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Exploring juvenile golden eagles' dispersal movements at two different temporal scales

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The spatial distribution of populations is the result of individuals' movements. In territorial species, the spatial dynamics of populations is to a large degree shaped by individuals' ranging behaviour during their juvenile dispersal. Here we use information on juvenile golden eagles (*Aquila chrysaetos*) tracked by satellite telemetry, to explore the effects of daily behavioural decisions on their dispersal strategy during their first year of life. When analysed on a biweekly basis, the large-scale movements of golden eagles did not differ from a correlated random walk (CRW) model of dispersal. Although in the long term such a strategy maximises the acquisition of information on good hunting areas, finding a mate and a vacant territory in a landscape, it is expensive in terms of energy requirements. At the finer scale of daily foraging movements, movement patterns were non-random, probably reflecting animals' oriented movements towards sites with high chances of successful hunting. We suggest that the key issue to take into account when exploring the factors determining individuals' dispersal strategies is how strongly the daily movements are influenced by an active search for food. This is to a large degree determined by food availability and individuals' ability to accumulate reserves. In our case, the individuals with the lowest proportion of foraging habitats within their dispersal areas showed large-scale movements more restricted than expected from a CRW. Also, distances covered by individuals in their biweekly movements were both larger and more variable in winter, when food availability diminishes.

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INTRODUCTION

Over the last decades there has been an increasing realization of the importance of understanding individual behaviour to understand populations' behaviour (SUTHERLAND & DOLMAN 1994; SUTHERLAND 1996, 1998; UCHMANSKI 2000; GRIMM & UCHMANSKI 2002; MORALES & ELLNER 2002; FERRER et al. 2004; NORRIS 2004), and an increasing awareness of the key roles of space in population dynamics, and individuals' dispersal for population persistence (TILMAN & KAREIVA 1997; HANSKI 1999; CLOBERT et al. 2001; PENTERIANI et al. 2005a, 2005b, 2006; HAWKES 2009; DELGADO et al. 2009, 2010a, 2010b). Understanding how animals disperse is key for the proper management and conservation of spatially structured populations (SUTHERLAND 1998; HANSKI 1999; REVILLA et al. 2004; PENTERIANI et al. 2005a, 2005b, 2006).

Animal movements have profound effects on biological processes at many organizational levels (NAMS 2006). Although there have been theoretical advances in linking ranging behaviour and population dynamics, empirical analyses testing theoretical expectations are still scarce (see e.g. TURCHIN 1991; ZOLLNER & LIMA 1999; REVILLA et al. 2004). One of the most widespread approaches used to account for the effects of individuals' movements on population dynamics is the analysis of diffusion models (KAREIVA & SHIGESADA 1983; TURCHIN 1991; LEVIN & PACALA 1997; TILMAN et al. 1997; HAWKES 2009). These models assume that random movement is a reasonable description of individuals' ranging behaviour (KAREIVA & SHIGESADA 1983; TURCHIN 1991; LEVIN & PACALA 1997; TILMAN et al. 1997). However, several analyses of animal movements have shown that individuals exhibit a range of movement strategies (KAREIVA & SHIGESADA 1983; FERRER 1993a; BERGMAN et al. 2000; CONRADT et al. 2000, 2001, 2003; BOWNE & WHITE 2004; PE'ER et al. 2004; REVILLA et al. 2004; NAMS 2006; BROOKS & HARRIS 2008), and that the type of movement performed by individuals has significant implications for the spatial dynamics of populations (TURCHIN 1998). Another limitation of diffusion models is that they use a mean-field approach to describe individuals' behaviour, usually assuming that they move in identical fashion and without influencing the movement of one another (TURCHIN 1991; LEVIN & PACALA 1997). This is hardly tenable in long-living animals with complex cognitive capacities, as interactions among individuals and differences in cognitive abilities, experience, and physiological state do have an effect on population dynamics (FERRER 1993b; FERRER & DONÁZAR 1996; SUTHERLAND 1996; UCHMANSKI 2000; GRIMM & UCHMANSKI 2002; GRIMM et al. 2003; FERRER et al. 2004; ROSSMANITH et al. 2005; SOUTULLO et al. 2006a; VUILLEUMIER & PERRIN 2006; HAWKES 2009; DELGADO et al. 2010a, 2010b).

Actually, to understand how behavioural decisions affect individuals' ranging behaviour and, thus, the dynamics observed at the population level, there is a need to understand which factors shape the strategies followed by dispersing individuals, and to consider the evolutionary pressures that generated and maintain them (HAWKES 2009; DELGADO et al. 2010b). Animals with a long dispersal period need to eat to survive and find a vacant territory to breed. There are two main kinds of movements animals can undertake to fulfil their needs: oriented and un-oriented movements. Oriented movements require a pre-fixed goal the animal wants (needs, prefers) to move towards, and some kind of long-distant orientation mechanism to locate it (NAMS 2006). Large

vertebrates use this kind of "far-sighted" strategy when moving across heterogeneous landscapes, which allows them to detect suitable habitats (the goal) within a given perceptual range (VUILLEMIER & PERRIN 2006). Oriented movements are an efficient strategy for locating suitable habitats when foraging (CONRADT et al. 2003).

However, oriented movements restrict animals to a limited set of fixed paths determined by local structures and corridors, with poorly attractive areas or frontiers acting as barriers, constraining the fraction of the whole landscape that is actually visited (CONRADT et al. 2003; VUILLEMIER & PERRIN 2006). For a dispersing individual in search of a breeding territory, random (un-oriented) movements constitute a better strategy, as they allow a complete examination of the whole landscape (VUILLEMIER & PERRIN 2006). Correlated random walks (CRW) are reasonable descriptions of many individuals' un-oriented movements (see e.g. BROOKS & HARRIS 2008). CRW models assume that although animals do not move in a preferred direction, the directions of consecutive moves are not completely independent (KAREIVA & SHIGESADA 1983; MCCULLOCH & CAIN 1989; ZOLLNER & LIMA 1999; BERGMAN et al. 2000; NAMS 2006). From a dispersal point of view such a "blind" strategy allows individuals to acquire better information on the distribution of hunting places and potential mates or breeding territories within their dispersal areas. Yet, this kind of strategy is the most demanding in terms of energy requirements (VUILLEMIER & PERRIN 2006), and thus can only be employed by animals that may accumulate reserves to fast for longer or can alternatively exploit food resources abundant enough to fulfil individuals' needs. When energy sources are in short supply, a "far-sighted" (oriented) strategy is more effective in energetic terms (CONRADT et al. 2003; VUILLEMIER & PERRIN 2006).

The golden eagle (*Aquila chrysaetos*) is a long-lived species with complex cognitive capacities, and thus is a useful model species to explore how behavioural decisions, at different temporal scales, affect dispersal dynamics. Like other large territorial raptors, after their first flight they spend several months improving their flying and hunting techniques within the parental territory (e.g., WATSON 1997; FERRER 2001). They do not usually breed until their fourth year of life (but see URIOS et al. 2007), and during the period between the time they become independent and their first breeding attempt, individuals explore an area of up to 18,000 km^2, acquiring information on the distribution of suitable sites for foraging and vacant territories for breeding (WATSON 1997; SOUTULLO et al. 2006c, 2006d; URIOS et al. 2007). Their spatial distribution as adults is the result of that process of juvenile dispersal, which in turn reflects the spatial and temporal availability of suitable territories for breeding (see e.g., LÓPEZ-LÓPEZ et al. 2007).

Here we used information on golden eagles tracked by means of satellite telemetry during their first year of juvenile dispersal, to test whether their movement patterns differed when analysed at different temporal scales. To this end we compared their observed dispersal pattern with a CRW dispersal model, considered as a proxy for many un-oriented dispersal patterns (see e.g. BROOKS & HARRIS 2008). We analysed movements at daily and biweekly scales. As daylong movements would better reflect daily foraging decisions, we expected that at this scale the movement pattern would deviate from randomness. This would reflect animals' oriented movements in search of food, with eagles remaining for longer in good hunting areas (i.e., with net displacement being smaller than expected from a CRW model), and just crossing (i.e., with net displacement being larger than expected from a CRW model) less favourable ones (ZOLLNER & LIMA 1999; NOLET & MOOIJ 2002). Yet, these daily movements scale up to shape the large-scale movements used by golden eagles to explore their dispersal

areas. Therefore, we also explored whether dispersing golden eagles use a more effective "blind" strategy when searching for a vacant territory (i.e., with net displacement being as expected from a CRW model), or if the high energy requirements of that strategy force them to move around a more restricted circuit, as expected from a "far-sighted" dispersing strategy (i.e., with net displacement being smaller than expected from a CRW model).

Finally, to evaluate whether food availability might explain the patterns observed, we tested for differences in (a) the pathways followed by individuals in winter, when food becomes scarcer, and the rest of the year, and (b) the proportion of foraging habitats within individuals' dispersal areas.

STUDY AREA

Birds were tracked throughout most of the northern and eastern Iberian Peninsula, covering an area of ca 150,000 km^2 (Fig. 1). The area encompasses a range of environments, including both high plateaus and mountain ranges, covered by deciduous and evergreen forests, scrublands and cultivated areas. The climate is also rather diverse, including mainly areas dominated by Mediterranean climate. This includes warm to hot summers with mild to cool winters and annual precipitation averaging 600 mm in the Northern and Eastern Mediterranean coast, and cold winters (depending mostly on altitude) and hot summers, with relatively dry weather (400–600 mm per year) in the inner plateau (SOUTULLO et al. 2007).
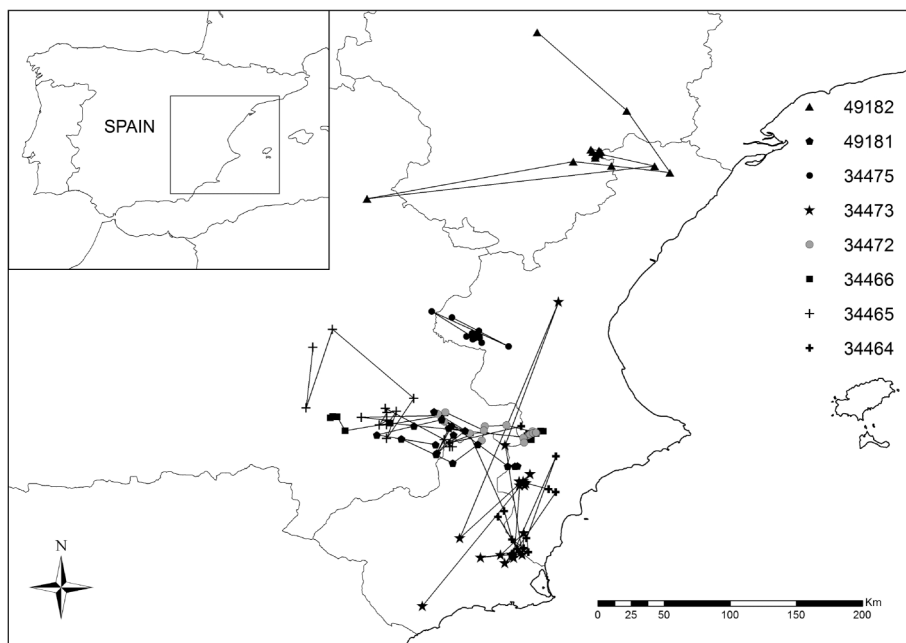

Fig. 1. — Biweekly movements of eight golden eagles during their first year of life in Spain. The different symbols indicate the centroids of the biweekly locations of each bird. Spanish Administrative units are shown.

MATERIALS AND METHODS

We used satellite telemetry to collect information on the locations of eight juvenile golden eagles tagged in eastern Spain. Individuals were captured between May 2002 and July 2004, while still in the nest, at an age of ca. 50 days old. At that age chicks have almost attained adult size but the risk of early fledging is limited (WATSON 1997). Platform transmitter terminals (PTTs) were fixed to the birds' backs using a breakaway Teflon harness, to allow for the PTTs to eventually fall off. Three types of PTTs, all manufactured by Microwave Telemetry Inc., were used: 45 g PTT-100, 50 g Solar PTT-100, and 70 g Argos/GPS Solar PTT-100. The equipment never exceeded 2.5% of the juveniles' body mass, below the 3% suggested by KENWARD (2001) to minimize the impact of the extra load on birds' behaviour and performance. For computational purposes all individuals were treated as if tagging had occurred when they were exactly 50 days old. Locations were collected using the Argos system. Argos assigns a measure of estimates' reliability (LC) to each position estimate, and two of the PTTs had a global positioning system (GPS) incorporated, providing locations with an accuracy of < 20 m (see SOUTULLO et al. 2007 and references therein). For the other six PTTs we did not consider locations assigned to LCs B (which are highly unreliable) for the analyses, and locations in LCs 0 and A were only used when they were consistent with golden eagles' behaviour in terms of distance covered in a given amount of time (see e.g., SOUTULLO et al. 2006b; CADAHÍA et al. 2007). Birds were tracked for as long as signal reception continued, although here we only report data from the eagles' first year of life. SOUTULLO et al. (2006c, 2006d) provide further details on the individuals studied, the tagging and tracking techniques, and PTTs' duty cycles.

Movements were analysed at daily and biweekly scales. For each individual we calculated the arithmetic mean of all locations from every day and 2-week period. These represent the centre of mass of the locations obtained during those periods, and given the relative inaccuracy of Argos locations this has been previously suggested as a reasonable approach to describe individuals' movements at those scales (e.g., SOUTULLO et al. 2006b, 2006c). Movements were represented as a series of straight-line moves using consecutive daily and biweekly location means to define such moves. Because each random draw is independent of the preceding random draws, the random draw process is a first-order Markov chain (KAREIVA & SHIGESADA 1983). To calculate the expected net square displacement (R_n^2), we used information on turning angles (measured clockwise) with respect to the previous move, and move lengths, to fit a CRW model. According to KAREIVA & SHIGESADA (1983), if an animal path can be described by a CRW, then after n consecutive moves, the expected square of the net distance travelled is:

$$E\left(R_n^2\right) = nE\left(l^2\right) + 2E\left(l\right)^2 \frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right) \tag{1}$$

where c is $E(cos\ \theta)$, θ being the turning angle, and l is the length of one move. $E(cos\theta)$ is estimated by the mean $cos(\theta)$, $E(l)$ is estimated by the mean move length and $E(l^2)$ is estimated by the mean (move length^2).

We calculated the biweekly moves for the eight individuals studied, whereas daily moves were only calculated for the two animals carrying a GPS PTT, as those are the only ones for which location accuracy and frequency were reasonably high enough to enable an accurate description of birds' movements at that temporal scale (see SOUTULLO et al. 2007). To test for deviations from CRW expectation in individuals' pathways we calculated NAMS' (2006) CRW_{diff} statistic and analysed deviations from the expected value for a CRW (i.e., 0) using the Jackknife procedure (SOKAL & ROHLF 1995) to calculate confidence intervals. Given that $\overline{R_n^2}$ represents the observed mean (net distance)^2 for each number of n consecutive moves, the CRW_{diff} statistic is calculated as follows:

$$CRW_{Diff} = \frac{1}{k}\sum_{n=1}^{k}\frac{\overline{R_n^2} - E\left(R_n^2\right)}{Max\,R_n^2 - E\left(R_n^2\right)} \tag{2}$$

where $Max\,R_n^2$ is the maximum value of $\overline{R_n^2}$ at that n.

CRW$_{diff}$ values with confidence intervals including the zero were considered as indicative of animals performing un-oriented movements. Values greater than zero were considered as indicative of animals performing straighter moves than expected from a CRW, with values lower than zero considered as reflecting pathways that were more tortuous than a CRW (NAMS 2006).

To test whether the sample of biweekly movement paths (as opposed to testing individual paths) matched the CRW expectations, we analysed all individual pathways together, as described in NAMS & BOURGEOIS (2004). This approach has the advantage of treating the individuals' data as a sample of the whole population from which these birds were drawn. Thus, it provides an overall estimate of the dispersal behaviour of the eagles of this population, and a more generalized inference on the movement patterns of golden eagles during their first year of juvenile dispersal. This analysis was not performed at the daily scale, as daily information was only available for two individuals.

Finally, to evaluate whether at the biweekly scale winter pathways differed from those observed the rest of the year, we used the t-test to compare the distance between successive centroids of winter locations with the distance between successive centroids of locations from the rest of the year. Data of all individuals were pooled together for this analysis. We also tested whether the proportion of the dispersal areas covered by the habitat types preferred for foraging (i.e., sclerophyllous vegetation and complex cultivation patterns) explained the different movement patterns observed. To do that we used a Mann-Whitney test to compare the percentage of these habitats within dispersal areas of individuals with pathways that fitted a CRW model of dispersal, with those of individuals that did not. Information on habitat availability within each individual dispersal area was obtained from SOUTULLO et al. (2008b).

RESULTS

Golden eagles showed different ranging behaviours at the two temporal scales. When the sample of all pathways was analysed, golden eagles' biweekly pathways did not differ from a CRW (t $= -0.49$, df $= 7$, $P > 0.6$). When individuals were analysed separately, however, the pattern was less clear, as individuals following paths that both differed and did not differ from a CRW were observed. Conversely, when analysed on a daily basis, movements were highly non-random, with observed R_n^2 being consistently smaller than expected from a CRW model (Table 1).

Distance between successive centroids was larger in winter than during the rest of the year (t $= 4.27$, df $= 133$, $P < 0.0001$), with differences among individuals and fortnights being also highest during these months (Fig. 2). For the six individuals for which information on habitat use was available, those that showed movement patterns consistent with a CRW model of dispersal had a larger proportion of their dispersal areas covered by the habitat types preferred for hunting (U $= 0$, n $= 6$, $P = 0.13$; Table 1).

DISCUSSION

Although large differences in individual behaviour were observed, when analysed on a biweekly basis, the large-scale movements of the individuals are consistent with a CRW model of dispersal. Conversely, when analysed at the finer scale of daily foraging movements, individuals' ranging behaviour is largely non-random, suggesting some degree of site fidelity (BERGMAN et al. 2000), as birds remain for longer in areas that are suitable for foraging. Interestingly, individuals that did not follow a CRW model of dispersal when large-scale movements were analysed are those with the smallest proportion of their dispersal areas covered by foraging habitats. This is in line with our expectations of birds restricting their movements to a few sites that ensure that their chances of successful hunting are high when food resources are scarce (SOUTULLO

et al. 2008b). Therefore, our observations reinforce the idea that large-scale movement patterns are to a large degree determined by behavioural decisions linked to foraging activities.

Table 1.

Deviations of the ranging behaviour of eight juvenile golden eagles from correlated random walks' (CRW) expectations analysed on both a biweekly and a daily basis. CRW_{diff} significantly different from zero are indicative of oriented movements; UCL and LCL indicate CRW_{diff} upper and lower 95% confidence interval limits; "CRW" indicates whether movement patterns are consistent with a CRW model of dispersal (Y) or not (N); "Foraging habitat" indicates the percentage of the dispersal area covered by habitat types preferred by golden eagles for foraging. SD, standard deviation.

| Individual (ID. #)	Mean (SD) move length (km)	Observed R_n^2 (km^2)	n	CRW_{diff}	UCL	LCL	CRW	Foraging habitat (%)
Biweekly movements								
34464	27.3 (24.5)	1776	15	−0.076	−0.033	−0.118	N	−
34465	27.6 (22.3)	12140	14	−0.045	−0.015	−0.075	N	17.6
34466	11.7 (21.3)	13887	13	−0.017	0.006	−0.040	Y	25.4
34472	9.6 (8.1)	3042	15	−0.054	0.028	−0.136	Y	31.6
34473	42.2 (54.3)	12395	16	−0.111	0.070	−0.292	Y	43.7
34475	13.2 (17.5)	420	12	−0.029	−0.014	−0.045	N	−
49181	21.3 (13.8)	819	15	0.244	1.259	−0.770	Y	32.9
49182	38.6 (51.2)	9511	13	−0.076	−0.007	−0.145	N	20.8
Daily movements								
49181	14.4 (16.8)	1165	195	−0.010	−0.009	−0.010	N	
49182	14.3 (30.7)	14111	98	−0.011	−0.007	−0.015	N	
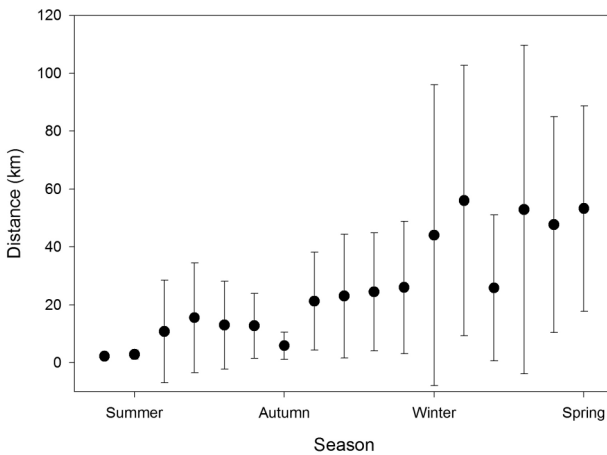
Fig. 2. — Biweekly distance (mean ± standard deviation) between the centroids of successive locations of eight golden eagles tracked in Spain throughout their first year of life.

During their juvenile dispersal raptors explore extensive areas of territory before restricting their movements to the area where they will eventually settle as adults (WATSON 1997; FERRER 2001; URIOS et al. 2007). Ranging behaviour during that stage is largely shaped by individuals' need to fulfil their food requirements and, hence, by food availability (NEWTON 1979). Thus, to understand how individual movements affect the spatial dynamics of populations, the key question is how to link the short-term foraging decisions that generate not-random patterns of foraging movements with the larger-scale patterns of dispersal movements.

Relating small-scale movements to larger-scale ones is actually one of the major challenges in spatial ecology (MORALES & ELLNER 2002). We suggest that the key issue to take into account when exploring answers to this question is how strongly the daily movements are influenced by an active search for food. If most of the time that individuals spend travelling they are in active search for food, then their movement pathways are expected to respond to the spatial distribution, abundance, catchability and quality of resources, and be non-random at both small and large scales (e.g., BOWNE & WHITE 2004). Yet, for species that are relieved from that pressure, and for which "wandering around" without pursuing a pre-fixed goal is relatively inexpensive, such as those that take advantage of water or air flows, then movement patterns at larger scales are more likely to be shaped by other evolutionary pressures.

In golden eagles flight activity is strongly influenced by thermal upwinds (HALLER 1996; WATSON 1997). Eagles use thermals to gain height and spend long periods in the air gliding. This facilitates long-distance un-oriented movements, which in terms of acquiring information are extremely valuable. In an evolutionary context, and as far as they are able to cope with the energy requirements of such a behaviour, birds that spend more time in soaring flight when they are not hunting would be rewarded with a larger chance of finding vacant places (as well as better hunting areas) than those that after feeding spend more time perching. Such a strategy not only increases the chances of finding a mate, but also the chances of finding it earlier, with an early start of reproductive life being a key determinant of lifetime reproductive output (PARTRIDGE 1989; WALLS et al. 1999; OLI et al. 2002).

Thus, even within a single population, differences in individual conditions (e.g., physiological condition or experience) and differences in the environmental conditions they are exposed to during dispersal (e.g., food availability) may favour different ranging strategies, with "blind" and "far-sighted" strategies representing extremes of a continuum. For example, in Spanish Imperial eagles, birds in better nutritional conditions perform longer exploratory movements during dispersal (FERRER 1992), with the time that individuals spend soaring decreasing when the time eagles have to spend hunting increases as a consequences of a decrease in prey availability (FERRER 1993d). This is in line with our observation that movement length but also its variability (among both fortnights and individuals) increases during winter, when food availability diminishes.

This might also explain differences in dispersal behaviour among golden eagles and other large raptors. Throughout their whole first year of life golden eagles increase the size of their dispersal area, exploring new sectors every month (SOUTULLO et al. 2006a, 2006d). In contrast, three or four months after independence other Mediterranean eagles such as juvenile Bonelli's (*Aquila fasciata*) and Spanish Imperial eagles (*Aquila adalberti*) restrict their movements to a few temporary settlements that they regularly use thereafter (FERRER 1993b, 1993c, 2001; BALBONTÍN 2005; CADAHÍA et al. 2005, 2007, 2009, 2010). Thus, whereas a "far-sighted" dispersal strategy may well explain the pattern of dispersal of Spanish Imperial and Bonelli's eagles, golden eagles'

behaviour is more in line with a "blind" strategy. This is not surprising considering that golden eagles may exploit a wider range of prey, and given their larger body size and lower metabolic rate they can store more reserves and fast for longer (Fevold & Craighead 1958; Soutullo et al. 2008b). In contrast, the other species need to hunt more frequently, and thus are forced to restrict their movements to a network of sites that ensure that their chances of successful hunting are always high (Ferrer 1993d; Soutullo et al. 2008a).

A similar scaling-up in movement patterns has been reported for other taxonomically distant organisms (Samu et al. 2003), with movement becoming less directional as the scale increases. In terms of golden eagles' survival and reproduction, behavioural decisions that generate a ranging behaviour that is not-random at foraging scales and random at dispersal ones are clearly advantageous. This also has population-level consequences, as a "blind" dispersal strategy maximises not only information acquisition during dispersal, but also population connectivity and the highest effective population size and, thus, decreases local extinction rates (Vuilleumier & Perrin 2006).

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