

Onset of natal dispersal in Peregrine Falcon from Mediterranean islands (Italy)

Salvatore BONDÌ, Enrico GUZZO, Rosario MASCARA & Maurizio SARÀ*

Received: April 05, 2018 – Revised: October 05, 2018 – Accepted: November 10, 2018

This is a contribution submitted to the Proceedings of the World Conference on the Peregrine Falcon in Budapest in September 2017.



Bondì, S., Guzzo, E., Mascara, R. & Sarà, M. 2018. Onset of natal dispersal in Peregrine Falcon from Mediterranean islands (Italy). – *Ornis Hungarica* 26(2): 201–221. DOI: 10.1515/orhu-2018-0029

Abstract Basic information on natal dispersal of Peregrine Falcons is virtually lacking in Europe, despite increased attention on this species, and the sensitivity of this stage in the Peregrines' life history. In this study, we collected satellite telemetry data during the onset of natal dispersal of 19 Peregrine Falcons tagged in Sicily and the Aeolian archipelago (Italy). We divided the onset of dispersal into the following 3 periods: post-fledging dependence period (PFDP), wandering, and wintering. PFDP lasted on average 47 ± 16 days, during which young peregrines moved very little (0.167 km), and explored small areas (0.226 km²) far from the nest cliff, and showed no sex differences. The wandering phase was highly individualistic, with median net displacements of 23.97 km. Both PFDP and wandering bearings were oriented towards NNE-ESE. Only five individuals went sporadically outside the island borders. During their first winter, Peregrines had a mean home range of 135.65 ± 82.31 km² spatially scattered across Sicily and mainly composed of open habitats, like cereal steppes, arboreal crops and agri-mosaics. Individuals had a dissimilar assortment in habitat composition, however the urban habitat was the most selected and the woodland the least. At night, during both wandering and wintering phases Peregrines used rocks, cliffs and electricity pylons in frequencies not statistically different between sex, phase and type of roost. Only two individuals had significant use of pylons and one of rocks. The multifaceted framework of Peregrine Falcon's natal dispersal was described here for the first time in a Mediterranean population.

Keywords: natal dispersal, Mediterranean islands, Peregrine Falcon, satellite telemetry, Sicily

Összefoglalás A kirepülés utáni diszperzió egy meghatározó szakasza a vándorsólyom életmenetének, azonban, a fokozott kutatási aktivitás ellenére sem ismerünk alapvető információkat erről a periódusról az európai populációk esetében. Tizenkilenc Szicíliaiban és a Lipari-szigeteken (Olaszország) műholdas jeladóval jelölt vándorsólymot követtünk kirepülés utáni diszperziójuk során. Ezt az életszakaszt három periódusra osztottuk: kirepülés utáni korai periódus (post-fledging dependence period, PFDP), kóborlás és telelés. A PFDP periódus átlagosan 47 ± 16 napig tartott, mialatt a fiatal sólymok nagyon kis távolságra (0,167 km) távolodtak el a fészektől, annak csak a közvetlen környékét fedezték fel (0,226 km²), és az ivarok sem különböztek ezekben a paraméterekben. A kóborlási fázis jelentős egyedi variabilitást mutatott 23,97 km medián eltávolodással. Mind a PFDP, mind a kóborlási fázisban a sólymok mozgása ÉÉNY-KDK irányt vett fel. Mindössze 5 egyed hagyta el rövid időkre Sziciliát. Az első telükön a fiatal vándorsólymok átlagosan $135,65 \pm 82,31$ km² területen, elszórta tartózkodtak a szigeten, jellemzően nyílt élőhelytípusokat – mint a gabonaföldek, gyümölcsfás ligetek és egyéb mozaikos mezőgazdasági területek – preferálva. Bár az egyedek különböztek az elfoglalt élőhelytípusok összetételében, a városi élőhely volt a leggyakrabban, míg az erdei élőhely a legritkábban használt. Éjszakai-zóhelynek sziklákat, sziklafalakat és elektromos oszlopokat használtak, a kóborló és a telelő időszakban egyaránt. Ezen helyek használatának gyakorisága azonban statisztikailag nem különbözött az egyedek, ivarok és életszakaszok között. Csupán két fiatal sólyom használta kimagaslóan gyakran az elektromos oszlopokat, míg egy a sziklákat preferálta éjszakai-zóhelyként. Tanulmányunk elsőként közöl részletes leírást a vándorsólyom mediterrán populációjának kirepülés utáni diszperziójáról.

Kulcsszavak: kirepülés utáni diszperzió, mediterrán szigetek, vándorsólyom, műholdas telemetria, Szicília

Department of Biological, Chemical and Pharmaceutical Sciences and Technologies Via Archirafi 18 – Palermo University (Italy).

** corresponding author: maurizio.sara@unipa.it*

Introduction

Biologging technologies, primarily satellite data-loggers, have opened new frontiers in the study of animal ecology, via the access to mass of high resolution data recorded on the daily activity and behaviour of single individuals moving in their habitats (Cooke *et al.* 2004, Cagnacci *et al.* 2010). This new scientific branch, called movement ecology (Nathan *et al.* 2008), applies to the investigation of all the relevant aspects of a species' life history, such as migration, space use, prospecting and dispersal (Bowler & Benton 2005, Ponchon *et al.* 2013).

The movement of an individual from one natal or living site to a new living site, currently defined as dispersal (Bullock *et al.* 2002, Ronce 2007), is an ecological process which has multi-level effects on the permanence, evolution and conservation of species (Bullock *et al.* 2002), because it determines individual survival, fitness costs, gene flow among populations, and species ranges (Bullock *et al.* 2002, Kokko & López-Sepulcre 2006, Nevoux *et al.* 2013). Furthermore, the spatial structure and connectivity of populations are directly linked to dispersal (Clobert *et al.* 2004).

Dispersal is basically the pattern of movements associated with both daily needs (e.g. foraging, roosting) and the search for a new habitat where to establish and reproduce (Doligez *et al.* 2002, Van Dyck & Baguette 2005). This adaptive force driving animal life can be further divided in 'natal dispersal', i.e. movement from the birthplace to the first breeding site; and 'breeding dispersal', i.e. movement between successive breeding sites (Greenwood 1980, Greenwood & Harvey 1982). Currently, the variety of movements associated with breeding biology and dispersal behavior in raptors and other bird species have been categorized in sequential, but distinct, phases, coded with a rather variable terminology (Bennetts *et al.* 2001, Andreassen *et al.* 2002, Bowler & Benton 2005, Penteriani & Delgado 2009), that Morrison and Wood (2009) tried to standardize.

A complex interaction between genetic and condition-dependent environmental forces gives rise to the development of animals' dispersal strategies (Bowler & Benton 2005). Indeed, individuals' behavioural characteristics may complement such an interaction and shape flexible dispersal strategies (Penteriani & Delgado 2009) with the ultimate purpose of settling in areas similar to the natal site (Doligez *et al.* 2002). In many species, including raptors, young birds collect public information by prospecting the quality of future breeding sites during their post fledging explorations (Boulinier *et al.* 1996, Reed *et al.* 1999, Doligez *et al.* 2002, Serrano *et al.* 2004, Nocera *et al.* 2006), or likewise explore the possibility for pair formation after a vacancy has occurred in natal areas (e.g. Ferrer 1996). Such an evaluation has a potentially relevant role in breeding habitat selection and helps individuals making optimal dispersal decisions often through prospecting and previous information of future reproductive success (Ponchon *et al.* 2013).

Since dispersal has also important consequences in raptor populations and community composition it is necessary to identify the factors that constrain (e.g. spatial distribution

of appropriate habitat, avoidance of territorial adults, etc.) the movement of young raptors when floating in search of stable settlement areas and/or breeding territories, as well as the effects they have on the communities of the settling area (Morrison & Wood 2009, Penteriani & Delgado 2009). Such effects can extend beyond their role as future breeders, as pointed out by Penteriani and Delgado (2009), in the case of predator-prey relationships and intra-guild predation of dispersing top predators.

In this context, a never addressed issue concerns how strategies of one species' natal dispersal can affect the occupancy patterns of species with similar ecological requirements, and hence can influence the competitive interactions among related species. This might occur between the Peregrine (*Falco peregrinus*) and the Lanner Falcon (*Falco biarmicus*) in Sicily, because the large and increasing population of the former species produces every year more offspring than the small and declining population of the latter one (Sarà *et al.* 2014). Hence, it might be the case that large numbers of Peregrine floaters could saturate the spatial niche available for Lanner Falcons in the medium- or long-term. Within the framework of an extensive investigation on the ecological interactions between the two species in Sicily (Amato *et al.* 2014, Sarà 2014, Sarà *et al.* 2016), we compare natal dispersal patterns of both species by satellite telemetry. We report here on the onset of natal dispersal occurring in juvenile Peregrine Falcons. In particular, in this first contribution we describe the individual patterns and sex differences during: i) the post-fledging dependence period, ii) the wandering phase, iii) the settling during the first winter of life and the related land-uses, iv) the nocturnal roosts used during wandering and wintering phases.

Material and Methods

Study area

Sicily is the largest Mediterranean island, as it extends over an area of 25,832 km² and is one of the most populated regions of Italy (193 inhabitants per km²). Its typically Mediterranean climate has remarkable variation from the northern areas facing the Tyrrhenian Sea, that mostly fall within the meso-Mediterranean sub-humid and meso-Mediterranean dry bioclimate to the southern areas that mostly fall within the thermo-Mediterranean dry bioclimate. Almost 24.4% of the Sicilian territory is mountainous, 61.4% is composed of highlands, while 14.2% of the surface is lowland. Deciduous forests and Mediterranean vegetation, of which almost 6–8% burns every year, cover 8.4% of the surface area, and are widespread mostly in the north-eastern part of the island, with beech (*Fagus sylvatica*) forests extending from 1200–1400 m a.s.l. in the northern ridge. Hilly and flat inland areas show great habitat heterogeneity, with cultivation zones (especially arable land, fodder, vineyards and olive orchards) intermingled with forest patches of non-native species (*Pinus* spp. and *Eucalyptus* spp.), natural evergreen woodlands (*Quercus* spp.), Mediterranean xeric grasslands, garrigues and shrub vegetation.

The Aeolian archipelago is a volcanic arch formed in the last 300,000 years before present and composed by seven major islands and several islets. Most of the archipelago

stretches in a more or less parallel way along the north eastern coasts of Sicily, from which is clearly visible. The nearest island (Volcano) is about 20 km from Sicily while the farthest (Stromboli) is about 50 km (Figure 1). Strongly exploited by agricultural activities in the past and by tourism today, the islands have lost most of the original vegetation that has been replaced by vineyards and non-native species. Nonetheless, significant patches of Mediterranean evergreen woodland and shrubland remain in the steep sides and at the top of the volcanos.

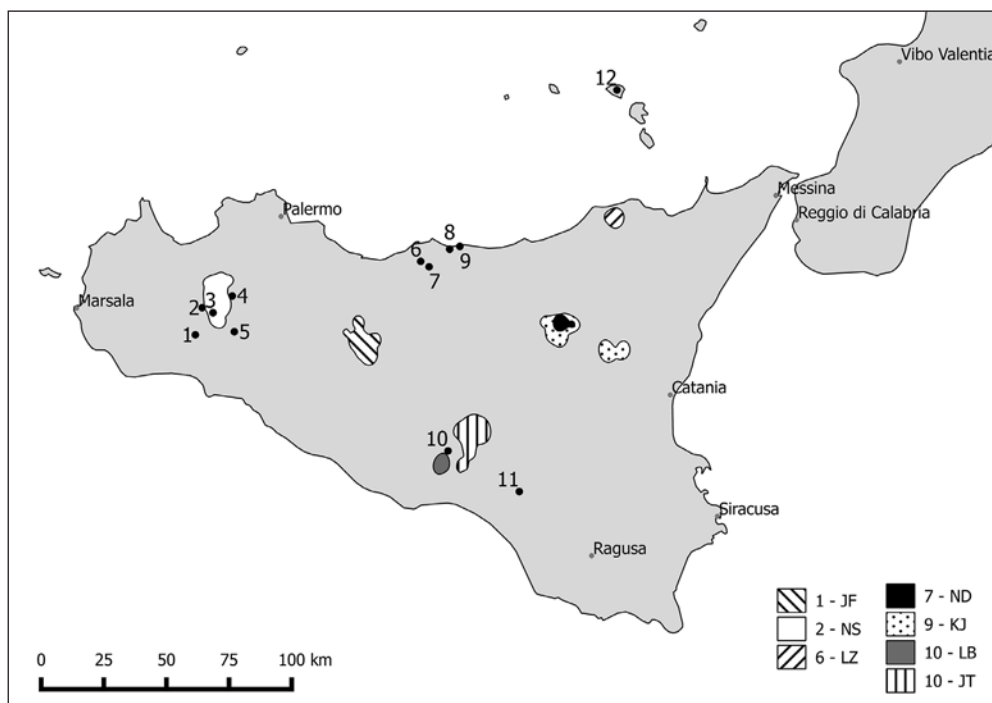


Figure 1. Map of study area with main towns, the twelve sampling sites (1-11 in Sicily and 12 in Salina, Aeolian archipelago) and 7 wintering areas (black, white and stippled or dashed) of juvenile Peregrine Falcons. Wintering individuals have been coded from both their natal site and lecture ring. For instance, 2-NS refers to falcon NS born in site 2 and wintering in the very close white area, etc., individuals have been listed in Table 2. All individuals but 10-JT are females, and all but 9-KJ had a single wintering area. The second wintering area of 9-KJ was used the year before by 7-ND, so the overlap is only spatial. Stromboli the foremost north-eastern Aeolian island, not showed because is out of map limits

1. ábra A vizsgálati terület térképe a jelentősebb városok, a 12 mintavételi (1-11 Szicíliában, a 12. Salina-n, – Lipari-szigetek) és 7 telető terület feltüntetésével (fekete, fehér és pöttyözött vagy sávozott). A telető egyedek jelölését a költőterület és a gyűrűszám kombinációja adja meg. Például, 2-NS az NS-sel jelölt sólymot jelenti, amelyik a 2-es mintavételi területen kelt ki, és a közeli, fehérrel jelölt területen telet. Az egyedek listája a 2. táblázatban található. A 10-JT egyedén kívül minden sólyom tojó, és mindnek, kivéve a 9-KJ egyednek, csak egyetlen telető területe volt. 9-KJ második telető területét az előző évben a 7-ND jelölésű sólyom használta, ezért átfedés kizárólag térben történt. A Stromboli, a Lipari-szigetecsoport legészakabbra fekvő szigete a lépték miatt nincs ábrázolva a térképen

Study species

The nearly-cosmopolitan Peregrine Falcon (White *et al.* 2013) is a sedentary and quite common species in both Sicily and Aeolian Islands, where it breeds in diverse coastal and inland habitats at altitudes up to 1300 m a.s.l. The Sicilian population currently assigned to *F. p. brookei* (White *et al.* 2013, but see Mengoni *et al.* 2018), was very likely only slightly hit by the massive world-wide decline occurring in the 20th century due to organochlorine pesticides (Cade *et al.* 1988, White *et al.* 2013). Past censuses (e.g. Schenk *et al.* 1983) estimated the population to be around 150 pairs, some 195–205 pairs were recorded after a review of local literature, and this baseline value was used to estimate a potential population of 216 ± 52 pairs by modeling the species' occupancy (Sarà 2008). Recent monitoring in 2014–2017, mapped the presence of 166 territories in nearly 65–70% of Sicily (Sarà *et al.* unpublished data), that would produce a prudential estimate of 240–250 territories in the whole island. Further 4–5 pairs are known in the Aeolian archipelago (Lo Cascio 2017). In both Sicily and Aeolian archipelago, the species is mainly threatened by direct human persecution (illegal shooting) and marginally by nest despoliation for illegal trading of eggs and chicks.

Field procedures and data treatment

To investigate the onset of natal Peregrine Falcon dispersal, we used a sample of known breeding sites, 11 distributed in northern, western and southern Sicily and 1 in Salina (Aeolian Island) during the 2014–2017 breeding seasons. Four northern sites and the Salina are coastal, while the others are located inland in Sicily (*Figure 1*). The entire sample was formed by natural nests, located on vertical cliffs in cavities, rocky ledges or old nests of Raven *Corvus corax*. Nests were accessed by a rock climber expert in raptor handling, who delivered the chicks to the base or to the top of the cliff for processing (collection of biometric data and genetic samples, ringing and tagging). We deployed 19 GPS-GSMs (model Saker ultra-light, Ecotone, Poland, weight 20 g) on juvenile Peregrine Falcons (6 males, 13 females, including duos of siblings from 4 sites), about 33–36 days old. Sex was inferred by body biometrics and then confirmed by genetic analysis (Mengoni *et al.* 2018). Transmitters were fixed as a backpack using a teflon harness (Rodríguez *et al.* 2009) and birds were released into their nest a maximum of 30–45 minutes after capture. The complete backpack weighed about 21 g, well below the 3% limit of body weight. Tagged birds were monitored once a week for the first month after marking, to check both bird and tag conditions. The satellite transmitters had a solar battery and were programmed to collect a GPS position every 6 of 24 hours of signal reception while chicks were in the nest, and every 1–2 hours after they have fledged out. To avoid biases associated to the non-independence of the data, positions obtained less than 2 hours after the previous one, were excluded from the analyses (Limiñana *et al.* 2007). Bird locations and routes were retrieved in geographical coordinates and then converted to UTM WGS84 coordinates for further calculation by QGIS 2.16 (QGIS Development Team 2016).

In this first contribution, we considered only locations corresponding to the period from the first fledging flight till the end of first winter of the young Peregrine Falcons. This 9-month

period, describing the onset of natal dispersal, was divided in three different phases, according to current literature (Weathers & Sullivan 1989, Morrison & Wood 2009, Penteriani & Delgado 2009): 1) post-fledging dependence period (hereafter PFDP), from the fledging day to the first day of leaving the natal area; 2) wandering, from the day of leaving the natal area until 30 November, was conventionally terminated by the start of next phase; and 3) first settling and wintering. As suggested for early-spring breeder species (Spina & Volponi 2008), this phase was considered from 1 December to 28 February.

To establish the end of PFDP and the start of wandering phase, we used both a visual observation of QGIS maps, and two standardized and quantitative methods: 1) net displacement (hereafter ND, Kareiva & Shigesada 1983, Turchin 1998), and 2) the cumulated coefficient of variation (hereafter ΔCV , Limiñana *et al.* 2008). For every individual, the ND procedure determines the Euclidean distance between the initial location and each subsequent relocation. We preferred not to transform ND values into squared NSD values (i.e. net squared displacement), because the nonlinearity of squared transformation alters distance values, so that the obtained movement timing would initiate and terminate later in the NSD framework compared to the ND scale (Beatty *et al.* 2013). ND differs by season, hence its interpretation depends on the timing and location of marking (Bunnefeld *et al.* 2011). This implies that the movement pattern for every individual marked in the nest shows an increase of ND values representing the onset of wandering or dispersal movements from the nest, followed by a second phase in which these values become quite stable and fluctuate around a maximum value, once the individuals have reached a given settling area (e.g. wintering grounds). In order to verify the start of wandering phase recorded by both visual observations and the ND method, we looked for the abrupt change in the movement pattern of every Peregrine Falcon, as expressed by the incremental coefficient of variation (ΔCV) between two subsequent bird locations. ΔCV shows a peak when the animal leaves the natal site and is flat when wandering movements become more continuous. This procedure allowed us to precisely identify both the start and duration of wandering movements per every tagged Peregrine Falcon (*Figure 2*).

To identify the geographical areas of both PFDPs and overwintering period, and their extensions, we calculated the 95% kernel (KDE95) using kernel density estimation and the Minimum Convex Polygon (MCP95) of the AniMove tool for ArcGis 9.3, by data obtained from ND and ΔCV calculations.

We used circular statistics (Batschelet 1981) to analyze whether PFDP and wandering directions, with respect to the geographic North and taking as reference the nest-site location of every individual, were different from a random dispersion and whether they differ by sex and siblings. Both PFDP and wandering directions obtained by QGIS were first transformed to rectangular polar coordinates to obtain the mean angle (azimuth) and the mean vector r . This latter measure of angular dispersion ranges from 0 (uniform dispersion) to 1 (complete concentration in one direction). Then, we used the Rayleigh's z statistics to test the null hypothesis that there is no mean direction of dispersion during the PFDP and wandering phases. The Watson-Williams' U statistics was used to test whether the male and female, as well as siblings Peregrine Falcons are significantly different in their main PFDP and wandering azimuths.

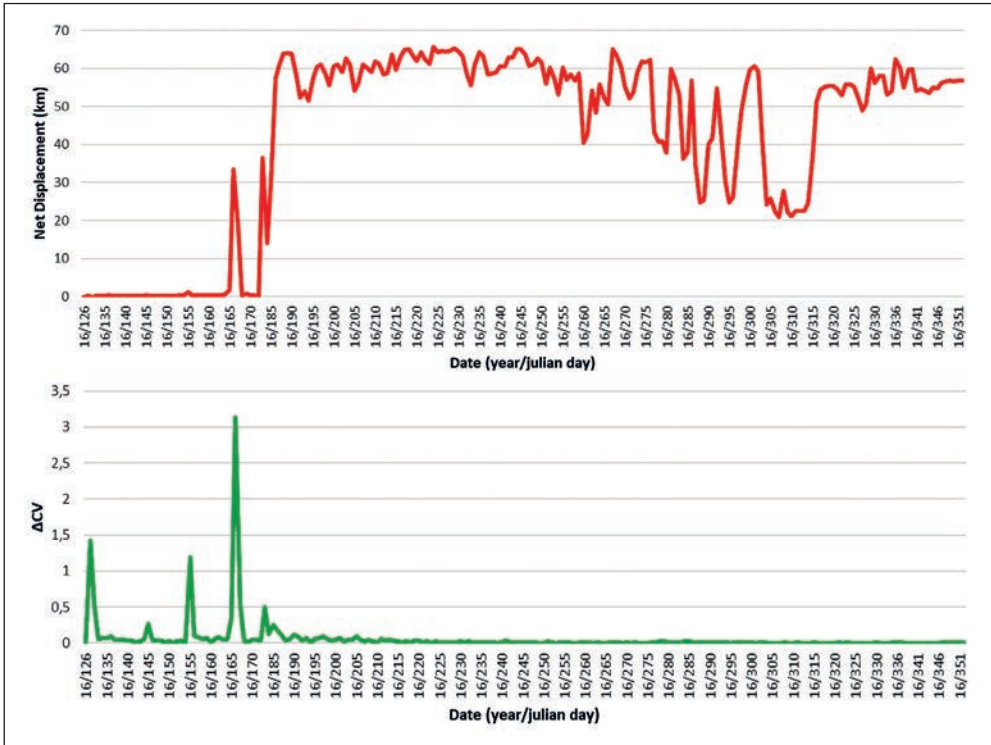


Figure 2. The end of PFDP and the start day of Peregrine Falcon LJ wandering is presented here as an example of the methodology followed to distinguish between the two phases. Above the first peak of movement from the nest cliff (Net Displacement). Below the highest increment of coefficient of variation (ΔCV) between two consecutive displacements. Both occurring on day 14 June 2016 (16/165), when wandering started after 32 days of PFDP

2. ábra

Az LJ jelölésű vándorsólyom PFDP periódusának végét és a kóborlási periódus kezdetét mutatja az ábra illusztrálva a módszert, amit a két periódus elkülönítésére használtunk. A felső panel a fészektől való első elmozdulási csúcsot mutatja (Net Displacement). Az alsó panel két egymást követő elmozdulás közötti legnagyobb variációs koefficiens növekményét (ΔCV) ábrázolja. Mindkettő 2016. június 14-én (16/165) történt, amikor a fiatal sólyom 32 napnyi PFDP után elkezdett kóborolni

We assessed whether net displacements, NDs, among individuals changed during dispersal phases (PFDP, wandering and wintering), by means of a general linear mixed model with 'ND' as dependent variable, 'sex' and 'phase' as fixed factors, 'individual' as a random factor, and a normal error distribution. To account for the predictor relationships, we employed a nested ANOVA design where 'sex' and 'phase' interact each other and are both nested in individual, sex was also nested in phase: so the resulting model was phase + sex(phase) + individual (sex*phase).

To investigate land use during winter we categorized land-cover as coded at the second or third hierarchical level (EEA, 2000) and acquired from GIS databases of CORINE Land Cover (CLC) digital maps (scale 1:25,000) of Sicily (<http://dataservice.eea.europa.eu/dataservice>). We considered the following 7 land-use categories: cereal steppes, grazeland, shrubland,

agri-mosaic (most herbaceous crops on irrigated land intermingled with other arboreal and herbaceous crops), arboreal crops (including vineyards), woodland (including both artificial and natural formations), and urban areas. To explore individual similarity of habitat uses during winter, we analyzed the diurnal locations (i.e. excluding nocturnal fixes, see below) per every individual in each land-use class using a multidimensional scaling (MDS) ordination. This procedure found the eigenvalues and eigenvectors of a matrix containing the similarities between all individuals' locations as expressed by the Bray-Curtis index of similarity, currently used for abundance data. Then to estimate the preference for land-use classes we compared KDE95, considered as used areas by Peregrine Falcons, with available areas as identified by MCP95s. We used a design of first type (i.e. used compared with known proportions of available units) and evaluated whether the use and availability of space differed among land-use classes by the standardized selection ratio B_i and the related chi-square test (Manly *et al.* 1993).

Finally, we made an analysis of nocturnal roost sites, by extracting all data recorded between 21:00 pm and 04:00 am, which corresponds to the darkness period through the whole year at the latitude of Sicily. We considered only the wandering and wintering phases and excluded the PFDP, because the roosts used at this stage are in or nearby the natal cliff, and hence depend from the habitat features of a given nesting site. We categorized nocturnal roosts as: a) trees, including bushes; b) cliffs and rock piles; c) electricity pylons, in order to perform a general linear mixed model with 'number of nocturnal fixes' as dependent variable, 'type of roost' and 'phase' as fixed factors, 'individual' as a random factor, and a normal error distribution. The 'individual*phase', 'individual*type of roost' and 'phase*type of roost' interactions were also modelled.

We used QGIS 2.6.1 to perform all spatial analyses, STATISTICA 10.0 (Statsoft inc.) and PAST 3.18 (Hammer *et al.* 2001) for all statistical analyses, setting the statistical significance threshold at $P < 0.05$. Dates were expressed as Julian calendar days (1st January = 1). To avoid overestimation of sample means due to averaging extreme values, we preferred to use the median and lower-upper (Q25-Q75) quartiles of ND values.

Results

Post-fledging dependence period

The mean fledging day of the 19 Peregrine Falcons tagged during 2014–2017 was 17 May, without sex difference (Student's test $t_{17} = 1.03$; $P = 0.32$), although males fledged on average four days earlier than females. The mean (\pm SD) duration of PFDP was 47 ± 16 days (min-max: 27-84), again without sex difference ($t_{17} = 0.06$; $P = 0.95$). The juvenile falcons ended their PFDP (and started their wandering phase) on average the 3 July (min-max: 10/6-10/8). Males tended to become independent four days earlier than females, although this difference was statistically not significant ($t_{17} = 0.52$; $P = 0.61$). The PFDP length did not show any linear correlation with fledging date of juvenile falcons (Pearson's $r = -0.109$; $P = 0.67$; $n = 19$); besides, the Julian day of fledging did not significantly correlate with the Julian day of wandering (Pearson's $r = 0.371$; $P = 0.13$; $n = 19$).

The GLM used to assess the factors predicting the net displacements of Peregrine Falcons was statistically significant ($F_{47} = 6674.183$; $P = 0.000$) and explained most of the original variability in the ND data set (Adjusted $R^2 = 0.874$). Two of the fixed factors, i.e. the intercept ($F_1 = 32.654$; $P = 0.000$) and the phase ($F_2 = 5.881$; $P = 0.006$), together with the random factor individual(sex*phase) ($F_{42} = 5401.04$; $P = 0.000$) were statistically significant, whereas the sex(phase) was not ($F_3 = 0.982$; $P = 0.410$).

The NDs during the PFDP were statistically shorter than those during wandering (Tukey's HSD with unequal N: $P = 0.00002$), and wintering (Tukey's HSD with unequal N: $P = 0.00002$). Nonetheless, all the 171 ND combinations among individuals during the PFDP are not statistically significant in the post hoc tests (Tukey's HSD with unequal N: P range = 0.196-1.000). The four pairs of siblings included in these 171 ND combinations were not significantly different, therefore displaying analogous net displacements from the natal cliffs.

Overall, their median displacement was 0.167 km from the natal cliff, and males did not differ from females (Tukey's HSD with unequal N: $P = 0.633$) (Table 1, Figure 3). Some individuals performed long flights, over 48 km in females and over 37 km in males, while still dependent on their parents (Table 1, Figure 3). During their PFDP the juvenile falcons stayed nearby the natal cliff, because the median KDE95 area explored was 0.226 km² (Q25-Q75: 0.087-0.454 km²) with a maximum value of 3.782 km². Males tended to explore smaller areas around the cliff than females, although this difference was not significant (0.17 km² in males vs 0.24 km² in females, Kruskal-Wallis $H_{1,19} = 0.377$; $P = 0.539$).

The directions of movements around the cliff site were statistically different from a uniform circular dispersion (Rayleigh's z value = 7.61; $P = 0.0002$; $n = 19$), as all individuals showed a clear tendency to explore more the northern, eastern and southern quadrants with

Table 1. Median values in kilometres of male and female juvenile Peregrine Falcons during onset of their natal dispersion in Sicily. All net displacement values (n fixes) have been calculated with respect to the nest-site of each individual. PFDP = Post-fledging dependence period; Q25 = lower quartile, Q75 = upper quartile

1. táblázat Szicíliai vándorsólymok költés utáni diszperziójának kezdeti fázisai alatt mért medián értékek kilométerben kifejezve. Minden nettó elmozdulási érték az egyedek fészékéhez van viszonyítva. PFDP = kirepülés utáni korai periódus (post-fledging dependence period), Q25 = alsó kvartilis, Q75 = felső kvartilis

Phase	Sex	N individuals	N fixes	Q25	Median	Q75	Minimum	Maximum
PFDP	F	13	7033	0.070	0.249	1.215	0.000	48.502
	M	6	3286	0.040	0.073	0.212	0.000	37.907
	Total	19	10319	0.055	0.167	0.897	0.000	48.502
Wandering	F	12	20085	7.024	24.879	64.849	0.004	218.405
	M	6	4864	8.330	18.548	147.469	0.004	249.786
	Total	18	24949	7.090	23.969	66.003	0.004	249.786
Wintering	F	9	7798	8.675	47.859	72.714	0.060	116.646
	M	2	2013	15.931	16.571	151.123	1.210	153.822
	Total	11	9811	8.734	41.117	75.739	0.060	153.822

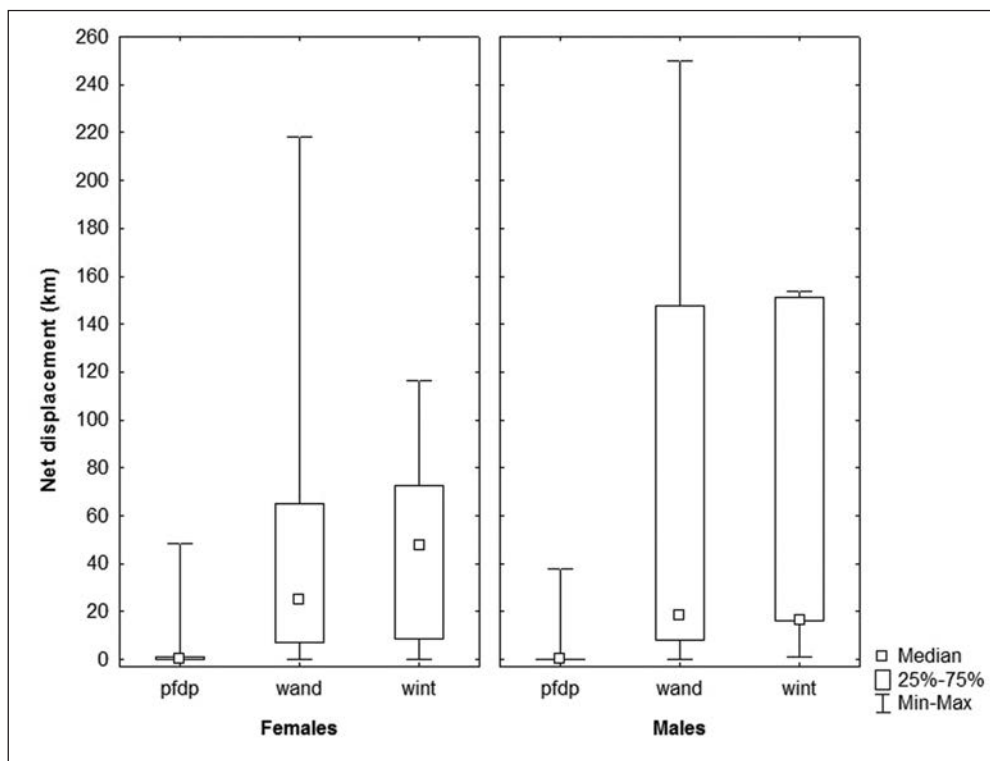


Figure 3. Median displacements values in kilometres of male and female Peregrine Falcons across the three initial phases of natal dispersal. All displacements have been related to the nest-site position of every individual. pfdp = post-fledging dependence period, wand = wandering, wint = wintering

3. ábra Hím és tojó vándorsólymok medián elmozdulásai (km) a kirepülés utáni diszperzió első három szakaszában. Minden elmozdulási érték az egyedek fészkéhez van viszonyítva. pfdp= kirepülés utáni korai periódus (post-fledging dependence period, PFDP), wand = kóborlás (wandering), wint= teletelés (wintering)

respect to the natal cliff location (Figure 4 above). The pattern for the total sample of juvenile falcons showed a quite high concentration of dispersion (mean vector $r = 0.633$) headed for directions with mean azimuth $\alpha = 95.49^\circ$ (bootstrapped 95% confidence = 66.16° – 121.4°). Males and females not differ in this pattern (Watson-Williams' $U_{1,17} = 2.483$; $P = 0.131$). Siblings from three pairs behaved heterogeneously, flying with bearings distant 22.5° ($n = 1$) and 67.5° ($n = 2$) each other, while those of the fourth pair tended to fly more or less with the same bearing ($< 10^\circ$), however the mean azimuth angles of the four sibling duos did not statistically differ (Watson-Williams' $U_{1,6} = 0.002$; $P = 0.881$).

Wandering

This second temporal segment, which is the first true dispersal moment in the life of young falcons, proved to be an idiosyncratic phase, and no pattern is actually emerging in our

sample, as juvenile falcons dispersed from the natal cliff in several ways (Table 2). Some of them (e.g. individuals KP and JA in Table 2) did short (4–7 days) nomadic explorations then came back to natal site, to move progressively far (JA) or to stand always close in following days (KP). Other individuals (NF black, LV, KL) stayed always very close (0.49–1.63 km) to natal site, moving back and forth the natal cliffs rather than beginning a true wandering phase, with maximum travel bouts of 40–60 km (Table 2), the remainders moved gradually far away. All individuals during wandering came back one or many times to natal cliffs, as showed by the minimum values in Table 2.

The total median net displacement during wandering was 23.969 km (Table 1, Figure 3), however the NDs during the wandering phase were statistically shorter than those during wintering (Tukey's HSD with unequal N: $P = 0.00002$). Females travelled significantly more

Table 2. Summary of net displacements in kilometres from natal cliffs during the wandering phase in Peregrine Falcons from Sicily and Salina Island (NP black and JL black). Every individual is named by its lecture ring code; same letter specifies the sibling duos. JL black was recovered and died in Salina island after a summer windstorm when still in PFDP. NA = not available

2. táblázat Nettó elmozdulások összesítése a kikelés helyétől számítva kilométerben a kóborlási periódus alatt Szicíliából és Salina-ról (NP black és JL black). Minden egyed a gyűrűkódja alapján van elnevezve; ugyanaz a betű testvérpárokat jelöl. A JL black jelölésű sólyom még a kirepülés utáni korai periódus alatt pusztult el Salina-n egy nyári szélvihar után. NA = nem hozzáférhető

Name	Sibling duo	Year	Sex	n	Q25	Median	Q75	Minimum	Maximum
NF black		2017	M	377	0.08	0.49	9.77	0.01	43.58
LV	a	2016	M	209	0.04	0.68	1.14	0.01	58.96
KP		2014	M	709	0.40	0.72	3.93	0.00	249.79
KL		2015	F	1988	1.48	1.63	2.35	0.00	62.81
LB	a	2016	F	2219	1.16	5.69	6.85	0.02	82.85
NS		2016	F	1852	6.56	8.68	8.86	0.03	51.71
LB black		2017	F	288	8.69	15.84	18.19	0.22	42.03
JT	b	2015	M	1526	14.83	15.94	17.18	0.00	128.28
JA		2014	F	2731	6.84	18.43	36.17	0.14	124.93
LP	b	2015	F	2346	16.59	19.95	43.43	0.06	149.74
NP black	c	2017	F	676	2.58	25.87	28.08	0.03	73.76
LJ		2016	F	2117	50.21	56.62	64.60	0.05	91.46
JF	d	2016	F	2096	61.14	64.18	73.74	0.01	101.21
ND		2016	F	1922	65.44	73.94	106.66	2.99	218.41
LZ		2016	F	1648	84.26	90.53	121.51	0.06	156.86
KJ black		2017	M	1894	147.42	147.50	149.32	0.79	164.85
JB	d	2016	M	149	18.93	177.06	210.76	0.02	236.20
KN		2015	F	202	192.35	194.49	196.54	27.47	198.76
JL black	c	2017	F	0	NA	NA	NA	NA	NA

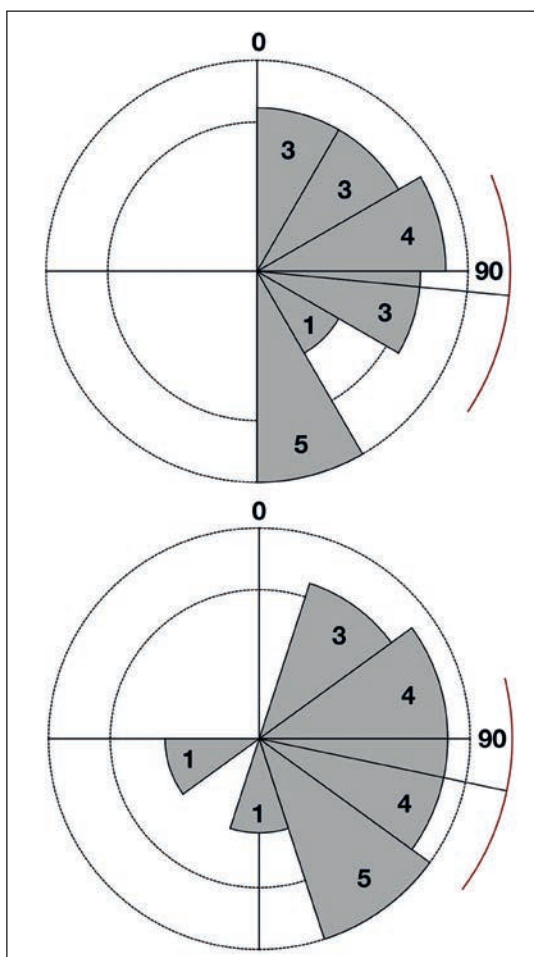
than males with median displacement values of 24.879 km and a maximum of 218.405 km with respect to males, which nonetheless showed the highest upper quartile (Q75) and the maximum absolute displacement of 249.786 km far from the nest cliff (*Table 1, Figure 3*). Only two pairs of siblings (b and d in *Table 2*) had statistically different travelling distances (Tukey's HSD with unequal N: $P = 0.00005$), but not the third pair (a in *Table 2*; Tukey's HSD with unequal N: $P = 0.980$).

The directions of leaving for the initial dispersal travel from the natal cliff (i.e. first day of wandering, see *Figure 2*) were statistically different from a uniform circular distribution (Rayleigh's z value = 14.51; $P = 0.0002$; $n = 18$), as all but one individual showed a clear tendency to fly away more to the northern, eastern and southern quadrants with respect to the nest-cliff location (*Figure 4* below). The pattern for the total sample of juvenile falcons showed a quite high concentration of dispersion (mean vector $r = 0.650$) headed for wandering directions with mean azimuth $\alpha = 101.85^\circ$ (bootstrapped 95% confidence = $76.4^\circ - 125.9^\circ$). Males and females did not differ in this pattern (Watson-Williams' $U_{1,16} = 0.019$; $P = 0.892$), as well as sibling duos (Watson-Williams' $U_{1,4} = 0.009$; $P = 0.928$). We found no significant correlation (circular correlation coefficient $r = -0.112$; $P = 0.61$; $n = 18$) between the individual azimuths of PFDP movements and those of the first day of wandering, meaning that the main direction of exploration during PFDP did not influence the direction of leaving the natal site.

Only five falcons exited the natal island borders and only for short periods.

Figure 4. Polar histogram of bearings, ordered clockwise from north (0°) and mean resultant bearing (with respect to East, 90°) taken by Peregrine Falcons during their post-fledging dependence period (above) and wandering phase (below) flights. The number of individuals taking a similar bearing is reported inside the grey inserts

4. ábra Elmozdulások iránya északról (0°) az óramutató járásának irányába rendezve, és ezeknek átlaga poláris hisztogrammal kifejezve. A felső panel a sólymok kirepülés utáni korai periódusát (PFDP) mutatja, míg az alsó a kóborló periódust. A hasonló irányba elmozduló egyedek száma a szürke cikkelyekben látható



Peregrine Falcon LZ did four short visits of 3-4 days each to Aeolian Island, from 24 August to 3 October 2016. Notably, two out the four visits of Falcon LZ were done reaching the Aeolian Island by nocturnal flights. Contrariwise, Falcon LJ did only a 4-hours trip to the Aeolian island of Filicudi, the 18 October 2017. Falcon ND crossed the Messina Strait the 15 July 2016 and went to Southern Calabria (Italy) for exactly one day before to come back Sicily. Falcon KJ flew over open sea for 4 hours to a maximum distance of 14 km, from the south-eastern coasts (far-off Siracusa, see *Figure 1*) and then came back. Eventually, Falcon NP, born in Salina island, from the 10 of August 2017, started moving back and forth among all the archipelago island but the far away Stromboli. The 20 of October 2017 reached in less than 2 hours inland eastern Sicily, near the Aetna volcano, where was unfortunately shot two days after the arrival, thus hampering us to gather information about its successive movements.

First wintering

Eleven of the 19 Peregrine Falcons provided complete (6 females, 1 males) or partial (3 females, 1 male) wintering data. Their median displacement value was 41.117 km distant from natal cliffs, with a maximum displacement of 153.822 km. Females displaced significantly farther than males during winter (Tukey's HSD with unequal N: $P = 0.00002$), but as in the case of wandering phase, a male had the highest upper quartile (Q75) and maximum winter displacement (*Table 1, Figure 3*). However, the net displacements of males referred to only two individuals and these results should be taken with caution (*Table 1, Figure 3*).

Complete data of seven falcons allowed focusing in more detail about the overwintering phase. All the seven falcons but one had a single wintering range, as falcon KJ had a double range in two nearby areas of 99.5 and 169.8 km², which it visited intermittently throughout the winter (*Figure 1*). Their average \pm SD home range during winter extended 135.65 ± 82.31 km² (min-max: 50.8-234.3) and is on average composed by cereal steppes (48%), arboreal crops (20%), agri-mosaics (12%), shrubland (9%), grazeland (7%), then urban areas (2%) and woodlands (2%). Such a quantitative composition is statistically different between all the seven falcons ($X^2_{36} = 3701.4$, $P = 0.0001$) as can be appreciated by the scatter in the bi-variate space of multidimensional scaling (*Figure 5*). The scatter arranges the individuals according to the decreasing quantity of cereal steppes used during winter (F1) and to the decrease of shrubland and increase of arboreal crops uses (F2). Thus, on F1 individuals JT and NS have 76.1% and 79.6% of cereal steppe composing their winter habitats while LZ has only 1.5%. On F2, shrubland decreases from 43.0% and 41.4% in ND and JA to 16.2% in LZ. This latter individual has on the contrary the highest quantity (i.e. 62.8%) of arboreal crops.

Despite these quantitative features of habitat configuration, the Peregrine Falcons were not randomly selecting the habitat in proportion to availability ($X^2_6 = 63.280$, $df = 72$, $P = 0.000$) and the standardized selection ratio B_i ranked the land-use classes by the probability of use such as: $B_{i-urban} = 0.21$, both $B_{i-agri-mosaic}$ and $B_{i-cereal} = 0.18$, $B_{i-arboreal\ crops} = 0.17$, $B_{i-shrubland} = 0.13$, $B_{i-grazeland} = 0.10$ and $B_{i-woodland} = 0.05$. Thus the probability of using the urban habitat, independently from its relative quantity in every individual's home range, is only slightly superior to that of agri-mosaics, cereal and arboreal crops, but two times more than grazeland and four times more than woodlands.

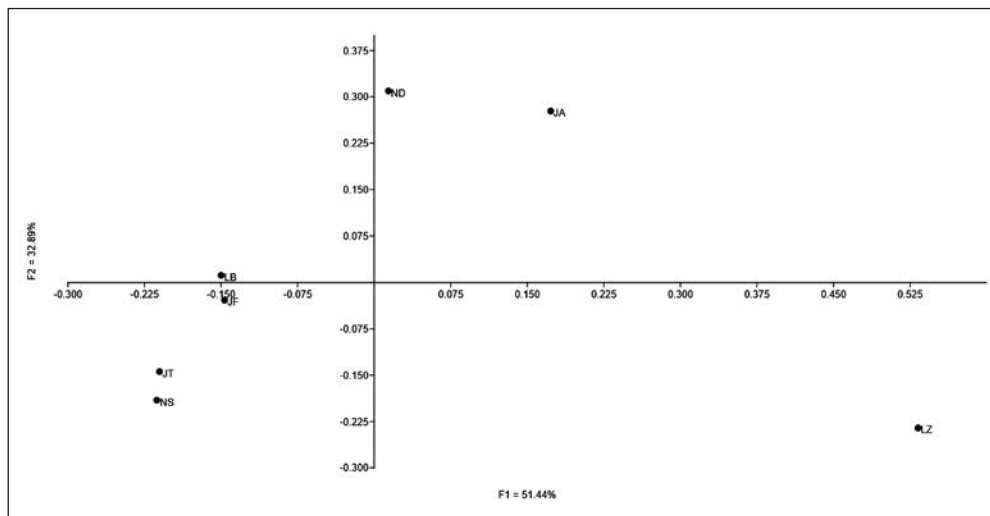


Figure 5. Scatter of seven juvenile Peregrine Falcons plotted in the bi-variate coordinate system of multidimensional scaling. The F1 and F2 axes express the percentage of variance accounted for by these factors and indicate their relative importance in explaining the spread in the data. Ordination along F1 expresses the decrease of cereal steppes use (from left to right), while along F2 expresses the decrease of shrubland and increase of areboreal crop use (from top to below) during winter. Each axis is scaled using the square root of its respective eigenvalue

5. ábra Fialat vándorsólymok élőhelyválasztása kétváltozós koordináta-rendszerben ábrázolva, többdimenziós skálázás segítségével. Az F1 és F2 tengelyek fejezik ki a két változó által magyarázott variancia százalékát és jelzik azok relatív fontosságát az eredmények kialakításában. Az F1 tengely mentén történő ordináció a gabonaföldek használatának csökkenését jelzi (balról jobbra), míg az F2 tengely csökkenő preferenciát jelez a bokros élőhelyek irányába és növekvőt a gyümölcsfás ligetek felé (fentről lefelé) a téli időszakban. Mindkét tengely a sajátértékeinek négyzetgyökével lett standardizálva

Data collection of nocturnal roost sites provided 4,475 locations during the wandering phase of 18 individuals, and 2,636 locations of 10 individuals during the wintering phase. At night during wandering juvenile falcons used 41.23% trees, 33.36% pylons and 25.41% rocks. These frequencies changed during wintering, with a decrease of tree use (24.09%) and an increase of pylon use (52.81%), while the frequency of rock use was similar (23.10%). Nonetheless, the GLMM yielded no significant results ($R^2 = 0.413$; $F_{65} = 1.898$; $P = 0.065$), as none of the tested single fixed effects (phase: $F_1 = 4.629$; $P = 0.06$; type of roost: $F_2 = 0.377$; $P = 0.688$), except for the intercept ($F_1 = 25.077$; $P = 0.000$), and neither the fixed interaction term (type of roost*phase: $F_2 = 1.682$; $P = 0.214$) were statistically significant. The random effect of 'individual' was not statistically significant either ($F_{17} = 0.897$; $P = 0.588$), and neither was its random interaction with phase (individual*phase: $F_9 = 0.785$; $P = 0.633$). Only the random interaction 'individual*type of roost' was statistically significant ($F_{34} = 2.297$; $P = 0.032$). This was occurring because few individuals, like for instance KL, disproportionately used more pylons (e.g. Tukey's HSD with unequal N: P of KL vs JB = 0.042; P of KL vs NS = 0.039; P of KL vs = 0.035, etc.) than the others.

Discussion

The onset of juvenile dispersal is a vital moment in the life history of raptors, since it is the time when juveniles definitively leave the nest but are still vulnerable and inexperienced (Newton 1979). Upon reaching independence, the foraging skills they acquire, as well as the moment they choose to leave, the places they visit, the distances they cover, and the general behavioural patterns they display will probably affect their chances of surviving and the severity of mortality rates (Bowler & Benton 2005, Walls *et al.* 2005, Kitowski 2009).

The availability of individual-based biollogging technologies has produced an exponential increase of published papers on bird movements in the last 30 years (e.g. *Figure 2* in López-López 2016). Nonetheless, most dispersal studies on Peregrine Falcons are still based on recoveries of banded birds (but see Dixon *et al.* 2012), besides focusing on migrating populations located in North America and North Eurasia (Dixon *et al.* 2012, Katzner *et al.* 2012, Dennhardt & Wakamiya 2013, Faccio *et al.* 2013, Mattox & Restani 2014), with few exceptions for the rest of Europe, like Zuberogoitia *et al.* (2009) who provided recovery distances from Spain.

Natal dispersal data presented here are the first study by satellite telemetry concerning juveniles from a Peregrine Falcon population living in Mediterranean island of Southern Europe. We distinguished a post-fledging dependence period (Morrison & Wood 2009, Penteriani & Delgado 2009) close to the natal cliff, including the temporary excursions (Walls & Kenward 1995) made by fledglings back and forth the natal cliff and usually within the same day. Departure from natal area, as indicated by a net displacement increase (Kareiva & Shigesada 1983, Turchin 1998) and peaks of cumulated coefficient of displacement variation (Limiñana *et al.* 2008), specified the first true step in the dispersal process of Peregrine Falcons, that we called wandering as in Penteriani and Delgado (2009). The third step related to the onset of natal dispersal we have analyzed, is the settlement in a territory during winter, when Peregrine Falcons occupy their first home-range choosing one or many roosts to exploit the habitat during the non-breeding season.

During post-fledging dependence period, altricial birds rely on their parents for food, while simultaneously developing the flight, foraging and social skills necessary for independent survival (Weathers & Sullivan 1989, Wheelwright & Templeton 2003). After fledging, Sicilian Peregrine Falcons stayed very close to the natal cliff and explored small areas nearby. In agreement with the few studies on raptors recording PFPD distances between sex (Seaton *et al.* 2008, López-López *et al.* 2014), we did not find significant difference between females and males. The duration of post-fledging dependence period differs among raptor species, ranging from 143–231 days in the Bearded Vulture *Gypaetus barbatus* (López-López *et al.* 2014) to 2–8 days in Lesser Kestrel *Falco naumanni* (Bustamante & Negro 1994). It likely does not only depend on body-size and/or lifespan, as it lasts longer in the smaller, magpie-size New Zealand Falcon *Falco novaeseelandiae* (76 days, Seaton *et al.* 2008), than in larger species like the Osprey *Pandion haliaetus* (18–46 days, Bustamante 1995) or the Black Kite *Milvus migrans* (15–36 days, Bustamante & Hiraldo 1989). Juvenile Peregrine Falcons would reach independence in two or more months

(Cramp & Simmons 1980), a figure comparable to the 47 days (range: 27–84) of PFDP shown in our sample, and to the 50–82 days of juveniles tracked in Iowa (Powell *et al.* 2002). However, Dzialak *et al.* (2009) recorded a shorter period (15–36 days) during another tracking programme in USA, and observed that different rearing and habitat conditions significantly influenced the PFDP duration.

Environmental conditions experienced by juveniles within the natal area soon after fledging may play the ultimate role in determining the timing and orientation of dispersal (Hanson *et al.* 2003, Pasinelli *et al.* 2004, Walls *et al.* 2005), and might explain better than body-size and/or lifespan, and according to Dzialak *et al.* (2009), the PFDP patterns observed in Peregrine falcons and other raptors. As in the Osprey we found no relation between fledging date and PDFP duration (Bustamante 1995), in contrast to what was found in the Black Kite, in which migratory urgency seems to affect the timing of family break-up (Bustamante & Hiraldo 1989). Despite the overall PFDP pattern described so far, we should emphasise the role of individual behaviour during this phase, because only some individuals made temporary daily excursions of 40–50 km when still dependent on parents. In addition, all falcons scattered their flights from NNE to SSE, regardless from sex and sibling condition, and this resulted in a non-random bearing of PFDP flights headed on average toward 95° East.

Wandering is another particularly important period, because juvenile raptors both explore new areas potentially suitable for future settlement, and start to hunt exclusively by themselves for the rest of their life. The start of wandering in Sicilian Peregrines occurs on average in early July and lasts until 30 November according to the conventional deadline we used to distinguish wandering from the wintering phase. In most avian species, with the remarkable exception of migratory birds which disperse much farther than resident species (e.g. Kassara *et al.* 2017), dispersers move relatively short distances, and long-distance dispersal is uncommon (Sutherland *et al.* 2000). Many raptor species, from small kestrels to large vultures, have been reported to exhibit great individual variation in the timing of dispersal (e.g. Bustamante & Hiraldo 1989, Bustamante & Negro 1994, Walls & Kenward 1998, López-López *et al.* 2014). In our study, Peregrine Falcons travelled relatively short median distances of some 25 km, but showed large individual variation. Strictly speaking, one third of the 18 individuals in which we measured this phase did not disperse, showing median movements less than 10 km far from the natal cliff, but with temporary excursions in the range of 50–250 km. The presence of non-dispersers has already been noted in raptor populations (e.g. Walls & Kenward 1998). The other Sicilian individuals moved a maximum median distance of 200 km, with independent trajectories and being apparently limited only by the size of the island. We documented only occasional trips taken outside the island borders, most of them directed to the well visible Aeolian Island. Vice versa the juvenile tagged in Salina moved to Sicily. Females dispersed farther than males, as occurs in many bird species, including raptors and Peregrine Falcons (Greenwood 1980, Sutherland *et al.* 2000, Zuberogoitia *et al.* 2009, Katzner *et al.* 2012, Faccio *et al.* 2014).

Excluding the group of poorly dispersing individuals, and considering the insular context, the distances travelled by the Sicilian juveniles are comparable to those of continental

populations. Female Peregrine Falcons from Northern Spain dispersed on average 80 km, and males 52 km during their pre-breeding movements (Zuberogoitia *et al.* 2009). In the New England (USA) population (Faccio *et al.* 2014), 75% of encounters occurred within the study area, with female dispersing greater distances (153 km) than males (88 km). However, the range of the remaining 25% of individuals extended until to Cuba and Nicaragua. Both Tordoff and Reding (1997) and Katzner *et al.* (2012) reported greater and much more variable dispersal distances, again with significant sex differences and with similar means (337 and 320 km for females, 161 and 176 km for males, respectively). As in the case of PFDPs, the first dispersal flights of Peregrine Falcons had a non-random bearing, on average toward 102° East. The main heading during PFDP did not influence the heading of the first dispersal flights. Juveniles, without sex differences, scattered mostly across the NNE and S quadrants, and only one individual did a westerly first dispersal flight. Non-random east-west bearing during dispersal has been already noted in Common Buzzard *Buteo buteo* (Walls & Kenward 1998), although with significant easterly directions only during the second wintering year. Such a non-random bearing in both PFDPs and first dispersal flights is probably related to the island geography, as already noted by Walls and Kenward (1998), who suggested that dispersing individuals cannot head south in their UK study area, due to the coasts, which act as barriers.

The seven individuals providing complete wintering data had independent home ranges scattered across Sicily and varying in size, the largest (234 km²) was 4 times larger than the smallest one (51 km²). We recorded a single case of spatial overlap of two falcons overwintering in the same area but in different years, and one individual had a double home-range and moved between the areas during the entire winter. Seven land-use classes were present in these wintering areas, however, falcons spent the majority of their time in cereal steppes, followed by arboreal crops, agri-mosaics and by the other land-use types. Habitat use indicates that juveniles choose open habitats, particularly human-managed and cultivated areas with both extensive non-irrigated cereal steppes and intensive (e.g. vineyards) crops. Nonetheless, land-use classes were not used proportionally to their availability, as the selection ratio (i.e. probability of use) specified, likely ranking the winter habitats according to the abundance of preferred prey flocks (feral and wood pigeons, starlings, jackdaws, magpies, etc.). Urban, arboreal crops, agri-mosaics and cereal steppes had a selection ratio higher than semi-natural habitats (shrubland, grazeland and woodland). This preference was consistent with the significant individual differences between the frequency of locations among the assortment of land-use classes. A similar use of open cultivated habitats during dispersal has been observed in the Bonelli's Eagle *Aquila fasciata* (Cadahía *et al.* 2010).

No data are currently available in the literature on roost use during the nights of the dispersal period. Overall, the frequency of chosen roost types was consistent between wandering and wintering with falcons roosting mostly on trees, rocks and pylons. Only three individuals had significantly different use of roost sites, roosting significantly more on pylons or rocks.

Concluding remarks

Judging from the onset of dispersal and genetic (see Mengoni *et al.* 2018) data available, the Peregrine Falcons living in Sicily and the surrounding island should be connected to a single and resident population, with still undetected but presumably poor connections to continental Italy. The progressing of investigation on natal dispersal will inform on the floater ecology of this population and will improve our understanding on the population dynamic of the Peregrine Falcons living in Mediterranean island.

Acknowledgements

We thank N. Antioco, E. Vitale, L. Zanca for the great field support during the study. Zoltán Németh made useful comments that improved notably the manuscript. Funding was provided by the Nando & Elsa Peretti Foundation project no. 442. This study complies with the current Italian laws regulating scientific research on animals.

References

- Andreassen, H. P., Stenseth, N. C. & Ims, R. A. 2002. Dispersal behaviour and population dynamics of vertebrates. – In: Bullock, J. M., Kenward, R. E. & Hails, R. S. (eds.) *Dispersal ecology*. – Blackwell Publishing, Oxford, pp. 237–256.
- Amato, M., Ossino, A., Brogna, A., Cipriano, M., D'Angelo, R., Dipasquale, G., Mannino, V., Andreotti, A. & Leonardi, G. 2014. Influence of habitat and nest-site quality on the breeding performance of Lanner Falcons *Falco biarmicus*. – *Acta Ornithologica* 49: 1–7. DOI: 10.3161/000164514X682841
- Batschelet, E. 1981. *Circular statistics for Biology*. – Academic Press, London
- Beatty, W. S., Kesler, D. C., Webb, E. B., Raedeke, A. H., Naylor, L. W. & Humburg, D. D. 2013. Quantitative and Qualitative Approaches to Identifying Migration Chronology in a Continental Migrant. – *PLoS ONE* 8(10): e75673. DOI: 10.1371/journal.pone.0075673
- Bennetts, R. E., Nichols, J. D., Lebreton, J. D., Pradel, R., Hines, J. E. & Kitchens, W. M. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals. – In: Clobert, E., Danchin, A. A., Dhondt, A. A. & Nichols J. D. (eds.) *Dispersal*. – Oxford University Press, New York, pp. 3–17.
- Boulinier, T., Danchin, E., Monnat, J. Y., Doutrelant, C. & Cadiou, B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. – *Journal of Avian Biology* 27: 252–256. DOI: 10.2307/3677230
- Bowler, D. E. & Benton T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biological Reviews* 80: 205–225. DOI: 10.1017/S1464793104006645
- Bunnfeld, N., Borger L., Van Moorter, B., Rolandsen, C. M. & Dettki, H. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. – *Journal of Animal Ecology* 80: 466–476. DOI: 10.1111/j.1365-2656.2010.01776.x
- Bullock, J. M., Kenward, R. E. & Hails, R. S. 2002. *Dispersal ecology*. – Blackwell Publishing, Oxford
- Bustamante, J. 1995. The duration of the post-fledging dependence period of Ospreys *Pandion haliaetus* at Loch Garten, Scotland. – *Bird Study* 42: 31–36. DOI: 10.1080/00063659509477145
- Bustamante, J. & Hiraldo, F. 1989. Post-fledging dependence period and maturation of flight skills in the Black Kite *Milvus migrans*. – *Bird Study* 36: 199–204. DOI: 10.1080/00063658909477025
- Bustamante, J. & Negro, J. J. 1994. The post-fledging dependence period of the Lesser Kestrel (*Falco naumanni*) in Southwestern Spain. – *Journal Raptor Research* 28: 158–163.
- Cadahía, L., López-López, P., Urios, V. & Negro, J. J. 2010. Satellite telemetry reveals individual variation in juvenile Bonelli's Eagle dispersal areas. – *European Journal Wildlife Research* 56: 923–930. DOI: 10.1007/s10344-010-0391-z

- Cade, T. J., Enderson, J. H., Thelander, C. G. & White, C. M. 1988. Peregrine Falcon populations: their management and recovery. – Boise, Idaho
- Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. – *Philosophical Transactions of the Royal Society B* 365: 2157–2162. DOI: 10.1098/rstb.2010.0107
- Clobert, J., Ims, R. A. & Rousset, F. 2004. Causes, mechanisms and consequences of dispersal. – In: Hanski, I. & Gaggiotti, O. E. (eds.) *Ecology, Genetics and Evolution of Metapopulations* – Academic Press, Cambridge, M., pp. 307–335.
- Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. & Butler, P. J. 2004. Biotelemetry: a mechanistic approach to ecology. – *Trends in Ecology and Evolution* 19: 334–343. DOI: 10.1016/j.tree.2004.04.003
- Cramp, S. & Simmons, K. E. L. 1980. *The Birds of the Western Palaearctic*, Vol. 2. – Oxford University Press, New York
- Dennhardt, A. J. & Wakamiya, S. M. 2013. Effective dispersal of Peregrine Falcons (*Falco peregrinus*) in the Midwest, U.S.A. – *Journal of Raptor Research* 47: 262–270. DOI: 10.3356/JRR-12-30.1
- Dixon, A., Sokolov, A. & Sokolov, V. 2012. The subspecies and migration of breeding Peregrines in northern Eurasia. – *Falco* 39: 4–9.
- Doligez, B., Danchin, E. & Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. – *Science* 297: 1168–1170. DOI: 10.1126/science.1072838
- Dzialak, M. R., Carter, K. M., Lacki, M. J., Westneat, D. F. & Anderson, K. 2009. Activity of post-fledging Peregrine Falcons in different rearing and habitat conditions. – *Southeastern Naturalist* 8: 93–106. DOI: 10.1656/058.008.0109
- EEA – European Environmental Agency 2000. *Corine Land Cover Technical Guide*. – Addendum 2000. Accessed 10 November 2013. <http://www.eea.eu.int>.
- Faccio, S. D., Amaral, M., Martin, C. J., Lloyd, J. D., French, T. W. & Tur, A. 2013. Movement patterns, natal dispersal, and survival of Peregrine Falcons banded in New England. – *Journal of Raptor Research* 47: 246–261. DOI: 10.3356/JRR-12-21.1
- Ferrer, M. 1996. Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti* – *Ibis* 135: 132–138. DOI: 10.1111/j.1474-919X.1993.tb02824.x
- Grémillet, D. & Boulinier, T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. – *Marine Ecology Progress Series* 391: 121–137. DOI: 10.3354/meps08212
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – *Animal Behaviour* 28: 1140–1162. DOI: 10.1016/S0003-3472(80)80103-5
- Greenwood, P. J. & Harvey, P. H. 1982. The natal and breeding dispersal of birds. – *Annual Review Ecology and Systematics* 13: 1–21. DOI: 10.1146/annurev.es.13.110182.000245
- Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. – *Palaeontologia Electronica* 4: 1–9.
- Hansson, B., Bensch, S. & Hasselquist, D. 2003. Heritability of dispersal in the Great Reed Warbler. – *Ecology Letters* 6: 290–294. DOI: 10.1046/j.1461-0248.2003.00436.x
- Kareiva, P. M. & Shigesada, N. 1983. Analyzing insect movement as a correlated random walk. – *Oecologia* 56: 234–238. DOI: 10.1007/BF00379695
- Kassara, C., Gangoso, L., Mellone, U., Piasevoli, G., Hadjikyriadou, T., Tsiopelas, N., Giokas, S., Lopez-Lopez, P., Urios, V., Figuerola, J., Silva, R., Bouten, W., Kirschel, A. N. G., Virani, M. Z., Fiedler, W., Berthold, P. & Gschwend, M. 2017. Current and future suitability of wintering grounds for a long-distance migratory raptor. – *Scientific Reports* 7: 8798. DOI: 10.1038/s41590-017-08753-w
- Katzner, T., Winton, J. D., McMorris, F. A. & Brauning, D. 2012. Dispersal, band encounters, and causes of death in a reintroduced and rapidly growing population of Peregrine Falcons. – *Journal of Raptor Research* 46: 75–83. DOI: 10.3356/JRR-10-93.1
- Kitowski, I. 2009. Social learning of hunting skills in juvenile Marsh Harriers *Circus aeruginosus*. – *Journal of Ethology* 27: 327–332. DOI: 10.1007/s10164-008-0123-y
- Kokko, H. & López-Sepulcre, A. 2006. From individual dispersal to species ranges: perspectives for a changing world. – *Science* 313: 789–791. DOI: 10.1126/science.1128566
- Limiñana, R., Soutullo, A. & Urios, V. 2007. Autumn migration of Montagu's Harriers *Circus pygargus* tracked by satellite telemetry. – *Journal of Ornithology* 148: 517–523. DOI: 10.1007/s10336-007-0182-9
- Limiñana, R., Soutullo, A., López-López, P. & Urios, V. 2008. Pre-migratory movements of adult Montagu's Harriers *Circus pygargus*. – *Ardea* 96: 81–96. DOI: 10.5253/078.096.0109

- Lo Cascio, P. 2017. Luoghi e Natura di Sicilia I: Le Isole Eolie [Sicily's Sites and Nature: The Aeolian Island, Vol. I.]. – Edizioni Danaus, Palermo
- López-López, P., Gil, J. A. & Alcántara, M. 2014. Post-fledging dependence period and onset of natal dispersal in Bearded Vultures (*Gypaetus barbatus*): new insights from GPS satellite telemetry. – Journal Raptor Research 48: 173–181. DOI: 10.3356/JRR-13-00072.1
- López-López, P. 2016. Individual-based tracking systems in ornithology: welcome to the era of big data. – Ardeola 63: 103–136. DOI: 10.13157/arla.63.1.2016.rp5
- Manly, B., Mc Donald, L. & Thomas, D. 1993. Resource selection by animals. – Chapman & Hall, London
- Mattox, W. G. & Restani, M. 2014. Migratory movements and mortality of Peregrine Falcons banded in Greenland, 1972–97. – Arctic 67: 433–440. DOI: 10.14430/arctic4420
- Morrison, J. L. & Wood, P. B. 2009. Broadening our approaches to studying dispersal in raptors. – Journal Raptor Research 43: 81–89. DOI: 10.3356/JRR-08-33.1
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E. 2008. A movement ecology paradigm for unifying organismal movement research. – Proceedings of the National Academy of Sciences 105: 19052–19059. DOI: 10.1073/pnas.0800375105
- Nevoux, M., Nicoll, M., Arlt, D., Jones, C. & Norris, K. 2013. The short- and long-term fitness consequences of natal dispersal in a wild bird population. – Ecology Letters 16: 438–445. DOI: 10.1111/ele.12060
- Newton, I. 1979. Population Ecology of Raptors. – T & AD Poyser, London
- Nocera, J. J., Forbes, G. J. & Giraldeau, L. A. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. – Proceedings Royal Society of London Series B 273: 349–355. DOI: 10.1098/rspb.2005.3318
- Pasinelli, G., Schiegg, K. & Walters, J. R. 2004. Genetic and environmental influences on natal dispersal distances in a resident bird species. – American Naturalist 264: 660–669. DOI: 10.1086/424765
- Penteriani, V. & Delgado, M. 2009. Thought on natal dispersal. – Journal of Raptor Research 43: 90–98. DOI: 10.3356/JRR-08-39.1
- Ponchon, A., Grémillet, D., Doligez, B., Chambert, T., Tveraa, T., González-Solís, J. & Boulinier, T. 2013. Tracking prospecting movements involved in breeding habitat selection: insights, pitfalls and perspectives. – Methods Ecology and Evolution 4: 143–150. DOI: 10.1111/j.2041-210x.2012.00259.x
- Powell, L. A., Calvert, D. J., Barry, I. M. & Washburn, L. 2002. Post-fledging survival and dispersal of Peregrine Falcons during a restoration project. – Journal Raptor Research 36: 176–182.
- QGIS Development Team 2016. QGIS Geographic Information System. – Open Source Geospatial Foundation Project
- Reed, J. M., Boulinier, T., Danchin, E. & Oring, L. W. 1999. Informed dispersal: prospecting by birds for breeding sites. – Current Ornithology 15: 189–259.
- Rodríguez, A., Negro, J. J., Fox, J. W. & Afanasyev, V. 2009. Effects of geolocator attachments on breeding parameters of Lesser Kestrels *Falco naumanni*. – Journal of Field Ornithology 80: 399–407. DOI: 10.1111/j.1557-9263.2009.00247.x
- Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annual Review of Ecology, Evolution and Systematics 38: 231–253. DOI: 10.1146/annurev.ecolsys.38.091206.095611
- Sarà, M. 2008. Breeding abundance of threatened raptors as estimated from occurrence data. – Ibis 150: 766–778. DOI: 10.1111/j.1474-919X.2008.00856.x
- Sarà, M. 2014. Spatial analysis of Lanner Falcon habitat preferences: Implications for agro-ecosystems management at landscape scale and raptor conservation. – Biological Conservation 178: 173–184. DOI: 10.1016/j.biocon.2014.08.004
- Sarà, M., Mascara, R. & López-López, P. 2016. Understanding the coexistence of competing raptors by Markov chain analysis enhances conservation of vulnerable species. – Journal of Zoology London 299: 163–171. DOI: 10.1111/jzo.12340
- Schenk, H., Chiavetta, M., Falcone, S., Fasce, P., Massa, B., Mingozi, T. & Saracino, U. 1983. Il Falco pellegrino: indagine in Italia [The Peregrine Falcon in Italy]. – Serie Scientifica LIPU, Parma
- Seaton, R., Holland, J. D., Minot, E. O. & Springett, B. P. 2008. Natal dispersal of New Zealand Falcon (*Falco novaeseelandiae*) in plantation forests. – Notornis 55: 140–145.
- Serrano, D., Forero, M. G., Donazar, J. A. & Tella, J. L. 2004. Dispersal and social attraction affect colony selection and dynamics of Lesser Kestrels. – Ecology 85: 3438–3447. DOI: 10.1890/04-0463

- Spina, F. & Volponi, S. 2008. Atlante della Migrazione degli Uccelli in Italia. 1. non-Passeriformi [Italian Bird Migration Atlas 1. Non-Passeriformes]. – Ministero dell’Ambiente e della Tutela del Territorio e del Mare – Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA). Tipografia CSR-Roma
- Sutherland, G. D., Harestad, A. S., Price, K. & Lertzman, K. P. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. – *Conservation Ecology* 4: 1–16. DOI: 10.5751/ES-00184-040116
- Tordoff, H. B. & Redig, P. T. 1997. Midwest Peregrine Falcon demography, 1982–1995. – *Journal of Raptor Research* 31: 339–346.
- Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. – Sinauer Associates, Sunderland, Massachusetts
- Van Dyck, H. & Baguette, M. 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? – *Basic Applied Ecology* 6: 535–545. DOI: 10.1016/j.baae.2005.03.005
- Walls, S. & Kenward, R. 1995. Movements of radio-tagged Buzzards *Buteo buteo* in their first year. – *Ibis* 137:177–182. DOI: 10.1111/j.1474-919X.1995.tb03237.x
- Walls, S. & Kenward, R. 1998. Movements of radiotagged Buzzards *Buteo buteo* in early life. – *Ibis* 140: 561–568. DOI: 10.1111/j.1474-919X.1998.tb04700.x
- Walls, S., Kenward, R. E. & Holloway, G. J. 2005. Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal. – *Journal Animal Ecology* 74: 190–197. DOI: 10.1111/j.1365-2656.2005.00914.x
- Weathers, W. W. & Sullivan, K. A. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. – *Ecological Monographs* 59: 223–246. DOI: 10.2307/1942600
- Wheelwright, N. T. & Templeton, J. J. 2003. Development of foraging skills and the transition to independence in juvenile Savannah Sparrows. – *Condor* 105: 279–287. DOI: 10.1650/0010-5422(2003)105[0279:DOFSAT]2.0.CO;2
- White, C. M., Cade, T. J. & Henderson, J. H. 2013. *Peregrine Falcons of the World*. – Lynx Edicions, Barcelona
- Zuberogoitia, I., Martínez, J. A., Azkona, A., Martínez, J. E., Castillo, I. & Zabala, J. 2009. Using recruitment age, territorial fidelity and dispersal as decisive tools in the conservation and management of Peregrine Falcon (*Falco peregrinus*) populations: the case of a healthy population in Northern Spain. – *Journal Ornithology* 150: 95–101. DOI: 10.1007/s10336-008-0321-y

