

# Pattern of repeatability in the movement behaviour of a long-lived territorial species, the eagle owl

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## Keywords

repeatability; animal movement; individual consistency; between-individual variation; long-lived species; *Bubo bubo*.

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## Abstract

Observed movement patterns are the response of the interaction between environmental variables and the animal internal state. Therefore, even individuals of the same species experiencing similar environmental conditions can exhibit different behavioural responses, as these responses can be highly repeatable within individuals. Here, we investigated the nocturnal movement behaviour of a territorial species, by radiotracking 26 eagle owls *Bubo bubo* in order to analyze within and between individual variation with respect to movement parameters and route choice. Owls showed a considerable individual consistency in all movement parameters and made repeated use of similar routes while moving within fixed home ranges. Thus, movement parameters varied much less between repeated nightly trajectories than between different individuals. Furthermore, when we compared different individuals inhabiting the same territory in different years, within-group repeatability was low or non-significant suggesting that the spatial configuration of habitat does not always represents one of the main drivers in animal movement behaviour. Similarly, male individuals appeared to exhibit greater repeatability than females. The overall pattern of repeatability we found seems to identify such consistent movement behaviour not only as the expression of individual response to external/internal inputs but also as an additional trait to include in the broad definition of animal personality.

## Introduction

The conceptual framework for movement ecology depicts movement as the interplay between four basic mechanistic components: (1) the internal state of individuals (e.g. physiological and neurological), (2) the motion (the set of traits that enables the focal individual to execute movement), and (3) navigation capacities (traits enabling animals to orient its movement in time and space), as well as (4) environmental factors. By applying such a paradigm to an actual system, we may expect that the resulting movement path of an organism feeds back to the internal and external components (Nathan *et al.*, 2008). While a large effort has been devoted to understanding the role of environmental factors (e.g. Morales & Ellner, 2002), our appreciation of the multiple internal components (e.g. motivation, physiological or neurological processes) involved in animal movement decisions is still incomplete (Börger, Danziel & Fryxell, 2008; Nathan *et al.*, 2008; Wolf *et al.*, 2009; Gautestad, 2011). Importantly, some other aspects potentially affecting animal movements, such as individual personality, have largely been ignored for many decades (Groothuis & Carere, 2005; Stamps, Briffa & Biro, 2012).

There has recently been a growing interest in the study of consistent differences in individual behaviour, given that repeatable behaviours seem to be common in wild populations, with important consequences for animal ecology and evolution (Réale *et al.*, 2007). Generally, behaviour is considered repeatable when individuals behave consistently through time and differently from other individuals (Bell, Hankison & Laskowski, 2009). In particular, repeated choices in movement behaviours have been described in several migratory species in relation to both trans-equatorial and trans-oceanic movements (Vardanis *et al.*, 2011; Dias, Granadeiro & Catry, 2013) as well as in marine and terrestrial organisms within their home ranges (Di Fiore & Suarez, 2007; Bosch *et al.*, 2010).

Territorial species are believed to have a complete knowledge of their surroundings, and the locations of some focal physical elements are periodically used in routine animal activities. For instance, animals may repeatedly use call or scent posts, roost sites or hunting posts to display social behaviour (e.g. territorial or courtship behaviour), reduce risk related to predation and improve foraging (e.g. sit-and-wait hunting strategy), respectively. The recurrent use of fixed locations (i.e. landmarks) might affect distances and time travelled by indi-

viduals and, consequently, favours repeated choices in animal movement behaviours. Yet, memory and the familiarity with the surroundings are not the only individual-level characteristics responsible for the observed repeatable movement patterns, since in some contexts where navigation by landmark recognition is not possible repeated movement behaviours arise as a result of a strong within-individual consistency (Vardanis *et al.*, 2011; Dias *et al.*, 2013). Such an alternative, but not exclusive, hypothesis receives support from the empirical observations that even individuals of the same species experiencing similar environmental conditions can exhibit different and consistent behavioural responses, as these responses are highly repeatable within the same individuals (Wilson, 1998; Bolnick *et al.*, 2003; Campioni *et al.*, 2013).

Although the definition of personality has become increasingly broad over the last few decades and now commonly refers to any consistent behaviour (Gosling, 2001; Réale *et al.*, 2010; Patrick, Charmantier & Weimerskirch, 2013), much of what we know about animal personality can mainly be attributed to the study of shy-bold continuum, namely, a fundamental axis of behavioural variation (Sih, Bell & Johnson, 2004) documented in short- to medium-lived species (Biro & Stamps, 2008). In fact, there are few studies considering the shy-bold axis of personality in long-lived species (e.g. Delgado & Penteriani, 2008; Patrick *et al.*, 2013) or examining their broadly defined personality traits (Quillfeldt, Voigt & Masello, 2010; Campioni *et al.*, 2013).

During a long-term study of eagle owls *Bubo bubo*, a territorial and long-lived species, in south-western Spain (e.g. Delgado *et al.*, 2010; Penteriani *et al.*, 2011; Campioni *et al.*, 2013), a large number of radio-tagged breeders were followed individually at a daily temporal scale for the duration of 7 years. Eagle owl home range behaviours and movement patterns have been analysed at different temporal and spatial scales with respect to internal and external factors, revealing a marginal effect of environmental composition on home range and movement patterns and a considerable importance of individual consistency in shaping movement behaviour (Campioni *et al.*, 2013). Moreover, it has been described that (1) from an early stage of life, dispersing eagle owls may exhibit different behavioural personality types (i.e. bold or shy) according to the social and environmental conditions (Delgado & Penteriani, 2008); (2) eagle owls that are permanently settled in an area, either as a floater during the last phase of dispersal or a territorial owner, change their movement behaviour as a consequence of learning about the main spatial features increasing local familiarity (Delgado, Penteriani & Nams, 2009; Penteriani & Delgado, 2012); and (3) eagle owls are endowed with a remarkable behavioural consistency when performing vocal displays (Penteriani *et al.*, 2010, 2014). All this evidence suggests that this species is particularly interesting for studying the repeatability of movement behaviour as an additional dimension in describing animal personality. In particular, on the base of previous results (Campioni *et al.*, 2013), we may expect that nightly movement paths of breeding eagle owls show high individual consistency. That is, movement path parameters will vary less within the same individual than between different individuals. If differences between males and females and

between territorial owners exist, then two new predictions can be formulated: (1) by comparing the movement paths of eagle owls which have been owners of the same territory in different years, we might expect a larger between-individual variation in movement parameters if individual repeatability plays a major role with respect to external input (territory composition or structure); (2) because male individuals have a strong territorial behaviour, we might expect them to display greater repeatability compared to female individuals whose range of movements is less constrained by the social context (Penteriani *et al.*, 2007; Campioni, Delgado & Penteriani, 2010); finally, (3) we might expect high repeatability in movement trajectories if eagle owls make reiterative use of spatial locations when travelling within their home ranges.

## Materials and methods

### Data collection

From 2004 to 2010, 26 breeding individuals (19 males and 7 females) from 19 nests were trapped (see Penteriani *et al.*, 2010; Campioni *et al.*, 2013 for more details) and fitted with a 30-g radio-transmitter, using a Teflon ribbon backpack harness (Biotrack; Wareham, Dorset, UK; <http://www.biotrack.co.uk>). The mass of the backpack was <3% of the mass of the smallest adult male (1.550 g) in our population (mean  $\pm$  SE = 1.667  $\pm$  105 g). Individual manipulation was always safe: during 7 years of trapping and continuous radiotracking of breeders (and ~150 dispersing individuals), we never recorded a potential adverse effect of the backpacks on bird survival or on breeding performance. Individuals were sexed by means of a molecular procedure, using DNA extracted from blood (Griffiths *et al.*, 1998).

We radiotracked territory owners individually throughout the night (from 1 h before sunset to 1 h after sunrise; total time duration = 3260 h) during 290 radiotracking sessions (mean number of radiotracking session per eagle owls  $\pm$  SD = 11  $\pm$  6, range = 4–25). The radiotracking sessions (mean time duration of a radiotracking session  $\pm$  SD = 11.3  $\pm$  1.8 h) were performed year-round in an attempt to sample behaviour throughout the different phases of the eagle owl's biological cycle until either the individual died or the battery of the transmitter failed (lifespan of transmitters ranged from ~1.5 to ~2.5 years). The locations of radiotagged individuals were determined by triangulations using three-element hand-held Yagi antennae (Biotrack) with Stabo (XR-100) portable ICOM receivers (IC-R20). Triangulation was generally performed within a short range from the focal eagle owl (100–300 m). On several occasions, direct observation of the focal owl was possible and used to validate triangulation points. To ensure independence between points and owing to the error in radiotracking localization (accuracy: mean  $\pm$  SE = 83.5  $\pm$  49.5 m), a distance of 150 m between locations was set as the minimum threshold to consider two position fixes as two real locations on a nightly scale (Delgado *et al.*, 2010). We recorded a new location (total number of locations = 5298) each time we detected a change in the position of the focal individual (for more details on movement detection, see Penteriani *et al.*, 2008; mean number of locations per radiotracking

session  $\pm$  SD = 17.2  $\pm$  5.2). Data analysis was performed employing only locations obtained by means of the triangulation method.

### Repeatability of movement parameter frequency distributions

Individual nightly movement behaviour was characterized by four variables: (1) total distance, calculated as the sum of the distance between successive steps of the nightly displacements; (2) step length, measured as the distance between successive locations; (3) speed, calculated as the step length divided by the time interval between successive locations; and (4) time step, recorded as the time elapsed between consecutive moves.

To have a visual representation of the patterns involved, we plotted a common histogram for each individual representing the actual frequency distribution of the four movement variables on a nightly scale. Because this type of data generally shows a right-skewed distribution, in which substantial information is hidden in the first bin of the common histogram and few scattered information is contained in its long-tail (Jovani, Mavor & Oro, 2008), we log-transformed the four variables to obtain 'movement parameter frequency log-linear distributions' (hereafter MPFD; Bak & Meesters, 1998). These MPFDs were comprehensively described by a combination of a few statistics (Jovani *et al.*, 2012), including: (1) minimum value, (2) maximum value, (3) median, (4) geometric mean and (5) coefficient of variation (CV = standard deviation/mean). Repeatability of these five statistics was then calculated to estimate individual consistency. Minimum values were very low in all movement parameters and thus we did not analyse their repeatability, given the lack of variability.

Within-individual repeatability ( $R$ ) was calculated for each MPFD statistics as  $R = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2)$ , where  $\sigma_a^2$  is the group (e.g. individual identity) variance and  $\sigma_e^2$  is the residual (error) variance (Sokal & Rohlf, 1995). Hence,  $R$  tells us about the strength of the differentiation between individuals ( $\sigma_a^2$ ) relative to the total variation. The total variation includes within-individuals variance (i.e. variance between measurements of behaviour of each individual;  $\sigma_e^2$ ) and the variance between individuals ( $\sigma_a^2$ ). These variances were retrieved from Linear Mixed Effects Models that included individual identity, territory and sex as random factors according to our different hypotheses. Parameter estimation was performed by means of Restricted Maximum-Likelihood following Nakagawa & Schielzeth (2010) employing the 'rptR' package (<http://rptR-forge.r-project.org/>) in the R environment (R Development Core Team 2009).

### Repeatability of movement trajectories

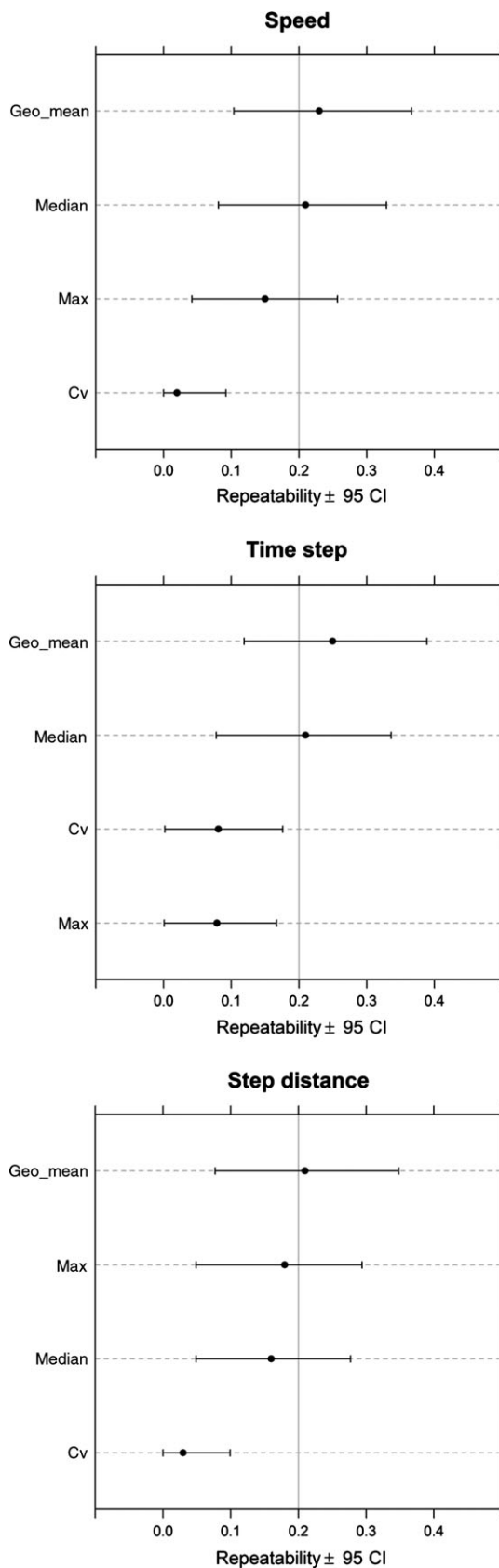
In order to obtain information on individual trajectories, we compared each actual route of each individual with 25 randomized ones. We compared the observed routes to those predicted by a null model, which describes the expectation in the case that individuals do not move following the same spatial paths. Thus, we denoted the location of the focal individual at time  $t$

using the formula  $\mathbf{z}(t) = (x(t), y(t))$ . Assuming that two consecutive data points of the focal individual have been acquired at times  $t_1$  and  $t_2$ , we asked if the observed location  $\mathbf{z}(t_2)$  was different from what would be expected from the knowledge of the location  $\mathbf{z}(t_1)$  and the null model of movement between the times  $t_1$  and  $t_2$ . That is, the null model defines a probability distribution of locations where the animal could have moved at time  $t_2$ , and the observed movement was compared to the distribution of the null locations. To construct the null model, we used observed step length, and accounted for a possible preference for habitat type by accepting the null model only in those locations which were in the same habitat (see Campioni *et al.*, 2013 for habitat classification) as the location to which the individual actually moved. With these two restrictions, the randomized trajectories were the most conservative; the removal of either of them would increase the chance of finding differences between actual routes and randomized ones. To compare the actual routes with the randomized ones, we performed a paired  $t$ -test.

## Results

### Within-individual consistency in MPFDs

The repeatability analysis of MPFDs for the 26 breeding eagle owls showed a considerable individual consistency in all movement parameters considered ( $R$  mean and range for all parameters; 0.16,  $\Delta R = 0.02$ –0.29, Fig. 1 for more details) except for CV, which showed a very low and non-significant repeatability in our analyses [ $R$  mean and range: 0.04 (0.001–0.08); all  $P > 0.10$ , Fig. 1]. Total distance displayed the highest repeatability [mean  $\pm$  SE and 95% CI; 0.29  $\pm$  0.08; (0.13–0.44), see also Fig. 2]. Moreover, when we analysed repeatability at the territory level ( $N = 8$ ; birds *per* territory ranged between 2 and 3), estimates were smaller, very close to zero ( $R$  range: 0.0–0.08,  $P > 0.10$ ). Namely, within-territory variability in MPFDs was remarkably high. More specifically, individuals moving within the same territory, i.e. in similar environmental conditions, seemed to show a substantial individuality (low repeatability). Additionally, male individuals ( $N = 19$ ) showed the highest repeatability of all movement parameters ( $R$  mean and range; 0.19,  $\Delta R = 0.04$ –0.30), although female individuals ( $N = 7$ ) seemed to be more consistent than male individuals with respect to time step ( $R$  mean and range; 0.18,  $\Delta R = 0.01$ –0.36). Accordingly, the 95% CI of repeatability estimates for most of the statistics were well above zero, demonstrating that they were statistically significant at  $\alpha = 0.05$ . Overall, these results suggest that eagle owls appear to have a consistent movement strategy night after night (i.e. with similar movement parameters) while maintaining some degree of variation across nights. Finally, the comparison between actual and randomized routes ( $\log_{10}$  transformed data paired  $t$ -test:  $t = -12.5012$ , d.f. = 25,  $P < 0.0001$ ) demonstrated that eagle owls preferentially followed the same routes every night, as each individual was more faithful to their actual routes than to the random ones.



**Figure 1** Repeatability estimates (error lines show 95% CI) of the four statistics (geo\_mean = geometric mean, CV = coefficient of variation, max = maximum value and median) employed to describe speed, time step and step distance frequency distributions (movement parameter frequency log-linear distributions) of 26 eagle owls. The four statistics are ordered according to their increasing value of repeatability while the grey line shows the repeatability value of 0.2 chosen as a reference value.

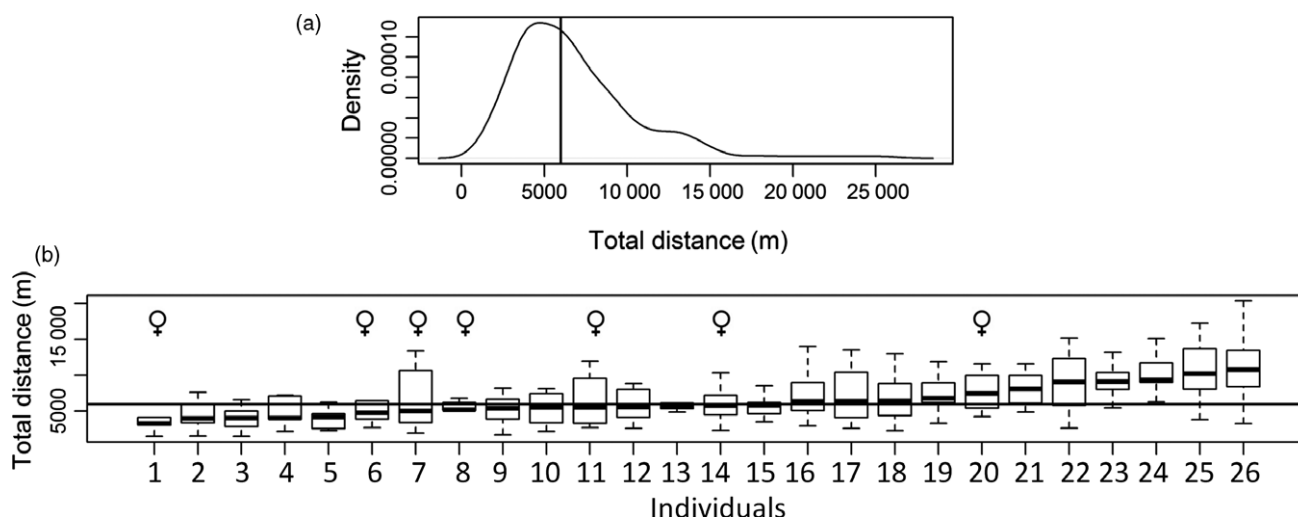
## Discussion

In the present work, we have shown that repeatability is a strong component of eagle owl movement behaviour. However, whereas individuals exhibited different degrees of repeatability in their movement parameters across nights according to the sex, we were not able to detect repeatability when different eagle owls have been owners of the same territory in different years. Finally, eagle owls were also consistently faithful to the use of preferential paths within their home ranges.

Although it is recognized that the movement decision-making process involves several internal- and environmental-level processes (Nathan *et al.*, 2008), we have highlighted in this study the importance of individuality, measured as within-individual repeatability, in the observed movement patterns. We previously found that the homogeneous distribution and unusual abundance of the main prey species characterizing a similar habitat composition between home ranges might explain why environmental factors poorly account for individual movement decisions (Campioni *et al.*, 2013). These previous results suggest an intriguing scenario in which behaviours may be mainly affected by individual-level attributes.

Important individual-level processes affecting movement behaviour include animal cognitive abilities, memory, and learning about the physical and social environments (Delgado *et al.*, 2009; Van Moorter *et al.*, 2009). These processes have been investigated as alternative mechanisms to stabilize home range boundaries of territorial species or of central place foragers (Van Moorter *et al.*, 2009). In fact, it is plausible to expect that the choice of eagle owls to reuse similar paths instead of random routes might be attributed to their ability to learn the location and quality of spatial elements (e.g. roost, call posts, foraging areas) used during their nightly activities (Delgado & Penteriani, 2007; Delgado *et al.*, 2009).

However, one of the most intriguing results we found is that when comparing different eagle owls that have inhabited the same territory (i.e. a natural way for controlling the territory effect), such groups of individuals showed low and non-significant levels of repeatability (i.e. small within-territory repeatability) in their movement parameters suggesting that consistent behavioural differences between individuals are maintained even when eagle owls confront the same spatial configuration. This result seems to support the hypothesis that movement behaviour in our study species is firstly related to the individual component and then to the external input, namely the spatial characteristics of the territory. It is generally difficult to separate these two sources of variation when studying animals in the field. Despite that, we provided some evidence that the



**Figure 2** Representation of population- and individual-level dispersion of total distance values ( $N = 290$ ) around the population median: (a) density distribution of total distance shown at the population-level describing how such a movement parameter is distributed around the population median value (black line). (b) Individual level boxplots of the total distance covered during nightly activity, illustrating that the boxplots of various owls lie below, in line with, and above the median value of the total distance calculated at the population level (black line). Mean number of total distance recorded per eagle owls ( $\pm$ SD) =  $11 \pm 6$ .

maintenance of behavioural traits can be strong and independent from environmental cues, even in species in which they have been recognized as one of the main source of between-individual variability in several traits (but see Delgado & Penteriani, 2008; Delgado *et al.*, 2010). Such a result does not exclude the possibility that in different phases of life (dispersal phase vs. breeding phase) these two non-mutually exclusive sources of heterogeneity, namely internal versus external inputs, might weigh differently on movement choice (see Delgado *et al.*, 2010).

The maintenance of consistent patterns of speed, step length, time step and route choice, might represent a good movement strategy to minimize time and energetic costs in relation to foraging activity (Stephens & Krebs, 1986). However, the peculiar environmental condition characterizing our study area (i.e. the high abundance of the main prey; Penteriani *et al.*, 2008; Campioni *et al.*, 2013) and the large amount of time spent by eagle owls perching on their roosts (Penteriani *et al.*, 2011) make it difficult to believe that eagle owls are undergoing strong time or energetic constraints. An alternative explanation is that consistent patterns of movement parameters, if not directly affected by external inputs and individual condition, might be due to an alternative endogenous trait that we can include in the broad definition of personality. In fact, there is evidence showing how repeatability in route choice must be of greater potential adaptive value for species moving over short distances as we found in eagle owls, which move through a home range of approximately 220 ha (Campioni *et al.*, 2013), than for those moving over large ranges and for long durations. In agreement with this idea, Vardanis *et al.* (2011) suggested predictability of relevant environmental cues to explain why Marsh harriers *Circus aeruginosus* displayed less repeatability in migration route choice (Vardanis *et al.*, 2011)

than homing pigeons *Columba livia* released a few kilometres away from the loft (Meade, Biro & Guilford, 2005).

Our findings are in accordance with the results of a recent review concerning the repeatability of behaviour which indicated that there might be important sex differences in repeatability, with adult males exhibiting more repeatability than females and immature individuals (Bell *et al.*, 2009). Notably, movement behaviour of territorial species such as eagle owls is linked to social dynamics and the rules that govern social interactions and spatial organization of territories (Penteriani & Delgado, 2008; Campioni *et al.*, 2010, 2012). Thus, certain biological features of eagle owls could explain this result. For example, it is recognized that, female eagle owls are remarkably free to move through other territories or to get close to neighbour nesting areas without suffering any physical injury (Penteriani *et al.*, 2007; Campioni *et al.*, 2010). Then a low level of risk (e.g. fights, injuries) when approaching conspecifics may potentially increase the variability of female movement decisions and accordingly decrease the relative individual consistency shown in the resultant frequency distributions of their movement parameters.

To conclude, our work leads to two main advances. Firstly, it provides a richer understanding of the subtle differences in movement behaviour exhibited by a year-round territorial species. Secondly, it affords a deeper understanding of behavioural traits outlining animal personality in long-lived species, those which may be integral to understand the evolution and maintenance of personality differences (Patrick *et al.*, 2013).

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