAL RETURNS OCCURRED WHEN JUVENILES WERE BETWEEN 321 AND 380 DAYS OLD (I.E. DURING MARCH-APRIL IN THE SECOND CALENDAR YEAR, FIG. 2C). THERE WAS LOW BETWEEN-INDIVIDUAL VARIATION IN NATAL RETURNS, WITH BIRD IDENTITY ACCOUNTING FOR ONLY 3.4% OF THE TOTAL VARIANCE (TABLE 3). WE DID NOT FIND STATISTICAL DIFFERENCES BETWEEN MALES AND FEMALES IN THE AGE AT FIRST NATAL RETURN ($U_{TEST} = 10$, $P = 1.00$, $N_1 = 5$, $N_2 = 4$).

ONLY TWO INDIVIDUALS WERE RECRUITED TO THE BREEDING POPULATION DURING THE STUDY PERIOD. FROM THE 16 JUVENILES RADIOTRACKED, TWO FEMALES MARKED IN 1998 WERE FOUND OCCUPYING A BREEDING TERRITORY DURING THEIR THIRD CALENDAR YEAR. THE BIRDS WERE 4.4 KM AND 120.8 KM FROM THEIR NATAL NESTS, RESPECTIVELY.

DISCUSSION

IN THIS STUDY, WE DETERMINED THE MOVEMENTS OF 16 JUVENILE BONELLI'S EAGLES IN SOUTHERN SPAIN. WE DID NOT DETECT GENDER DIFFERENCES IN THE AGE AT FIRST DEPARTURE FROM NATAL AREAS, THE AGE AT THE FIRST TEMPORARY SETTLEMENT, OR THE AGE AT FIRST RETURN TO NATAL AREAS. EXPLORATORY FLIGHTS TOOK PLACE DURING THE WHOLE TRANSIENT PHASE OF DISPERSAL, ALTERNATING WITH TEMPORARY SETTLEMENTS AND WITH NATAL RETURNS. SPECIFICALLY, EXPLORATORY FLIGHT WAS AN IMPORTANT ACTIVITY DURING DISPERSAL UP TO THEIR SECOND CALENDAR YEAR, AND SETTLEMENTS IN TEMPORARY AREAS OCCURRED AROUND NOVEMBER IN THE FIRST CALENDAR YEAR. TIME DEDICATED TO EXPLORING SURROUNDING AREAS INCREASED AGAIN IN MALES BUT NOT FEMALES AFTER THE AGE OF 501 DAYS, WHICH IS AROUND THE END OF THE SUMMER IN THEIR SECOND CALENDAR YEAR.

AS HAS BEEN SHOWN IN OTHER BIRD SPECIES, MOVEMENTS PERFORMED BY JUVENILES DIFFER STRONGLY FROM TERRITORIAL ADULTS (FERRER 1993A, FERRER & HARTE 1997, CADAHÍA ET AL 2005, BALBONTÍN 2004, SOUTULLO ET AL 2008). MOVEMENT PATTERNS OF JUVENILE BONELLI'S EAGLES WERE SIMILAR TO THOSE PERFORMED BY OTHER LARGE BIRDS OF PREY, SUCH AS SPANISH IMPERIAL EAGLES (FERRER 1993B) AND GOLDEN EAGLES (SOUTULLO ET AL 2006). IN GENERAL, WE FOUND THAT GENDER DID NOT HAVE A STRONG EFFECT ON THE MOVEMENT PATTERNS OF JUVENILE EAGLES. HOWEVER, EXPLORATORY FLIGHT WAS SIGNIFICANTLY MORE FREQUENT IN MALES THAN IN FEMALES AFTER THE AGE OF 501 DAYS. AT THAT AGE, EAGLES ARE IN THEIR SECOND YEAR AND NEARING THE TIME OF MOULTING TO A SUB-ADULT PLUMAGE STAGE, DURING WHICH BREEDING MAY COMMENCE (BALBONTÍN ET AL 2003). THEREFORE, THE INCREASE IN EXPLORATORY FLIGHTS ONLY BY MALES DURING THE FINAL PERIOD OF THE TRANSIENT PHASE COULD BE ASSOCIATED WITH AN INCREASE IN THE TIME DEDICATED TO SEARCHING FOR VACANT BREEDING TERRITORIES OR SEARCHING FOR POTENTIAL MATES WITHIN OR NEAR THE NATAL AREAS. IN BIRDS, NATAL DISPERSAL IS NORMALLY FEMALE-BIASED (GREENWOOD 1980). IF THE FREQUENCIES OF NATAL RETURNS OR EXPLORATORY FLIGHTS INFLUENCE THE DISTANCE AT WHICH JUVENILE EAGLES WILL BE RECRUITED INTO THE BREEDING POPULATION, THEN THIS OUTCOME COULD BE EXPECTED. FOR EXAMPLE, IF AN INCREASE IN THESE ACTIVITIES COULD ALSO INCREASE THE PROBABILITY OF FINDING A VACANT TERRITORY NEAR THE NATAL AREA, THEN MALES WOULD MORE LIKELY RECRUIT NEAR NATAL AREAS THAN FEMALES. HOWEVER, FURTHER STUDIES OF THE RELATIONSHIP BETWEEN MOVEMENT BEHAVIOUR DURING DISPERSAL AND NATAL DISPERSAL DISTANCE ARE REQUIRED TO PROVIDE A BETTER UNDERSTANDING OF THE MECHANISMS GOVERNING NATAL DISPERSAL.

THE INDIVIDUALS THAT SETTLED DURING THIS STUDY DID NOT DO SO UNTIL THEY WERE APPROXIMATELY NINE MONTHS OLD. INDEED, COMPETITION (INTER- OR INTRA-SPECIFIC) MIGHT EXIST AMONG JUVENILE EAGLES FOR TEMPORARY SETTLEMENT AREAS. FERRER (1993A) REPORTS THAT JUVENILE SPANISH IMPERIAL EAGLES USED BETWEEN THREE AND EIGHT TEMPORARY SETTLEMENT AREAS IN ROTATION. FERRER (1993D) ALSO OBSERVED THAT THE HUNTING SUCCESS RATIO DECREASED FROM THE BEGINNING OF SETTLEMENT TO ABANDONMENT DESPITE INCREASED HUNTING EFFORT, A FINDING THAT IS INTERPRETED AS INDICATING A DECLINE IN AND/OR DEPLETION OF FOOD RESOURCES IN THE TEMPORARY SETTLEMENT AREAS. IN OUR STUDY, SETTLEMENT AREAS WERE USED EVEN BY JUVENILE EAGLES COMING FROM DISTANT POPULATIONS (>1000 KM, ALCÁNTARA ET AL. 2001, REAL & MAÑOSA 2001). THIS SITUATION, IN WHICH A HIGH NUMBER OF LARGE EAGLES TRY TO SETTLE IN A SUITABLE AREA, MIGHT RESULT IN AN OVERCROWDING EFFECT, THUS MAKING IT MORE DIFFICULT FOR AN INDIVIDUAL TO SETTLE SUCCESSFULLY.

THE DISTANCE EAGLES DISPERSED FROM NEST SITES (I.E. AVERAGE DISTANCE 48.35 KM) WAS DIFFERENT IN THIS STUDY COMPARED TO DISTANCES REPORTED IN OTHER STUDIES ON THE SAME SPECIES (ALCÁNTARA ET AL. 2001, REAL & MAÑOSA 2001, CADAHÍA ET AL. 2005). FOR INSTANCE, CADAHÍA ET AL. (2005) FOUND, USING SATELLITE TRACKING TECHNOLOGY, THAT THE DISTANCE OF DISPERSAL TO THE BREEDING AREA RANGED FROM 87 TO 536 KM IN A SAMPLE OF 13 JUVENILE EAGLES FROM EASTERN SPAIN. ON THE OTHER HAND, REAL & MAÑOSA (2001) REPORTED THAT 57% AND 33% OF RESIGHTED BIRDS IN A WING-TAGGING STUDY (122 EAGLES WERE RING AND WING-TAGGED) REMAINED WITHIN 100 KM AND 200 KM FROM THEIR NESTS, RESPECTIVELY. THE DIFFERENCES IN DISTANCE TO THE NATAL NEST OF DISPERSING JUVENILES FOUND AMONG THE THREE STUDIES COULD BE DUE EITHER TO METHODOLOGICAL FACTORS LINKED TO THE SCALE OF MEASUREMENTS, OR TO TRUE DIFFERENCES AMONGST POPULATIONS. SPECIFICALLY, SATELLITE TRACKING PROVIDES LARGER-SCALE DATA THAN CONVENTIONAL RADIOTRACKING, WHICH IN TURN CAN COVER A GREATER AREA THAN SIMPLE WING-TAGGING METHODS, AND THIS MAY EXPLAIN SOME OF THE DIFFERENCE AMONGST THESE POPULATIONS/STUDIES. ALTHOUGH LONG-DISTANCE MOVEMENT WAS BIASED IN OUR STUDY DUE TO THE METHOD EMPLOYED, WE CONTROLLED RADIOTAGGED EAGLES FOR MORE THAN 80% OF THE TIME (I.E. THE MAJORITY OF THE TIME AN EAGLE REMAINED WITHIN AN AVERAGE DISTANCE OF ABOUT 50 KM FROM THEIR NATAL AREAS) AND HENCE PROBABLY THE DIFFERENCE FOUND AMONG THE SPANISH POPULATIONS COULD BE ATTRIBUTED TO DIFFERENCES AMONG POPULATIONS.

IN CONCLUSION, IT IS CLEAR FROM THIS STUDY THAT DETAILED INVESTIGATIONS OF RANGING BEHAVIOUR DURING THE TRANSIENT

PHASE OF DISPERSAL IN LONG-LIVED SPECIES WITH DEFERRED MATURATION CAN PROVIDE NEW INSIGHTS INTO IMPORTANT ECOLOGICAL AND BEHAVIOURAL QUESTIONS, SUCH AS THOSE RELATING TO THE EVOLUTION OF NATAL DISPERSAL IN NATURAL POPULATIONS. FOR INSTANCE, THOSE ACTIVITIES ASSOCIATED WITH THE EAGLES' MOVEMENTS, SUCH AS EXPLORATORY FLIGHTS, COULD VARY BETWEEN SEXES AT THE END OF THE TRANSIENT PHASE OF DISPERSAL, WHEN INDIVIDUALS SHOULD START SEARCHING FOR MATES OR VACANT BREEDING TERRITORIES. FURTHERMORE, GATHERING INFORMATION DURING THIS CRITICAL LIFE-HISTORY PERIOD CAN PROVIDE IMPORTANT INFORMATION FOR USE IN THE MANAGEMENT OF ENDANGERED SPECIES SUCH AS BONELLI'S EAGLE.

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