

Philopatry and natal dispersal in a sedentary population of western marsh harrier

A. Sternalski¹, C. Bavoux², G. Burneleau³ & V. Bretagnolle¹

¹ CEBC-CNRS, Beauvoir-sur-Niort, France

² Le Marais aux Oiseaux, Les Grissotières, Dolus-d'Oléron, France

³ Rue du Port de Chiffeu, Mauzac, Saint-Just-Luzac, France

Keywords

philopatry; natal dispersal; sex bias; home range; *Circus aeruginosus*; Marsh Harrier; radio tracking.

Correspondence

Audrey Sternalski, CEBC-CNRS, 79360

Beauvoir-sur-Niort, France.

Email: sternalski@cebc.cnrs.fr

Received 2 January 2007; accepted

9 July 2007

doi:10.1111/j.1469-7998.2007.00372.x

Abstract

Dispersal is a key life-history trait because it influences population dynamics and population genetic structure. From a behavioural perspective, the study of natal dispersal requires some understanding of the mechanisms that affect individual movements, because movements of an animal form a path that is continuous throughout its life. Our aim was to investigate juvenile dispersal strategies in the western marsh harrier *Circus aeruginosus*, between fledging and first breeding attempt (from 1 to 4 years later, depending on the sex and individual). Using radio tracking, we monitored dispersing juvenile harriers and their home-range size variations within a sedentary population in central western France from 2001 to 2007. Juvenile dispersal strategy was mainly characterized by a very high natal philopatry (i.e. birds that remained within the study area) and short-distance dispersal. All but one bird (out of 39) remained within the study area between their first winter and their first spring, and 96.0% during their first spring. The distance moved at 2 years of age was significantly larger for males than for females ($3800 \pm \text{SD } 3593$ m and $935 \pm \text{SD } 481$ m for seven males and six females, respectively), in contrast to most bird species studied so far. Home-range size was not sex biased and significantly decreased with age. In addition, non-breeding birds had larger home ranges ($1603 \pm \text{SD } 2128$ ha) than breeders ($349 \pm \text{SD } 185$ ha). Using data obtained from other populations, juvenile marsh harrier dispersal strategies appeared to be determined by migratory status (migratory birds dispersing farther) and demographic parameters (juvenile survival or fecundity).

Introduction

Dispersal is a key life-history trait because it has profound influences on population dynamics as well as on population genetic structure (Dieckmann, O'hara & Weisser, 1999). As a consequence, it has long been studied from both ecological and evolutionary perspectives (Sutherland *et al.*, 2000). In long-lived animals, two forms of dispersal have been identified (see Clobert, Ims & Rousset, 2004): breeding and natal dispersal. Natal dispersal, that is the movement of an individual from where it was born to its first breeding site (Greenwood, 1980), has been particularly investigated in birds. Females were found to disperse further than males from natal sites, and two main hypotheses have been proposed to account for this bias: the resource defence hypothesis (Greenwood, 1980) and the inbreeding avoidance hypothesis, which relies on the presumed advantages of dispersal in reducing breeding with close relatives (Pusey & Wolf, 1996).

Dispersal may also be viewed from a behavioural perspective (Clobert, de Fraipont & Danchin, 2005), considering dispersal as a state-dependent process that accounts for

spatial and temporal environmental constraints, resulting in individual dispersal strategies, that is whether to disperse, how and where to travel and where to settle (Kenward *et al.*, 2002). Dispersal data are, however, still missing for many species because they are difficult to collect, often requiring intensive, large-scale and long-term demographic studies (Koenig, Van Vuren & Hooge, 1996). Furthermore, although studies of marked and recaptured animals provide data on natal dispersal, they usually do not account for the transition movement. Before the emergence of telemetry methods, transition movement was assumed to be a straight line between the nest and the first breeding place. Radio tracking now allows movements to be studied in greater detail, in particular to measure natal dispersal as a transition movement vector from the natal to the breeding site, consisting of several temporally separated home ranges (Walls & Kenward, 1998).

Raptors are long-lived species that may disperse over several years before acceding to first reproduction. During juvenile dispersal, individuals settle within different home ranges and acquire skill efficiency and experience. Several radio tracking studies have been conducted on juvenile

dispersal in medium-size raptors (Tyack, Walls & Kenward, 1998; Walls *et al.*, 1999; Kenward, Walls & Hodder, 2001). In the genus *Circus*, a single study on Northern Harrier *Circus hudsonius* (Beske, 1982), and a pilot study on 19 juveniles Western Marsh Harrier *Circus aeruginosus* (Bavoux *et al.*, 1992, 1998) that were monitored only during 4–8 months after fledging, have been published. Here, we use a much larger sample size of birds of this latter species, radio-tags that were long lived (several years) and much more numerous and precise locations. Our aims were to investigate juvenile dispersal strategies in the Marsh Harrier, and in particular (1) to describe and compare individual juvenile dispersal patterns, by calculating dispersal distances between nest sites and subsequent seasonal individual home ranges and (2) to analyse the effects of sex, age, experience and breeding status on seasonal home-range size and dispersal distance variations. More specifically, we predicted that females should disperse further than males, that home-range size should decrease with age and that home-range size should be larger for non-breeding individuals than for breeders.

Materials and methods

Study area and species

The western marsh harrier (hereafter, marsh harrier) has been studied since 1982 by two of the authors (C. B. and G. B.) in the *Marais de Brouage* (c. 120 km², 45°51'N–01°04'W, Fig. 1). This wetland is an old marine gulf managed as saltmarsh, crossed by a large network of canals (c. 1900 km

and small ponds. The landscape of the study area is mainly composed of grassland (86%) and cultivated area (14%), with many small patches of reed bed. There is also a wide network of roads or tracks (c. 770 km), allowing easy travel throughout the study area. The study area is a homogeneous habitat, which is suitable for harriers, but is surrounded by unsuitable habitat (intensive agriculture, forests, cities). The closest neighbour suitable patch is c. 10 km away (Ile d'Oléron). This particular topography (i.e. bounded area) allowed us to define philopatric behaviour in contrast to dispersing behaviour: if individuals remained within the study area, they were considered to be philopatric individuals (whatever their dispersal distance within the study site, which was quantified); otherwise, they were considered to be dispersing individuals.

The marsh harrier is an abundant raptor in the *Marais de Brouage*: c. 100 breeding pairs (with the highest densities of 36 nests in 15.6 km²), and around 400 birds were counted in communal roosts in winter (Bavoux & Burneleau, 2004). Forty-seven birds were equipped with backpack transmitters: 42 as chicks (24 males and 18 females) and five as adults (two males and three females). The transmitter of one male chick failed < 4 months after fledging (before November: see Table 1). The 47 harriers (four in 2001, eight in 2002, nine in 2003, three in 2004 and 23 in 2005) belonged to 24 different nests, and were fitted with TW3 tags (Biotrack Ltd., Wareham, UK) mounted with a harness of a 9 mm-wide Teflon ribbon (Dunstan, 1972). The tags fitted during 2001–2002 transmitted for about 2 years, but later ones transmitted for a maximum of 4 years. Radio transmitters weighed < 5% of a bird's body mass (including harness), which is 609 g for

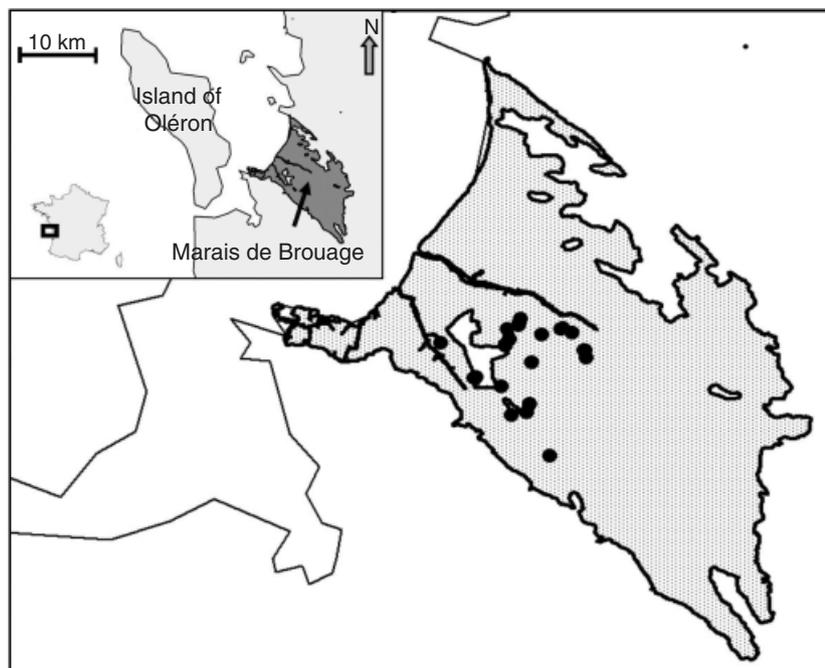


Figure 1 Map of the study area showing the *Marais de Brouage* (shaded) where marsh harriers *Circus aeruginosus* were radio tracked. Dots represent the 24 nests from which fledglings were radio-tagged (see Materials and methods).

males and 813.8 g for females (see Bavoux, Burneleau & Bretagnolle, 2006), and were thus unlikely to impact harrier survival and behaviour (Mech & Barber, 2002). Chicks were ringed and genetically sexed (Fridolfsson & Ellegren, 1999).

Data collection

Radio tracking data were collected between August 2001 and February 2007. Birds were tracked by car in the study area and its surroundings, under favourable climatic conditions, and were located using a three-flexible elements Yagi antenna and portable receiver (Yaesu FT-817, Cypress, CA, USA). Signals could usually be detected at 4–5 km maximum distance when birds were flying. A total of 12 235 locations (9245 in the daytime and 2990 at communal night roosts) were obtained. Only daytime locations were considered for the present study, because night roosts can be several kilometres away from the zone occupied during the day (A. Sternalski, C. Bavoux, G. Burneleau, V. Bretagnolle, pers. obs.). Daytime locations were collected under two sampling designs, that is ‘burst’ and sequential samplings (Swihart & Slade, 1997; Barg, Jones & Robertson, 2005). For the former (30% of the data), successive observations were separated by short time intervals (i.e. one location every *c.* 10 min). For the latter (70% of the data), observations were collected with longer intervening time intervals (i.e. one or two locations per day). All tagged birds that died were recovered in the field. Transmitters that failed were always confirmed visually (i.e. survival of the individual was confirmed) with individual colour rings. Therefore, the fraction of dispersing birds was calculated as the fraction of birds that left the area that did not die and whose transmitters did not fail.

A coordinate grid system ($100 \times 100 \text{ m}^2$) was set up across the entire study area and all locations were automatically positioned on their square’s centre (i.e. all locations were positioned within a 70-m maximum radius). Exact coordinates (Lambert II carto – Paris) were projected under the ‘Systèmes Français Méridien de Paris’. When individuals were detected visually (34% of 9245 locations), their position was reported on maps (70 m precision). Other locations (66%) were determined by triangulation and plotted on the study map with an estimated precision of *c.* 140 m. Two seasons were defined *a priori*: winter, that is the non-breeding season (November–February), and spring, the breeding season (March–July). Analyses were divided into nine periods: post-fledging period, from the hatching date to the end of October, and then eight consecutive periods, corresponding to the first, second, third and fourth winters and springs.

Home-range size estimates

Home range has been defined as an area repeatedly traversed within a specified time period (Kenward *et al.*, 2001). In this study, the time period is set at the season, and therefore, up to nine seasonal home ranges could be estimated. We used the 95% fixed kernel method for calculating

home ranges in order to reduce the impact of outlier locations from excursions. Fixed, rather than an adaptive kernel was preferred because the latter, allowing a varying smoothing parameter according to location density in space, may introduce a systematic variation in home-range estimation. Data were first standardized by the method of ‘Unit Variance’ (Rodgers & Carr, 1998). The smoothing parameter, *h*, is usually calculated with the least-square cross-validation technique (Seaman *et al.*, 1999), but Hemson *et al.* (2005) recently advised caution regarding this method when large samples or samples containing a large number of points that are very close together are used, and argued that in such cases, the reference smoothing parameter h_{ref} is preferable. As our sampling design contained ‘burst’ samplings, we used a fixed h_{ref} . This single value was determined by calculating h_{ref} for all individuals \times period with ≥ 20 locations, then plotting this distribution (Fig. 2a) and taking the median of the distribution as our *h* value. The smoothing parameter (0.486) was used for all individuals and all seasons.

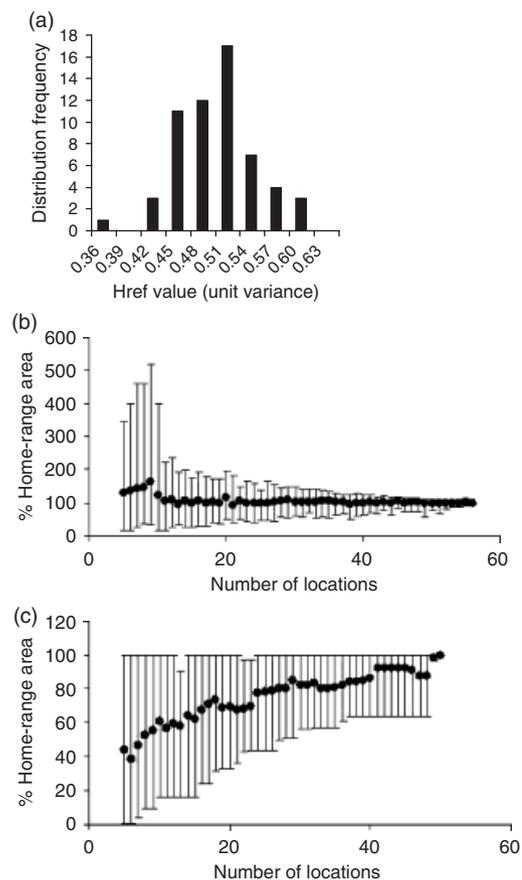


Figure 2 Frequency distribution of H_{ref} values calculated for all individuals \times period (only with ≥ 20 locations available). Example of an individual bootstrap to determine the minimum sample size necessary to estimate the home ranges (in this example, an asymptote is reached at around 20 locations). Incremental area analysis with all individuals with ≤ 50 locations per season (using RANGES VI software).

Dispersal distances

Dispersal distances (from the nest and between seasonal ranges) were calculated for all birds, including philopatric birds defined as those remaining within the study area. Measurement of distances between successive home ranges is difficult because a home range is not an exact point in space. We used the harmonic mean function of ranges VI (Lair, 1987; Kenward *et al.*, 2002) to estimate a focal point for each home range (range 5–813 locations per individual per period). Although harmonic mean function is less robust mathematically than kernel functions, this method is rather insensitive to outliers (Kenward *et al.*, 2002; Kenward, South & Walls, 2003). Seasonal movements and dispersal were calculated, according to season, either by the absolute distance separating the natal nest position and the harmonic mean centre of each subsequent seasonal home range, or by the relative distance between successive harmonic mean centres (i.e. between period i and period $i+1$). Natal dispersal distance was calculated as the straight-line distance between the nest position and the first breeding settlement. However, in order to increase the sample size (as not all fledglings bred during the study period), we calculated natal first- and second-year dispersal as the distance between the natal nest and the harmonic mean centre at 1, and 2 years of age, respectively. Two years is the median age of first breeding in this population. By convention, individuals were considered within the breeder category in successive winters from their first breeding attempt (with laid eggs).

Statistical analyses

The accuracy of kernel density estimation may be affected by two sampling artefacts: the time interval between consecutive locations, which may affect the level of statistical autocorrelation in the data (Swihart & Slade, 1985), and sample size (Seaman *et al.*, 1999). Marsh harriers typically behave periodically, with short hunting stages alternating with long resting stages where a bird remains in exactly the same location for up to 2 h (Bavoux *et al.*, 1992). In addition to our sampling design containing 'burst' sampling sessions, this periodic behaviour produces a high level of autocorrelation in the data. Achieving statistical independence may be at the cost of sample size as well as biological significance (e.g. De Solla, Bonduriansky & Brooks, 1999), and therefore we preferred a biological rather than a statistical definition of independence, that is a sampling time interval long enough to allow individuals to traverse their home range entirely (Lair, 1987), considering first their maximal moving speed. This resulted in keeping locations spaced by more than 10 min. In order to validate this method, we additionally tested two further approaches. The second method considered the mean (rather than maximal) moving speed, which resulted in a 41-min lag in order to obtain independent locations. The third method, based on the length of long resting stages, was set at 120 min. We did not detect any significant differences between home-range areas estimated

with the three approaches (mixed model, individual as a random factor: $F_{158,2} = 0.07$, $P = 0.93$, $n = 189$). Given that the sample size decreased from 89 to 63 home-range estimations, we chose to retain the largest sample size (i.e. we excluded from the dataset all locations separated by < 10 min).

Usually, 15–20 locations are considered to be necessary to obtain stable home-range size estimates (e.g. Kenward *et al.*, 2003). Here, we used two bootstrap approaches to determine the minimum sample size necessary to estimate correctly the individual home ranges (i.e. cover the entire home-range area). First, for each individual successively, we started with a sample size of five locations and increased it by increments of one location until the total sample size was reached. For each sample size, we ran 50 iterations of the procedure. We then examined the resulting sample size–area relationships to assess whether it reached an asymptote (Barg *et al.*, 2005; see Fig. 2b for an example). Second, we used the incremental area analysis implemented in Ranges VI (Fig. 2c). Both analyses agreed in suggesting that birds with ≥ 20 locations per season reached the asymptote (Fig. 2b and c; see sample sizes in Tables 1 and 2).

All home-range size estimations were performed using the Home Range (HRE, Rodgers & Carr, 1998) and Spatial Analyst Extensions of ArcView3.2 (Hooge & Eichenlaub, 1997). We checked for normality of all variables before performing parametric tests, and log-transformed them if necessary. We used generalized linear mixed models (PROC MIXED in SAS 9.2) to analyse individual variability in natal dispersal distances. Means are expressed as \pm SD.

Results

Philopatry and survival rate of juveniles

Philopatry (i.e. birds that remained within the study area) and survival rates of juveniles were calculated for each period separately (therefore, sample sizes vary; see Table 1). Marsh harriers appeared to be highly philopatric at post-fledging (from fledging until October), as 100% of the 39 fledglings (two of the 41 birds were found dead during that period) were subsequently recovered within the study area during their first winter. All but one of the 29 harriers (i.e. 96.6%) that could be monitored between their first winter and their first spring remained in the area (six birds died and the transmitters of four others failed during their first winter: Table 1). Then, only two birds left the study area, during their first and second springs. The philopatry rate was thus 95.2% at 2 years of age. Of the 41 fledglings, eight were recovered dead before the age of 1, mainly during the winter period, another one was found dead in its second winter, two others at the age of 1 and finally, two were recovered dead at 2 years of age. Based on radio-tracking data, the survival rate of fledging birds at 1 year of age was 78.3%, and 72.1% at 2 years of age.

Table 1 Sample sizes (males and females) used to analyse philopatry and survival rates of juvenile marsh harriers *Circus aeruginosus*

	Post-fledging	First winter	First spring	Second winter	Second spring	Third winter	Third spring	Fourth winter	Fourth spring
Total number of birds at the start of the period	41	39	28	24	23	9	7	6	4
Males	23	21	16	13	12	5	3	3	3
Females	18	18	12	11	11	4	4	3	1
Total number of birds lost during the period due to	2	11	4	1	14	2	1	2	4
Dispersal	0	1	1	0	1	0	0	0	0
Death	2	6	2	1	1	0	0	0	0
Transmitter failure	0	4	1	0	1	2	0	2	0
End tracking session ^a	0	0	0	0	(11)	0	(1)	0	(4)
% philopatry per period ^b	100	96.6	96.0	100	95.2	100	100	100	100
% survival per period ^c	95.1	82.3	96.2	95.8	95.2	100	100	100	100

^aThis number corresponds to the birds that reached that age when the study stopped (February 2007).

^bCalculated as the number of birds still within the study site out of the number of birds present at the start of the period, excluding dead birds and birds with transmitter failure during the period.

^cCalculated as the number of birds still alive at the end of the period out of the number of birds present at the start of the period, excluding dispersed birds and birds with transmitter failure during the period.

Numbers are detailed for all nine consecutive periods of the study (see Materials and methods for terminology and details).

Table 2 Sample sizes (males and females, and total number of locations available) used to analyse dispersal (left) and home range (right) of juvenile marsh harriers *Circus aeruginosus*

	Post-fledging	First winter	First spring	Second winter	Second spring	Third winter	Third spring	Fourth winter	Fourth spring
Number of tracked birds	32/0	33/26	28/17	23/23	13/12	7/6	5/3	4/2	2/0
Males	16/0	17/11	15/10	11/11	7/6	3/3	3/3	3/2	2/0
Females	16/0	16/15	13/7	12/12	6/6	4/3	2/0	1/0	0/0
Age of birds	0.2	0.5	1	1.5	2	2.5	3	3.5	4
Total locations	321/0	1932/1603	2443/1895	1593/1283	1213/998	596/458	698/538	76/57	11/0

Numbers are detailed for all nine consecutive periods of the study (see Materials and methods for terminology and details). The age of the birds at each period is provided in the last line (average age, in years, from birth month).

Dispersal distances

Distances from the natal nest could be obtained for all 47. Successive movements from the natal nest were significantly influenced by period (mixed model on log-transformed distance, data from third and fourth winter, and third and fourth spring pooled because of sample size, and individual as a random factor: $F_{88,6} = 20.77$, $P < 0.0001$, $n = 147$) and sex ($F_{88,1} = 4.81$, $P = 0.03$), but not by their interaction ($F_{88,5} = 1.21$, $P = 0.31$). The period and sex effects arose mainly from the post-fledging period (in which birds of both sexes dispersed less than later: Fig. 3a), because excluding post-fledging period from the analysis resulted in non-significant effects of sex, period and their interaction (all $P > 0.1$). At post-fledging, males dispersed less than females (104 ± 81 m vs. 765 ± 1838 m) but the difference was not significant (Kruskal–Wallis Test: $\chi^2 = 2.22$, $n = 32$,

$P = 0.14$). Conversely, at 1 year of age, males dispersed further than females (2062 ± 1208 and 1581 ± 2126 m, respectively: $\chi^2 = 3.48$, $n = 38$, $P = 0.06$), and this was even more marked at 2 years of age (3800 ± 3593 m for males, 935 ± 481 m for females: $\chi^2 = 5.22$, $n = 13$, $P = 0.02$). Natal dispersal distance was 2098 ± 1565 and 856 ± 616 m for four breeding males and four breeding females, respectively. As there was no period effect when excluding post-fledging for the two sexes, we pooled all data and investigated whether sex and breeding status (breeder vs. non-breeder) had an effect on dispersal distance. We found no sex effect, status effect or interaction between factors on dispersal distance (see Fig. 4a).

Given that the sample sizes and individuals retained in analyses varied across periods, we further considered a reduced sample of individuals that could be monitored during six consecutive periods (i.e. from first winter to third

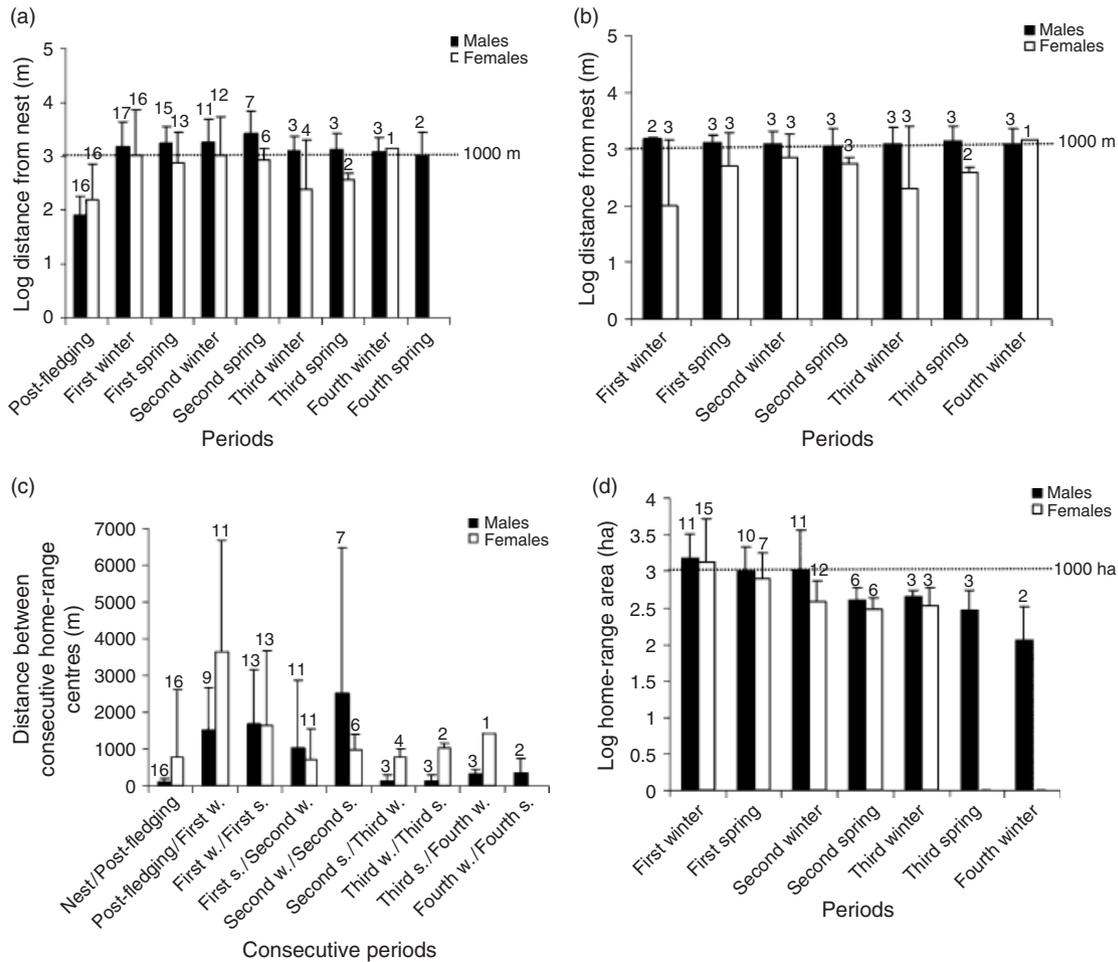


Figure 3 Dispersal distances from the natal nest (in metres, log-transformed, means expressed \pm SD) to the home range centroid at consecutive periods of the study a, b, successive distances between consecutive seasonal home-range centres c, and home-range area variations (in ha, log-transformed) over consecutive periods of the study d, with males (solid bars) and females (open bars) for: -all individuals: a (see Table 2 for sample size), c and d (sample size above bars) -a reduced sample of six individuals (sample size above bars) that have been monitored between the first winter and the third spring: b. The horizontal dotted lines represent a distance of 1000 m and an area of 1000 ha.

spring), consisting of three males and three females. The larger dispersal distances in males compared with females and its stability during consecutive stages were similarly found with this reduced sample size (Fig. 3b). We also considered dispersal distances as being calculated by increments, that is the distance between a seasonal centre of home range at period i and the seasonal centre of home range at period $i+1$. In both sexes, the distances moved during post-fledging were smaller than between post-fledging and first winter, and then decreased regularly (Fig. 3c). However, for both sexes, there was again an increase in movements from second winter to second spring.

Home-range size variation

Seasonal home-range sizes could be estimated within five periods (post-fledging excluded because of a small sample size

and third spring and fourth winter excluded because only males were available), and for 16 males and 15 females (Table 2). Home-range size was significantly influenced by period (mixed model: $F_{48,6} = 5.75$, $P = 0.0001$, $n = 89$) but not by sex ($F_{48,1} = 1.24$, $P = 0.27$, interaction not significant, Fig. 3d), males and females having similar home ranges (1378 ± 1909 ha, $n = 46$ and 1318 ± 2043 ha, $n = 43$, respectively). Considering the reduced sample of six individuals, the same pattern and the same statistical results were observed. In contrast to dispersal distance, there was a significant effect of the reproductive status on home-range size ($F_{56,1} = 13.74$, $P = 0.0005$, $n = 89$; sex effect and interaction not significant): home range was greater for non-breeding (1603 ± 2126 ha, $n = 71$) than for breeding individuals (349 ± 185 ha, $n = 18$, Fig. 4b). We also found a positive relationship between dispersal distance and home-range size (mixed model, individual as a random factor: $F_{57,1} = 5.06$, $P = 0.03$, $n = 89$, Fig. 5).

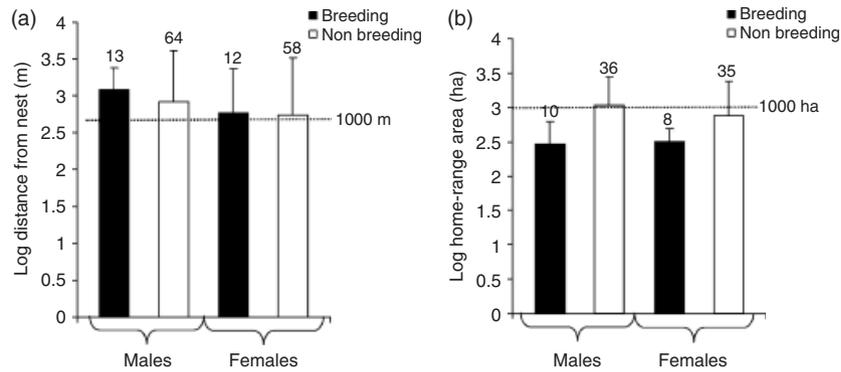


Figure 4 (a) Dispersal distance from the natal nest (in metres, log-transformed, means expressed \pm sd) of breeding and non-breeding individuals. Males with solid bars and females with open bars. The horizontal dotted line represents a distance of 1000 m. (b) Home-range area (in ha, log transformed) of breeding and non-breeding individuals. The horizontal dotted line represents an area of 1000 ha. In the winter season, individuals were considered to be breeders from their first breeding stage.

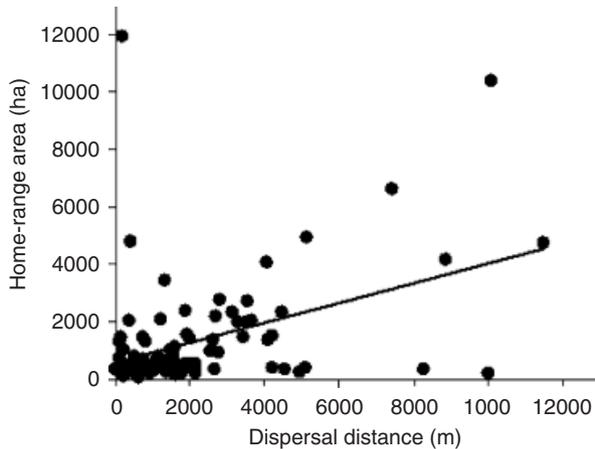


Figure 5 Relationship between dispersal distance (m) and home-range size (ha).

Discussion

Natal dispersal in marsh harrier

Our results showed a very high natal philopatry (96.6% in first winter, 96.0% in first spring, 100% in second winter, 95.2% in second spring and 100% later) and very short-distance dispersal for this population during this study. Although higher, these rates are consistent with a previous study carried out using wing-tagging on a neighbour sedentary population (*île d'Oléron*, 175 km², located *c.* 10 km from the present study area): on average, 40.8% of 191 wing-tagged chicks (belonging to four cohorts) remained in the study area during their first winter (Bavoux *et al.*, 1992). In addition, 28.4% of 334 wing-tagged and/or ringed chicks bred, or at least have been seen, in *île d'Oléron* (see Bavoux *et al.*, 1995). Two other studies investigated natal dispersal in marsh harrier, using resightings of ringed and wing-tagged birds: both reported much lower values of fledglings recovered as breeders in the study site (5.8% at 2 years of age

and 7.7% at 3 years of age: Witkowski, 1989; 7.1% at 2 or 3 years of age: Buczek, 1995). Dispersal data obtained by resighting methods are known to underestimate dispersal range compared with radio-tracking approaches (Koenig *et al.*, 1996). The two latter studies also involved migratory populations of marsh harrier (Clarke, 1995), a behaviour known to affect dispersal pattern (see Sutherland *et al.*, 2000 for a recent review). Paradis *et al.* (1998) reported that migratory species disperse further than resident ones, and Weatherhead & Forbes (1994) found that natal philopatry is less common in migratory species than in resident ones. Demographic parameters also affect the dispersal pattern: Johst & Brandl (1999) showed by using a modelling approach that in vertebrates living in a temporally constant environment, a low natal dispersal is favoured in populations showing low birth rates. Similarly, Altwegg *et al.* (2003) found a strong covariation between survival and emigration of barn owls *Tyto alba*, with more individuals emigrating in years of low survival. In our study, we found a rather low juvenile (1 year old) mortality rate, *c.* 21%. This population also shows low fecundity, at around only one fledgling per laying pair (Bavoux *et al.*, 1989 and unpubl. data). High natal philopatry in our study population may therefore result from low mortality and fecundity rates, in contrast to migratory populations in which breeding success is twice that in our study area (see, Bavoux *et al.*, 1989 and Witkowski, 1989). Moreover, in migratory populations, juvenile mortality is higher (46%, Buczek, 1995).

Sex-biased dispersal

Female-biased dispersal in birds is widespread and is supposed to arise from females benefiting by moving away from their natal site and by assessing a wide variety of territories and mates, whereas males should benefit by staying in a familiar territory, that is near to their natal site (Wheelwright & Mauck, 1998). In contrast to many bird species studied so far, and especially raptors (Newton & Marquiss, 1983; Korpimäki, 1993), we found no female bias in natal

dispersal. Actually, considering philopatric birds (i.e. birds that remained within the study area), males moved longer distances than females. Female-biased dispersal has not been found in all species (Clarke, Saether & Roskaft, 1997), and even within a species, the pattern may change according to populations (Lahaye, Gutierrez & Dunk, 2001). Indeed, the study performed on *île d'Oléron* suggested a slight sex bias in distances moved from birth site during first winter (males: 6.1 ± 5.4 km, $n = 35$ and females: 7.4 ± 5.4 km, $n = 29$; Bavoux *et al.*, 1992). In addition, of the chicks recovered as breeders, 21.9% of the males ($n = 32$) and no females ($n = 28$; Fischer exact-test: d.f. = 1, $P = 0.01$) settled close to their natal nest (i.e. <200 m; Bavoux *et al.*, 1995). Polygyny, which is relatively common in our study population, may also act indirectly on dispersal. While polygyny is usually related to a biased adult sex ratio (specifically, an excess of adult females may promote polygamy: Simmons, 2000), the adult sex ratio in this population is unbiased (49.1% male, Bavoux *et al.*, 2006). As some males mate with several females, others therefore remain unpaired, leading to possibly intense male intra-sexual competition, and as a consequence, male-biased distance moved from natal nest.

Home range and the effects of age and breeding status

In raptors, home range is mainly delineated by breeding place and hunting area, and its variation in size depends on the type of habitat, local food resources and food requirements (Marquiss & Newton, 1981), age (Walls & Kenward, 2001) and individual skills (Pärt, 1995). Dispersal distance and home-range size also vary proportionately across bird species (Bowman, 2003), a result that we confirm intra-specifically. More generally, we found that home-range size, as dispersal distance, was influenced by the age and sex of the individuals. In particular, home ranges were shown to decrease with age and/or experience. In raptors, home-range size in juveniles is larger than that of adults (Forero, 1999), resulting from individual experience and skill increasing with age (Pärt, 1995). Moreover, among sexually dimorphic raptors such as *Accipiter*, females (the larger sex) have a larger home range than males (Marquiss & Newton, 1981; Boal, Andersen & Kennedy, 2003). We failed to detect any difference in home-range size between males and females, possibly in relation to reduced sexual dimorphism in this species.

In contrast to dispersal distances, home-range size was influenced by reproductive status. In montagu's harrier *Circus pygargus* Salamolard (1997) reported no home-range size differences between non-breeding and breeding males. In contrast, non-breeding marsh harriers had larger home ranges than breeding ones. Breeders are expected to show smaller home ranges, because of breeding commitments (males have to provide food for females and young, and therefore return frequently to the nest, whereas females remain in the vicinity of the nest). In order to reduce their energy expenditure, males restrict their hunting movements to the nest area and thus contract their home-range size

during the breeding season. In contrast, montagu's harriers, even breeding birds, do not defend feeding territories (Garcia & Arroyo, 2005).

Acknowledgements

This study was conducted under a license delivered by the CRBPO (*Muséum National d'Histoire Naturelle*). Particular thanks are due to several trainees and volunteers of *Le Marais aux Oiseaux* for their dedicated help during the field work, particularly L. Mimaud. We are grateful to D. Carslake for commenting and improving the English of a first draft.

References

- Altwegg, R., Roulin, A., Kestenholz, M. & Jenni, L. (2003). Variation and covariation in survival, dispersal, and population size in barn owls *Tyto alba*. *J. Anim. Ecol.* **72**, 391–399.
- Barg, J. J., Jones, J. & Robertson, R.J. (2005). Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. *J. Anim. Ecol.* **74**, 139–149.
- Bavoux, C. & Burneleau, G. (2004). Busard des roseaux *Circus aeruginosus*. In *Rapaces nicheurs de France. Distribution, effectifs et conservation: 75–79*. Thiollay, J.-M. & Bretagnolle, V. (Eds). Paris: Delachaux & Niestlé.
- Bavoux, C., Burneleau, G. & Bretagnolle, V. (2006). Gender determination in the western marsh harrier (*Circus aeruginosus*) using morphometrics and discriminant analysis. *J. Raptor Res.* **40**, 57–64.
- Bavoux, C., Burneleau, G., Leroux, A. & Nicolau-Guillaumet, P. (1989). Le Busard des roseaux *Circus a. aeruginosus* en Charente-Maritime (France). II. Chronologie et paramètres de reproduction. *Alauda* **57**, 247–262.
- Bavoux, C., Burneleau, G., Nicolau-Guillaumet, P. & Picard, P. (1992). Le Busard des roseaux *Circus a. aeruginosus* en Charente-Maritime (France). V. Déplacements et activité journalière des juvéniles en hiver. *Alauda* **60**, 149–158.
- Bavoux, C., Burneleau, G., Nicolau-Guillaumet, P., Picard, P. & Sahuc, C. (1998). Dependence and emancipation in juvenile Marsh Harriers *Circus a. aeruginosus*. In Meyburg, B.-U., Chancellor R.D. & Ferrero J.J. (eds), *Holarctic Birds of Prey*: 91–100. Mérida/Berlin: ADENEX/WWGBP.
- Bavoux, C., Burneleau, G., Nicolau-Guillaumet, P. & Picard, P. (1995). Le Busard des roseaux *Circus a. aeruginosus* en Charente-Maritime (France). VIII. Attachement au site de reproduction et appariements. *Alauda* **63**, 273–280.
- Beske, A.E. (1982). Local and migratory movements of radio-tagged juvenile harriers. *J. Raptor Res.* **16**, 39–53.
- Boal, C.W., Andersen, D.E. & Kennedy, P.L. (2003). Home range and residency status of northern goshawks breeding in Minnesota. *The Condor* **105**, 811–816.

- Bowman, J. (2003). Is dispersal distance of birds proportional to territory size? *Canadian J. Zool.* **81**, 195–202.
- Buczek, T. (1995). Natal site tenacity and fidelity to breeding place in individually marked marsh harriers (*Circus aeruginosus*). *Notatki Ornitologiczne* **36**, 323–329.
- Clarke, A.L., Saether, B.-E. & Roskaft, E. (1997). Sex biases in avian dispersal: a reappraisal. *Oikos* **79**, 429–438.
- Clarke, R. (1995). *The marsh harrier*. London: Hamlyn.
- Clobert, J., de Fraipont, M. & Danchin, E. (2005). L'évolution de la dispersion. In *Ecologie comportementale*: 199–232. Danchin, E., Giraldeau, L.-A. & Cézilly, F. (Eds). Paris: Dunod.
- Clobert, J., Ims, R. & Rousset, F. (2004). Causes, mechanisms and consequences of dispersal. In *Ecology, genetics, and evolution of metapopulations*: 307–335. Hanski, I. & Gaggiotti, O.E. (Eds). London: Academic Press.
- De Solla, S.R., Bonduriansky, R. & Brooks, R.J. (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *J. Anim. Ecol.* **68**, 221–234.
- Dieckmann, U., O'hara, B. & Weisser, W. (1999). The evolutionary ecology of dispersal. *Trends Ecol. Evol.* **14**, 88–90.
- Dunstan, T.C. (1972). A harness for radio-tagging raptorial birds. *Inland Bird Banding News* **44**, 4–8.
- Forero, M.G. (1999). Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology* **80**, 1298–1310.
- Fridolfsson, A.K. & Ellegren, H. (1999). A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30**, 116–121.
- Garcia, J.T. & Arroyo, B.E. (2005). Food-niche differentiation in sympatric hen *Circus cyaneus* and montagu's harriers *Circus pygargus*. *Ibis* **147**, 144–154.
- Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162.
- Hemson, G., Johnson, P., South, A.B., Kenward, R.E., Ripley, R. & Macdonald, D. (2005). Are kernels the mustards? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J. Anim. Ecol.* **74**, 455–463.
- Hooge, P.N. & Eichenlaub, B. (1997). *Animal movement extension to Arcview, Ver. 1.1*. Anchorage, AL: Alaska Science Center, Biological Science Office, US Geological Survey.
- Johst, K. & Brandl, R. (1999). Natal versus breeding dispersal: evolution in a model system. *Evol. Ecol. Res.* **1**, 911–921.
- Kenward, R.E., Rushton, S.P., Perrins, C.M., Macdonald, D.W. & South, A.B. (2002). From marking to modelling: dispersal study techniques for land vertebrates. In *Dispersal ecology*: 50–71. Bullock, J.H., Kenward, R.E. & Hails, R.S. (Eds). Oxford: British Ecological Society.
- Kenward, R.E., South, A.B. & Walls, S.S. (2003). *Ranges6 v1.2: for the analysis of tracking and location data*. Online manual. Wareham, UK: Anatrack Ltd.
- Kenward, R.E., Walls, S.S. & Hodder, K.H. (2001). Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. *J. Anim. Ecol.* **70**, 1–13.
- Koenig, W.D., Van Vuren, D. & Hooge, P.N. (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.* **11**, 514–517.
- Korpimäki, E. (1993). Does nest-hole quality, poor breeding success or food depletion drive the breeding dispersal of Tengmalm's owls? *J. Anim. Ecol.* **62**, 606–613.
- Lahaye, W.S., Gutierrez, R.J. & Dunk, J.R. (2001). Natal dispersal of the spotted owl in southern California: dispersal profile of an insular population. *The Condor* **103**, 691–700.
- Lair, H. (1987). Estimating the location of the focal centre in red squirrel home range. *Ecology* **68**, 1092–1101.
- Marquiss, M. & Newton, I. (1981). A radio-tracking study of the ranging behaviour and dispersion of European sparrowhawks *Accipiter nisus*. *J. Anim. Ecol.* **51**, 111–133.
- Mech, L.D. & Barber, S.M. (2002). *A critique of wildlife radio-tracking and its use in national parks: a report to the US national park service*. Jamestown: US Geological Survey, Northern Prairie Wildlife Research Center (<http://www.npwrc.usgs.gov/resource/wildlife/radiotrk/radiotrk.pdf>).
- Newton, I. & Marquiss, M. (1983). Dispersal of sparrowhawks between birthplace and breeding place. *J. Anim. Ecol.* **52**, 463–477.
- Paradis, E., Baillie, S.R., Sutherland, J. & Gregory, R.D. (1998). Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* **67**, 518–536.
- Pärt, T. (1995). The importance of local familiarity and search costs for age- and sex-biased philopatry in the collared flycatcher. *Anim. Behav.* **49**, 1029–1038.
- Pusey, A. & Wolf, M. (1996). Inbreeding avoidance in animals. *Trends Ecol. Evol.* **11**, 201–206.
- Rodgers, A.R. & Carr, A.P. (1998). *HRE: the home range extension for ArcView*. Thunder Bay: Ontario Ministry of Natural Resources, Centre for Northern Forest (Ecosystem Research <http://blue.lakeheadu.ca/hre/>).
- Salamolard, M. (1997). Utilisation de l'espace par le Busard cendré *Circus pygargus*. Superficie et distribution des zones de chasse. *Alauda* **65**, 307–320.
- Seaman, D.E., Millsbaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999). Effects of sample size on kernel home range estimates. *J. Wildl. Mgmt.* **63**, 739–747.
- Simmons, R.E. (2000). *Harriers of the world. Their behaviour and ecology*. Oxford: Oxford University Press.
- Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P. (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conserv. Ecol.* **4**, 16 (<http://www.consecol.org/vol4/iss1/art16>).
- Swihart, R.K. & Slade, N.A. (1985). Influence of sampling interval on estimates of home-range size. *J. Wildl. Mgmt.* **49**, 1019–1025.

- Swihart, R.K. & Slade, N.A. (1997). On testing for independence of animal movements. *J. Agric. Biol. Environ. Statistics* **2**, 48–63.
- Tyack, A.J., Walls, S.S. & Kenward, R.E. (1998). Behaviour in the post-nestling dependence period of radio-tagged common Buzzards *Buteo buteo*. *Ibis* **140**, 58–63.
- Walls, S.S. & Kenward, R.E. (1998). Movements of radio-tagged Buzzards *Buteo buteo* in early life. *Ibis* **140**, 561–568.
- Walls, S.S. & Kenward, R.E. (2001). Spatial consequences of relatedness and age in buzzards. *Anim. Behav.* **61**, 1069–1078.
- Walls, S.S., Mañosa, S., Fuller, R.M., Hodder, K.H. & Kenward, R.E. (1999). Is early dispersal enterprise or exile? Evidence from radio-tagged buzzards. *J. Avian Biol.* **30**, 407–415.
- Weatherhead, P.J. & Forbes, M.R.L. (1994). Natal philopatry in passerine birds: genetic or ecological influences? *Behav. Ecol.* **5**, 426–433.
- Wheelwright, N.T. & Mauck, R.A. (1998). Philopatry, natal dispersal, and inbreeding avoidance in an island population of savannah sparrows. *Ecology* **79**, 755–767.
- Witkowski, J. (1989). Breeding biology and ecology of the marsh harrier (*Circus aeruginosus*) in the Barycz Valley, Poland. *Acta Ornithol.* **25**, 223–320.