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Geidel Laure

Inter-individual variation in home range construction during post-dispersal settlement

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Directed by A.J.M. Hewison



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This report is an informative exercise, which does not commit the responsibility of the welcome laboratory.

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Abstract

During natal dispersal, *i.e.* an individual's movement from its natal home range to its first breeding home range, the settlement in a post-dispersal home range may be influenced by an individual's condition, *i.e.* its phenotype or its internal state, and/or by an individual's natal context, *i.e.* the environment within its natal home range. Inter-individual variability during settlement in a post-dispersal home range has strong consequences for individual fitness, population dynamics and gene flow. A better understanding of the mechanisms underlying variability in settlement during dispersal is thus of primary interest. We focused on the temporal process of postdispersal home range construction (e.g. temporal variation in home range's size and habitat composition during home range's construction) in juvenile roe deer (Capreolus capreolus) living in a heterogeneous landscape and monitored by GPS collars. Our aim was to assess inter-individual variability in the temporal construction process of the post-dispersal home range. We expected a natal disperser's condition such as its body mass and/or a natal disperser's natal context such as the features of its natal home range (e.g. size, proportion of woodland, habitat diversity) to influence the temporal process of post-dispersal home range construction. First, we described a gradual construction of the post-dispersal home range. Second, we showed that natal dispersers constructed their post-dispersal home range differently depending on their condition: the size of the post-dispersal home range increased with increasing individual body mass. Finally we highlighted the influence of an individual's natal context on the temporal construction process of the post-dispersal home range. Contrary to copse-born individuals, forest-born individuals seemed to first settle in a post-dispersal home range highly similar to their natal home range and seemed to explore progressively new habitats during the construction of their postdispersal home range. Our study revealed that the settlement in a post-dispersal home range is highly dependent on an individual's condition and natal context. In further studies, we propose to assess the influence of individual personality on the construction process of the post-dispersal home range.

Key words: natal dispersal; behaviour of post-dispersal home range construction; inter-individual variation; settlement; ungulate

Résumé

La dispersion natale concerne le mouvement d'un individu depuis son site de naissance jusqu'à son site de première reproduction. La condition (phénotype ou état interne) et le contexte natal (environnement natal) d'un individu pourraient influencer la dernière phase de la dispersion, c'est-à-dire l'établissement dans un domaine vital post-dispersion. Pendant la dernière phase de la dispersion, la variabilité interindividuelle a des conséquences importantes en termes de fitness des individus, de dynamique des populations et de flux de gènes. Il est donc indispensable de mieux comprendre les mécanismes induisant la variabilité interindividuelle lors de l'établissement pendant la dispersion. Dans cette étude, nous nous sommes intéressés au processus temporel de construction du domaine vital post-dispersion (ex. variation temporelle de la taille et de la composition en habitats du domaine vital post-dispersion pendant sa construction) dans une population de chevreuils évoluant dans un paysage hétérogène et suivie par télémétrie. Notre objectif était d'évaluer la variabilité interindividuelle concernant la construction temporelle du domaine vital post-dispersion. Nous nous attendions à ce que la construction temporelle du domaine vital post-dispersion soit influencée par la condition des individus, par exemple leur masse corporelle, et/ou par leur contexte natal comme les caractéristiques de leur domaine vital natal (ex. taille, proportion de bois, diversité d'habitat). Nous avons d'abord décrit une construction graduelle du domaine vital post-dispersion. Ensuite, nous avons montré que les disperseurs construisaient leur domaine vital post-dispersion différemment en fonction de leur condition : la taille des domaines vitaux post-dispersion augmente avec la masse corporelle des individus. Finalement, nous avons souligné l'influence du contexte natal sur le processus temporel de construction du domaine vital post-dispersion. Pendant la construction de leur domaine vital post-dispersion, contrairement aux individus nés en milieu ouvert, les individus nés en milieu fermé semblaient d'abord s'établir dans un domaine vital post-dispersion fortement similaire à leur domaine natal. Ils semblaient ensuite explorer progressivement de nouveaux habitats. Notre étude révèle que l'établissement dans un domaine vital post-dispersion, dépend fortement de la condition et du contexte natal des individus. De plus, nous proposons de s'intéresser à l'influence de la personnalité sur la construction du domaine vital post-dispersion dans de futures études.

Mots-clés: dispersion natale ; comportement de construction du domaine vital post-dispersion ; variabilité interindividuelle ; établissement, ongulé

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1. Introduction

Natal dispersal, *i.e.* an individual's movement from its natal habitat to its first breeding site (Howard 1960), includes departure from the natal habitat, transience through the landscape and establishment in a post-dispersal home range (Clobert *et al.* 2001). Dispersal is a key process because it is linked with individual fitness, population dynamics and gene flow (Jhost & Brandl 1997, Stamps & Blozis 2006). The process of natal dispersal is condition and context-dependent (Clobert *et al.* 2009). In fact, as dispersal enhances costs at the three stages of its process (classified into energetic, time, risks and opportunity costs), the management of those costs at the individual level may lead to inter-individual variation in dispersal (Bonte *et al.* 2012). Thus, the condition of an individual, *i.e.* an individual's internal state or phenotype, and the natal context, *i.e.* an individual's natal environment may influence the three stages of dispersal.

The condition of juveniles has an impact on natal dispersal as there is much evidence for phenotype related individual variation in the departure from the natal home range. In fact, phenotypic differences between dispersers and non-dispersers (i.e. philopatrics) have been described in a wide range of taxonomic groups (Clobert et al. 2009). These phenotypic differences may imply (i) physiological traits as variation in dispersal rate of butterflies is for example linked with variation in flight physiology (Haag et al. 2005), (ii) morphological traits such as a difference of body mass between dispersers and philopatrics of male Belding's ground squirrel (Spermophilus beldingi) (Holekamp, 1983) or in the common shrew (Sorex araneus) where dispersers have longer tibia and hind foot than philopatrics (Hanski et al. 1991), (iii) behavioural traits as in great tits (Parus major) where dispersing juveniles have a higher exploratory behaviour than philopatrics (Dingemanse et al. 2003). (iv) and life-history traits as in dispersing Glanville fritillary butterflies (Melitaea cinxia) which have a higher fecundity than philopatrics (Hanski et al. 2006). Whereas many studies have been conducted on inter-individual variation in dispersal linked to juvenile condition during the departure process, less research is available on inter-individual variation linked to differences in condition during transience (Clobert et al. 2009) and settlement. However, some variation in dispersal distance has been shown to be related to phenotypic traits. Indeed, the morphology of dispersing individuals may impact their dispersal distance. In newly emerged Chinook salmon (Oncorhynchus tshawytscha) larger individuals disperse further than smaller ones (Bradford & Taylor, 1997) and in juvenile eagle owls (Bubo bubo) individuals in better condition disperse further than individuals in poorer condition (Delgado et al. 2010). Although, behavioural traits such as sociality or even exploration have been correlated to dispersal distance, *e.g.* in the invasive mosquitofish (*Gambusia affinis*) more asocial individuals disperse further than more social individuals (Cote *et al.* 2010a) and in great tits dispersing females which explore more seem to disperse further than females which explore less (Dingemanse *et al.* 2003). Despite evidence for condition dependent dispersal in the departure from the natal home range and in the transience through the landscape, condition dependence at settlement in a post-dispersal home range has not been studied yet.

Similarly, dispersal is highly dependent on the natal context as an individual's external natal environment experienced before dispersal has an influence on dispersal behaviour and thus lead to inter-individual variation in dispersal outcomes (Clobert *et al.* 2009). Indeed, the natal context of an individual may have direct effects on its dispersal behaviour or it may have indirect effects on dispersal by modifying an individual's phenotype (*e.g.* maternal effects) (Ims & Hjermann 2001).

Evidence for context dependent natal dispersal has been described in the three stages of the dispersal process. First, the decision to leave the natal home range has been linked with the environment experienced in the natal home range such as (i) the size of the natal home range as in the colonial lesser kestrel (*Falco naumanni*) where the probability of natal dispersal decreases with the size of the natal home range (Serrano *et al.* 2003); (ii) the social environment of the natal home range for example in the degus (*Octodon degus*) where the probability of dispersal increases with increasing number of degus in the group (Quirici *et al.* 2011); (iii) and the behaviour of individuals in the population of birth as the population mean boldness and sociality scores influence for example the likelihood to disperse in the invasive mosquitofish (Cote *et al.* 2011). Indeed, individuals from populations composed of more asocial individuals or less bold individuals (Cote *et al.* 2011).

Second, an influence of the natal context during transience has also been highlighted. In particular, dispersal distance and the direction taken during transience may be shaped by an individual's natal context. In the American redstart (*Setophaga ruticilla*), the dispersal distance and the direction taken during natal dispersal depends on the latitude of the natal site (Studds *et al.* 2008).

Finally, settlement in a post-dispersal home range at the end of the dispersal process may also be affected by a disperser's experience in its natal home range thus leading to interindividual variation in this last stage of dispersal. Dispersers may for example choose a postdispersal range that most resemble their natal range (Stamps & Davis, 2006). Natal habitat preference induction (NHPI), where experience of stimuli in an individual's natal home range increases the probability that the individual will select a post-dispersal home range that contains comparable stimuli (Davis & Stamps 2004), has been observed in several taxa (Sacks *et al.* 2005, Stamps & Blozis 2006, Mabry & Stamps 2008, Selonen *et al.* 2007). For example, in the Siberian Flying squirrel (*Pteromys volans*), patch size and nest localization were similar in the natal home range and in the post-dispersal home range (Selonen *et al.* 2007). Furthermore, the quality of the natal habitat may have an impact on a disperser's selectivity and competitive ability at settlement, thus leading to a silver spoon effect (Stamps, 2006). For example, Van de Pol *et al.* have shown that oystercatchers (*Haematopus ostralegus*) that were reared on high-quality natal ranges had a higher probability of settling in high-quality postdispersal ranges (2006). Experience of high-quality habitat may also increase a disperser's assessment of its chances of subsequently encountering another high-quality habitat, and hence reduce its chances of accepting a lower-quality habitat (Stamps & Davis, 2006). For example, European populations of the parasitoid *Cotesia glomerata* are more selective when they encounter high-quality habitat before selecting where to lay their eggs (Vos & Vet 2004).

Establishment in a post-dispersal home range is of particular importance as spatial variation in resources and predation risk directly influence an individual's survival and reproductive success (Low et al. 2010). Furthermore, as dispersal has an impact on population dynamics and gene flow (Jhost & Brandl 1997, Stamps & Blozis 2006), individual variation in dispersal may play an important role in population dynamics. If an individual selects a post-dispersal home range as a function of its natal context, this may for example influence the genetic structure between populations so that natal habitat preference induction may lead to the establishment of independent genetic pools. In Californian coyotes, a settlement biased toward post-dispersal ranges with cues similar to those of the natal home range contributes to divide the population into four genetic pools (Sacks et al. 2005). Despite, the consequences of inter-individual variability in the settlement stage of dispersal for individual fitness, population dynamics and gene flow, the relationship between a disperser's behaviour and its condition and/or natal context has received so far little attention. This lack of studies dealing with settlement in a post-dispersal home range is probably due to the difficulty of acquiring high quality data on this stage of the dispersal process. Thus, in order to better understand the ecological and evolutionary consequences of inter-individual variability in dispersal it seems of great importance to provide more studies on condition and natal context dependence in the last stage of the dispersal process, *i.e.* the settlement in a post-dispersal home range.

To our knowledge, those few studies focusing on settlement in a post-dispersal home range at the end of natal dispersal have described inter-individual variability in habitat selection behaviour during this stage, but they have not described the process of post-dispersal home range construction. In order to select their post-dispersal home range, individuals must use a set of external cues such as habitat quality, vegetation type, food availability, predation risk or even the risk of parasitism and competition with heterospecifics (Marzluff 1988, Clark & Shutler 1999). For the purpose of describing how individuals construct their post-dispersal home range we may thus study how cues used in order to select the post-dispersal home range vary temporally during the construction process of the post-dispersal home range. In view of the marked importance of the natal context on habitat selection at the end of natal dispersal and of the role of natal condition in the dispersal process that we highlighted above, our study aimed to describe the influence of an individual's natal context and condition on the process of post-dispersal home range construction during settlement in a widespread large herbivore, the roe deer (*Capreolus capreolus*). Therefore we focused on the last stage of the dispersal process, the settlement in a post-dispersal home range.

The roe deer is a particularly pertinent species for the study of inter-individual variability in temporal variation of the post-dispersal home range during its construction. Indeed, roe deer exploit a variety of habitats in terms of composition and structure (Hewison et al. 2001). In addition, a substantial proportion of juveniles disperse and the dispersal process seems to be both condition and natal context dependent. In particular, an individual's propensity to disperse is linked with both its body condition and its behaviour. Individuals who have a high body mass and explore more tend to disperse, whereas individuals with a lower body mass and less exploratory behaviour do not (Debeffe et al. 2012; Debeffe et al. 2013). Furthermore, Debeffe described an influence of an individual's condition on the settlement strategy when natal dispersers selected a post-dispersal home range (2013). Indeed, heavier individuals were more likely to settle in a post-dispersal home range that resembled their natal home range than lighter individuals (Debeffe 2013). Thus, natal habitat preference induction was more observed in individuals in good condition than in individuals in worse condition (Debeffe 2013). Second, an individual's natal context seems also to have an impact on the dispersal process in roe deer. Indeed according to Debeffe et al., forest-dwelling individuals disperse less than those living in more heterogeneous habitats (2012). Highly precise data on roe deer movements living in a spatially heterogeneous agricultural landscape, and more precisely on juvenile movements during dispersal, are available from an intense and

Post- dispersal HR features	Explanatory variables	Biological effect	Expectation
Size (log area) & Proportion of woodland (exponential) &	Time (month of post- dispersal HR construction) Individual body mass Proportion of woodland in the individual's natal HR	Gradual post-dispersal HR construction Proxy for individual phenotypic quality or condition Proxy for individual natal context	 Post -dispersal HR features vary temporally during the construction of the post-dispersal HR as individuals construct their post-dispersal HR gradually in a novel environment. Temporal variation in post-dispersal HR features varies with individual condition because an individual's condition influences its ability to cope with conspecifics. Thus individuals in poorer condition should have less temporally stable post-dispersal HRs. Temporal variation in post-dispersal HR features varies with the proportion of woodland in the natal HR as forest-dwelling individuals should have more stable home ranges according to Cargnelutti <i>et al.</i> (2002) if we assume that juveniles exhibit the same behaviour than adults.
Habitat heterogeneity (Shannon diversity index)	Habitat heterogeneity in the individual's natal HR	Proxy for individual natal context	Temporal variation in post-dispersal HR features varies with habitat heterogeneity in the natal HR as individuals used to a high diversity of habitats should be more used to variable habitat features in their HR. Thus individuals with high habitat heterogeneity in their natal HR should have less temporally stable post-dispersal HRs.
Habitat disimilarity	Time (month of post- dispersal HR construction) Individual body mass	Gradual post-dispersal HR construction Proxy for individual phenotypic quality or condition	The habitat dissimilarity of the post-dispersal HR with the natal HR increases temporally during the construction of the post-dispersal HR as individuals may first try to construct a post-dispersal HR highly resembling their natal HR and gradually explore new habitats. Temporal variation in habitat dissimilarity between the natal HR and the post-dispersal HR decreases with decreasing individual condition because an individual's condition influences its ability to settle in appropriate habitats. Thus individuals in poorer condition should have less temporally stable post-dispersal HRs.
disimilarity with the natal HR (Manly similarity distance)	Proportion of woodland in the individual's natal HR Habitat heterogeneity in the individual's natal HR	Proxy for individual natal context Proxy for individual natal context	Temporal variation in habitat dissimilarity between the natal HR and the post-dispersal HR increases with increasing proportion of woodland in the natal HR as forest-dwelling individuals should be less active and have thus more temporally stable post-dispersal HRs. Temporal variation in habitat dissimilarity between the natal HR and the post-dispersal HR increases with increasing habitat heterogeneity in the natal HR as individual's used to a high diversity of habitats should be more used to variable habitat features in their HR. Thus individuals with high habitat heterogeneity in their natal

Table 1: Hypotheses about the influence of an individual's condition and natal context on the temporal variation of its post-dispersal home range (HR: home range).

long term GPS monitoring study making it possible to study inter-individual variation in the construction of the post-dispersal home range (Morellet *et al.* 2011).

In order to study inter-individual variability in the temporal construction process of the post-dispersal home range, we focused on temporal variation in post-dispersal home range size and in habitat features such as the proportion of woodland, the habitat diversity and the habitat resemblance with the natal home range of successive monthly post-dispersal home ranges. Moreover, we described the features of natal dispersers' natal home range in terms of proportion of woodland and habitat diversity. Therefore, the way an individual's condition (body mass) and natal context (natal home range features) shape the dispersal process was studied. We expected a natal disperser's condition such as its body mass and a natal disperser's natal context such as the habitat features of its natal home range to influence temporal variation in the features of the post-dispersal home range during its construction (Table 1), revealing a last stage of dispersal highly dependent on individual's condition and natal context.

2. Material and methods

2.1. Model species

The roe deer (*Capreolus capreolus*) is a slighty dimorphic and sedentary species (Andersen *et al.* 1998). Roe deer home range size varies between approximately 80 ha in wooded areas and 150 ha in open agricultural areas (Hewison *et al.* 1998). Juvenile roe deer stay close to their mother until their 11^{th} month. Then, approximately in April, a proportion of juveniles initiate natal dispersal (34%, Debeffe *et al.* 2013) whereas the remaining individuals stay in their natal home range (*i.e.* philopatric, their post-dispersal home range overlaps their natal home range). During the period prior to dispersal, some individuals leave their natal home range for a short period and explore the surrounding environment. Those explorations occur more often in dispersing individuals than in philopatric individuals (Debeffe *et al.* 2013). During natal dispersal, roe deer leave their natal home range (departure stage), travel a variable distance through the habitat matrix (between 1 and 40 km in the studied population) over around 45 days (transience stage) and finally select a post-dispersal home range (settlement stage) (Debeffe 2013). This stage of the roe deer's life cycle does not differ between sexes as females disperse as often as males (Debeffe 2013).

2.2. Study site

The study was conducted in a hilly and heterogeneous agricultural landscape in the South-West of France (N 43°13', E 0°52') (Figure 1). The climate of this region is oceanic. The study site covers around 10 000 ha (Debeffe 2013) with a variable proportion of woodland and two large forest patches. Those two forest patches are surrounded by semi-open and open cultivated landscapes. Within the study site, roe deer density averages 9.3 roe deer/100 ha (+/-1.32, min = 6.6, max = 10.9) outside the forests and is about two times higher in the forests (unpublished data, A. J. M. Hewison).

2.3. Captures and individual monitoring

Roe deer were caught from 2002 to 2013 during winter using 50 meter-long and 2 meterhigh nets disposed along a 4km long line. All capture, handling and collaring were done according to French law for animal welfare and procedures were approved by the French administration. Once an individual is captured, its sex and its body mass are recorded to the nearest 0.1kg. The individual's body mass provides a good proxy of individual quality and therefore of individual condition (Toigo *et al.* 2006). Indeed heavy adult females have a higher probability to reach old age (Gaillard *et al.* 2000) and heavy males have a higher reproductive success (Vanpé *et al.* 2010). Juveniles (individuals younger than 1 year old) can be distinguished from older individuals by the presence of a tri-cuspid third premolar milk tooth (Ratcliffe & Mayle 1992). This age estimation enables us to distinguish potential natal dispersers. Before releasing, roe deer are equipped with a Global Positioning System (GPS) collar (Lotek 3300 GPS or Lotek Small WildCell GSM). Those collars are programmed to monitor the individuals for 48 weeks. They are programmed to record the roe deer's location every 4h (in 2002-2004) or every 6h (in 2005-2013).

In this study location data for the first week after capture were excluded because capture and handling induce transient modifications of roe deer spatial behaviour (Morellet *et al.* 2009). Then, because fixes might sometimes be inaccurate, we removed 15 aberrant points from the data set. Aberrant points were defined following a fix rule (Figure 2). Furthermore, only locations of the calendar year corresponding to the year of potential dispersal event were kept for the analysis.



Figure 1: Map of the study site highlighted in the orange frame.



Figure 2: Definition of aberrant points.

The point B is considered as being aberrant when (i) the distance between A and B is larger than two times the distance between A and C and the angle φ is higher than 2.5 radians and the speed at which the animal moved from A to B is higher than 500m/h or (ii) the distance between A and B and the distance between B and C is larger than 1000m.

2.4. Definition of dispersers and dispersal stages

Following preliminary analyses using different methods (based on residency time segmentation and Net Squared Displacement segmentation) in order to distinguish dispersing individuals from philopatrics and to define the different stages of the dispersal process (departure from the natal home range, transience, settlement in a post-dispersal home range) we chose Börger and Fryxell's (2012) method based on the Net Squared Displacement (NSD) combined with a non-linear hierarchical modeling framework. The NSD which measures the straight line distances between the first location of an individual and the subsequent locations of the same individual (Bunnefeld et al. 2011) was obtained with the library adehabitatLT in R (Callenge 2009). Börger and Fryxell's method (2012) allowed us to assign a movement strategy (philopatric or disperser) to each individual depending on the change of its NSD with time (Julian date) (Figure 3). The NSD of each individual was compared to three models (i) a null model were the NSD is constant, (ii) a philopatric model were the NSD has a linear increase before reaching a constant and (iii) a disperser model were the NSD is asymptotic. Concerning model selection, the model with the highest concordance correlation coefficient (CC), which determines the goodness of fit of each model, was selected (Börger & Fryxell's 2012). When CC is equal to or lower than 0, the model has a bad fit. As this method systematically attributed a movement strategy to the individual based on the highest CC and because some movement strategies seemed questionable, we retained individuals assigned as dispersers only when the CC of the dispersal model was higher than 0.6. This threshold value was chosen because it allowed us to include those individuals where the visual inspection of their trajectory indicated for sure that they dispersed in the sample of natal dispersers defined using Börger and Fryxell's method (2012).

40 dispersers were thus identified using this method. Individual's which were monitored less than 2 months following settlement were not taken in account for the analysis because we needed a longer monitoring to study the temporal process of post-dispersal home range construction. Thus, this study was conducted on 32 natal dispersers.

Furthermore, the method of Börger and Fryxell (2012) allowed us to obtain the individual parameters of the dispersal model and thus to define the departure date from the natal home range and the settlement date in the post-dispersal home range for each individual. As, from visual inspection, the model output for the departure date from the natal home range of one individual (individual 634_11) was too early because of an exploratory movement



<u>Figure 3:</u> NSD (m²) as a function of time (Julian date) for two individuals, one defined as disperser (A) and another defined as philopatric (B) according to Börger and Fryxell's method (2012).

Figure 4: Definition of monthly post-dispersal home ranges.

preceding the true departure from the natal home range, we defined the date of its departure from the natal home range visually looking at its trajectory.

2.5. Statistical analysis

2.5.1. Natal context

Individual natal home ranges were estimated using a fixed- kernel method based on an *ad hoc* approach for the smoothing parameter and a grid of 2.5 pixels at the 90% isopleth (which corresponds to the smallest size on which the probability to relocate the animal is equal to 0.90) (Börger *et al.* 2006 ; Worton 1989). The locations used to estimate the 90% home range and its size corresponded to the beginning of an individual's monitoring (one week after the capture event) until the day preceding its departure from the natal home range defined using Börger and Fryxell's method (2012) (see above). The library adehabitatHR (Calenge 2006) from the R software (R development core team 2010) was used to estimate the 90 % natal home range and its size (area).

Several features of the natal home range were then measured in order to assess an individual's natal context. Using a GIS of the study site available for most years and the software ArcGIS 10 (ESRI, 2011), the habitat within the natal home range was determined using the GIS of the year corresponding to the year of monitoring of each individual or, where this was not available, to the closest year to the year of monitoring of the individual. The GIS of the study site contains 38 habitat categories describing the kind of vegetation (*e.g.* crops, natural meadow, artificial meadow, corn, leguminous plant, fallow land, forested sizes, etc...), roads, tracks, human infrastructures and other habitats.

First, the proportion of woodland in the natal home range was calculated for each individual. This corresponded to the areas of forest patches and hedges within the size (area) of the natal home range.

Second, the habitat diversity within the natal home range was estimated using the Shannon-Weaver diversity index as recommended by Priego-Santander *et al.* (2013) for each individual. This index was calculated on the 38 habitat categories of the GIS of the study site. The Shannon-Weaver diversity index (SWDI) takes into account the proportion (p(i)) of each habitat category and the total number of habitat categories (n) and is calculated as:

 $SWDI = \sum_{i=1}^{n} (p(i) * \ln(p(i)))$

2.5.2. Temporal construction of the post-dispersal home range

In order to study the temporal process of post-dispersal home range construction, we segmented the post-dispersal period (from the first day after settlement in the post-dispersal home range defined using Börger and Fryxell's method (2012) to the end of the monitoring) on a monthly basis. Thus we estimated monthly post-dispersal home ranges (at the 90% isopleths using the method described above) (Figure 4). Monthly post-dispersal home ranges which were estimated based on less than 56 locations (half of the median number of locations per monthly home range) were removed. Furthermore, because female roe deer home range size varies over time in relation to seasonality (Morellet *et al.* 2013), juvenile home range size may also vary in relation to seasonality. Thus, to control for potential variation in home range size due to seasonality, we decided to focus on the first four months following dispersal as day length was relatively stable during this period. Whereas for 30 individuals we could estimate 4 monthly post-dispersal home ranges, 2 individuals were monitored for a shorter period and we were thus able to estimate only 3 monthly post-dispersal home ranges for them.

In order to focus on temporal variation in post-dispersal home range features during the construction process, several characteristics were described for each monthly postdispersal home range. First, using the same GIS of the study site and the same method as described for the natal home range, the size, the proportion of woodland and the habitat diversity within each monthly post-dispersal home range were calculated for each individual. Second, the habitat dissimilarity between each monthly post-dispersal home range and the natal home range was described using the GIS of the study site. The habitat proportion of each of the 38 habitat categories was first calculated for each monthly post-dispersal home range. Then, for each individual and for each monthly post-dispersal home range, the habitat dissimilarity with the natal home range was calculated using Manly's distance (a distance commonly used for percentages) with the libarary ade4 (Dray & Dufour 2007). Manly's distance takes values between 0 and 1. Whereas a value of 0 indicates a low dissimilarity (high similarity in habitat composition) between the natal home range and the considered monthly post-dispersal home range, a value of 1 indicates a high dissimilarity (low similarity in habitat composition) between the natal home range and the considered monthly postdispersal home range. Manly's distance takes into account the proportion of each kind of habitat in each monthly post-dispersal home range (p(i)) and the proportion of habitat in the natal home range (q(i)) as follows:

Manly's distance $=\frac{\sum |p(i)-q(i)|}{2}$

2.5.3. Proportion of woodland at settlement

The size of the post-dispersal home range may be influenced by the proportion of woodland in the surrounding environment. Indeed, Cargnelutti *et al.* (2002) highlighted a relationship between the proportion of woodland and the home range size of roe deer. Therefore, we defined a variable indexing the proportion of woodland within the local landscape of the post-dispersal home range. Thus, we first defined for each individual the location of the overall post-dispersal home range as the locations from the first day after settlement in the post-dispersal home range defined based on Börger and Fryxell's method (2012) to the end of the monitoring. We then calculated the center of gravity of the overall post-dispersal home range for each individual. Following that, using ArcGIS 10 and the appropriate GIS of the study site, we constructed a buffer with a diameter of 600m and centered on the center of gravity of the overall post-dispersal home range of each individual and extracted the habitat within each buffer. Finally, we calculated the proportion of woodland in each buffer *i.e.* in the overall post-dispersal home range for each individual.

2.5.4. Model construction and selection

In order to test our hypotheses on the influence of an individual's condition (body mass) and natal context (features of the natal home range) on the temporal process of postdispersal home range construction, we used mixed effect models with the individual and the year as random effects in each model to account for repeated measures for each individual (3 or 4 monthly post-dispersal home ranges) and for an effect of the cohort. As environmental conditions may vary between years and thus influence the temporal process of post-dispersal home range construction, taking in account an effect of cohort seems of great importance. For example, variation in precipitations between years may lead to variation in phenology and thus to variation in the temporal process of post-dispersal home range construction as roe deer are highly dependent on forage availability for their survival. Linear mixed effect models (library lme4 in R) were used to model the size (log size) of monthly post-dispersal home ranges and habitat diversity (exponential) within monthly post-dispersal home ranges (Bates &. Maechler 2010). The size of monthly post-dispersal home ranges was log transformed and the habitat diversity of monthly post-dispersal home ranges was subject to exponential transformation in order to satisfy normality of model residuals. To model the proportion of woodland within monthly post-dispersal home ranges and the habitat dissimilarity between the natal home range and each monthly post-dispersal home range, generalized mixed effect models were conducted with a beta regression (library glmmADMB in R) (Bolker *et al.* 2012). The beta regression allows a wider range of distribution for dependent variables within the interval]0,1[(Cribari-Neto & Zeileis 2010).

We expected a natal disperser's condition such as its body mass and a natal disperser's natal context such as the habitat features of its natal home range to influence temporal variation in the features of the post-dispersal home range during its construction (Table 1), revealing a last stage of dispersal highly dependent on an individual's condition and natal context.

As we expected a natal disperser's condition (*i.e.* body mass) and a natal disperser's natal context (*i.e.* habitat features of its natal home range) to influence temporal variation in the features of the post-dispersal home range during its construction , we predicted a two way interaction between the month of the construction process and the body mass, a two way interaction between the month of the construction between the month of the construction process and the proportion of woodland within the natal home range and a two way interaction between the month of of ur process and the habitat diversity within the natal home range. Prior to the construction of our models, we checked if the coefficient of determination (R^2) between the explanatory variables we wanted to test was not too high. The highest R^2 was that of the relation between the habitat diversity and the proportion of woodland within natal home ranges (R^2 adjusted = 0.41) (Appendix 1).

Furthermore, when constructing our models, we controlled for several confounding effects, thus instead of basing model selection on a null model, we constructed reference models. First, as an influence of the proportion of woodland in the habitat on roe deer's home range size has been previously demonstrated (Cargnelutti *et al.* 2002), when modeling the size of monthly post-dispersal home ranges, we added the proportion of woodland within a buffer surrounding the center of gravity of the entire post-dispersal home range as an additive effect. This allowed us to control for the proportion of woodland available around the post-dispersal home range and thus to account for a potential influence on the proportion of woodland available around the post-dispersal home range on the size of monthly post-dispersal home ranges. Second, as the size of the natal home range may have an influence on the size of monthly post-dispersal home ranges, we added the size of the natal home range as an additive effect when modeling the size of monthly post-dispersal home range as an additive and available around the post-dispersal home range may have an influence on the size of monthly post-dispersal home range as an additive effect when modeling the size of monthly post-dispersal home range as an additive effect when modeling the size of monthly post-dispersal home range as an additive effect when modeling the size of monthly post-dispersal home range as an additive effect when modeling the size of monthly post-dispersal home range as an additive effect when modeling the size of monthly post-dispersal home range as an additive and available around the post-dispersal home range during the post-natal period may also tend to have a large post-dispersal home range because when natal dispersers leave their natal home range and settle in a new home range (post-dispersal home range) they may express the same behaviour

as in their natal home range, due to a natal imprinting mechanism. Third, as the proportion of woodland and the habitat diversity in monthly post-dispersal home ranges probably depends on the size of those monthly post-dispersal home ranges (a high proportion of woodland should be linked with a small home range size according to Cargnelutti *et al.* 2002 and a high habitat diversity should be linked with a large home range size), we added the size of monthly post-dispersal home ranges as an additive effect when modeling the proportion of woodland and the habitat diversity. In order to model habitat dissimilarity between the natal home range and monthly post-dispersal home ranges, we used a null model instead of a reference model because we had no particular expectation of confounding effects.

Then, we used a backward approach to select the best model based on the second order Akaike Information Criterion parameter (AICc) (Appendix 2, Appendix 3, Appendix 4). As we worked on a sample size of 32 individuals and as our models had many parameters, we used the AICc (Burnham & Anderson 1998). When several models had a difference of AICc (Delta_AICc) smaller than or equal 2, we selected the more parsimonious of the models by retaining the model with the fewest parameters. For more clarity in the presentation of the results we presented only the models with a delta AICc<2 and the model following those models.

All the analyses were conducted on a sample size of 32 individuals (with 4 monthly post-dispersal home ranges for 30 individuals and 3 monthly post-dispersal home ranges for 2 individuals).

3. Results

3.1. Temporal variation in the size of monthly post-dispersal home ranges

The most parsimonious model describing variation in the size (logarithmic) of monthly postdispersal home ranges revealed that the variation in the size of monthly post-dispersal home ranges was explained by the month of the construction process and the individual's body mass as additive effects (AICc=199.82 ; AICc weight=0.29 ; K=10) (Tables 1 and 2, Appendix 5). According to model predictions, the size of monthly post-dispersal home ranges decreased markedly between the first and the second month of the construction process (27.0% of size (ha) decrease) (Figure 5). Then, between the second and the fourth month of the construction process, the size of monthly post-dispersal home ranges constant (Figure 5). Furthermore, individuals with a higher body mass always had larger monthly postdispersal home ranges than lighter individuals. The size of the monthly post-dispersal home range increases by 278% when individual body mass increases by 54% (Figure 7).

Two other models had a $\Delta AICc \le 2$ with the most parsimonious model. Whereas the first included the month of the construction process, the body mass and the habitat diversity within the natal home range as additive effects ($\Delta AICc=0.82$; AICc=200.64; AICc weight=0.2; K=11), the second included the month of the construction process, the body mass and the proportion of woodland within the natal home range as additive effects ($\Delta AICc=1.32$; AICc=201.14; AICc weight=0.15; K=11) (Tables 1 and 2).

3.2. Temporal variation in the proportion of woodland within monthly postdispersal home ranges

Third, as the proportion of woodland and the habitat diversity in monthly postdispersal home ranges probably depends on the size of those monthly post-dispersal home ranges (a high proportion of woodland should be linked with a small home range size according to Cargnelutti *et al.* 2002 and a high habitat diversity should be linked with a large home range size), we added the size of monthly post-dispersal home ranges as an additive effect when modeling the proportion of woodland and the habitat diversity.

Concerning, the variation in the proportion of woodland within monthly post-dispersal home ranges, the most parsimonious model was the model of reference which included the individual and the year as random effects and the size of monthly post-dispersal home ranges as additive effects (AICc=-232.07; AICc weight=0.27; K=10) (Tables 1 and 3, Appendix 6). This suggests that the variables we used to index an individual's condition and natal environment could not explain the variation in the proportion of woodland within monthly post-dispersal home ranges. However, the model which included an interaction between the month of the construction process and the individual's body mass, but also an interaction between the month of the construction process and the proportion of woodland in the natal home range, had an $\Delta AICc \leq 2$ with the most parsimonious model ($\Delta AICc=0.62$; AICc=-231.45; AICc weight=0.2; K=16) (Tables 1 and 3).

3.3. Temporal variation in habitat diversity within monthly post-dispersal home ranges

Model selection for variation in habitat diversity (exponential) of monthly postdispersal home ranges revealed that the most parsimonious model was the reference model including the individual and the year as random effects and the size of monthly post-dispersal home ranges as additive effects (AICc=383.66; AICc weight=0.65; K=5) (Tables 1 and 4,

Abbreviation	Meaning
Ind	Individual
Year	Year
Woodland _{Buffer}	Proportion of woodland in a buffer surrounding the center of gravity of the overall post-dispersal home range
Size _{natalHR}	Size (ha) of the natal home range (log transformed)
Size _{postHR}	Size (ha) of monthly post-dispersal home ranges (log transformed)
Month	Month of the construction process of the post-dispersal home range
BM	Individual body mass
Woodland _{natalHR}	Proportion of woodland in the natal home range
Diversity _{natalHR}	Habitat diversity in the natal home range

<u>Table 1:</u> List of abbreviations and their meanings used in the models

<u>Table 2:</u> Performance of the linear mixed effects models with a Delta_AICc<2 and of the model following those models for explaining variation in the size (log transformed) of monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Models	AICc	Delta_AICc	AICcWt	Κ
$Month + BM + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	199.82	0	0.29	10
$Month + BM + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	200.64	0.82	0.2	11
$Month + BM + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	201.14	1.32	0.15	11
Month + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	202.9	3.08	0.06	9

<u>Figure 5:</u> Predictions (black points) and confidence interval (bars) for temporal variation in monthly post-dispersal home range size (ha) from the model explaining temporal variation in the size of monthly post-dispersal home ranges with additive effects of the month of the construction process and individual body mass. The other variables were fixed to their median values for presentation.

<u>Figure 6:</u> Predictions (dark line) and confidence interval (grey lines) for the relationship between the size (ha) of monthly post-dispersal home ranges and individual body mass from the model explaining variation in the size of monthly post-dispersal home ranges with additive effects of the month of the construction process and the individual body mass. Only the month of the construction process was represented and the other variables were fixed to their median value for presentation.

Appendix 7). All the other models had a $\Delta AICc>2$ with the most parsimonious model selected (Tables 1 and 4). This suggests that variation in habitat diversity of monthly post-dispersal home ranges was not explained by the variables we used to index an individual's condition and natal environment.

3.4. Temporal variation in habitat dissimilarity between the natal home range and each monthly post-dispersal home range

The most parsimonious model for variation in habitat dissimilarity between the natal home range and each monthly post-dispersal home range revealed that variation in habitat dissimilarity between the natal home range and each monthly post-dispersal home range was explained by an interactive effect between the month of the construction process and the proportion of woodland in the natal home range (AICc=-208.38; AICc weight=0.36; K=11) (Tables 1 and 5, Appendix 8). Habitat dissimilarity during the construction process of the post-dispersal home range varied differently for individuals which we classified as having a high proportion of forest in their natal home range (>18% of woodland in their natal home range, as 18% corresponded to the median proportion of woodland in the natal home ranges of dispersers in the population we studied) compared to individuals which we classified as having a low proportion of forest in their natal home range (<18% of woodland in their natal home range). Indeed, for individuals with a high proportion of forest in their natal home range, habitat dissimilarity between their natal home range and their monthly post-dispersal home range (i) increased by 42 % between the first and the second month of the construction process and (ii) remained more or less constant between the second and the fourth month of the construction process (Figure 7) For individuals with a low proportion of forest in their natal home range, habitat dissimilarity between their natal home range and their monthly postdispersal home range (i) increased by 5 % between the first and the second month of the construction process, (ii) decreased by 5% between the second and the third month of the construction process and (iii) increased by 4% between the third and the fourth month of the construction process (Figure 7). Thus for individuals with a low proportion of forest in their natal home range, habitat dissimilarity between their natal home range and their monthly postdispersal home range remained more or less constant during the construction process of their post-dispersal home range (Figure 7).

All other models had a $\Delta AICc>2$ with the most parsimonious model selected (Tables 1 and 5).

<u>Table 3:</u> Performance of the generalized linear mixed effects models with a Delta_AICc<2 and of the model following those models for explaining variation in the proportion of woodland within monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Models	AICc	Delta_AICc	AICcWt	Κ
$Size_{postHR} + Ind + Year$	-232.07	0	0.27	5
Month * BM + Month * Woodland _{natalHR} + Size _{postHR} + Ind + Year	-231.45	0.62	0.2	16
$Month + BM + Size_{postHR} + Ind + Year$	-229.35	2.71	0.07	9

<u>Table 4:</u> Performance of the linear mixed effects models with a Delta_AICc<2 and of the model following those models for explaining variation in habitat diversity (exponential transformed) within monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Models	AICc	Delta_AICc	AICcWt	Κ
$Size_{postHR} + Ind + Year$	383.66	0	0.65	5
Month + Size _{postHR} + Ind + Year	388.03	4.37	0.07	8

<u>Table 5:</u> Performance of the generalized linear mixed effects models with a Delta_AICc<2 and of the model following those models for explaining variation in habitat dissimilarity between the natal home range and each consecutive post-dispersal home range. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Models	AICc	Delta_AICc	AICcWt	Κ
Month * Woodland _{natalHR} + Ind + Year	-208.38	0	0.36	11
Month * Woodland _{natalHR} + BM + Ind + Year	-206.35	2.03	0.13	12
Month * Woodland _{natalHR} + BM + Diversity _{natalHR} + Ind + Year	-203.89	4.49	0.04	13

in the natal home range (F=high proportion of woodland, O=low proportion of woodland).

<u>Figure 7:</u> Predictions (black points) and confidence interval (bars) for variation in habitat dissimilarity between the natal home range and each monthly post-dispersal home range from the model explaining habitat dissimilarity between the natal home range and each monthly post-dispersal home range with an interaction between the month of the construction process and the proportion of woodland in the natal home range. For comprehension simpler presentation, individuals were divided in two categories depending on the proportion of woodland in their natal home range (F=individuals having a high proportion of woodland in their natal home range, *i.e.* >18% of woodland in their natal home range, *i.e.* <18% of woodland in their natal home range, *i.e.* <18% of woodland in their natal home range.

4. Discussion

A natal disperser's condition, *i.e.* its internal state or phenotype, and natal context, *i.e.* its natal environment, lead to inter-individual variation in dispersal (Clobert *et al.* 2009). Whereas condition and natal context dependence have been mostly described in the first stage of dispersal (Cote *et al.* 2011, Dingemanse *et al.* 2003, Haag *et al.* 2005, Hanski *et al.* 1991, Hanski *et al.* 2006, Quirici *et al.* 2011, Serrano *et al.* 2003), to our knowledge, studies focusing on the influence of an individual's condition and natal context in the settlement in a post-dispersal home range during natal dispersal are scarce. However, inter-individual variability in the settlement stage of dispersal is of particular importance for individual fitness, population dynamics and gene flow (Low *et al.* 2010, Duckworth & Badyaev 2007, Sacks *et al.* 2005). Indeed the condition such as the behavioural traits of an individual may influence its probability of success during settlement in a post-dispersal home range (Duckworth & Badyaev 2007). For example, in mountain bluebird, more aggressive individuals have a higher settlement success at the end of natal dispersal than less aggressive ones (Duckworth & Badyaev 2007).

Furthermore, the natal context of an individual may influence its settlement choice at the end of natal dispersal as individuals may tend to select a post-dispersal home range that resemble their natal home range (Davis & Stamps 2004). Thus, in order to better understand the ecological and evolutionary consequences of inter-individual variability in dispersal it seems of great importance to provide more studies on condition and natal context dependence in the last stage of the dispersal process, *i.e.* the settlement in a post-dispersal home range.

In this study, we were interested in inter-individual variability during the settlement in a post-dispersal home range at the end of natal dispersal. Our study aimed thus more precisely to describe the influence of an individual's natal context and condition on the temporal process of post-dispersal home range construction during settlement in a population of roe deer exploiting a variety of habitats in terms of composition and structure (Hewison *et al.* 2001).

The construction of the post-dispersal home range in a novel environment appeared to be a temporally gradual process in roe deer natal dispersers. Furthermore, we described interindividual variability in the construction of the post-dispersal home range during dispersal. First, the condition of roe deer natal disperser's affected the construction of the post-dispersal home range as individuals with a higher body mass always constructed a larger home range than individuals with a lower body mass. Second, the temporal construction process of the post-dispersal home range appeared to depend on the environmental features in a disperser's natal home range. Indeed, depending on the proportion of woodland in their natal home range, natal dispersers constructed their post-dispersal home range differently in time.

Our results suggest a last stage of the dispersal process condition- and natal contextdependent in a large herbivore: the roe deer. To our knowledge, our study is the first to focus on the influence of an individual's condition and natal context on the temporal construction process of the post-dispersal home range. As described by Debeffe *et al.* (2012) for the first stage of dispersal (*i.e.* the departure from the natal home range), the body mass of natal dispersers and the proportion of woodland in their natal home range lead to inter-individual variability in roe deer natal dispersal.

4.1. Gradual construction of the post-dispersal home range

As we expected, roe deer natal dispersers constructed their post-dispersal home range gradually. Indeed, the size of monthly post-dispersal home ranges and the dissimilarity with the natal home range of monthly post-dispersal home ranges varied during the construction process.

During the first month of the construction process, the size of the post-dispersal home range appeared much larger than later in the construction where the size of the post-dispersal home range remained more or less constant (27 % larger first month's post-dispersal home range than second month's post-dispersal home range). Thus, as roe deer natal dispersers first construct a large monthly post-dispersal home range and as they then tend to have a reduced and quite constant monthly post-dispersal home range size, we may suppose that during the first month of post-dispersal home range's construction, dispersing juveniles explore their novel local environment to refine the composition and/or the limits of their new home range. Furthermore, when natal dispersers arrive in a novel environment they probably do not know their social environment. Therefore, natal dispersers may also refine the limits of their postdispersal home range depending on agonistic interactions with conspecifics during the first month of the construction of their post-dispersal home range. Indeed, in Siberian jays (Perisoreus infaustus) it has for example been shown that resident individuals constrain settlement of dispersers (Griesser et al. 2008). As roe deer adult males are territorial between March and August (Hoem et al. 2007), i.e. during a period including the settlement period at the end of roe deer natal dispersal (between April and July), they may thus push out natal dispersers from their territory and constraints natal dispersers to have an unstable postdispersal home range at the beginning of the construction process. For example, Wahlström (1994) described adult roe deer agonism toward yearling males. Once natal dispersers have refined the limits of their post-dispersal home range depending on the habitat composition and on the social context, their post-dispersal home range may remain more or less stable as suggested by the less variable post-dispersal home range size between the second and the fourth month of the construction process. As there is little available published information on post-dispersal settlement, we may compare the behaviour of post-dispersal home range construction for natal dispersers with that of home range construction for released animals in management operations. Thus, instability in the post-dispersal home range of roe deer natal dispersers might be compared with observed home range instability following animal release in a new site for example during reintroductions. Indeed it has been shown that the home range size of released individuals is often larger directly after release than some weeks later. This is for example the case in birds such as the puaiohi (Myadestes palmeri), in the whitetailed deer (Odocoileus virginianus), in red squirrels (Sciurus vulgaris), and in fishes such as the black-spot tukfish (Choerodon schoenleinii) where the size of the home range is larger directly following release than some weeks later probably because of explorations and learning of the novel environment and because of intraspecific and interspecific competition (Tweed et al. 2003, Beringer et al. 2002, Wauters et al. 1997, Kawabata et al. 2008). This comparison, between released animals and natal dispersers has limitations because the latter are not forced to leave their natal home range and then to settle in a new environment but also because released animals may be raised in captivity. However, for both natal dispersers and released animals, the environment encountered at settlement is new.

Similarly, habitat dissimilarity between the natal home range and each successive post-dispersal home range varied during the construction process of the post-dispersal home range. This observation reveals that the habitat cues experienced in the natal home range may be used by a natal disperser in order to construct its post-dispersal home range. As those variations in habitat dissimilarity between the natal home range and each successive post-dispersal home range depended on the natal context of natal dispersers, we will describe them further.

Contrary to our expectations, the proportion of woodland and the habitat diversity of monthly post-dispersal home ranges did not vary during the construction process. These results indicate that roe deer natal dispersers had a constant proportion of woodland and constant habitat diversity in their post-dispersal home range over the stages of the construction process of the post-dispersal home range. This may be due to a need for a certain fixed amount of woodland, for example for purposes of feeding or shelter (Hewison et al. 1998), and a certain fixed habitat diversity for example in order to insure feeding as roe deer are selective opportunists (Duncan et al. 1998). Indeed, Cargnelutti et al. (2002) described an identical surface area of woodland in absolute terms in both copse-living deer and forest deer, despite the fact that home range size differed between copse-living deer and forest deer. They suggested that roe deer require a certain base area of woodland in their home range for food, shelter and social functions (Cargnelutti et al. 2002). However, the absence of observed variation in the proportion of woodland and in the habitat dissimilarity of monthly postdispersal home ranges during the construction process of the post-dispersal home range may be due to a too small sample size in our study to describe such influence (e.g. small AICc differences concerning model selection for the variation in the proportion of woodland of monthly post-dispersal home ranges) or it may be due the use of inaccurate proxies for the description of the post-dispersal home range. Indeed, when dispersing roe deer construct their post-dispersal home range, they may not base their choice on the proportion of woodland but rather on the proportion of deciduous woodland as they often feed on the leaves of deciduous trees (Duncan et al. 1998). Moreover, the description of post-dispersal home range habitat diversity we used may not be biologically pertinent for roe deer as it is difficult to evaluate which categories of habitat should be included when measuring habitat diversity in roe deer home ranges. In fact, when measuring habitat diversity in monthly post-dispersal home ranges, we attributed the same weight to human infrastructures and roads than to different categories of vegetation. It may be interesting to separate habitat categories that may be avoided by roe deer such as roads when measuring habitat diversity within their home ranges.

Together with a marked difference in roe deer home range size between the first month and the second month of the construction of the post-dispersal home range, the absence of temporal variation in proportion of woodland and habitat diversity during the construction process of the post-dispersal home range may suggest that the construction of the postdispersal home range took only one month. In the future, it would thus be interesting to look at the stability in space of monthly post-dispersal home ranges in order to define when the post-dispersal home range stabilizes. For that purpose, a measure of the distances between the centers of gravity of successive monthly post-dispersal home ranges combined with a measure of the overlap between monthly successive post-dispersal home range may be used. Moreover, we may suppose that the month considered as the first month of construction of the post-dispersal home range may actually belong to the transience stage of the dispersal process and not to the settlement stage of dispersal. However, when looking at the trajectory of roe deer natal dispersers, their speed of moving seem highly different between the transience stage and the settlement stage. Further studies should measure the speed of moving of individuals during the different dispersal stages in order to verify that the different stages of dispersal were defined appropriately.

4.2. Inter-individual variability during the construction of the postdispersal home range

First, we described evidence for condition dependence (Clobert et al. 2009) in the last stage of the dispersal process (*i.e.* the settlement in a post-dispersal home range). Indeed, the condition of roe deer natal dispersers, indexed here according to their body mass, had an influence on the size of monthly post-dispersal home ranges. While we supposed that individuals in better condition would have a more stable home range than individuals in poorer condition, *i.e.* that the size of monthly post-dispersal home ranges would vary less during the construction of the post-dispersal home range for individuals in better condition than for individuals in poorer condition, the influence of an individual's body mass on the size of monthly post-dispersal home ranges was independent of the month of the construction process. Individuals with a higher body mass always had larger monthly post-dispersal home ranges than lighter individuals (278 % larger post-dispersal home ranges for 54% heavier individuals). An individual's condition could be linked with its ability to cope with conspecifics. Thus individuals in better condition (*i.e.* with a higher body mass) may be able to exploit and maintain a larger post-dispersal home range than individuals in poorer condition. Evidence for a better ability to cope with conspecifics for individuals in better condition than for individuals in poorer condition has been described in the roe deer as heavier reproducing territorial males had a higher yearly breeding success than lighter males (Vanpé et al. 2009). The same pattern for the ability to cope with conspecifics may occur in juvenile roe deer. Another hypothesis to explain the observed difference in post-dispersal home range size between light and heavy individuals could be that heavier individuals may have higher energetic needs and so require larger home ranges. For example, female roe deer seemed to adjust the size of their home range to their energetic needs (Tufto et al. 1996).

Second, settlement in a post-dispersal home range appeared natal context dependent (Clobert *et al.* 2009). Indeed the natal context of dispersing roe deer influenced the construction of the post-dispersal home range as the proportion of woodland in the natal home range had an influence on the variation in habitat dissimilarity between the natal home range and each successive monthly post-dispersal home range during the construction process of the

post-dispersal home range. Furthermore, as we expected but not in the same manner than we predicted, the influence of the natal context (i.e. the proportion of woodland in the natal home range) depended on the month of construction of the post-dispersal home range. That is, whereas habitat dissimilarity between the natal home range and each successive monthly postdispersal home range varied during the construction of the post-dispersal home range for individuals with a high proportion of woodland in their natal home range (individuals born in mostly forested habitats, *i.e.* forest-born individuals), habitat dissimilarity between the natal home range and each successive monthly post-dispersal home range remained more or less constant during the construction of the post-dispersal home range for individuals with a low proportion of woodland in their natal home range (individuals born in more open, mixed habitats, *i.e.* copse-born individuals). For forest-born individuals, habitat dissimilarity between the natal home range and the first month's post-dispersal home range was lower than habitat dissimilarity between the natal home range and the subsequent successive monthly post-dispersal home ranges (between the first and the second month of the construction process, habitat dissimilarity between the natal home range and monthly post-dispersal home ranges increased by 42%). Following the first construction month of the post-dispersal home range, habitat dissimilarity between the natal home range and each monthly post-dispersal home range remained more or less constant for forest- and copse-born natal dispersers. The observed difference between forest- and copse-born individuals in temporal variation of habitat dissimilarity between the natal home range and each monthly post-dispersal home range reveales behavioural differences between those two kinds of natal dispersers during settlement. Debeffe et al. (2012) already described differences in dispersal behaviour between forest- and copse-born natal dispersers. Indeed forest-born individuals dispersed less and when they dispersed, they travelled less far than copse-born individuals (Debeffe et al. 2012). Because forest-born individuals tend to disperse less than copse-born individuals (Debeffe et al. 2012), we may suppose that they were more bound to their natal home range than copseborn individuals. Indeed, forest-born individuals may be more afraid of novelty, *i.e.* have a higher level of neophobia (Mettke-Hofmann et al. 2009), than copse-born individuals. Thus, when forest individuals disperse and finally settle in a post-dispersal home range, they may first try to find a post-dispersal home range highly similar to their natal home range in terms of habitat composition, then they may gradually explore new habitats leading to an increase in habitat dissimilarity between the natal home range and monthly post-dispersal home ranges between the first and the second months of construction of the post-dispersal home range. This result suggests that forest individuals may rely on cues resembling those cues they experienced in their natal home range when they begin to settle in a post-dispersal home range. Natal habitat preference induction, *i.e.* the phenomenon of a habitat selection following dispersal biased toward stimuli encountered in an individual's natal habitat (Davis & Stamps, 2004), has already been observed in roe deer as the resemblance between the natal home range and the post-dispersal home range (overall post-dispersal home range) varied between individuals (Debeffe 2013). Those variations in natal dispersers' settlement strategies were linked to an individual's condition (body mass and sex) but the influence of the natal context on settlement was not studied (Debeffe 2013). Therefore, natal habitat preference induction may be used as a strategy in order to settle in a post-dispersal home range (Davis & Stamps, 2004) in forest individuals but not in copse-living individuals. Furthermore, a preliminary study on the settlement behaviour of roe deer natal dispersers seemed to describe an influence of an individual's level of neophobia and its settlement behaviour in a post-dispersal home range (Geidel, 2014). Indeed, individuals with a high level of neophobia settled in a postdispersal home range with a lower habitat dissimilarity with their natal home range than individuals with a low level of neophobia (Geidel, 2014). Differences in strategies for the construction of the post-dispersal home range may be observed because individuals with different natal contexts may have different personalities, i.e. on stable and repeatable individual behavioural differences over time and across situations (Réale et al. 2007). For example forest-born individuals may have a higher level of neophobia than copse-born individuals. Therefore, further studies should try to assess how an individual's natal context influences its personality. Once the relationship between an individual's natal context and its personality will have been described, we may have more facilities to explain how an individual's natal context shapes its settlement behaviour during natal dispersal.

4.3. Conclusion and prospects

Our study highlighted that the last stage of the dispersal process is dependent on both an individual's condition and natal context. As evidence for both condition and natal context dependence in settlement is scarce (Clobert *et al.* 2009), our study provides a rare example of condition and natal context dependence in the settlement in a post-dispersal home range in a free ranging large herbivore. Besides focusing on inter-individual variability in the settlement stage of the dispersal process, we described the temporal process of post-dispersal home range construction. To our knowledge, it is the first time that the temporal construction process of the post-dispersal home range at the end of natal dispersal was studied. We pointed out the influence of an individual's condition, particularly of its body mass, and of an individual's natal context, here the proportion of woodland in its natal home range, on the last stage of the dispersal process. These results are coherent with the results already obtained concerning condition and natal context dependence in roe deer natal dispersal (Debeffe *et al.* 2012). Indeed, previous studies described the marked influence of individual's body mass and of the proportion of woodland in individual's natal home range on earlier stages of the dispersal process (in particular, on the probability to disperse and on the distance travelled during dispersal) (Debeffe *et al.* 2012). Furthermore, in addition to the influence of an individual's personality on dispersal propensity. In fact, dispersal propensity was linked to juveniles' energetic budget and to their level of neophobia (Debeffe *et al.* 2014). Natal dispersers had a higher energetic budget and a lower level of neophobia than philopatric individuals (Debeffe *et al.* 2014).

Because the personality of individuals, may influence dispersal behaviour in roe deer, but also in some other animal species such as in great tits, in the invasive mosquitofish (Cote et al. 2010b; Dingemanse et al. 2003, Cote et al. 2010a) and in the mountain bluebird (Sialia currucoides) where more aggressive individuals disperse further than less aggressive individuals (Duckworth & Badyaev 2007), it would be interesting to study how personalities influence the construction process of the post-dispersal home range in dispersing roe deer and how it generates inter-individual variability in the behaviour of post-dispersal home range construction. The link between an individual's level of neophobia and its behaviour of postdispersal home range construction seems of particular interest. Indeed, when natal dispersers settle in a post-dispersal home range, they are confronted to a novel environment and need to construct their post-dispersal home range in this new environment. Thus, natal dispersers may vary in the strategy they use in order to construct their post-dispersal home range as a function of their fear of novelty. We may suppose that natal dispersers with a high level of neophobia will rely on habitat cues encountered in their natal home range at the beginning of the construction of their post-dispersal home range and that they will progressively explore new habitats. To the contrary, individuals with a low level of neophobia are less afraid of novelty and should rely less on the habitat cues of their natal home range when they construct their post-dispersal home range than individuals with a high level of neophobia.

Finally, our study highlighted the importance of integrating the effects of the condition and of the natal context in studies on settlement during natal dispersal. The effects of both factors may generate complex movement patterns as they influenced the settlement in a postdispersal home range. Therefore, a better understanding of condition and natal contextdependent settlement during natal dispersal may help us better understand population dynamics and colonization processes (Clobert *et al.* 2009).

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Appendix

<u>Appendix 1:</u> Adjusted coefficient of determination (R²) between explanatory variables of interest (using linear models).

	Body mass	Proportion of woodland in the natal home range	Habitat diversity in the natal home range
Body mass		-0.0081	0.011
Proportion of woodland in the natal home range			0.41
Habitat diversity in the natal home range			

Hypotheses	Models
Null	$Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Gradual construction	Month + Woodland _{Buffer} + Size _{natalHR} + Ind + Year
Condition	$Month + BM + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition	Month * BM + Woodland _{Buffer} + Size _{natalHR} + Ind + Year
Natal context	$Month + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Natal context	Month * Woodland _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year
Natal context	$Month + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Natal context	Month * $Diversity_{natalHR}$ + $Woodland_{Buffer}$ + $Size_{natalHR}$ + Ind + $Year$
Condition & natal context	$Month + BM + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month * BM + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month * Woodland_{natalHR} + BM + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month * BM + Month * Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month + BM + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month * BM + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	Month * Diversity _{natalHR} + BM + Woodland _{Buffer} + Size _{natalHR} + Ind + Year
Condition & natal context	Month * BM + Month * Diversity _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year
Natal context	$Month + Woodland_{natalHR} + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Natal context	Month * Woodland _{natalHR} + Diversity _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year
Natal context	$Month* Diversity_{natalHR} + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Natal context	$Month * Woodland_{natalHR} + Month * Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month + BM + Woodland_{natalHR} + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month* BM + Woodland_{natalHR} + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month * Woodland_{natalHR} + BM + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month*Diversity_{natalHR}+BM+Woodland_{natalHR}+Woodland_{Buffer}+Size_{natalHR}+Ind+Year$
Condition & natal context	$Month * BM + Month * Woodland_{natalHR} + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month* BM + Month* Diversity_{natalHR} + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	$Month*Woodland_{natalHR} + Month*Diversity_{natalHR} + BM + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$
Condition & natal context	Month * BM + Month * Woodland _{netalHR} + Month * Diversity _{natalHR} + Woodland _{Buffar} + Size _{natalHR} + Ind + Year

Appendix 2: Candidate linear mixed effect models for explaining variation in the size (log transformed) of monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Hypotheses	Models
Null	$Size_{postHR} + Ind + Year$
Gradual construction	Month + Size _{postHR} + Ind + Year
Condition	Month + BM + Size _{postHR} + Ind + Year
Condition	Month * $BM + Size_{postHR} + Ind + Year$
Natal context	$Month + Woodland_{natalHR} + Size_{postHR} + Ind + Year$
Natal context	Month * Woodland _{natalHR} + Size _{postHR} + Ind + Year
Natal context	Month + Diversity _{natalHR} + Size _{postHR} + Ind + Year
Natal context	Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year
Condition & natal context	$Month + BM + Woodland_{natalHR} + Size_{postHR} + Ind + Year$
Condition & natal context	Month * BM + Woodland _{natalHR} + Size _{postHR} + Ind + Year
Condition & natal context	Month * Woodland _{natalHR} + BM + Size _{postHR} + Ind + Year
Condition & natal context	Month * BM + Month * Woodland _{natalHR} + Size _{postHR} + Ind + Year
Condition & natal context	$Month + BM + Diversity_{natalHR} + Size_{postHR} + Ind + Year$
Condition & natal context	Month * BM + Diversity _{natalHR} + Size _{postHR} + Ind + Year
Condition & natal context	Month * Diversity _{natalHR} + BM + Size _{postHR} + Ind + Year
Condition & natal context	Month * BM + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year
Natal context	$Month + Woodland_{natalHR} + Diversity_{natalHR} + Size_{postHR} + Ind + Year$
Natal context	Month * Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year
Natal context	Month * Diversity _{natalHR} + Woodland _{natalHR} + Size _{postHR} + Ind + Year
Natal context	Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year
Condition & natal context	$Month + BM + Woodland_{natalHR} + Diversity_{natalHR} + Size_{postHR} + Ind + Year$
Condition & natal context	Month * $BM + Woodland_{natalHR} + Diversity_{natalHR} + Size_{postHR} + Ind + Year$
Condition & natal context	Month * Woodland _{natalHR} + BM + Diversity _{natalHR} + Size _{postHR} + Ind + Year
Condition & natal context	Month * $Diversity_{natalHR} + BM + Woodland_{natalHR} + Size_{postHR} + Ind + Year$
Condition & natal context	$Month * BM + Month * Woodland_{natalHR} + Diversity_{natalHR} + Size_{postHR} + Ind + Year$
Condition & natal context	$Month* BM + Month* Diversity_{natalHR} + Woodland_{natalHR} + Size_{postHR} + Ind + Year$
Condition & natal context	$Month * Woodland_{natalHR} + Month * Diversity_{natalHR} + BM + Size_{postHR} + Ind + Year$
Condition & natal context	Month * BM + Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year

<u>Appendix 3:</u> Candidate generalized or linear mixed effect models for explaining respectively variation in the proportion of woodland and in habitat diversity (exponential transformation) within monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Hypotheses	Models
Null	Ind + Year
Gradual construction	Month + Ind + Year
Condition	Month + BM + Ind + Year
Condition	Month $*$ BM + Ind + Year
Natal context	$Month + Woodland_{natalHR} + Ind + Year$
Natal context	Month * Woodland _{natalHR} + Ind + Year
Natal context	Month + Diversity _{natalHR} + Ind + Year
Natal context	Month * Diversity _{natalHR} + Ind + Year
Condition & natal context	$Month + BM + Woodland_{natalHR} + Ind + Year$
Condition & natal context	Month * BM + Woodland _{natalHR} + Ind + Year
Condition & natal context	Month * Woodland _{natalHR} + BM + Ind + Year
Condition & natal context	Month * BM + Month * Woodland _{natalHR} + Ind + Year
Condition & natal context	$Month + BM + Diversity_{nataHR} + Ind + Year$
Condition & natal context	Month * BM + Diversity _{natalHR} + Ind + Year
Condition & natal context	Month * Diversity _{natalHR} + BM + Ind + Year
Condition & natal context	Month * BM + Month * Diversity _{natalHR} + Ind + Year
Natal context	$Month + Woodland_{natalHR} + Diversity_{natalHR} + Ind + Year$
Natal context	Month * Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year
Natal context	Month * $Diversity_{natalHR} + Woodland_{natalHR} + Ind + Year$
Natal context	Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Ind + Year
Condition & natal context	Month + BM + Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year
Condition & natal context	Month * BM + Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year
Condition & natal context	Month * Woodland _{natalHR} + BM + Diversity _{natalHR} + Ind + Year
Condition & natal context	Month * Diversity _{natalHR} + BM + Woodland _{natalHR} + Ind + Year
Condition & natal context	Month * BM + Month * Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year
Condition & natal context	Month * BM + Month * Diversity _{natalHR} + Woodland _{natalHR} + Ind + Year
Condition & natal context	Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + BM + Ind + Year
Condition & natal context	Month $*$ BM + Month $*$ Woodland _{natalHR} + Month $*$ Diversity _{natalHR} + Ind + Year

<u>Appendix 4:</u> Candidate generalized linear mixed effect models for explaining variation in habitat dissimilarity between the natal home range and each monthly post-dispersal home range. The individual and the year were included as random effects in the model and the other variables as fixed effects.

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Models	AICc	Delta_AICc	AICcWt	K
$Month + BM + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$		0	0.29	10
$Month + BM + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	200.64	0.82	0.2	11
$Month + BM + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	201.14	1.32	0.15	11
Month + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	202.9	3.08	0.06	9
$Month + BM + Woodland_{natalHR} + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	202.96	3.14	0.06	12
Month * BM + Diversity _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	203.37	3.55	0.05	14
$Month * BM + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	203.88	4.06	0.04	14
$Month + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	204.13	4.31	0.03	10
$Month + Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	204.62	4.81	0.03	10
Month * BM + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	204.91	5.09	0.02	12
$Month * BM + Woodland_{natalHR} + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	205.82	6.01	0.01	15
Month * Diversity _{natalHR} + BM + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	206.39	6.57	0.01	14
$Month + Woodland_{natalHR} + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	206.5	6.68	0.01	11
Month * Woodland _{natalHR} + BM + Woodland _{Buffer} + Size _{natalHR} + Ind + Year		7.44	0.01	14
Month * Diversity _{natalHR} + BM + Woodland _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year		9.02	0	15
$Month * Woodland_{natalHR} + BM + Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	209.19	9.38	0	15
$Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	209.74	9.93	0	6
Month * $Diversity_{natalHR}$ + $Woodland_{Buffer}$ + $Size_{natalHR}$ + Ind + $Year$	209.75	9.93	0	13
Month * BM + Month * Diversity _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	209.89	10.07	0	17
$Month * BM + Month * Woodland_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	210.32	10.51	0	17
Month * Woodland _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	210.61	10.79	0	13
$Month * Woodland_{natalHR} + Month * Diversity_{natalHR} + BM + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	211.89	12.07	0	18
Month * Diversity _{natalHR} + Woodland _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	212.24	12.43	0	14
Month * BM + Month * Woodland _{natalHR} + Diversity _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year		12.58	0	18
Month * BM + Month * Diversity _{natalHR} + Woodland _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year		12.67	0	18
Month * Woodland _{natalHR} + Diversity _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	212.6	12.78	0	14
$Month * Woodland_{natalHR} + Month * Diversity_{natalHR} + Woodland_{Buffer} + Size_{natalHR} + Ind + Year$	215.13	15.31	0	17
Month * BM + Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Woodland _{Buffer} + Size _{natalHR} + Ind + Year	215.67	15.85	0	21

<u>Appendix 5:</u> Performance of the 28 candidate linear mixed effect models explaining variation in the size (log transformed) of monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Models	AICc	Delta_AICc	AICcWt	K
$Size_{postHR} + Ind + Year$	-232.07	0	0.27	5
Month * BM + Month * Woodland _{natalHR} + Size _{postHR} + Ind + Year	-231.45	0.62	0.2	16
Month + BM + $Size_{postHR}$ + Ind + $Year$	-229.35	2.71	0.07	9
Month + Size _{postHR} + Ind + Year	-229.08	2.99	0.06	8
Month * BM + Month * Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-229.02	3.04	0.06	17
Month * BM + Woodland _{natalHR} + Size _{postHR} + Ind + Year	-228.58	3.49	0.05	13
Month * BM + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-228.55	3.52	0.05	13
Month * Woodland _{natalHR} + BM + Size _{postHR} + Ind + Year	-228.52	3.55	0.05	13
Month * Woodland _{natalHR} + Size _{postHR} + Ind + Year	-228.27	3.8	0.04	12
Month + BM + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-227.09	4.98	0.02	10
Month + BM + Woodland _{natalHR} + Size _{postHR} + Ind + Year	-227.06	5.01	0.02	10
Month * $BM + Size_{postHR} + Ind + Year$	-226.92	5.15	0.02	11
Month + Woodland _{natalHR} + Size _{postHR} + Ind + Year	-226.8	5.26	0.02	9
Month + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-226.77	5.3	0.02	9
Month * BM + Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-226.36	5.71	0.02	14
Month * Woodland _{natalHR} + BM + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-226.32	5.75	0.02	14
Month * Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-225.87	6.2	0.01	13
Month + BM + Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-225.03	7.04	0.01	11
Month + Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	-224.56	7.51	0.01	10
Month * BM + Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	-223.93	8.13	0	20
Month * BM + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	-222.81	9.25	0	16
Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + BM + Size _{postHR} + Ind + Year	-221.76	10.3	0	17
Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	-221.23	10.83	0	16
Month * Diversity _{natalHR} + BM + Size _{postHR} + Ind + Year	-220.9	11.16	0	13
Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	-220.76	11.3	0	12
Month * BM + Month * Diversity _{natalHR} + Woodland _{natalHR} + Size _{postHR} + Ind + Year	-220.49	11.58	0	17
Month * $Diversity_{nataHR} + BM + Woodland_{nataHR} + Size_{postHR} + Ind + Year$	-218.71	13.35	0	14
Month * Diversity _{natalHR} + Woodland _{natalHR} + Size _{nostHR} + Ind + Year	-218.43	13.64	0	13

<u>Appendix 6:</u> Performance of the 28 candidate generalized linear mixed effect models for explaining variation in the proportion of woodland within monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

Models	AICc	Delta_AICc	AICcWt	K
Size _{postHR} + Ind + Year	383.66	0	0.65	5
Month + Size _{postHR} + Ind + Year	388.03	4.37	0.07	8
$Month + BM + Size_{postHR} + Ind + Year$	388.33	4.66	0.06	9
$Month + Woodland_{natalHR} + Size_{postHR} + Ind + Year$	388.74	5.07	0.05	9
$Month + BM + Woodland_{natalHR} + Size_{postHR} + Ind + Year$	389.06	5.4	0.04	10
$Month + Woodland_{natalHR} + Diversity_{natalHR} + Size_{postHR} + Ind + Year$	390.14	6.48	0.03	10
Month + $Diversity_{natalHR}$ + $Size_{postHR}$ + Ind + $Year$	390.35	6.69	0.02	9
$Month + BM + Diversity_{natalHR} + Size_{postHR} + Ind + Year$	390.66	7	0.02	10
$Month + BM + Woodland_{natalHR} + Diversity_{natalHR} + Size_{postHR} + Ind + Year$	390.77	7.11	0.02	11
Month * Woodland _{natalHR} + Size _{postHR} + Ind + Year	392.6	8.93	0.01	12
Month * Woodland _{natalHR} + BM + Size _{postHR} + Ind + Year	393.02	9.36	0.01	13
Month * BM + Size _{postHR} + Ind + Year	393.49	9.83	0	12
Month * Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	394.11	10.45	0	13
Month * BM + Woodland _{natalHR} + Size _{postHR} + Ind + Year	394.43	10.77	0	13
Month * Diversity _{natalHR} + Woodland _{natalHR} + Size _{postHR} + Ind + Year	394.83	11.17	0	13
Month * Woodland _{natalHR} + BM + Diversity _{natalHR} + Size _{postHR} + Ind + Year	394.85	11.19	0	14
Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	394.92	11.26	0	12
Month * Diversity _{natalHR} + BM + Size _{postHR} + Ind + Year	395.36	11.7	0	13
Month * $Diversity_{natalHR} + BM + Woodland_{natalHR} + Size_{postHR} + Ind + Year$	395.61	11.95	0	14
Month * BM + Diversity _{natalHR} + Size _{postHR} + Ind + Year	395.96	12.3	0	13
Month * BM + Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	396.2	12.53	0	14
Month * BM + Month * Woodland _{natalHR} + Size _{postHR} + Ind + Year	398.67	15.01	0	16
Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	400.45	16.78	0	16
Month * BM + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	400.53	16.87	0	16
Month * BM + Month * Woodland _{natalHR} + Diversity _{natalHR} + Size _{postHR} + Ind + Year	400.56	16.9	0	17
Month * BM + Month * Diversity _{natalHR} + Woodland _{natalHR} + Size _{postHR} + Ind + Year	400.9	17.24	0	17
Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + BM + Size _{postHR} + Ind + Year	401.21	17.55	0	17
Month * BM + Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Size _{postHR} + Ind + Year	407.04	23.38	0	20

<u>Appendix 7:</u> Performance of the 28 candidate linear mixed effect models explaining variation in habitat diversity (exponential transformed) within monthly post-dispersal home ranges. The individual and the year were included as random effects in the model and the other variables as fixed effects.

monthly post dispersal none range. The individual and the year were mended as random effects in the r	nodel and the other variat	les us fixed effe		
Models	AICc	Delta_AICc	AICcWt	K
Month * Woodland _{natalHR} + Ind + Year	-208.38	0	0.36	11
Month * Woodland _{natalHR} + BM + Ind + Year	-206.35	2.03	0.13	12
Month * Diversity _{natalHR} + Ind + Year	-206.13	2.25	0.12	11
Month * Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year	-206	2.38	0.11	12
Month * Diversity _{natalHR} + Woodland _{natalHR} + Ind + Year	-204.14	4.24	0.04	12
Month * Diversity _{natalHR} + BM + Ind + Year	-204.13	4.25	0.04	12
Month + Ind + Year	-203.9	4.48	0.04	7
Month * Woodland _{natalHR} + BM + Diversity _{natalHR} + Ind + Year	-203.89	4.49	0.04	13
Month + Woodland _{natalHR} + Ind + Year	-202.06	6.32	0.02	8
Month + BM + Ind + Year	-202.02	6.36	0.01	8
Month * Diversity _{natalHR} + BM + Woodland _{natalHR} + Ind + Year	-202.02	6.36	0.01	13
Month $*$ BM + Month $*$ Woodland _{natalHR} + Ind + Year	-201.88	6.5	0.01	15
Ind + Year	-201.75	6.63	0.01	4
Month + Diversity _{natalHR} + Ind + Year	-201.67	6.71	0.01	8
Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + Ind + Year	-201.6	6.78	0.01	15
$Month + BM + Woodland_{natalHR} + Ind + Year$	-200.15	8.23	0.01	9
Month + Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year	-199.81	8.57	0	9
Month + BM + Diversity _{natalHR} + Ind + Year	-199.79	8.59	0	9
Month * Woodland _{natalHR} + Month * Diversity _{natalHR} + BM + Ind + Year	-199.34	9.04	0	16
Month * BM + Month * Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year	-199.28	9.11	0	16
Month * BM + Month * Diversity _{natalHR} + Ind + Year	-199.03	9.35	0	15
Month + BM + Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year	-197.81	10.57	0	10
Month * BM + Ind + Year	-197.68	10.7	0	11
Month * BM + Month * Diversity _{natalHR} + Woodland _{natalHR} + Ind + Year	-196.78	11.6	0	16
Month * BM + Woodland _{natalHR} + Ind + Year	-195.69	12.69	0	12
Month * BM + Diversity _{natalHR} + Ind + Year	-195.33	13.05	0	12
Month $*$ BM + Month $*$ Woodland _{natalHR} + Month $*$ Diversity _{natalHR} + Ind + Year	-193.99	14.39	0	19
Month * BM + Woodland _{natalHR} + Diversity _{natalHR} + Ind + Year	-193.23	15.15	0	13

<u>Appendix 8:</u> Performance of the 28 candidate generalized linear mixed effect models for explaining variation in the dissimilarity between the natal home range and each monthly post-dispersal home range. The individual and the year were included as random effects in the model and the other variables as fixed effects.