Elodie Wielgus

2nd year Master’s degree – Ecologie Fonctionnelle, Comportementale et Evolutive
2015/2016

Are individual roe deer (*Capreolus capreolus*) distributed randomly or according to their behavioral profiles in a heterogeneous environment?

Research internship carried out in the *Comportement et Ecologie de la Faune Sauvage* department (C.E.F.S) in the *Institut National de la Recherche Agronomique* (I.N.R.A)

Directed by **Nicolas Morellet** and **Michel Goulard**

Presented the 16th June

ACKNOWLEDGEMENTS

At the first step, I would like to thank Stéphane Aulagnier and Mark Hewison for having accepted me and in the INRA-CEFS laboratory.

I would like to give a special thanks to Nicolas Morellet to have offered me this opportunity to realize this internship and to follow me during the different stages of my internship. I would like to thank him for helping me during the construction of the hypotheses, during the analyses and the interpretation of the results. I thank him for his valuable assistance, for always being attentive to answer my questions and for its recommendations on statistical analyses on R. Moreover, thank you for your comments during the reading of my report, sometimes even during the week-end.

A particular thanks to Michel Goulard for helping me during statistical analysis, in particular in geostastical models and PLS regression. I would like to thank him for his valuable assistance and presence to answer my questions. He was always ready to come to the laboratory to discuss the topic and bring me answers, and I am particularly grateful to him.

Many thanks to Yannick Chaval for his participation in the study. He gave me the access to data-base and explained me the functioning. I do not forget all hours he spent to build buffers in QGIS and extract the land use sometimes into late in the evening or during his holidays. Thank you for your help.

I also want to thank Bruno Lourtet, without whom the realization of this study would have not been possible because he took hours in order to input the GIS of the study site.

Great thanks to Ophélie Couriot for introducing me to the telemetry method during two weeks. These few weeks were great, during which I learned many things, although the weather was not really sunny or welcoming! I also think about Chloé Monestier for advices she provided me during the interpretation of the results, explications about personality concepts and others discussions that I appreciated.

I also thank my interns co-workers, Laura Gervais and Pauline Hessenauer for their welcome, their good mood and for the atmosphere in the office. With Ophélie, Chloé and Anaïs Denailhac, thank you for all these good moments in particularly outside the laboratory that I appreciated a lot.

Finally, thanks to everybody of the laboratory for their cordial welcome and for the field experiments. In particular, I thank Mark, Nicolas, Yannick, Ophélie, Chloé, Bruno Cargnelutti, Nicolas Cebe, Hélène Verheyden, Erwan Quéméré, Joël Merlet, Denis Picot, Jean Joachim, Jean-Luc Rames, for roe deer captures and other people who helped to collected data that I used during my internship. I enjoyed those months spent with you!

SOMMAIRE

INTRODUCTION

During their life, animals face multiple energy demands to reproduce and to ensure their maintenance in a broad manner (e.g. growth, predator or pathogens avoidance, …). Resource acquisition is consequently crucial for animals, in particular the acquisition of food resource, but also acquisition of others resources that are essential for the survival and/or reproduction of an animal like for example finding a sexual partner, a refuge or a territory for a nesting site (Tilman 1982). The optimal foraging theory determines the individual's behavioral tactic when searching for food, defined as a set of decisions, which allows the animal to maximize its survival and its reproductive success (Cézilly and Benhamou 1996). This theory depends both on risk of predation and resources availability. Resources are often limited in the environment and are not distributed homogeneously (Croxall *et al.* 1988). Indeed, the landscape in which animal species live is dynamic and evolves naturally through processes for example plant succession, climatic variations or due to seasonality. According to Mueller and Fagan (2008), resources availability changes in time and in space across four axes: (1) resource abundance, (2) spatial configuration of resource, (3) temporal variability of resource locations and (4) temporal predictability of resources. Therefore, resources are generally distributed in several patches and the temporal variability or predictability of resources is influenced by seasonality in temperate zones or between the rainy and dry seasons in tropical zones, for example. This temporal variability of resources can be seen at different scales: among years, among seasons, within a season or even within a day (Gaillard *et al.* 2010). As a result, animals face a heterogeneous landscape of resources, in which they develop multiple adaptations to survive, notably through movements across and within patches (Nathan *et al.* 2008). Natal dispersal defined by movements of an individual from its natal habitat to its first breeding site (Clobert *et al.* 2005) is a key process that allows to respond to heterogeneity of resources availability by avoiding competition for resources access, such as food or a sexual partner (Bowler and Benton 2005). In addition, the phenomenon of migration described as a regular movement of individuals over long distances in relation to the regular fluctuations in environmental conditions (Dingle and Drake 2007) as well as a nomadic behavior are also responses adopted by species or some individuals from a species (partial migration) to cope with temporal variability and predictability of resources (Mueller and Fagan 2008). However, distribution of animals across patches may not always only result in maximizing the foraging opportunities. In prey species, individuals must balance between the need to obtain sufficient energy and avoiding the risk of predation, which they face during foraging (Brown 1988; Lima and Dill 1990). The use of a patch by individuals is greatly influenced by predation (Lima 1998; Brown 1999; Brown and Kotler 2004). In consequence, in addition to the spatio-temporal heterogeneity of resources, animal species have to avoid risk generally also structured in space and time (Lima and Bednekoff 1999; Creel and Winnie 2005) which generates a landscape of fear (Laundré *et al.* 2001), with the topography defined as the level of predation risk that prey meet in habitat.

In prey species, individuals face a trade-off between resource acquisition and potential risk of predation, and it may be more pronounced in human's dominated landscapes because of human activity (hunting) and global changes. Indeed, the intensification of agricultural practices and the extension of urban areas have greatly modified landscapes by increasing farmed areas and fragmentation of natural habitats (Sotherton 1998; Robinson and Sutherland 2002) and the amplification of climate change can lead to temporal changes in availability and predictability of resources (Cahill *et al.* 2013), resulting in marked spatio-temporal heterogeneity in both resource distribution and risk in these habitats. Moreover, landscape changes via human activities, including transport networks building, logging or urbanization are disturbances that animal species face, in addition to natural constraints. Consequently, animals can use risky habitats to search for higher quality food resources (Hewison *et al.* 2009) to ensure their maintenance, but the use of these habitats increase the exposition to both direct lethal (hunting and vehicle collisions) and non-lethal risks (recreational activities and presence of domestic species as dogs and livestock) by the contact with humans or natural predators (Jayakody *et al.* 2008; Webb *et al.* 2011). Hence, Frid and Dill (2002) considered that humans and disturbances created by human activity are a form of predation. Therefore, the search for food can force prey to forage in areas with a higher predation risk or can limit the ability of prey to detect a predator (Lima and Dill 1990). In order to maximize their search for food and minimize the risk to being preyed, animals may respond by modifying (1) morphological traits as changes in shape in gray treefrog (*Hyla chrysoscelis*) tadpoles induced by the presence of a predator that allow them to increase swimming speed and thus, help them to avoid predators (McCollum and Leimberger 1997), (2) physiological traits as higher metabolic rates in grasshoppers (*Melanoplus femurrubrum*) in the presence of predators (Hawlena and Schmitz 2010) and (3) behavioral traits as increasing of vigilance behavior of impala (*Aepyceros melampus*) and wildebeest (*Connochaetes taurinus*) in sites where felids were re-introduced (Hunter and Skinner 1998). Vigilance is a crucial anti-predator behavior that reduces the vulnerability to predation (Lima and Dill 1990), and several studies highlighted the increase of this behavior in presence of predators (Monclus *et al.* 2006; Benhaiem *et al.* 2008). However, the increase of vigilance level can be habitat-dependent, especially in red deer (*Cervus elaphus*), in which vigilance level of an individual is higher in open habitats such as meadows than in closed habitats, like forest (Jayakody *et al.* 2008). In this landscape of fear, in order to forage, animals may also reduce the potential predation risk by altering their habitat use from riskier to safer areas in time and/or in space (Bonnot *et al.*

2013) or their movement patterns (Fortin and Andruskiw 2003; Webb *et al.* 2011) or by increasing group size (Creel and Winnie 2005).

Individuals of a same population may differ in their response to predation risk by expressing contrasting behaviors that depend on their phenotypic traits and their sensitivity to stressors (Koolhaas *et al.* 1999; Martin and Réale 2008). To days, it is acknowledge that individuals within a same population show consistent behavioral differences over their life time and when they appear in stressful situations, in presence of predators for instance, the behavioral differences are interpreted as "coping style" (Koolhaas *et al.* 1999). These authors defined a coping style as "a coherent set of behavioral and physiological stress response which is consistent over time and which is characteristic to a certain group of individuals". Five behavioral dimensions are commonly used to describe behavioral profile and form the "Big Five" theory (Réale *et al.* 2007): shyness-boldness (or reactivity-proactivity), exploration-avoidance, activity, sociability and aggressiveness. Facing to a stressful situation, the behavioral responses are described by a continuum of proactivity. On the one hand, proactive individuals are more active, highly aggressive, impulsive in decision-making and take risks in the face of potential dangers and on the other hand, reactive individuals are less active, lowly aggressive, avoid the risky situations and tend to react to dangers by freezing (Koolhaas *et al.* 1999, 2010). It is also defined that proactive individuals are bold, whereas reactive individuals are shy. For instance, when faced with a trade-off between resource acquisition and risk avoidance, some individuals prioritize foraging opportunities but, therefore, may expose themselves to a higher risk of predation whereas others may prefer to minimize risk by foraging in secure habitats, even if food quality is lower.

European roe deer (*Capreolus capreolus*) is a concentrate selector (Hofmann 1989) but also a generalist herbivore which feeds on a large number of plant species (Sempéré *et al.* 1996; Tixier and Duncan 1996). Roe deer are well-adapted to modern agricultural landscapes (Sempéré *et al.* 1996), thanks to its behavioral plasticity and diet composition flexibility (Abbas *et al.* 2011). However, as contacts with humans increase through recreational activities for example, roe deer face risk of predation by human disturbances, such as roads or hunting (Bonnot *et al.* 2013), in addition to risk by natural predators (principally wolves and lynx but red foxes, dogs and wild boars can killed fawns). In humans dominated landscape, open environments have higher quality food resources (Hewison *et al.* 2009) but also higher human disturbance (hunting) (Padié *et al.* 2015), thus, roe deer face to a behavioral trade-off between food acquisition and risk avoidance in these environments (Bonnot *et al.* 2013). One behavioral adaptation is an altering of their activity patterns between nighttime and daytime by the use of risky habitats during nighttime and safer habitats during day time (Bonnot *et al.* 2013). However, it persists individual differences in the way individuals solve the trade-off, in relation to individual's personality (Monestier *et al.* 2015). For example, although ungulates often used open habitats during nighttime and safer habitats during daytime, reactive roe deer used less open habitats during daytime when risk is higher than proactive individuals (Bonnot *et al.* 2015). However, proactive individuals increased their vigilance level to counterbalance this high level of predation. In addition, the inter-individual differences in behavior may have strong impacts on fitness (Smith and Blumstein 2008). For example, in North American red squirrels (*Tamiasciurus hudsonicus*), the mother aggressiveness influenced her offspring survival and its activity impacted her offspring growth rate (Boon *et al.* 2007). However, this study highlighted a temporal variation in fitness consequences of personality, because these effects of mother personality on her offspring varied across life-history stages and over time, probably due to food availability. In roe deer, Monestier *et al.* (2015) had shown that inter-individual differences in the coping style of the mother roe deer impacted early offspring survival and, thereby, female fitness. However, this study had also highlighted that consequences of coping styles on female fitness were habitat-dependent, because offspring survival was dependent on both the coping style and the habitat use of their mother. Indeed, offspring of proactive mothers survived better in open habitats whereas, in closed habitats, fawns of reactive mothers had the highest survival. This suggests a landscape of fitness costs that differs among individuals of a same population and that behavioral profiles are more adaptable in terms of fitness in some environments than in others. Therefore, this supposes that some of behavioral profiles should be favored in some contexts. For instance, in Eastern chipmunks (*Tamias striatus*), Martin and Réale (2008) have found that the most exploratory and docile individuals lived in areas that were most frequented by humans. These results indicate a non-random distribution of animals in the landscape as animals distribute themselves in relation to both personality and human disturbance. To our knowledge, few studies have focused on spatial distribution of behavioral profiles, even though some recent studies have highlighted that specific behavioral profiles occur more frequently in some contexts than in others (Dingemanse *et al.* 2003; Stamps and Groothuis 2010; Pearish *et al.* 2013).

We carried out a study on a free-ranging population of roe deer in order to study the distribution of individuals in a humans dominated agricultural landscape in relation to their personality. We expected that specific behavioral profiles occur more frequently in some contexts than in others, which may generate a spatial distribution in the landscape of coping styles. Roe deer is defined as a forest-dwellings species and prefers forest habitats, croplands with small woodland patches but also high-grassy meadows with some shrubs (Sempéré *et al.* 1996 However, as proactive roe deer used more open habitats during daytime than reactive individuals (Bonnot *et al.* 2015), we first expected that environment of reactive individuals should include more woodland patches than environment of proactive individuals. Then, forests habitats are one of the most important habitats for roe deer because they offers refuge but they have been severely affected by landscape changes and the remaining woodlands are often highly fragmented, which can alter the movement abilities of roe deer for example (Coulon *et al.* 2004). In this way, because reactive individuals should avoid the stressful situations (Koolhaas *et al.* 1999), we hypothesized that the woodland fragmentation in habitat of these individuals should be lower in order to move in favorable matrix because unfavorable habitat in terms of predation risk does not provide cover against predator, compared to woodland habitat of proactive individuals, which can be more fragmented because they are more impulsive in decision-making when they have to face dangers. Third, because human activity induce some disturbances for roe deer (Bonnot *et al.* 2013) and they avoid areas with human activity, as roads and human dwellings (Coulon *et al.* 2008), we expected that proactive individuals, which are more impulsive in decision-making and more prone to take risks in the face of potential dangers may accept more human disturbances in their habitat than reactive individuals. Finally, we also expected that in open environments, which are heavily dominated by crops and humans, individuals should be more active in order to counterbalance the high risk of predation in this environment (Padié *et al.* 2015). In contrast, as the forest environments are more secure areas than open areas we expected that individuals are less active in forest than in open areas.

In order to test whether there is a spatial distribution of individuals in the landscape according to their personality, we investigated relationships between individual's behavioral traits and individual's environmental context. For that, we used several variables describing the individual's environmental context and two different behavioral traits: an index of proactivity and an index of activity level.

MATERIAL AND METHODS

1. Study site

The study was carried out in a hilly and heterogeneous agricultural landscape in the South-West of France, about 60 km south-west of Toulouse (Fig. 1). This area covers around 7500 ha and it has suffered modification over the last century due to intensification of agricultural practices, an increase in average field size, a loss of woodlands and hedges and the planting of new crop types like corn and sorghum. The climate of this region is oceanic with an average annual temperature of 11.7°C and an average annual precipitation of 800 mm. It is a fragmented landscape in which the human population is present everywhere, including in villages and farms surrounded by a considerable road network. The study site is made up of meadows, crops and the wooded areas are divided into two large forests and several small woodlands.

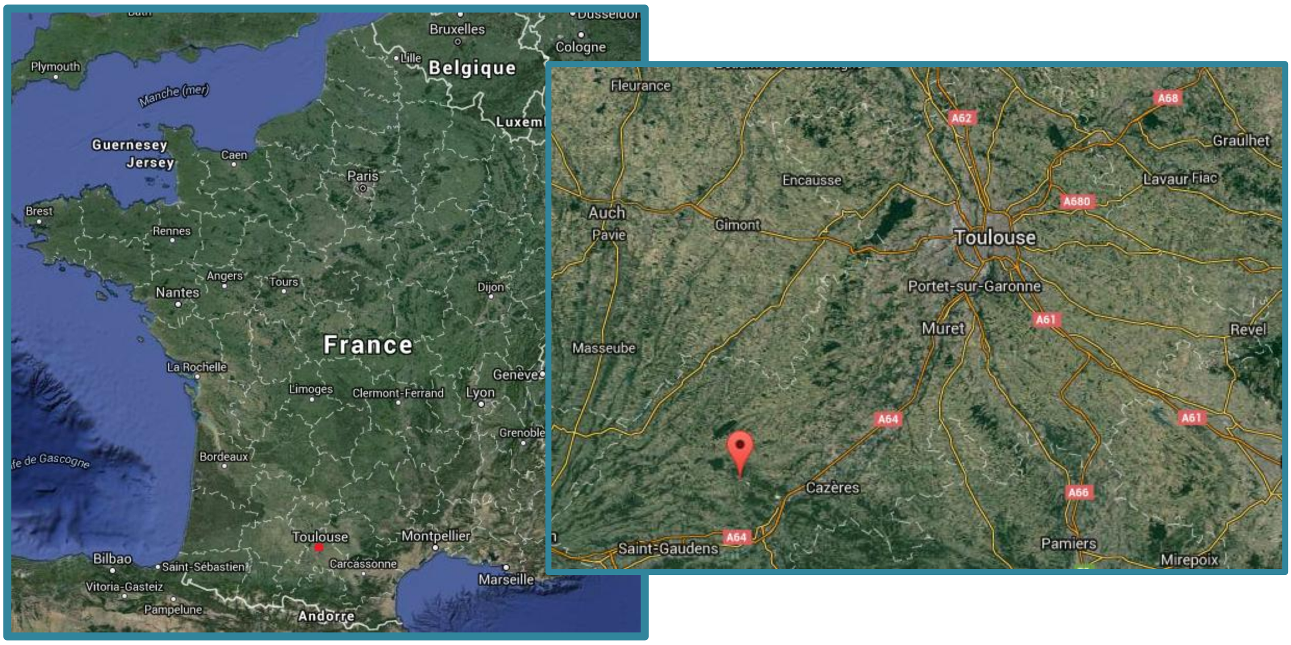


Figure 1: Location of study site (red point on the right picture). The study site is situated close to Aurignac, about 60 km of Toulouse.

2. Data collection

2.1 Capture events: behavioral data

Since 2002, winter captures of roe deer in the Aurignac population are performed from November to March. Every winter among six and eight captures are carried out on eleven sites chosen throughout the study site in order to cover the whole gradient of landscape heterogeneity. To capture individual’s roe deer, about 4 km of nets are used. The day of capture event a hundred people push animals towards the nets and when roe deer is caught in a net, it is tranquillized with an intra-muscular injection of 0.3 mL of acepromazine (Calmivet). Next, the individual is transferred into a small wooden retaining box to limit its stress until the end of the capture.

During marking, for each animal, we measured its body mass with an electronic balance to the nearest 0.1 kg, its sex and its age (in three age classes: juveniles, less than 1 year old, yearling, between 1 and 2 years old and adults). Juveniles are recognized by the presence of a tri-cupsid third premolar milk tooth (Ratcliffe and Mayle 1992). Then, most of individuals are equipped with a VHF, GPS or GSM collar (Lotek 3300 GPS or Lotek Small WildCell GSM).

Since 2009, behavioral data are collected to index the individual's reactivity to the capture event (Debeffe *et al.* 2014; Bonnot *et al.* 2015; Monestier *et al.* 2015), and to determine the inter-individual differences in the response to a stressful situation (Réale *et al.* 2000). We retained the behavior of animal throughout the capture event, at capture and during handling. In addition to behavior in the net (struggle or not) and in the wooden box (turning upside down), the struggle and painting levels on the marking table, the behavior and the running type at release (panic or calm, flight speed, attempts to remove its collar) are recorded.

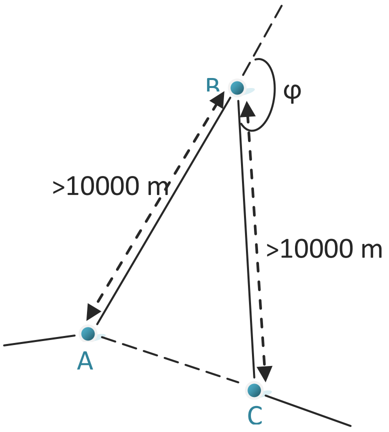
2.2 Individual monitoring: spatial data and activity

The majority of roe deer are equipped with GPS collars during the marking procedure. These collars allow following individual movements as they record the locations of individual thanks to the satellites. In fact, collars were programmed to collect GPS locations with a specified schedule. Between 2002 and 2004 the collars provided one GPS fix every 4 hours and since 2005 every 6 hours. In addition most collars are also equipped with an activity sensor that provides information on activity through head position (Gottardi *et al.* 2010). In fact these activity sensors give the sum of the number of vertical and horizontal head movements every 5 mins. Monestier *et al.* (2015) have shown that vertical head movements were consistent over time as a result of a high repeatability ($r = 0.682$), suggesting that this measure of activity characterize a personality traits.

3. Indexing individual's environmental context and behavioral profile

3.1 Environmental context

In order to describe the environmental context of a roe deer, we used the locations recorded by GPS collars to measure a center of gravity for each individual per year. It allows estimating the position in the landscape of the environment of an individual and then, describing the environment around the center of gravity, corresponding to the environmental context of an individual. Because these spatial data were necessary to describe the environment of a roe deer and the land cover mapping of the study site was only available from 2005, we focused our study on roe deer followed from 2005, *i.e.* individuals with locations every 6 hours. On the other hand, we considered only yearlings and adults roe deer because fawns have the same environment as their mother and they are emancipated at one year old. Individuals which were monitored less than 30 days following release were not taken into account in this study because we needed a longer monitoring to index habitat in which a roe deer live. We also removed location data for the first week after capture because this event induces modifications of roe deer spatial behavior (Morellet *et al.* 2009). Indeed, after release, roe deer show a strategy that consists of seeking a refuge, with limited displacement. In addition, because locations might sometimes be inaccurate, we removed 25 aberrant points from the full data set. Aberrant points were defined following a fix rule (Fig. 2). Overall, 180 environmental context were described for 169 individuals (some of individuals were followed several years). One individual had much of its habitat outside the land cover mapping of the study site, thus we could not describe his environment and we excluded this individual from the analysis. Finally, we have described the environmental context for 179 individuals monitored.



The point B is considered as being aberrant if (1) the distance between A and B is larger than two times the distance between A and C and the speed at which the animal moved from A to B is higher than 1000 m/h and the angle φ is higher than 2.5 radians or (2) the distance between A and B and the distance between B and C is larger than 10000 m.

Figure 2: Definition of aberrant points.

For this study, we used three terms related to landscape ecology which we defined as follows: (1) habitat is defined as a suitable element or not of the landscape for roe deer such as crops, forest or human dwellings, (2) landscape is defined as a set of suitable habitat for one species, which isolated from one another by a hostile matrix and (3) environment describes the place of life of an individual, taking into account several types of habitats. In order to describe the surrounding environment for each individual, several features of the landscape were measured. For that, we considered several buffers with a radius ranging from 100 m to 1500 m with an interval of 100 m centered on the center of gravity of each individual. As each type of habitat (crops, forest, hedgerows, …) have a different degree of connectivity (With *et al.* 1997), the perception of landscape by animals can vary according to the type of habitat. In addition, the spatial scale at which roe deer perceives its environment is unknown. Therefore, the use of several buffers allows taking into account different spatial scales, and overcome the lack of information on the spatial scale at which roe deer perceives its environment. Otherwise, the environment is so complex that a single spatial scale would not describe totally the environmental context. Thus, the small scales represent local environment, whereas the others cover the surrounding environment. Then, using the land cover mapping of the study site described each year and the software QGIS, the environments were determined the year of monitoring for each individual. The GIS of the study site contains 38 habitat categories describing the vegetation type (crops, natural meadow, artificial meadow, forested patches, hedges, …), roads, tracks, human infrastructures and other habitats. To describe the environment, we reclassify the habitats into three classes based on the degree of habitat openness: (1) the "open habitats" corresponding largely to crops, artificial and natural meadows and grassy strips, (2) the "forest habitats" characterized by wood, hedge and fallow land and (3) the "human habitats" taking into account ways, parkings, roads and human infrastructures (Fig. 3). Then, in order to characterize the environmental context within buffers, the "ClassStat" function within the package SDMTools (VanDerWal *et al.* 2014) from the R software was used to calculate the metrics for three habitat classes ("open habitats", "forest habitats" and "human habitats"). Among all the indexes obtained for each habitat classes, we chose the most appropriate to describe the environmental context of roe deer. First, roe deer is considered as a species of closed, predominantly wooded landscapes (Sempéré *et al.* 1996), thereby, we chose indexes describing the forest habitat. We defined the proportion of woodland corresponding to the proportion of forest patches within the area of the buffer. In addition, it is widely known that the intensification of agricultural practices and the extension of urban areas have greatly modified landscapes and create fragmented landscapes (Sotherton 1998; Robinson and Sutherland 2002). Forests habitats have been severely affected by landscape changes and the remaining woodlands are often highly fragmented, which lead to a large number of small and isolated patches immersed in an agricultural matrix. The fragmentation of woodland can affect roe deer's population, altering the movement abilities of animals for example (Coulon *et al.* 2004). Thus, we described the fragmentation of woodland by an aggregation index of forest habitats. This last index range from 0 to 100 and explain spatial configuration of forest patches with a value maximal when woodlands patches are aggregated into a single and compact patch. Second, even if roe deer are well adapted to modern agricultural landscapes (Sempéré *et al.* 1996) and then to human dominated landscapes, it avoids still areas with human activity, as roads and human dwellings (Coulon *et al.* 2008). Thus, we also described the roe deer environmental context by the proportion of human habitats corresponding to the proportion of human patches within the area of the buffer. A last index was estimated in order to quantify the diversity in habitats in the environmental context of a roe deer. For that, the "ClassStat" function was still used to calculate the Simpson's diversity index based on the proportion of categories describing the vegetation types (*e.g.* woodland, corn, rapeseed, wasteland, fallow land, wooded hedges, lucerne, parks, sorghum, soya and others leguminous plants, meadows, sunflower, polygonaceae plants, orchard and vine). Roads, human infrastructures and other human habitats were not taken into account in the calculation of the index. Then, the Simpson's diversity index was calculated using the following formula: $1 - \sum_{i=1}^{n} Pi^2$, with Pi, the proportion of a given habitat category and *n*, the total number of vegetation categories. A high Simpson's diversity index indicates a high diversity of vegetation.

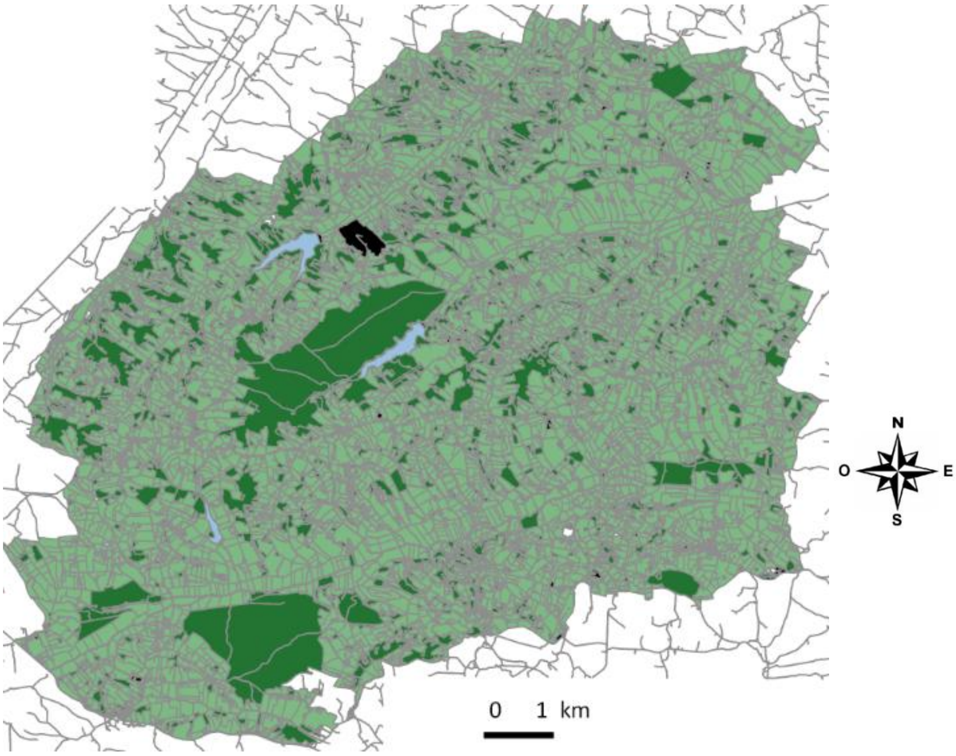


Figure 3: Study site cartography into three classes defined to describe the habitat of roe deer: open habitats (light green), forest habitats (dark green) and humans' habitats (dark).

3.2 Individual's behavioral profile

To describe the individual's reactivity to the risky situation of roe deer, according to a reactivity-proactivity gradient, we used behavioral parameters collected during capture events, which have been shown as being proxies of personality traits (Monestier *et al.* 2015). The behaviors recorded at capture and during handling are summarized into a behavioral score. In fact we attributed a score of 1 (occurrence) or 0 (absence) for each of the considered behaviors (Tab. 1) and then, an index of reaction to this stressful event was calculated as the mean of the sum of the scores for these 5 behavioral items. This index describes a stress profile gradient ranging from 0 to 1, with 1 indicating an individual with a high response to a stressful situation, a proactive individual (Monestier *et al.* 2015). For analyses, only individuals for whom the behavioral score was calculated with at least four behavioral items were kept (n = 95).

Table 1: Behavioral items used for the calculation of behavioral score. A behavioral score was then calculated as the mean of the sum of the scores for theses 5 behavioral items and it range from 0 to 1.

Capture phase	Behavioral items	Scores
In net	Struggle	No (0) Yes (1)
In box	Turning upside down in the box	No (0) Yes (1)
During handling	Struggle and panting on the table	No (0) Struggle or panting only (0.5) Struggle and panting (1)
At release	Speed running	Trotting (0) Moderate running (0.5) High speed running (1)
	Attempt to remove its collar	No (0) Yes (1)

The individual's behavioral profile was also described by the activity level of an individual. Activity corresponds to one of five behavioral dimensions usually identified and forming the "Big Five" theory (Réale *et al.* 2007). Activity corresponds to the general level of an individual's activity. This personality trait is supposed to be measured in non-risky and non-novel environment in order to be independent of the proactivity-reactivity personality dimension. In order to index the individual's activity, we used the activity data through head movement provided by activity sensor (Monestier *et al.* 2015). For that, we estimated the mean activity for the vertical movements during summer. We chose to this season because of a low hunting activity, a high resources availability and this is a key periods for the roe deer. Indeed, energy demands in this season are high due to lactation for females and rut for males (Maublanc 1991), leading to an increase of feeding activity. We considered that the level of head movements was an index of the level of activity during summer, *i.e.* individuals with high values of head movements had a high level of activity.

4. Statistical analyses

In order to test whether there was a spatial distribution of individuals in the landscape according to their behavioral profile (behavioral score and activity level), we analyzed the link between the behavioral score and the activity level with several environmental variables organized in space to describe the landscape (the proportion of forest habitat, the index of aggregation of forest habitat, the proportion of human habitat and the Simpson's diversity index at several scales). To be able to take into account the spatial structure of the data, we used geostatistical analyzes with the environmental variables as independent variables in each model. As the habitat use and habitat selection differ between males and females, we expected some differences between sexes in terms of spatial distribution of individuals in the landscape. Indeed, the habitat use of females is directly influenced by the availability of resources (Tufto *et al.* 1996) and females distribute themselves according to the resources availability, as predict by the ideal free distribution (Walhstrom *et al.* 1995 but see Pettorelli *et al.* 2003), whereas the distribution of males is mainly influenced by the females availability (Vanpé *et al.* 2009). In addition, the risk avoidance - resource acquisition trade-off differs between males and females (Monestier *et al.* 2015), which may lead to differences in the spatial distribution of males and females according to their behavioral profile (*i.e.* their behavioral score and their activity). As we expected difference between sexes, we considered two-way interactions between sex and each environmental variable, *i.e.* we used 121 independents variables (2 sexes, 4 environmental variables and 15 scales). As the number of independent variables was very important, we used a partial least square regression (PLSR) (Tenenhaus *et al.* 1995) in order to reduce the number of independent variables integrated into the geostatistical models. This method allows modeling a dependent variable by a set of independent variables and thus, the construction of predictive models, when the number of independents variables is really high (in particular when the number is similar to or higher than the number of observations). The PLSR consists in carrying out a principal component analysis of the set of independents variables, in such a way that the components are most possible related to the response variable in terms of the covariation (Tenenhaus *et al.* 1995). Then, the principle is to find a linear regression on a set of orthogonal components. Therefore, the PLSR was used to model the behavioral profile (*i.e.* the behavioral score and the activity level) according to the environmental variables, the sex and the two-way interaction between the sex and each environmental variables in order to reduce the number of independent variables to a few components, which are linear combinations of the initial variables. We used 95 observations to model the behavioral score and 142 for the activity level. We performed the PLSR using the “plsr” function within the package pls (Mevik and Wehrens 2007) in R. We scaled (consisting in centering and dividing by the variance) the independents variables in order to give the same importance and to be able to compare the coefficients of these variables. The number of components considered in the PLSR (behavioral score and activity level) was selected by the cross-validation method plotting the estimated root mean squared error of prediction (RMSEP) as a function of the number of components.

As previously stated, the PLSR was used in order to reduce the number of independent variables considered in the geostatistical modeling. We performed geostatistical analyses to take into account the potential spatial dependence of residuals, not accounted for the environmental variables (package geoR in R; Ribeiro and Diggle 2001). The models integrated in the geostatistical analyses were based on the PLS components, with as much variables as the number of components of the PLSR retained by the cross-validation approach. For each response variable, we considered all possible geostatistical models ("likfit" function in geoR package) and to selected the "best" model according to the Akaike Information Criterion (AIC). We selected the best model by retaining the model with the lowest AIC. As a first step, we plotted the empirical variogram of the behavioral score and the activity level data in relation to the independents variables in order to estimate initials parameters of each model. The variogram describes the spatial dependence in data, which shows the spatial variance between pairs of points as a function of the distance separating these points. To test the spatial correlation in the residuals of the behavioral score and the activity level data, we performed Monte-Carlo tests based on these variograms. This approach computes envelops for empirical variograms based on permutations of the data values on the spatial locations, i.e. the envelopes were built under the assumption of no spatial correlation. When all points are within the envelope, we cannot reject the spatial independence of the residuals of the dependent variable, which means that the spatial information was mainly taken into account by the environmental variables. For each dependent variable considered (i.e. the behavioral score and the activity level), the residuals were spatially independents then we have considered that we did not need to perform a geostatistical modeling. Hence, we used the PLSR to analyze the effects of the environmental variables on the behavioral profile. The PLSR provided coefficients for all independent variables (*i.e.* the environmental variables, the sex and the two-way interaction between sex and each environmental variable) and we calculated the variable importance of prediction (VIP) (Tenenhaus 1998) to index the importance of each variable in the different models. The VIP allows classing the environmental variables in relation to their explanatory power of the dependent variables. According to Tenenhaus (1998), the most important variables in the construction of the dependent variable are those having a high VIP, i.e. > 0.8.

RESULTS

The aim of this study was to test whether there was a spatial distribution of individuals in the landscape according to their behavioral profile. For that, we assessed the relationships between the behavioral score of the individuals (n = 95) and the activity level in summer (n = 142) with the environmental variables, which are organized in space. We have considered the proportion of forest habitat, the index of aggregation of forest habitat, the proportion of human habitat and the Simpson's diversity index at several scales and all the two-way interactions between sex and each environmental variable, using a PLSR analysis. The behavioral score describe the individual's reactivity to the risky situation, according to a reactivity-proactivity gradient and a high behavioral score indicates a high response of individual to stressful situation by being impulsive in decision-making whereas a low behavioral score indicates a low response of individual to stressful situation (Monestier *et al.* 2015). Activity corresponds to the general level of an individual's activity.

No differences were detected in the behavioral score between sexes, the difference between sexes was very low (0.002) with a small VIP. In contrast, there were differences in the activity level in summer between sexes: the difference was 0.54 in favor of males and this effect was very important (VIP > 0.8), indicating that the males were more active than females in summer. Otherwise, there were strong spatial structuring of roe deer behavioral score and activity level for the two sexes (Figs. 4 and 5).

The behavioral score was negatively correlated with the proportion of forest habitat whereas the activity level in summer was positively correlated with the proportion of forest habitat, whatever the sex and the scale (Figs. 4a, 4b, 5a and 5b). Thus, individuals with a high proportion of forest habitat in their surrounding environment tended to be more active in summer but not reactive to danger.

In addition, whatever the spatial scales, the behavioral score decreased when the index of aggregation of forest habitat increased, indicating that individuals had a low behavioral score when forest patches were highly aggregated (Figs. 4c and 4d). In contrast, the effect of the index of aggregation of forest habitat on the activity level differed among the spatial scales (Figs. 5c and 5d). Within a radius of 100 m, the effect was positive and strong but decreased until almost zero within a radius of 400 m. Then, even if the effects of the index of aggregation of forest habitat on the activity level were higher when the spatial scale was expanded, the relationship was reversed for radius larger than 1000 m. This pattern was similar for males and females. Therefore, individuals tended to be less reactive to dangers and more active in summer when they live in an environment where woodland patches are highly aggregated.

The behavioral score and the activity level of individuals were also influenced by the vegetation diversity index (Figs. 4e, 4f, 5e and 5f), but these effects differed among the spatial scales and between the sexes. Indeed, the behavioral score was negatively correlated with the vegetation diversity index, except for small scales (within a radius of 300 m), where the correlation was positive. This pattern was similar for males and females, even if the influence of the vegetation diversity index was slightly more pronounced for males within a radius of 300 m. In fact, for small scales, the behavioral score increased when the vegetation diversity index increased whereas for larger scales, the behavioral score decreased when the vegetation diversity index increased. The effect of the vegetation diversity index on the activity level also differed among the spatial scales and between the sexes. Indeed, the activity level of males increased when the vegetation diversity index increased, except for the largest scales and this result was also observed for females, but only within radius of less than 900 m. For larger scales, the positive effect of the vegetation diversity index on the activity level of females decreased and reversed, even if this relationship was not very relevant (VIP < 0.8). Therefore, for the smallest scales, females and males seemed to be more reactive to a potential danger and more active during summer when they live in a diversified environment. In contrast, for larger scales, females and males were less reactive to a potential danger when the environment was more diversified.

The proportion of human habitat had a negative effect on the behavioral score of roe deer, except for very large scales (Figs. 4g and 4h): individuals generally had a low behavioral score in habitat with a high proportion of human dwellings, roads and others infrastructures, and this effect was slightly more pronounced for males than for females. In contrast, the effects of the proportion of human habitat on the activity level differed among the spatial scales and this pattern was similar for males and females (Figs. 5g and 5h). Indeed, this relationship is complex and it is reversed several times according to the spatial scale considered. Therefore, the individuals living in a heavily human dominated environment were less reactive to dangers and presented highly contrasting activity level according to the spatial scale considered.

Even if the behavioral score and the activity level were influenced by the four environmental variables, the proportion of human habitat was the most influential variable, in particular on the activity level (Figs. 4g, 4h, 5g and 5h). The proportion of forest habitat had the lowest influence both on the behavioral score and on the activity level. Lastly, the index of aggregation of forest habitat and the vegetation diversity index influenced strongly the behavioral score, but weakly the activity level.

Finally, the habitat variables and the two-way interaction between the sex and each environmental variable explained 38.4% and 29.5% of the spatial structure of the behavioral score and the activity level, respectively.

Figure 4. Barplots of the coefficients of the PLSR analysis carried out to explain the behavioral score of roe deer by four environmental variables described at 15 scales. (a),(c),(e) and (g) are the coefficients for females and (b),(d),(f) and (h) are the coefficients for males. The ordinate axis gives the values of the coefficients of the environmental variables and the abscissa axis corresponds to the radius of the buffer used to describe the environment. Error bars represent the confidence interval at 95% and the stars the relevance of the variables in the analysis from the VIP.

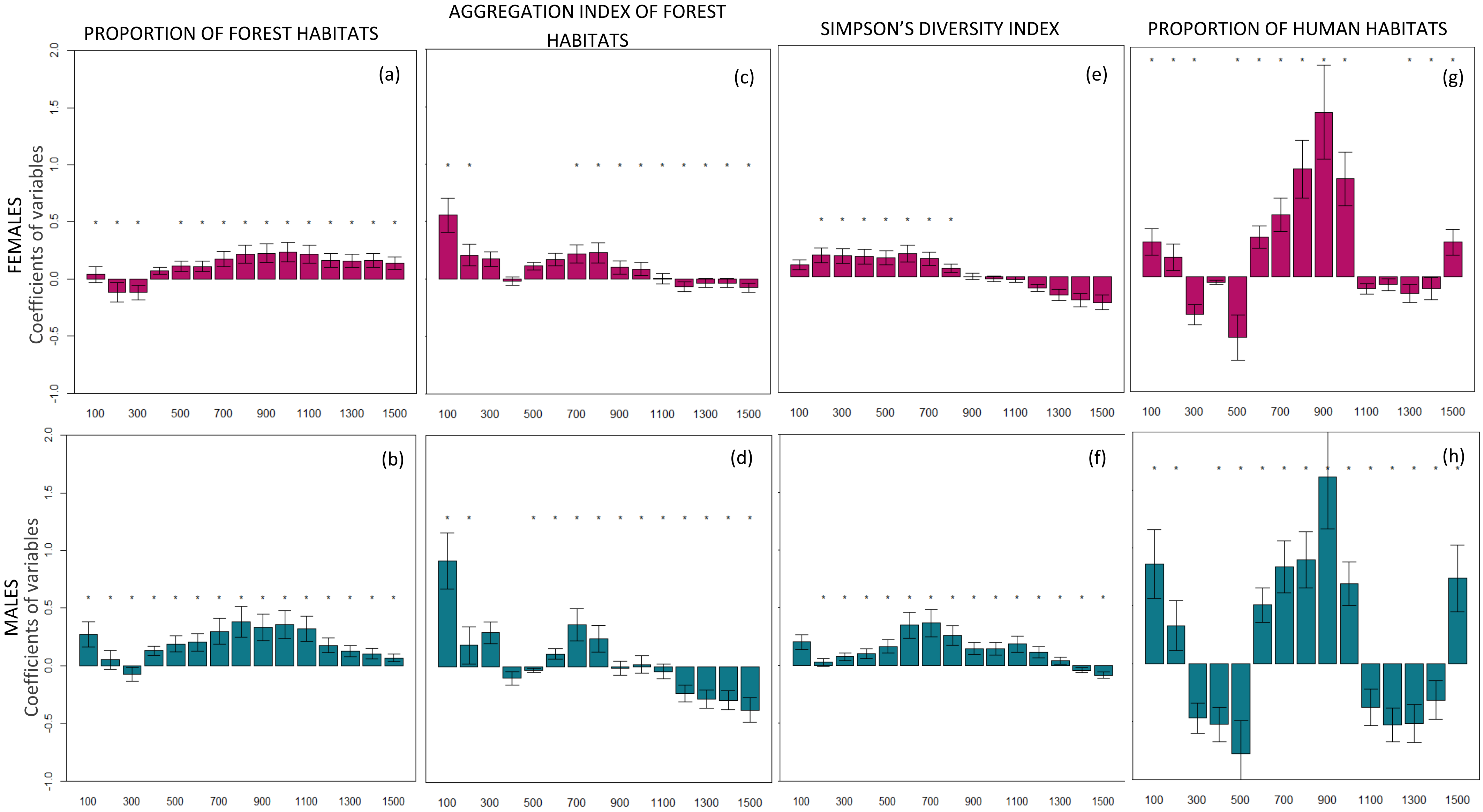


Figure 5. Barplots of the coefficients of the PLSR analysis carried out to explain the activity level of roe deer during summer by four environmental variables described at 15 scales. (a),(c),(e) and (g) are the coefficients for females and (b),(d),(f) and (h) are the coefficients for males. The ordinate axis gives the values of the coefficients of the environmental variables and the abscissa axis corresponds to the radius of the buffer used to describe the environment. Error bars represent the confidence interval at 95% and the stars the relevance of the variables in the analysis from the VIP.

DISCUSSION

The aim of this study was to investigate if individual's roe deer in a free-ranging population distribute themselves across a humans dominated agricultural landscape in relation to their behavioral profile. Some recent studies provided evidence for behavioral profile – environment correlations, for example in a natural population of three-spined stickleback (*Gasterosteus aculeatus*) (Pearish *et al.* 2013). They have shown that individuals emerged from a refuge more quickly after a disturbance when they were in shoals compared to animals that were alone. Our study provides evidence for behavioral profile – environment correlations in a natural population of roe deer; roe deer were not distributed randomly in relation to their behavioral profile and their distribution varied with the spatial scales. These results are consistent with some of our hypotheses. As expected, for most of the considered spatial scales, less reactive individuals to dangers, corresponding to a reactive coping style *(i.e.* individuals which are weakly aggressive and tend to avoid the risky situations; Koolhaas *et al.* 1999) occupied closed environments defined as heavily forested environments where woodland habitat is weakly fragmented whereas the more reactive individuals to dangers (*i.e.* a proactive coping style) lived in open environments where woodland habitat were scarce and highly fragmented. In contrast, some of our results are not in agreement with our prediction. Indeed, we expected that proactive individuals, which are more impulsive in decision-making and more prone to take risks in the face of potential dangers may accept more human disturbances in their environment than reactive individuals. However, our results showed the opposite: the more "reactive" individuals occupied an environmental context where human presence is high and the more "proactive" individuals lived in areas where human activities are lower. In addition, our results on the correlation between the environmental context and the individual's activity during summer were contrary to our predictions: we found that the individuals from open environments were less active than those living in closed environments.

This non-random distribution of behavioral profiles in the landscape might be explained in four ways according to habitat selection or natural selection: (1) roe deer could actively seek areas with certain characteristics of habitat because of their intrinsic differences in their behavioral profile (niche picking; Stamps and Groothuis 2010) to potentially increase their fitness, (2) an individual might influence its environment in which it live (niche construction; Stamps and Groothuis 2010), (3) roe deer could show different behavioral profiles because they lived in different environments, *i.e.* the environment influence the individual's behavior and (4) roe deer could show different behavioral profiles in specific environments because certain behavioral profile would be consistently selected in different environments by natural pressure of selection. According to the first hypothesis, Stamps and Groothuis (2010) defined the niche-picking as the fact that "an individual with a given phenotype choose a particular set of conditions in which to live". For example, an animal could select its environmental context according to its behavioral profile. The habitat matching theory predicts that individuals might move through the landscape in order to find and settle in the environment that maximizes their fitness according to their phenotype (Jacob *et al.* 2015). In addition, when fawns become independent and disperse (Debeffe *et al.* 2012), at the end of the dispersal process, the settlement in a post-dispersal home range may be affected by a disperser's experience in its natal home range in such a way dispersers select a post-dispersal range that resemble their natal home range (Stamps and Davis 2006). According to Stamps *et al.* (2009), the natal habitat preference induction predicts that favorable experiences in a natal home range will increase the probability that the individual choose a post-dispersal range that resembles the natal home range. In roe deer, females with high body mass, presumably born in higher quality habitat, were more prone to choose a similarly post-dispersal home range (Debeffe *et al.* 2013). In this way, as offspring of proactive mothers survived better in open habitats and fawns of reactive mothers survived better in closed habitats (Monestier *et al.* 2015), if theses fawns choose their post-dispersal home range according to their experiences in the natal home range and to maximize their fitness, it may generate a spatial distribution in the landscape of behavioral profiles. With the second hypothesis, a roe deer may influence the environment in which it lives via niche construction defined as the fact that "an individual with a given phenotype shape the conditions in which it lives" (Stamps and Groothuis 2010). However, even if locally, roe deer can alter the environment by nutrient transfer from cropland to forest patches (Abbas *et al.* 2012) or by seeds dispersal (as in deer; Gill and Beardall 2001) for example, it is very unlikely that the roe deer completely changes the environment, in a way that a spatial distribution according to the behavioral profiles occurs for the spatial scales considered. In addition, the environment of the study site is complex and highly controlled by humans, thus, landscape changes are mainly due to human activities, as the intensification of agricultural practices and the extension of urban areas. According to the third hypothesis, roe deer may distribute themselves across landscape in relation to their behavioral profile because environments in which they live influence their behavior. For instance, being in a safe environment could encourage individuals to be bolder. However, our result are opposite with this suggestion because individuals living in a closed secure environment had a reactive coping style, *i.e.* individuals trend to avoid the risky situations or to react by freezing (Koolhaas *et al.* 1999), corresponding to shy individuals. According to the last hypothesis, roe deer may distribute themselves across landscape in relation to their behavioral profile because the well-suited behavioral profiles to a given environment would be selected. Indeed, as offspring of proactive mothers survived better in open habitats and fawns of reactive mothers survived better in closed habitats (Monestier *et al.* 2015) and behavioral profiles are heritable (Réale *et al.* 2009, Dochtermann *et al.* 2015), it seems that individuals selected for a given environment are different by demographic parameters associated with their behavioral profile. In this way, individuals selected to live in open environments would be proactive and individuals selected to live in closed environments would be reactive, resulting in a non-random distribution of the behavioral profile. The mechanisms that generate non-random distribution are probably non-exclusive and might interact with each other. Distinguishing between the four explanations is difficult without examining the behavioral profile, dispersal patterns and the habitat selection of juveniles from their natal home range, even if the most likely explanations are the hypothesis (1) and (4) : roe deer choose to occupy areas with certain characteristics of habitat because of their intrinsic differences in their behavioral profile or certain behavioral profile would be consistently selected in different environments by natural pressure of selection. In order to test theses hypothesis, it would be interesting to manipulate the environment of individuals experimentally, moving individuals of their initial environment to a different environment. We expected that an individual with a given behavioral profile could actively seek areas with certain characteristics of habitat for which it is well-suited. Indeed, if the individual is mal-adapted to the environment in which it lives, its fitness will decreased, likewise, if the environment is not the one it has chosen. A control would also need to be sure that the loss of fitness is not due to the transfer between environments. Nevertheless, moving individuals from their initial environment to a different environment is difficult in roe deer. However, whatever the causes of this spatial distribution across landscape in relation to their behavioral profile, the existence of such a distribution may have important implications for conservation and management studies.

We found a relationship between environmental context and the individual's behavioral score: individuals from open environments, defined with a high fragmentation of wooded habitat and a low wooded surface area, were more "proactive" facing to dangers. We also found a behavioral profile – environment correlation between environmental context and the individual's activity during summer: individuals from open environments were less active than those living in closed environments. These results show that there is a negative correlation between the activity during summer and the behavioral score (*i.e.* reaction to stressful situation) of an individual, which is contrary to the definition of proactivity gradient given by Koolhaas *et al.* (1999), which defines the "proactive" individuals as very active individuals and the "reactive" individuals as less active individuals. Otherwise, it is surprising that individuals occupying open environments are less active during summer than those inhabiting closed environments. Indeed, open environments are heavily dominated by crops and the presence of humans, so we expected that the highly active individuals live in these environments, where predation risk is high demanding a significant activity to avoid being predated (Padié *et al.* 2015). In contrast, the forested environments are secure areas where predation risk is relatively low, so we expected that individuals are less active. These results might be explained in two ways, according to the trade-off between (1) resource acquisition and (2) risk avoidance. According to the first component of the trade-off, the activity of individuals may reflect the foraging efficiency rather than the mobility. Indeed, we considered that the level of head movements was an index of the level of activity during summer. Nevertheless, because the collar with activity sensor is placed around the animal's neck, the activity sensor could be more influenced by head movements than the whole body, in particular the legs movements (Gervasi *et al.* 2006). Thus, it is probable that behaviors such as vigilance or grazing could lead to high activity values, while walking behaviors such as constant and direct locomotion could lead to lower activity values. As a consequence, the head movements may reflect foraging efficiency rather than a general activity, in particular in terms of mobility. In this way, the individuals living in forest environments would be more active because food resources are less abundant, more scattered and of low nutritional value whereas the individuals in open environments would be less active due to an access to abundant resources of a high quality level (Hewison *et al.* 2009, Abbas *et al.* 2011). According to the second component of the trade-off, the activity of individuals would be a response to predation risk. In open environments, although the quality of food resources for roe deer is better (Hewison *et al.* 2009, Abbas *et al.* 2011), the risk of predation is also highest in these environments (Padié *et al.* 2015). In this way, for the individuals living in open environments, a low activity may decrease the risk of detection by predators, especially by humans, who preferentially hunt in these environments due to a high visibility. In addition, during summer, females have to ensure the survival of their fawns, in addition to their own survival. In contrast, closed environments are more secure areas for roe deer, thus, they could be more active, especially as they have to search intensively for food, which are scarcer in these environments. So, the difference in activity level of individuals between closed and open landscapes could be a response environment-dependent to solve the trade-off between resource acquisition and risk avoidance.

Although we showed behavioral profile – environment correlations, the relationships between environmental context and the individual's behavioral score or individual's activity during summer varied among spatial scales. Roe deer were not distributed randomly in relation to their behavioral profile but, according to the spatial scale considered, their distribution varied. Our results have shown that the proportion of woodland and the index of aggregation of forest habitat have the same influence on the behavioral score whatever the spatial scale but with a more pronounced effect of the proportion of woodland on behavioral score of males with smaller scales. In contrast, the environmental diversity does not affect in the same way the behavioral score: at small scales, proactive individuals occupied diverse environments while at larger scales, reactive individuals inhabited diverse environments. The relationship could in part be explained by the proportion of woodland in the individual’s environmental context. Indeed, for small scales, reactive individuals could live in purely forest environments with low habitat diversity. The habitat diversity would be higher for proactive individuals, living in open environments. When the spatial scale expands, the relationship was opposite. It could be that habitat diversity of proactive individual’s environments does not vary, but that habitat diversity of reactive individual’s environment increases because the scale would include other types of habitat, other than forest habitat. We also found a complex relationship between the proportion of human activities and the behavioral score. These results show that according to the spatial scale considered, the conclusions regarding the spatial distribution of behavioral profiles in the landscape would be different. We suggest that the spatial configuration of landscape elements may explain the complexity of the relationships between the individual’s environment and its behavioral profile. Indeed, the elements are not randomly distributed in the landscape, especially human dwellings, which are mainly concentrated and usually surrounded by crops, although some are far away. In addition, some of our results may be difficult to interpret due to the complexity or the anisotropy of the landscape. This study is one of the first studies demonstrating the influence of landscape features on the distribution of behavioral profiles taking into account different spatial scales.

This study highlighted that specific behavioral profiles occur more frequently in some contexts than in others, already shown in some recent studies (Dingemanse *et al.* 2003; Stamps and Groothuis 2010; Pearish *et al.* 2013). As the woodland habitat constitute secure areas for roe deer, the “reactive” and active individuals seems to minimize risk by occupying closed environments, whereas the “proactive” and less active individuals prioritize the acquisition of resources, by inhabiting open environments with a better access to nutrient rich (Hewison *et al.* 2009). However, our result on the link between the proportion of human activities in the environment and the individual’s behavioral score is not consistent with this suggestion. As human activity induce some disturbances for roe deer (Bonnot *et al.* 2013) and roe deer avoid areas with human activity, such as roads and human dwellings (Coulon *et al.* 2008), we expected that the “proactive” individuals, which are more prone to take risks in the face of potential dangers may accept more human disturbances in their environment than the “reactive” individuals. Surprisingly, our results showed that the “reactive” individuals appeared in an environmental context where human presence is high, as opposed to the “proactive” individuals who lived in areas where human activities are lower. Even though our results are not conform to our prediction, they are consistent with a study by Martin and Réale (2008) where the most docile individuals, corresponding to a “reactive” coping style (Koolhaas *et al.* 1999) occupied home range in the most frequented area by humans. We suggest that the spatial configuration of forest habitats may explain the high proportion of human presence in the environment of the “reactive” individuals. Indeed, because these individuals occupy mainly closed environments, they could accept more proximity with human activities than the "proactive" individuals, living in open environments with then a higher visibility and/or exposition to human activities. However, individuals living in open environments could counterbalance the high predation risk by increasing their flight distance (Bonnot *et al.* 2015).

As some behavioral profiles occur more frequently in some contexts, the behavior of an individual is context-dependent. Otherwise, many studies have shown that personality traits affect life-history traits such as dominance (Dingemanse and de Goede 2004), reproductive success (Both *et al.* 2005), offspring survival (Monestier *et al.* 2015), natal dispersal (Debeffe *et al.* 2014) and other fitness components of individuals (Smith and Blumstein 2008). In this case, as personality traits are context – dependent and personality traits affect individual's fitness, it means that the fitness consequences of personality may be context – dependent both in time and in space. Indeed, the fitness consequences of personality can vary according to environmental conditions. For example, Dingemanse *et al.* (2004) have found that the survival of adult great tits (*Parus major*) was related to their exploratory behavior in novel environments and theses effects differed between sex and among years. This study has also shown that the number of offspring surviving to breeding was related to their parents' personalities, and that selection varied among years. This study provides evidence that fitness consequences of personality are context – dependent in time. In this way, Boon *et al.* (2007) also highlighted a temporal variation in fitness consequences of personality in North American red squirrels (*Tamiasciurus hudsonicus*). The mother aggressiveness influenced her offspring survival and its activity impacted her offspring growth rate, but these effects of mother personality on her offspring varied across life-history stages and over time, probably due to food availability. Thus, there was a temporal heterogeneity in the influence of behavior on individual performance. A recent study has also provided evidence that fitness consequences of coping style are habitat – dependent in roe deer (Monestier *et al.* 2015). The inter-individual differences in the coping style of the mother roe deer impacted early offspring survival and, thereby, female fitness. However, this study had also highlighted that consequences of coping styles on female fitness were habitat-dependent, because offspring survival was dependent on both the coping style and the habitat use of their mother. In open habitats, fawns born to more proactive mothers survived better than those born to more reactive mothers whereas, in closed habitats, fawns of more proactive mothers survived less well than fawns of more reactive mothers. Therefore, as fitness consequences of behavioral profile are habitat – dependent, it seems that according to the environmental context, individuals are selected differently depending on their behavioral profile. Our study provides clear evidence that according to the environment, the selected individuals are not the same in relation to their behavioral profile, which means individuals would select environments for which they are particularly well suited, as predicted by habitat matching theory. In this way, heterogeneity of the environment could allow the maintenance of behavioral differences, with more proactive individuals in highly fragmented environments and more reactive individuals in forest environments. Thus, global changes, such as the extension of urban areas, the deforestation and the fragmentation of wooded habitat could lead to a gradual disappearance of reactive individuals either because they cannot adapt to landscape modification or because they adapt and change their behavioral profiles. In roe deer, integrating behavioral profile into studies of the response of wildlife to landscape heterogeneity could therefore help us understand the impact of global changes on their distribution. In addition, the behavioral profiles should be taking into account in management studies or conservation of roe deer and wildlife.

CONCLUSION

Our study highlighted a non-random distribution of roe deer in a heavily modified landscape by humans. To days, many studies have documented the effects of recent modification of landscapes on wildlife demographic parameters or on physiological or behavioral traits directly related to this stressful situation (Diffendorfer *et al.* 1995; Bonnot *et al.* 2013), but few studies have investigate how behavioral profile affects the way that individuals respond to landscape modification and distribute themselves. Our study provides a rare example of a non-random spatial distribution of individuals in relation to their behavioral profile in a free ranging population of a large herbivore, resulting in a more likely occurrence of particular behavioral profile in certain environments. However, the underlying mechanisms to this distribution are probably many and future studies should perform experiments to better identify the mechanisms involved in order to explain why specific behavioral profiles occur in certain environments. Otherwise, this study was conducted at several spatial scales, showing different influences of the landscape on the behavioral profile according to the scale considered. However, some of our results are difficult to interpret according to the scale, probably due to the complexity or the anisotropy of the landscape. It would require further works to understand the observed differences among the spatial scales. This study, providing evidence for behavioral profile – environment correlations have important ecological and evolutionary implications and conclude that landscape heterogeneity could play a major role in the maintenance of behavioral differences among individuals.

APPENDIX

Appendix 1. Calculation of individual’s behavioral score

```
######
### 1. Ouverture des données
comportement=read.csv("data_personnalite.csv",header=T,sep=";")
        ## Ce tableau contient l’occurrence des comportements relevés à la capture pour chaque
        individu (0/1 ou NA). Pour le calcul de la note comportemental, seulement 5 comportements
        étaient utilisés.


######
### 2. Calcul de la note comportementale
        ## On ne prend pas en compte les individus pour lesquelles aucun comportement n’a été
        renseigné.
comportement2 = subset (comportement, (lutte_filet & retourne & lutte_halete_table &
lache_gratte_collier & course_bolide) ! = "NA")

        ## Calcul de la moyenne sur les 5 comportements sélectionnés, donnant la note à la capture
comportement2$note_capture = NA
for (i in 1:length(comportement2$lutte_filet)) {
        x=c(comportement2$lutte_filet[i],comportement2$retourne[i],comportement2$lutte_halete_t
        able[i],comportement2$lache_gratte_collier[i], comportement2$course_bolide[i])
          comportement2$note_capture[i]=mean(x,na.rm=TRUE)
}

######
### 3. Calcul du nombre de comportements utilisés pour le calcul de la note
        ## Cette valeur est utilisée pour sélectionner les individus à conserver : seuls ceux dont la note
        à la capture a été calculée avec au moins 4 comportements renseignés sur les 5 ont été
        conservés pour les analyses.
comportement2$note_capture_sum=NA
for(i in 1:length(comportement2$cpt_id)) {
        x=c(comportement2$lutte_filet[i],comportement2$retourne[i],comportement2$lutte_halete_t
        able[i],comportement2$lache_gratte_collier[i], comportement2$course_bolide[i])
          comportement2$note_capture_sum[i]=sum(x,na.rm=TRUE)
}
## Cette boucle calcule la somme des valeurs associées à chaque comportement (0/1). Comme il y a 5
comportements, cette valeur peut varier entre 0 et 5. La ligne de code suivante permet d’obtenir le
nombre de comportements qui a été pris en compte pour le calcul pour chaque individu. Seuls les
individus dont la note à la capture a été calculée avec au moins 4 comportements ont été conservés
comportement2$total_score= (comportement2$note_capture_sum/comportement2$note_capture)
```

Appendix 2. Calculation of individual’s center of gravity

```
######
### 1. Ouverture des données
tab = read.csv ("sans_points_aberrants.csv", header = T, sep=",")
        ## Ce tableau contient toutes les informations sur les animaux suivis (identifiant, année de
        suivi, âge, …) et les positions GPS de latitude et longitude toutes les 6h.
```

```
######
### 2. Coordonnées géographiques de chaque individu : on fait un tableau où on garde seulement les
coordonnées x, y de chaque individu
coord = subset (tab, select = c(cap_bague, posx, posy, cap_annee_suivi))
        ##On sélectionne seulement les colonnes indiquant l’identifiant de l’animal suivi (cap_bague),
        les positions GPS (posx et posy) et l’année de suivi de l’animal (cap_annee_suivi)

######
### 3. Calcul du barycentre par individu (ani_etiq + cap_annee_suivi)
barycente = aggregate (list(x = coord$posx, y = coord$posy), list(ind = coord$cap_bague, annee =
coord$cap_annee_suivi), mean, na.rm = T)
        ## La fonction « aggregate » permet de faire la moyenne des positions x et y en fonction de
        l’identifiant de l’animal et de son année de suivi.

######
### 4. Transformation de l’objet en objet spatial
        ## Cette étape permet de créer les barycentres spatiaux des chevreuils, de façon à pouvoir
        ensuite les représenter sous QGIS.

library(sp) ; library(rgdal)
class(barycentre)
        ## Bien que les données comportent des coordonnées géographiques, pour le moment elles
        ## sont stockées sous forme d'un data.frame non spatialisé.
        ## Il faut donc indiquer que ces données possèdent une information spatiale.
        ## Je convertis ces données en objet spatial ponctuel possédant une table d'attributs, un
        SpatialPointsDataFrame.

bary_spatial <- SpatialPointsDataFrame (coords = barycentre[,3:4], data = barycentre[,1:2], proj4string
= CRS("+init=epsg:27573"))
        ## L’attribut ‘coords’ permet d’identifier les données spatiales, ‘data’ indique les données
        associées aux coordonnées spatiales (en l’occurrence l’identifiant et l’année de suivi de
        l’animal) et l’attribut ‘proj4string’ permet d’indiquer le système de géoréférencement des
        coordonnées géographiques (ici, en lambert III, dont le code EPSG est 27573)

        ## L’objet crée contient ainsi les barycentres des coordonnées géographiques des individus
        spatialisés. Cependant, l’assolement disponible en SIG a un système de géoréférencement en
        lambert 93.
        ## Conversion du système de projection en Lambert 93
bary_spatial_lambert93 <- spTransform(x = bary_spatial, CRSobj = CRS("+init=epsg:2154"))

######
### 5. Information sur l'objet spatial crée 'bary_spatial_lambert93'
slotNames(bary_spatial_lambert93)
        ## Affichage du nom des slots : L'objet contient 5 slot : data, coords.nrs, coords, bbox et
        proj4string, donnant des informations sur ce que l’objet contient.

######
### 6. Exportation des données spatiales dans un shapefile
writeOGR(obj = bary_spatial_lambert93, dsn = "C:/Users/sav/Documents/Elodie/Données/
Barycentre_spatial_sans_points_aber", layer = "barycentre_spatial_sans_points_aber", driver = "ESRI
Shapefile")
```

Appendix 3. Calculation of metrics of three habitat classes for a given radius of buffer (here, 100 m)

```
######
### 1. Ouverture des données à partir de la base de données
spdf <- dbReadSpatial(con, schemaname="public", tablename="t_bary_bar_100_grps",
geomcol="geom")
        ## dbReadSpatial est un script permettant de lire des tables issues de la base de données.
        spdf est un SpatialPolygonsDataFrame, décrivant tous les polygones à l'intérieur des buffers de
        rayon 100m des individus.

######
### 2. Calcul des statistiques des trois classes d'habitat : habitats fermés, habitats ouverts et habitats
anthropiques
num_individu = c(levels (as.factor (spdf$cap_bague)))
        ## Vecteur contenant tous les identifiants des individus suivis, à savoir 179.

stat_indi = data.frame()
indice_tot = data.frame()
        ## Construction de deux data frame vides, qui seront remplis par la boucle.

for (a in 1:length(num_individu)) {
  indi = subset(spdf, cap_bague == num_individu[a])
        ## Sélection de tous les polygones expliquant l'habitat de l'individu a.
  toto = extent(indi)
  r <- raster(ncol = toto[2] - toto[1], nrow = toto[4] -toto[3])
        ## Création d'un raster de dimension
  extent(r) <- extent(indi)
        ## Ajustement des emprises (étendues)
  indi$GRD_CAT = NA
  indi$GRD_CAT [indi$grd_cat=="bois"]=1
  indi$GRD_CAT [indi$grd_cat=="culture"]=2
  indi$GRD_CAT [indi$grd_cat=="humain"]=3
        ## Attribution de numéros aux catégories d'habitat, de façon à utiliser la fonction « rasterize »
  indi_ras <- rasterize(indi, r, "GRD_CAT", fun='first')
        ## Pixellisation de l'objet spatial indi, à partir du raster de référence r et par rapport aux
        catégories d'habitat
  stat_indi = ClassStat(indi_ras)
        ## ClassStat calcule les statistiques des classes d'habitat à partir du raster 'indi_ras'
        représentant l'habitat rastérisé de l'individu donné. Parmi les valeurs obtenues, il y la
        proportion de chaque classe d'habitat dans le buffer et un indice d'agrégation pour chacune
        des classes d'habitat.
  stat_indi$cap_bague = num_individu[a]
        ## Ajout de l'identifiant de l'animal
  indice_tot = rbind(indice_tot,stat_indi)
}

        ## Nous avons lancé ce script pour tous les buffers, c'est-à-dire 15 fois.
```

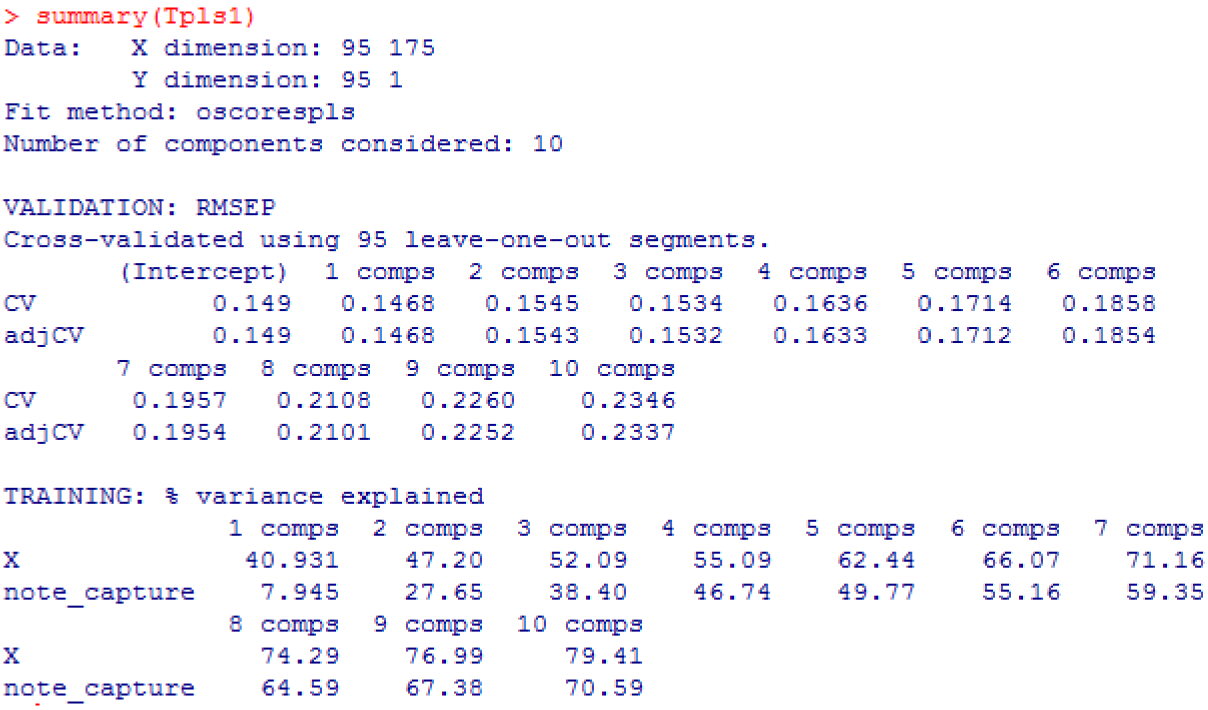
Appendix 4. PLS regression used to model the behavioral score according to the environmental variables, the sex and the two-way interaction between the sex and each environmental variable

This method was used in order to reduce the number of independent variables to a few components

```
require(geoR) ; library(pls)
        ## Chargement des packages
######
### 1. Ouverture des données
note_cap = read.table("Modele_note_capture.txt")
        ## Ce tableau contient les valeurs de la variable dépendante pour chaque individu, à savoir
        note à la capture (« behavioral score ») ainsi que les valeurs des variables indépendantes, en
        l'occurrence, la proportion d'habitats forestiers, l'indice d'agrégation de l'habitat forestier,
        l'indice de diversité du couvert végétal et la proportion d'habitats anthropiques, chacune pour
        les 15 buffers de rayons croissantes.
note_cap2 = subset ( note_cap , is.na ( aggregation.index.humain_400) == F & is.na (
aggregation.index.fermes_100 ) == F)
        ## Suppression des NA car la régression PLS supprimer les individus avec données valant NA
note_cap3=scale(note_cap2[4:90])
        ## On centre-réduit les variables indépendantes
note_cap4=cbind(note_cap2[,c(1:3,91:94)],note_cap3)


######
### 2. Régression PLS
        ## 1. Modèle PLS avec 10 composantes en incluant une validation de type croisée : leave-one-
        out
Tnom=names(note_cap4)
Tnom=Tnom[8:94]
Tform=paste("note_capture~",Tnom[1],"*ani_sexe")
for(i in 2:length(Tnom)) Tform=paste(Tform,paste(Tnom[i],"*ani_sexe"),sep="+")
        ## Boucle permettant d'écrire le modèle entre la variable dépendante et les variables
        indépendantes, à inclure ensuite dans la PLS

Tpls1 = plsr(as.formula(Tform), data = note_cap4,ncomp=10, validation = "LOO", method =
"oscorespls", scale = T)
        ## Cette ligne de code prédit un modèle avec 10 composantes et inclue une validation de type
        croisée : leave-one-out .
summary(Tpls1)
```



```
> summary(Tpls1)
Data:    X dimension: 95 175
         Y dimension: 95 1
Fit method: oscorespls
Number of components considered: 10

VALIDATION: RMSEP
Cross-validated using 95 leave-one-out segments.
       (Intercept)  1 comps  2 comps  3 comps  4 comps  5 comps  6 comps
CV           0.149   0.1468   0.1545   0.1534   0.1636   0.1714   0.1858
adjCV        0.149   0.1468   0.1543   0.1532   0.1633   0.1712   0.1854
       7 comps  8 comps  9 comps  10 comps
CV      0.1957   0.2108   0.2260    0.2346
adjCV   0.1954   0.2101   0.2252    0.2337

TRAINING: % variance explained
              1 comps  2 comps  3 comps  4 comps  5 comps  6 comps  7 comps
X              40.931    47.20    52.09    55.09    62.44    66.07    71.16
note_capture    7.945    27.65    38.40    46.74    49.77    55.16    59.35
              8 comps  9 comps  10 comps
X               74.29    76.99     79.41
note_capture    64.59    67.38     70.59
```

Cet affichage résume les résultats de la régression. La première partie donne la racine de l'erreur quadratique moyenne de prédiction (RMSEP) associée à chaque composante lorsqu'une validation croisée est effectuée. Il y a deux estimations de validation croisée: CV est l'estimation ordinaire, et adjCV est une estimation corrigée, mais pour une validation croisée LOO, la différence est moindre. C'est grâce à la RMSEP qu'on peut choisir le nombre de composante, l'idée étant de minimiser l'erreur ainsi que le nombre de composantes. La deuxième partie de cet affichage renseignent les proportions cumulées de variance des variables explicatives retranscrites par les facteurs pour la variable réponse (note_capture).

2. Choix du nombre de composantes à conserver

rmsepcv.plsr < -RMSEP(Tpls1, intercept=F, estimate = c("CV","adjCV"))
plot(rmsepcv.plsr,legendpos="topright")

Il est souvent plus simple de juger les RMSEP en les traçant: Evolution du RMSEP en fonction du nombre de composantes de la régression sur composante principale

plot(explvar(Tpls1),type="l",main="")

Evolution de la part de variance (en %) prise en compte par chaque composante

3. Modele PLS à 3 composantes

Tpls2=plsr(as.formula(Tform),ncomp = 3,data=note_cap4,validation = "LOO",method="oscorespls", scale = T)
summary(Tpls2)

4. Ajout des scores issus de la PLS dans le tableau 'note_cap4'

note_cap5=cbind(note_cap4,Tpls2$scores[,1:3])
names(note_cap5)[95:97]=c("comp1","comp2","comp3")

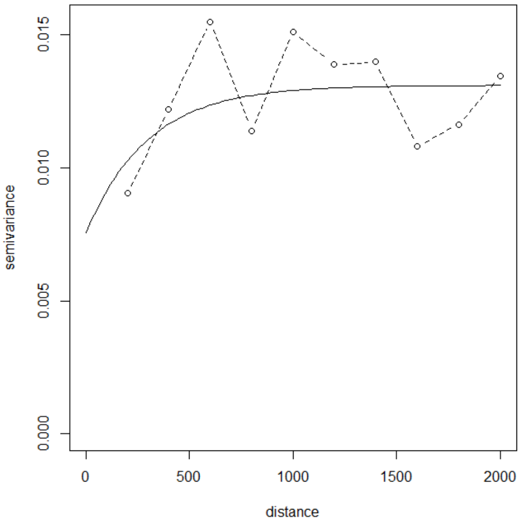
######
3. Analyse géostatistique

1. Transformation du data.frame en objet spatial

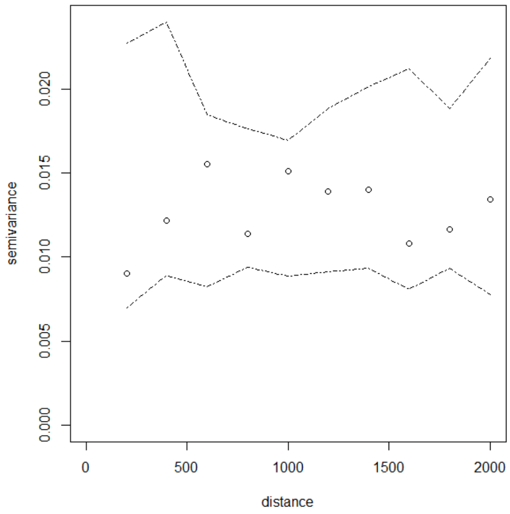
note_cap6<- as.geodata(note_cap5,coords.col = 2:3, data.col = 7, covar.col = c(95:97),borders = TRUE)

Les attributs 'coods.col' indique

```
    ## 2. Variogrammes empiriques et enveloppe
var2 <- variog(note_cap6, max.dist = 2000,trend = ~ comp1 + comp2 + comp3, uvec = seq(200,2000,by = 200))
plot(var2)
lines(var2,type="b",lty=2)
wls2 <- variofit(var2, ini.cov.pars = c(0.01,300), cov.model = "exp", nugget = 0.01)
    ## Ajustement du variogramme
lines.variomodel(wls2)
```

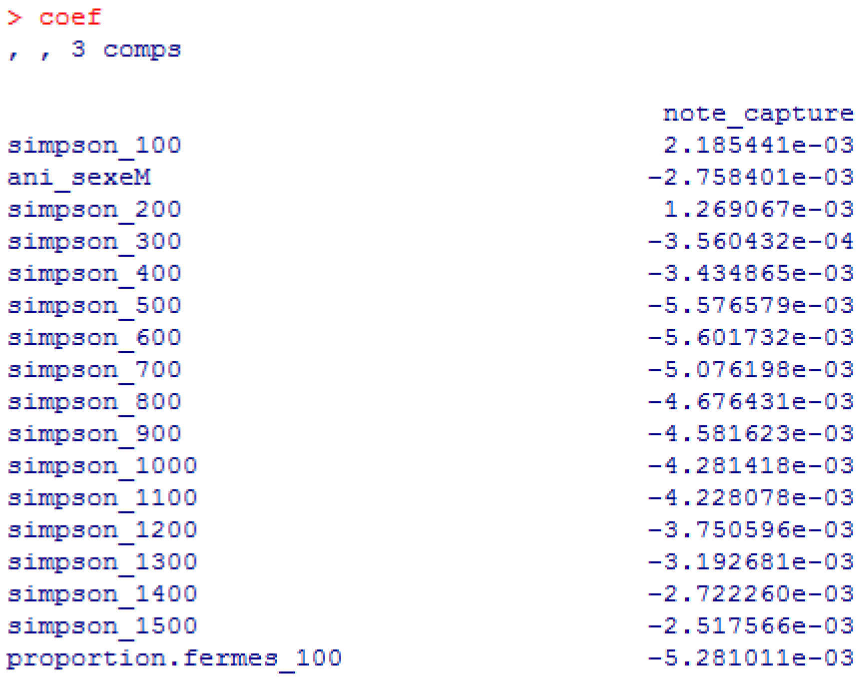


```
Tenv=variog.mc.env(note_cap6,obj=var2)
plot(var2,env=Tenv)
```



```
    ## Le variogramme empirique est contenu complètement dans l'enveloppe, on ne peut donc pas rejeter l'indépendance spatiale. Les erreurs ne sont pas spatialement corrélées, c'est-à-dire que les résidus sont indépendants spatialement. De ce fait, nous avons utilisé la PLS pour analyser les effets des variables environnementales sur le profil comportemental, et non pas pour réduire le nombre de composantes à intégrer ensuite dans un modèle géostatistiques.

######
### 3. Importance des variables indépendantes (habitats + sexe + interaction habitat/sexe)
    ## 1. Coefficients des variables explicatives
coef = coefficients (Tpls2)
```



```
> coef
, , 3 comps

                                      note_capture
simpson_100                           2.185441e-03
ani_sexeM                            -2.758401e-03
simpson_200                           1.269067e-03
simpson_300                          -3.560432e-04
simpson_400                          -3.434865e-03
simpson_500                          -5.576579e-03
simpson_600                          -5.601732e-03
simpson_700                          -5.076198e-03
simpson_800                          -4.676431e-03
simpson_900                          -4.581623e-03
simpson_1000                         -4.281418e-03
simpson_1100                         -4.228078e-03
simpson_1200                         -3.750596e-03
simpson_1300                         -3.192681e-03
simpson_1400                         -2.722260e-03
simpson_1500                         -2.517566e-03
proportion.fermes_100                -5.281011e-03
```

Ce code donne les coefficients de chaque variable initiale de la PLSR à 3 composantes.

Manipulation pour que le nom des variables explicatives soient considérés comme une variable à part, et non pas comme le numéro des lignes

```
coef2 = as.data.frame(coef)
coef2$nom = row.names(coef2)
rownames(coef2) = NULL
names(coef2) = c("coef","nom")
```

Ces quelques lignes de codes permettent de considérer le nom des variables explicatives comme une variable à part, et non pas comme le numéro des lignes.

2. Calcul des VIP (Variable Importance in Projection)

```
source ("VIP.R")
vip = VIP(Tpls2)
```

Ce script calcule directement les VIP associés aux coefficients des variables indépendantes d’une PLS. A chaque coefficient d’une variable indépendante et pour chaque modèle (à 1, 2 ou 3 composantes) est associé un VIP.

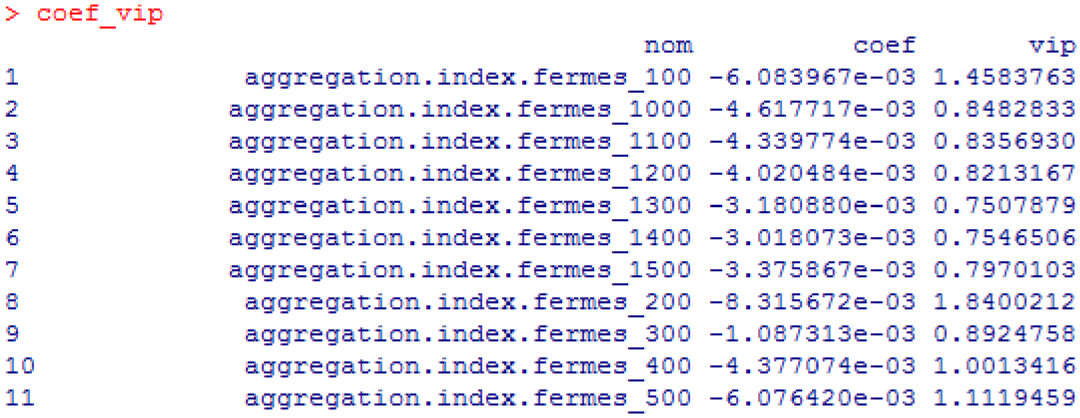
```
vip2=t(vip)
vip3=vip2[,3]
```

Sélection seulement des VIP qui correspondent aux variables pour le modèle cumulé avec trois composantes.

```
vip3 = as.data.frame(vip3)
vip3$nom = row.names(vip3)
rownames (vip3) = NULL
names(vip3) = c("vip","nom")
```

Ces quelques lignes de codes permettent de considérer le nom des variables explicatives comme une variable à part, et non pas comme le numéro des lignes.

```
coef_vip = merge(coef2,vip3,by="nom",all.x=T)
```



```
> coef_vip
                                 nom          coef       vip
1          aggregation.index.fermes_100 -6.083967e-03 1.4583763
2         aggregation.index.fermes_1000 -4.617717e-03 0.8482833
3         aggregation.index.fermes_1100 -4.339774e-03 0.8356930
4         aggregation.index.fermes_1200 -4.020484e-03 0.8213167
5         aggregation.index.fermes_1300 -3.180880e-03 0.7507879
6         aggregation.index.fermes_1400 -3.018073e-03 0.7546506
7         aggregation.index.fermes_1500 -3.375867e-03 0.7970103
8          aggregation.index.fermes_200 -8.315672e-03 1.8400212
9          aggregation.index.fermes_300 -1.087313e-03 0.8924758
10         aggregation.index.fermes_400 -4.377074e-03 1.0013416
11         aggregation.index.fermes_500 -6.076420e-03 1.1119459
```

```
coef_vip2=subset(coef_vip,vip>0.8)
dim(coef_vip2)
        ## Sélection des variables indépendantes dont le coefficient à un VIP > 0.8.

######
### 4. Barplots
        ## 1. Calcul de la matrice de variance-covariance des coefficients des variables pour la représentation des barres d'erreurs

        ## Soit Y, la variable réponse (note_capture)
Y=note_cap4$note_capture
        ## X, la matrice des variables de départ et T, la matrice des observations sur les composantes PLS
T=Tpls2$scores
        ## La variable réponse peut aussi s'écrire : Y = T.b = X.coef, avec b, les loadings associés à chaque composante, et coef, les coefficients de la PLS associés à chaque variable explicatives. Afin de calculer la matrice de variance-covariance des coefs, nous devons d'abord passer par les composantes PLS (T.b).

        ## Etant donné que la PLS est une régression linéaire, b peut être obtenu par :
b=lm(Y~T)
        ## Ainsi, la matrice de variance covariance des b est :
V = vcov(b)[-1,-1]
         ## On supprime l'intercept

        ## Or, ce qui nous interésse, ce sont les coef, coefficients associés aux variables initiales. On sait que T peut s'écrire : T = XH, avec H,  la matrice des projections des variables explicatives sur les composantes PLS.
        ## Donc Y = T.b = XH.b = X.beta, d'où, beta = Hb. La transformation entre les coef et les b se fait par H :
H=Tpls2$projection
        ## Comme beta = Hb, la matrice de variance-covariance des coef avec 3 composantes est :
V1= H%*% vcov(lm(Y ~ T))[-1,-1] %*% t(H)

# La diagonale de cette matrice donne les variances associées à chacun des coefficients des variables explicatives 'coef'
D = diag(V1)

D1 = as.data.frame(D)
D1$nom = row.names(D1)
```

```
rownames(D1)=NULL
names(D1)=c("variance","nom")
        ## Ces quelques lignes de codes permettent de considérer le nom des variables explicatives
        comme une variable à part, et non pas comme le numéro des lignes.

        ## Création d'un tableau contenant les coefficients associés aux variables explicatives et la
        variance
res=merge(coef2,D1,by="nom")

        ##2. Représentation des coefficients des variables d’indice d’agrégation du bois pour les
        femelles
bp = barplot ( res [ c ( 1, 8:15, 2:7), 2], col="#B50F67", names.arg = c("100", "200", "300", "400", "500",
"600", "700", "800", "900", "1000", "1100", "1200", "1300", "1400", "1500"), ylim = c ( -0.02, 0.02),
ylab = "Coefficients of variables")
arrows(bp, res$coef[c(1,8:15,2:7)]- 1.96 * (sqrt(res$variance)[c(1,8:15,2:7)]),bp, res$coef[c(1,8:15,2:7)]
+ 1.96 *(sqrt(res$variance)[c(1,8:15,2:7)]), lwd=1.5, angle=90,length=0.1,code=3)
```

REFERENCES

Abbas, F., Morellet, N., Hewison, A.J.M., Merlet, J., Cargnelutti, B., Lourtet, B., Angibault, J.-M., Daufresne, T., Aulagnier, S., and Verheyden, H. (2011). Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. Oecologia *167*, 401–411.

Abbas, F., Merlet, J., Morellet, N., Verheyden, H., Hewison, A.J.M., Cargnelutti, B., Angibault, J.M., Picot, D., Rames, J.L., Lourtet, B., et al. (2012). Roe deer may markedly alter forest nitrogen and phosphorus budgets across Europe. Oikos *121*, 1271–1278.

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M., Morellet, N., and Verheyden, H. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour *76*, 611–618.

Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., and Hewison, A.J.M. (2012). Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research *59*, 185-193.

Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., Klein, F., Hewison, A.J.M., and Morellet, N. (2015). Interindividual variability in habitat use: Evidence for a risk management syndrome in roe deer? Behavioral Ecology *26*, 105-114.

Boon, A.K., Réale, D., and Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. Ecology Letters *10*, 1094–1104.

Both, C., Dingemanse, N.J., Drent, P.J. and Tinbergen, J.M. (2005). Pairs of extreme avian personalities have highest reproductive success. Journal of Animam Ecology *74*, 667–674.

Bowler, D.E., and Benton, T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews *80*, 205–225.

Brown, J.S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology *22*, 37–47.

Brown, J.S. (1999). Vigilance, patch use and habitat selection: Foraging under predation risk. Evol. Ecol. Res. 1, 49-71. Evolutionary Ecology Research *1*, 49–71.

Brown, J.S., and Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. Ecology Letters *7*, 999–1014.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., and Wiens, J.J. (2013). How does climate change cause extinction? Proceedings of the Royal Society, B. Biological Sciences *280*, 20121890.

Calenge, C., Maillard, D., Invernia, N., and Gaudin, J.-C. (2005). Reintroduction of roe deer Capreolus capreolus into a Mediterranean habitat: Female mortality and dispersion. Wildlife Biology *11*, 153–161.

Cézilly, F., and Benhamou, S. (1996). Les stratégies optimales d'approvisionnement. Revue d'Ecologie (Terre Vie) *51*, 43–86.

Clobert J., De Fraipont, M. and Danchin, É. (2005). L'évolution de la dispersion In : Danchin E., Giraldeau L.-A. et Cézilly F. Écologie comportementale : Cours et questions de réflexion. Paris : DUNOD, 637p. ISBN 2-10-005499-6

Coulon, A., Cosson, J.F., Angibault, J.M., Cargnelutti, B., Galan, M., Morellet, N., Petit, E., Aulagnier, S., and Hewison, A.J.M. (2004). Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual–based approach. Molecular Ecology *13*, 2841–2850.

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.-M., and Hewison, A.J.M. (2008). Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. Landscape Ecology *23*, 603–614.

Creel, S., and Winnie Jr., J.A. (2005). Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour *69*, 1181–1189.

Croxall, J.P., Davis, R.W., and O'Connell, M.J. (1988). Diving patterns in relation to diet of gentoo and macaroni penguins at south Georgia. The Condor *90*, 157–167.

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J.-M., and Mark Hewison, A.J. (2012). Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further Journal of Animal Ecology *81*, 1327–1337.

Debeffe, L. (2013). La dispersion chez le chevreuil européen, Capreolus capreolus, dans un paysage hétérogène. Mémoire de thèse. Université de Toulouse, Université Toulouse III - Paul Sabatier.

Debeffe, L., Morellet, N., Bonnot, N., Gaillard, J.M., Cargnelutti, B., Verheyden-Tixier, H., Vanpé, C., Coulon, A., Clobert, J., Bon, R., et al. (2014). The link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore. Proceedings of the Royal Society of London B: Biological Sciences *281*, 20140873.

Diffendorfer, J.E., Gaines, M.S. and Holt, R.D. (1995). Habitat fragmentation and movements of three small mammals (Sigmodon, Microtus and Peromyscus). Ecology *76*, 827-839.

Dingemanse, N.J. and de Goede, P. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behavioral Ecology *15*, 1023–1030.

Dingemanse, N.J., Both, C., Drent, P.J., and Tinbergen, J.M. (2004). Fitness consequences of avian personalities in a fluctuating environment. Proceedings of the Royal Society of London B: Biological Sciences *271*, 847–852.

Dingemanse, N.J., Both, C., Noordwijk, A.J. van, Rutten, A.L., and Drent, P.J. (2003). Natal dispersal and personalities in great tits (Parus major). Proceedings of the Royal Society of London B: Biological Sciences *270*, 741–747.

Dingle, H., and Drake, V.A. (2007). What Is Migration? BioScience *57*, 113–121.

Dochtermann, N.A., Schwab, T., and Sih, A. (2015). The contribution of additive genetic variation to personality variation: heritability of personality. Proceedings of the Royal Society of London B: Biological Sciences *282*, 20142201.

Eklöv, P., and Halvarsson, C. (2000). The trade-off between foraging activity and predation risk for Rana temporaria in different food environments. Canadian Journal of Zoology *78*, 734–739.

Fortin, D., and Andruskiw, M. (2003). Behavioral Response of Free-Ranging Bison to Human Disturbance. Wildlife Society Bulletin *31*, 804–813.

Frid A. et Dill L. (2002**)**. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., & Van Moorter, B. (2010) Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B: Biological Sciences *365*, 2255-2265.

Gervasi, V., Brunberg, S., Swenson, J.E., and Bowman, J. (2006). An Individual-Based Method to Measure Animal Activity Levels: A Test on Brown Bears. Wildlife Society Bulletin *34*, 1314–1319.

Gill, R.M.A. and Beardall, V. (2001). The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry *74*, 209-218.

Gottardi, E., Tua, F., Cargnelutti, B., Maublanc, M.-L., Angibault, J.-M., Said, S., and Verheyden, H. (2010). Use of GPS activity sensors to measure active and inactive behaviours of European roe deer (Capreolus capreolus). Mammalia *74*, 355–362.

Hawlena, D., and Schmitz, O.J. (2010). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. PNAS *107*, 15503–15507.

Hewison, A.J.M., Morellet, N., Verheyden, H., Daufresne, T., Angibault, J.-M., Cargnelutti, B., Merlet, J., Picot, D., Rames, J.-L., Joachim, J., et al. (2009). Landscape fragmentation influences winter body mass of roe deer. Ecography *32*, 1062–1070.

Hofmann, R.R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia *78*, 443–457.

Hunter, L.T.B., and Skinner, J.D. (1998). Vigilance Behaviour in African Ungulates: The Role of Predation Pressure. Behaviour *135*, 195–211.

Jarle Tufto, J.D.C.L. (1996). Habitat Use and Ecological Correlates of Home Range Size in a Small Cervid: The Roe Deer. Journal of Animal Ecology *65*, 715–724.

Jayakody, S., Sibbald, A.M., Gordon, I.J., and Lambin, X. (2008). Red deer Cervus elephus vigilance behaviour differs with habitat and type of human disturbance. Wildlife Biology *14*, 81–91.

Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W., and Blokhuis, H.J. (1999). Coping styles in animals: current status in behavior and stress-physiology. Neuroscience & Biobehavioral Reviews *23*, 925–935.

Koolhaas, J.M., de Boer, S.F., Coppens, C.M., and Buwalda, B. (2010). Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. Frontiers in Neuroendocrinology *31*, 307–321.

Laundré, J.W., Hernández, L., and Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology *79*, 1401–1409.

Lima, S.L. (1998). Nonlethal Effects in the Ecology of Predator-Prey Interactions. BioScience *48*, 25–34.

Lima, S.L., and Bednekoff, P.A. (1999). Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. The American Naturalist *153*, 649–659.

Lima, S.L., and Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. *68*, 619–640.

Martin, J.G.A., and Réale, D. (2008). Animal temperament and human disturbance: implications for the response of wildlife to tourism. Behavioural Processes *77*, 66–72.

Maublanc, M.-L., Cibien, C., Gaillard, J.M., Maizeret, C., Bideau, E. and Vincent J.P. (1991). Le chevreuil. Revue d'Ecologie (Terre Vie) *6*, 155-183.

McCollum, S.A., and Leimberger, J.D. (1997). Predator-induced morphological changes in an amphibian: predation by dragonflies affects tadpole shape and color. Oecologia *109*, 615–621.

Mevik, B.-H., and Wehrens R. (2007). The pls Package: Principal Component and Partial Least Squares Regression in R. Journal of Statistical Software *18*, 1-23.

Monclús, R., Rödel, H.G., and Von Holst, D. (2006). Fox Odour Increases Vigilance in European Rabbits: A Study under Semi-Natural Conditions. Ethology *112*, 1186–1193.

Monestier, C., Morellet, N., Gaillard, J.-M., Cargnelutti, B., Vanpé, C., and Hewison, A.J.M. (2015). Is a proactive mum a good mum? A mother's coping style influences early fawn survival in roe deer. Behavioral Ecology, 00: 1-9.

Morellet, H.V.N. (2009). The Effect of Capture on Ranging Behaviour and Activity of the European Roe Deer *Capreolus capreolus*. Wildlife Biology *15*, 278–287.

Mueller, T., and Fagan, W.F. (2008). Search and navigation in dynamic environments - from individual behaviors to population distributions. Oikos 117, 654-664.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P.E. (2008). A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America *105*, 19052-19059.

Padié, S., Morellet, N., Hewison, A.J.M., Martin, J.-L., Bonnot, N., Cargnelutti, B., and Chamaillé-Jammes, S. (2015). Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos *124*, 1536–1546.

Pearish, S., Hostert, L., and Bell, A.M. (2013). Behavioral type-environment correlations in the field: a study of three-spined stickleback. Behavioral Ecology Sociobiology *67*, 765-774.

Pettorelli, N., Gaillard, J.-M., Duncan, P., Maillard, D., Van Laere, G., and Delorme, D. (2003). Age and density modify the effects of habitat quality on survival and movements of roe deer. Ecology *84*, 3307-3316.

Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C., and Bonenfant, C. (2014). Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. Plos Biology 12, e1001828.

Ratcliffe, P.R. and Mayle, B. (1992). Roe deer biology and management. Forestry Commission Bulletin *105*, 1-28.

Réale, D., Gallant, B.Y., Leblanc, M., and Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. Animal Behaviour *60*, 589–597.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. and Dingemanse N.J. (2007). Integrating animal temperament within ecology and evolution. Biological Reviews 82:291–318.

Réale, D., Martin, J., Coltman, D.W., Poissant, J., and Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. Journal of Evolutionary Biology *22*, 1599–1607.

Ribeiro Jr., P.J. and Diggle, P.J. (2001) geoR: A package for geostatistical analysis. R-NEWS, Vol 1, No 2, 15-18. ISSN 1609-3631.

Robinson, R.A., and Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology *39*, 157–176.

Sempéré, A.J., Sokolov, V.E. and Danilkin, A.A. (1996). Mammalian species : Capreolus capreolus. American Society of Mammalogists *538*, 1-9.

Smith, B.R., and Blumstein, D.T. (2008). Fitness consequences of personality: a meta-analysis. Behavioral Ecology *19*, 448–455.

Sotherton, N.W. (1998). Land use changes and the decline of farmland wildlife: An appraisal of the set-aside approach. Biological Conservation *83*, 259–268.

Stamps, J.A., and Davis, J.M. (2006). Adaptive effects of natal experience on habitat selection by dispersers. Animal Behaviour *72*, 1279–1289.

Stamps, J., and Groothuis, T.G.G. (2010). The development of animal personality: relevance, concepts and perspectives. Biological Reviews *85*, 301–325.

Stamps, J.A., Krishnan, V.V., and Willits, N.H. (2009). How different types of natal experience affect habitat preference. The American Naturalist *174*, 623–630.

Tenenhaus, M., Gauchi, J.-P. and Ménardo, C. (1995). Régression PLS et applications. Revue de Statistique Appliquée *13*, 7-63.

Tenenhaus, M. (1998). La régression PLS : Théorie et pratique. Editions TECHNIP, 254 pages.

Tilman, D. (1982). Resource competition and community structure. Monogr Popul Biol *17*, 1–296.

Tixier, H., and Duncan, P. (1996). Are European roe deer browsers? A review of variations in the composition of their diets. Revue d'Ecologie (Terre Vie) *51*, 3–17.

Tufto, J., Andersen, R., and Linnell, J. (1996). Habitat Use and Ecological Correlates of Home Range Size in a Small Cervid: The Roe Deer. Journal of Animal Ecology *65*, 715–724.

VanDerWal, J., Falconi, L., Januchowski, S., and Storlie, L.S. and C. (2014). SDMTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modelling exercises.

Vanpé, C., Morellet, N., Kjellander, P., Goulard, M., Liberg, O., and Hewison, A.J.M. (2009). Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. Journal of Animal Ecology *78*, 42-51.

Wahlstrom, L.K. and Kjellander, F. (1995). Ideal free distribution and natal dispersal in female roe deer. Oecologia *103*, 302-308.

Webb, S.L., Dzialak, M.R., Harju, S.M., Hayden-Wing, L.D., and Winstead, J.B. (2011). Effects of human activity on space use and movement patterns of female Elk. Wildlife Society Bulletin *35*, 261–269.

With KA, Gardner RH, Turner MG (1997) Landscape connectivity and population distributions in heterogeneous environments. Oikos *78*, 151–169.

Résumé

Au cours de leur vie, les animaux doivent répondre à de multiples demandes énergétiques afin de se reproduire et d'assurer leur survie. Les individus font face à un compromis comportemental entre l'acquisition des ressources et l'évitement du risque de prédation. Malgré une adaptation générale des individus au sein d'une population, il est largement admis que les individus d'une population présentent des réponses comportementales différentes aux contraintes imposées par ce compromis. Par ailleurs, les différences interindividuelles dans le comportement peuvent avoir des conséquences importantes sur la valeur adaptative individuelle. Dans ce contexte, il a récemment été démontré chez le chevreuil, que la survie des juvéniles était influencée par le profil comportemental maternel, mais que les conséquences dépendaient de l'habitat maternel. Cela suggère une distribution spatiale des individus selon leur profil comportemental. Dans la présente étude, l'objectif était d'évaluer la distribution spatiale des individus présentant différents profils comportementaux au sein du paysage par l'analyse des relations entre traits comportementaux et caractéristiques paysagères. Nous avons supposé que certains profils comportementaux seraient plus fréquents dans certains environnements, traduisant une corrélation entre profil comportemental et environnement. Nous trouvons que les individus les moins réactifs face aux dangers vivent principalement dans les environnements fermés, globalement forestiers, à l'inverse des individus plus réactifs qui occupent davantage les environnements ouverts. D'autre part, il semble que les individus moins réactifs acceptent mieux la proximité avec les habitations humaines. Cette étude est l'une des premières à mettre en évidence des corrélations entre profil comportemental et environnement dans une population animale sauvage et conclue sur l'importance de l'hétérogénéité du paysage pour le maintien des différences comportementales interindividuelles.

Mots-clés : Profil comportemental, compromis, environnement, activité, stress

Abstract

Animals face multiple energy demands to reproduce and to ensure their maintenance in a broad manner through their lifespan. Then, individuals face a behavioral trade-off between resource acquisition and predation risk. Despite a general adaptation of animal's behavior within a population, it is largely acknowledge that individuals within a same population show consistent behavioral differences over their life time related to the constraint imposed by this trade-off. The inter-individual differences in behavior may have strong impacts on fitness. It has recently been demonstrated that maternal behavioral profile do influence the survival of the offspring in roe deer, but the consequences of coping styles on female fitness were habitat-dependent. This suggests a spatial distribution of individuals in relation to their behavioral profile. Therefore, in this study, we wanted to estimate the spatial distribution of roe deer according to their behavioral profile by analyzing the link between behavioral traits and landscape features. We hypothesized that specific behavioral profile of individuals are more common in a given environment, resulting in the existence of behavioral profile – environment correlations. We found that less reactive individuals to danger occupied mainly closed environments where woodland habitat was abundant whereas the more reactive individuals to danger lived in open environments. In addition, the less reactive individuals accepted more proximity with human activities. This study provides some of the first evidence for behavioral profile – environment correlations in a free-ranging animal population and concludes that landscape heterogeneity could allow the maintenance of behavioral differences among individuals.

Keywords: Behavioral profile, trade-off, environment, activity, stress