



Studying spatial interactions between sympatric populations of large herbivores: a null model approach

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Sympatric populations of species with similar ecology are limited by competition for available resources. While quantifying niche overlap between species in interaction offers a useful description of coexistence patterns, the lack of correspondence between niche overlap and competition prevents any functional interpretation. Using an innovative approach for analysing spatial distributions of individuals from two sympatric species, we aim to fill the gap. We applied our models to data collected on sympatric females of roe deer and red deer. Using the null model approach commonly applied in community ecology, we tested in a first model for deviation from a random distribution of female roe deer in relation to female red deer. We took into account constraints generated by both the marked sedentary habits and habitat use (avoidance of mature forest) of roe deer in this null model. In a second null model, we removed the habitat constraints to avoid any lack of power of our tests. We then compared the overlap index calculated from roe deer and red deer locations with the distribution expected under each of these null models. As we failed to reject the null model in both cases, we tested a third null model simulating an identical distribution of roe deer and red deer home ranges and we rejected it. Our results show that the distribution of female roe deer does not depend on the distribution of female red deer, indicating an absence of competitive interactions between the deer species. This conclusion relies on the application of the null model approach, which provides a suitable way of performing a formal test of interspecific competition rooted in explicitly defined hypotheses, and could not have been reached using simple overlap indices as generally performed when assessing competitive interactions. We thus encourage scientists to apply this null model analysis to population ecology.

Studying competition and identifying its effect on species distributions is central to community ecology. Many methodological tools have been developed in this field to tackle this topic. Simple indices such as niche overlap measures have been developed because the amount of overlap in resource utilization is assumed to be proportional to the intensity of competition between two species (Schoener 1974). However, the link between these indices and competition and their interpretation have been hotly debated (Colwell and Futuyma 1971, Hurlbert 1978, Schoener 1982). Simply demonstrating some overlap in resource use by animals of two sympatric species as often performed in population ecology studies can provide evidence either for or against the existence of interspecific competition. For instance, based on experimental studies of small mammals in the field, Schröder and Rosenzweig (1975) showed that a high overlap in habitat use between two sympatric species of small mammals does not lead to competitive interactions, whereas Koplin and Hoffmann (1968) found that spatial segregation can result from high

competition. On the other hand, in community ecology, the approach based on null models allows a reliable assessment of species coexistence (Gotelli 2001). According to Gotelli and Graves (1996), a null model is a pattern-generating model that is based on randomization of ecological data and is designed with respect to some ecological or evolutionary process of interest. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism. Thus, certain elements of the data are held constant, and others are allowed to vary stochastically to create new assemblage patterns (Gotelli and Graves 1996). Null models deliberately exclude the mechanism being tested (i.e. competition here). They have been widely used in community ecology (Connor and Simberloff 1979, Roxburgh and Matsuki 1999, Gotelli 2000, Wiegand and Moloney 2004). According to Gotelli (2001), the null model analysis involves three steps in community ecology. First, an index of community structure, such as the amount of niche overlap, is measured for the observed data. Second, a null community is generated

according to an algorithm or set of rules for randomization, and this same index is measured for the null community. A large number of null communities are usually built to generate a frequency histogram of index values expected when the null hypothesis is true. Lastly, the position of the observed index in the tail of this null distribution is used to assign a probability value to the pattern.

This approach has been met with large success in community ecology (see Krasnov et al. 2011 for a recent case study) because it provides both specificity and flexibility in data analysis, which are often not possible to get using conventional statistical testing. Null model analysis thus provides a way of studying a mechanism where experimental studies are not possible (Gotelli and Graves 1996). Despite its wide use in community ecology, the null model approach has not been previously used in population ecology to study interactions between animals. To our knowledge, Martin et al. (2008) proposed the only application of the null model approach to population ecology, in the context of habitat selection of brown bear *Ursus arctos*. Such a gap between population ecology and community ecology illustrates the 'lack of communication between paradigms' (Austin 1999). However, the null model approach could be useful to population ecologists by providing the missing link between spatial overlap indices among species and the intensity of competition.

We aim here to provide the first null model analysis for assessing competitive interactions between sympatric species. We took advantage of the detailed monitoring of both roe deer *Capreolus capreolus* and red deer *Cervus elaphus* at La Petite Pierre National Hunting and Wildlife Reserve (northeastern France) to illustrate our approach. This case study nicely fitted requirements for conducting such analyses on interspecific interactions. First, these species are both large herbivores with quite similar food requirements and are both distributed over the entire reserve, leading to the expectation of a high potential competition (MacArthur and Levins 1964, Pianka 1974, Sale 1974). Moreover, the vegetation in the study area has both a low quality and a slow dynamics (Klein and Hamann 1999). The soil is indeed made up of sandstone and is thereby not highly fertile. Previous studies on this red deer population have shown that density-dependent responses of life history traits occurred (Bonenfant et al. 2002), suggesting that resources were limiting when red deer density was high. In a context of limited resources, there was a potential for competition between deer species (Richard et al. 2010). We thus assessed whether both deer species foraged at the same places by examining how the two species were distributed relative to each other. This study therefore provides an assessment on the reliability of using null models in population ecology to tackle several issues related to interspecific competition based on individual data.

Methods

Study area

The La Petite Pierre National Hunting and Wildlife Reserve is a 27 km² forest located in northeastern France (48.5°N,

7°E), in the Vosges mountains. The mean elevation is 300 m a.s.l. and the climate is continental with oceanic influences, involving cool summers and relatively mild winters (mean January and mean July temperatures are 0.6 and 18.4°C, respectively, data from Météo France, Phalsbourg weather station, 10 km from La Petite Pierre). The forest is structured with even-aged tree stands and includes approximately equal proportions of broadleaved (mainly beech *Fagus sylvatica*) and coniferous species (mainly silver fir *Abies alba*, Norway spruce *Picea abies*, and Scots pine *Pinus sylvestris*, Hamann et al. 1997). Three species of large ungulates are present in the reserve and hunted, with an average of 40 red deer, 50 roe deer and 150 wild boars *Sus scrofa* shot every year. Based on nocturnal counting, Garel et al. (2010) found on average, for the 2004–2008 time period, 0.740 (± 0.119) red deer km⁻¹ which corresponds to a population size of 445 (± 93) individuals in the whole reserve. However, the study area is not enclosed and animals can move easily. This number of individuals is probably overestimated because it takes into account animals that do not live throughout all the year in the reserve. We lack a comparable density estimate for roe deer. However, using less complete information, Richard et al. (2010) reported that an average of 0.51 roe deer were detected km⁻¹ for the same period.

Species description

Red deer are intermediate feeders because they can eat both low (such as grasses) and high (such as fruit or leaves) quality food (Gebert and Verheyden-Tixier 2001). Roe deer are more selective and their diet is only composed of ligneous and semi-ligneous species (Storms et al. 2008). Red deer and roe deer do not feed on exactly the same resources, as red deer are able to consume all resources consumed by roe deer, whereas the opposite is not true (Storms et al. 2008). Therefore, if competition occurs between the two species, the roe deer should be more affected by the presence of the red deer than the reverse (Richard et al. 2010), leading to asymmetric competition. Moreover, both species do not have the same activity patterns. Roe deer alternate feeding and resting phases during the day (Cederlund 1981, Jeppesen 1989), whereas red deer are rather biphasic, foraging more during the night than during the day and resting more during the day than during the night (Georgii and Shröder 1983). Both species therefore do not necessarily forage at the same time of the day, so that if competition occurs, it should be exploitative competition (Birch 1957).

Data collected

Twenty-five different female roe deer and twenty-four different female red deer were captured between 2004 and 2008 in the reserve, using drive-netting or traps. The captures sites were not randomly distributed throughout the reserve (more captures sites in the western than in the eastern part) due to accessibility constraints (i.e. road and tracks, Fig. 1). Female deer were equipped with GPS collars (Lotek Wireless, ON, Canada). One year later, collars fell on the ground and we located them with radio-telemetry. Once a

collar was recovered, we downloaded one year of location data, which included one location every four hours, two days a week. We used different GPS collars according to the species' body mass. For roe deer, which is a small ungulate (20–30 kg), we used the 3300S GPS, whereas for red deer, which is much larger (130 kg), we used either the 3300L or the 4400M, according to female neck width. To account for seasonal changes in resource availability, we distinguished three seasons: spring (May–June), summer (July–August) and winter (November–February). We obtained a total of ninety four and sixty seven 'female-season-year' for roe deer and red deer, respectively. By 'female-season-year' we mean the set of locations collected for a given female during a given season in a given year (Table 1). In addition, since red deer have a biphasic activity pattern (Georgii and Shröder 1983), we distinguished day from night in the analyses.

Randomization procedure

We used a null model approach to assess the spatial interactions between roe deer and red deer. We tested one model for each season (i.e. spring, summer and winter) and for each possible time of the day (i.e. night, day, or night and day pooled) because space use may vary with the time of the day and with the season. We also took into account the fact that different animals were monitored during different years when designing the null model. For each possible combination of season and time of the day, we calculated an index of overlap between the two deer species as follows: for a given year, we first pooled the locations of all monitored red deer and we calculated a 'global' utilization distribution (UD) using the kernel method (smoothing parameter set to 140 m). We also estimated the UD for each female roe deer monitored during that year using the kernel method (smoothing parameter set to 70 m). The ad-hoc smoothing parameter (h_{ref}) was estimated for each monitored animal (Worton 1989), and the average value of h_{ref} was chosen as the smoothing parameter for a given species. Pellerin et al. (2008) showed that fixing the smoothing parameter to the same value for all home ranges of a given species provides a reliable way of comparing the home range of different individuals. We retained different smoothing parameters for roe deer and red deer because of the large between-species difference in home-range size. We then estimated the probability of finding a red deer in the 95% home range of each roe deer during that year from these species-specific UD (PHR index, Fieberg and Kochanny 2005, Appendix 1). We then calculated the mean PHR index, averaged over all roe deer monitored during that year. Finally, we averaged these mean PHR indices over all years to obtain a global overlap index (GOI). We used this GOI as the metric for quantifying the association between females of the two deer

species. We then carried out a randomization procedure to test the significance of the observed GOI under different null models that keep some structure of the data to preserve the biological phenomenon that is being explored. We focused on the random distribution of roe deer females because, from a biological point of view, roe deer are more likely to be affected by the red deer presence than the reverse (see above Species description).

First, we tested a null model describing the spatial independence between female roe deer and female red deer. For each possible combination of seasons and times of the day, we generated a theoretical statistical distribution of GOI expected under the null hypothesis of independence as follows (Table 2).

1) For each roe deer and each year (Fig. 2a), we first randomly rotated the whole set of GPS locations around its centre of gravity by an angle α sampled in a uniform distribution. This allowed randomizing the orientation of the roe deer home range around its centre of gravity (Fig. 2b).

2) We then randomly drew a new centre of gravity for a given roe deer in a given year (Fig. 2c). The sedentary habits of adult female roe deer are very strong (Strandgaard 1972, Pettorelli et al. 2003). In our study, the overlap between home ranges reached 66, 70, and 80% from one year to another, one season to another, and between night and day, respectively. In addition to this high site fidelity, roe deer home range size is remarkably small (around 30 ha and typically < 50 ha in forest, Saïd et al. 2005, 2009, mean of 42 ha at La Petite Pierre from the data available in this study). Being much larger and showing less marked sedentary habits, red deer adult females have home ranges about ten times larger than roe deer (typically around 300–500 ha in forest, Catt and Staines 1987, with a mean of 433 ha at La Petite Pierre from the data available in this study). Therefore, the capture site of a roe deer should be much closer to its home range barycentre than for red deer. We thus took into account the high sedentary habits of roe deer females in our randomization. Then, for a given roe deer and in a given year, we randomly sampled: 1) a capture site among all capture sites available in the study area during that year; 2) a distance d to this capture site in the set of observed distances between the centre of gravity of the home range of monitored roe deer and their capture site; and 3) an angle β drawn from a uniform distribution, corresponding to the angle between the east direction and the line segment connecting the centre of gravity of the home range and the capture site (Fig. 2c). This allowed generating randomly a new centre of gravity for the locations of roe deer females. We then shifted the set of locations rotated at the step 1 so that the centre of gravity of the locations corresponded to this new location.

For a given year, applying the steps 1 and 2 to all monitored female roe deer allowed us to generate randomly a spatial distribution of roe deer locations under the

Table 1. Number of deer included in analyses for each season (Sp: spring, Su: summer, W: winter) and each year. 'Sum' corresponds to the number of 'individuals/season/year'.

	2004			2005			2006			2007			2008			Sum
	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	Sp	Su	W	
Roe deer	1	8	8	5	6	5	5	5	5	8	8	7	8	8	7	94
Red deer	5	5	3	4	4	4	3	2	2	2	4	5	6	10	8	67

Table 2. Description of each model tested. For each model, the biological meaning of the null model, the constraints entered in the model, and the outcome of the test are provided.

	Null hypothesis	Model constraints	Outcome
Model 1	Random distribution of one species in relation to the other.	<ul style="list-style-type: none"> - Random orientation of roe deer home range and centre of gravity. - Proximity to capture site. - Habitat constraint: 80% of individuals with < 30% of locations in mature forest. 	No rejection of null hypothesis. No avoidance or attraction between distribution of the two species.
Model 2	Random distribution of one species in relation to the other.	<ul style="list-style-type: none"> - Random orientation of roe deer home range and centre of gravity. - Proximity to capture site. 	No rejection of null hypothesis. No avoidance or attraction between distribution of the two species.
Model 3	Similarity of space use between species.	<ul style="list-style-type: none"> - Random orientation of roe deer home range and centre of gravity. - Proximity to capture site. - New centre of gravity of the set of locations of roe deer randomly sampled among all red deer locations. 	Rejection of null hypothesis. The two species do not use exactly the same geographic areas.

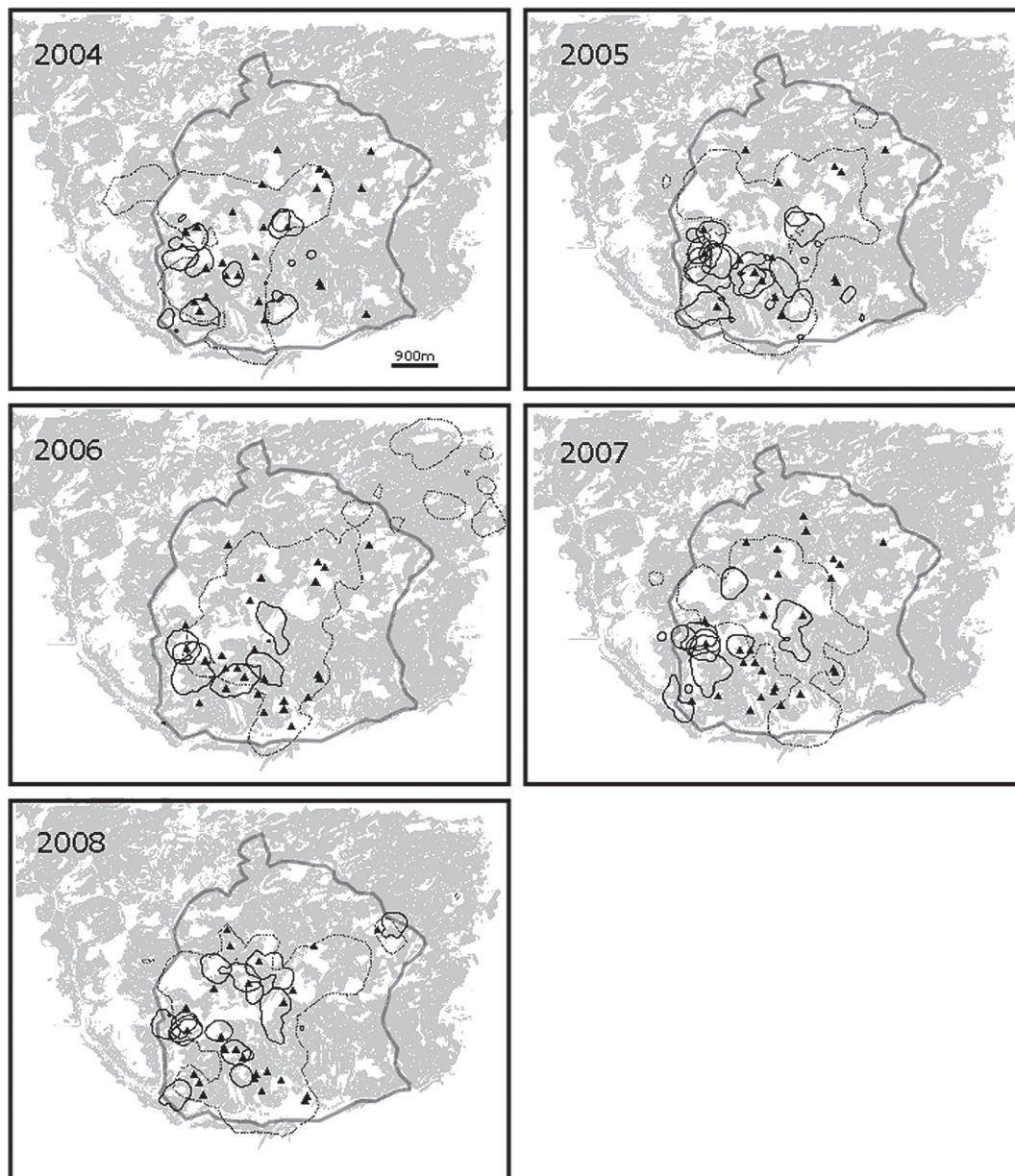


Figure 1. Deer home ranges for each year from 2004 to 2008. The grey background represents mature forest areas, the grey line is the delimitation of the reserve, the dark line defines each roe deer home range for the entire year, and the discontinuous line defines the home range of all red deer for the entire year. We did not distinguish among seasons or times of day for a clearer representation. Capture sites are represented with a triangle.

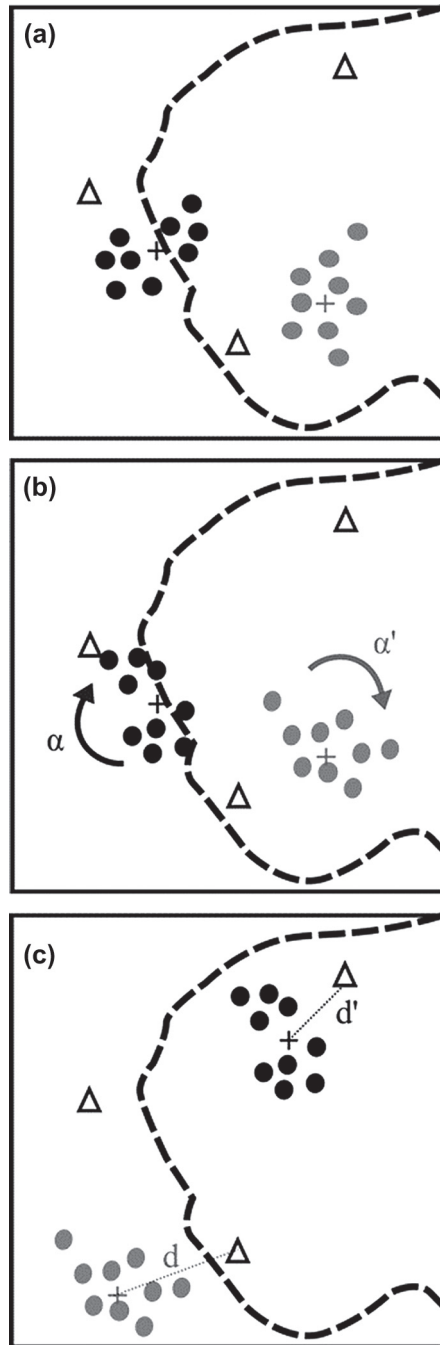


Figure 2. Diagram of the randomization procedure. (a) Points represent GPS locations of roe deer (two individuals are represented, one in black and one in grey) and crosses represent their centre of gravity. The discontinuous line defines the home range of all monitored red deer. Triangles are capture sites. (b) For each roe deer, we randomly rotated the whole set of GPS locations around its centre of gravity by an angle α sampled in a uniform distribution. (c) For each roe deer and each year, we randomly sampled a capture site among all capture sites available and a distance d to this capture site in a set of observed distances between the centre of gravity of the home range and the capture site. Finally, we calculated the overlap between the roe deer home range and the home range of all red deer. This description of the randomization is available for the second model but the first and the third both show some variation. In the first model we constrained 80% of individuals to have $< 30\%$ of their locations within mature forest. In the last null model, one roe deer location is on a red deer location.

hypothesis of random space use. This approach allowed us to maintain the ‘biological reality’ in the model by taking into account the high sedentary habits of roe deer (as the average of the randomized locations strongly depended on the location of the capture site) and the movement behaviour (as the structure of the location pattern – i.e. the number and the size of core areas – was not changed by our randomization process).

3) Roe deer females do not use space randomly, because habitat selection occurs (Pellerin et al. 2010). Roe deer females avoid mature forests and select for clearings, which have been shown to improve markedly their lifetime reproductive success (McLoughlin et al. 2007). At La Petite Pierre, 80% of the monitored roe deer females had $< 30\%$ of their locations in mature forest, whereas mature forests cover about 66% of the study area (Fig. 1). Not taking into account the avoidance of mature forests by roe deer females in our model might have resulted in the null model being rejected independently from the interaction process we were aiming to assess (the so-called Jack Horner effect, Wilson 1995). To correct for that confounding effect of habitat selection, we added a ‘habitat constraint’ in our randomization process. We thus retained a distribution of roe deer locations generated using the above algorithm only when 80% or more female roe deer had $< 30\%$ of their locations in mature forests.

4) We thus generated 1000 datasets using this null model, taking into account the high sedentary habits, the movement behaviour (i.e. home range spatial structure), and the habitat selection of female roe deer. We calculated a value of GOI for each one. We finally compared the expected distribution of the GOI with the observed value to test the independence between space use by females in both species.

The constraints on the null model are very strong. In particular, the habitat constraint may lead to distributions that are too similar to the observed distribution, leading to a low power of the test (the so-called Narcissus effect, Wilson 1995). To avoid that problem, we also simulated a second null model to test the independence between the two species, by performing again 1000 simulations of the first null model without the habitat constraint (i.e. all spatial distributions generated using steps 1, 2, and 4 were included in the test).

Finally, we simulated the similarity of space use between roe deer and red deer using a third model based on the null hypothesis that both species use preferentially the same places. This third model was similar to the second one, except that the new centre of gravity of the set of locations was, in addition to steps 1 and 2, randomly sampled among all

Table 3. Season-specific proportion of female roe deer home range covered by red deer female home range (nocturnal and diurnal home ranges are pooled) as measured using the Fieberg and Kochanny (2005) PHR method (see main text).

	Spring	Summer	Winter
Mean	0.28	0.35	0.53
Standard deviation	0.37	0.41	0.37
Minimal value	0	0	0
Maximal value	1	1	1
n	27	36	32

Table 4. Summary results for three randomization procedures, for the three seasons (spring, summer and winter), for each time of day (day, night, or day and night pooled called all day). I+HC corresponds to the model of independence with habitat constraint (first model); I–HC is the model of independence without habitat constraint (second model), and ID is the model of identity of space use (third model). Observed and expected GOI are the observed and expected global overlap index, respectively (see the main text for a detailed description). Variance is the variance of the expected GOI.

Null model	Season	Time of day	Observed GOI	Expected GOI	Variance	p-value	
I+HC	spring	day	0.0163	0.0141	3.83×10^{-5}	0.68	
	spring	night	0.0105	0.0113	5.61×10^{-5}	0.50	
	spring	all day	0.0143	0.0131	3.11×10^{-5}	0.62	
	summer	day	0.0193	0.0214	5.38×10^{-5}	0.42	
	summer	night	0.0218	0.0199	5.61×10^{-5}	0.71	
	summer	all day	0.0216	0.0215	3.45×10^{-5}	0.54	
	winter	day	0.0291	0.0370	4.2×10^{-4}	0.48	
	winter	night	0.0326	0.0394	4.2×10^{-4}	0.49	
	winter	all day	0.0324	0.0408	4.2×10^{-4}	0.46	
	I–HC	spring	day	0.0163	0.0134	3.78×10^{-5}	0.69
		spring	night	0.0105	0.0114	2.88×10^{-5}	0.49
		spring	all day	0.0143	0.0130	2.98×10^{-5}	0.64
summer		day	0.0193	0.0213	5.45×10^{-5}	0.44	
summer		night	0.0218	0.0195	5.48×10^{-5}	0.73	
summer		all day	0.0216	0.0217	3.73×10^{-5}	0.50	
winter		day	0.0291	0.0366	4.07×10^{-4}	0.49	
winter		night	0.0326	0.0391	4.05×10^{-4}	0.49	
winter		all day	0.0324	0.0402	4.18×10^{-4}	0.47	
ID		spring	day	0.0163	0.1215	1.75×10^{-4}	10^{-8}
		spring	night	0.0105	0.1142	1.68×10^{-4}	10^{-8}
		spring	all day	0.0143	0.1130	1.58×10^{-4}	10^{-8}
	summer	day	0.0193	0.0983	1.38×10^{-4}	10^{-8}	
	summer	night	0.0218	0.0821	1.67×10^{-4}	10^{-8}	
	summer	all day	0.0216	0.0876	1.05×10^{-4}	10^{-8}	
	winter	day	0.0291	0.0885	3.12×10^{-4}	10^{-8}	
	winter	night	0.0326	0.0794	3.13×10^{-4}	10^{-8}	
	winter	all day	0.0324	0.0819	2.96×10^{-4}	10^{-8}	

red deer locations. Therefore, the new set of GPS locations generated for a given roe deer was more likely to be located where there were many red deer locations. Similarly, for each roe deer, we estimated a kernel utilization distribution from the randomized set of GPS locations, and we estimated the mean PHR for the whole set of roe deer. The distribution of the 1000 values of PHR expected under the hypothesis of similar space use was then compared to the observed value (Table 2 for further details on models, Appendix 2).

All calculations were performed using the free packages `adehabitatLT` and `adehabitatHR` (Calenge 2006) for R 2.11.0 software (R Development Core Team 2011). Note that we added several functions that allow performing easily this kind of null model analysis with the `adehabitatLT` package (in particular the `testNM` function). The vignette of `adehabitatHR` explains how to reproduce the kind of calculations carried out in this paper.

Results

There was a large individual variability in the proportion of roe deer home range covered by a red deer home range (Table 3). Our data indicated that a large overlap between the two deer species occurs during all seasons and during both night and day. These results were supported by our null model analysis. Indeed, for all seasons at night or during the day, we did not reject the hypothesis that

female roe deer are randomly distributed in relation to female red deer, both with or without including the habitat constraint (i.e. model 1 and model 2, all p-values > 0.4) (Table 4). However, for each season and each time of the day (night, day, and night and day pooled), we rejected the model 3 stating that female roe deer and female red deer select the same places (Table 4, all p-values < 10^{-8}). Consequently, areas most intensively used by female roe deer were not located at the same place as those of female red deer.

Discussion

We have defined a null model describing the independence in space use between females of roe deer and red deer, which accounted for highly sedentary habits, movement behaviour (i.e. home range spatial structure), and habitat selection of female roe deer. We did not find any difference between the statistical distribution of the overlap index expected under this null model and the observed overlap index. Performing the same test after removing the habitat constraint to gain statistical power led to the same result. We only rejected the null model of identical spatial distribution of female red deer and female roe deer after accounting for sedentary habits and movements of roe deer and after forcing the centre of gravity of roe deer home ranges to correspond to a red deer female location. This result indicates

that the places where the animals spent most of their time differed between roe deer and red deer females.

The non-rejection of the two first null models we tested could result from a lack of statistical power of our null model analysis. Such a situation has been described as the Narcissus effect (Wilson 1995) and occurs when the simulated data is too similar to the original dataset. However, we did not detect any avoidance between the deer species when not including habitat constraints in the null model analysis (i.e. trading bias for increased statistical power), suggesting that statistical power was not involved in the results. The non-rejection could also indicate a too rough criterion to detect competitive interactions between the two deer species (Gotelli 2000). However, we used the same GOI criterion when we rejected the third null model, indicating that when a strong overlap pattern occurs in the data, the GOI criterion allows detecting the signal. We could thus discard methodological explanations to account for our results, which rather indicate a low intensity of competition between the two deer species. In support of that, some female roe deer had a large spatial overlap with female red deer (Fig. 1), indicating that resources were probably not limiting for deer during our study period.

The three null models we implemented all rely on the randomization of the distribution of roe deer home ranges, while keeping the spatial distribution of the red deer fixed. At first sight, it is tempting to try the reverse exercise, i.e. to randomize the spatial distribution of red deer females while keeping the distribution of roe deer females fixed. However, this would be hard to justify from a biological point of view. Given that red deer feed on a wider range of plant species than roe deer (Storms et al. 2008), roe deer should be more affected by the red deer than the reverse. Previous studies on red deer and roe deer interactions support the asymmetry of competition between these species (Latham 1999). In addition, we lack required biological information about sedentary habits and required habitat type for randomizing red deer. Under such conditions, null models based on randomized red deer locations would not be realistic.

The intensity of interspecific competition depends on both the number of competing individuals and their ability to compete (Stewart et al. 2002). Red deer and roe deer can potentially compete because red deer can use the entire roe deer feeding niche (Storms et al. 2008), but the reverse is not true. At the La Petite Pierre reserve, both roe deer and red deer are hunted (forty individuals of each species, each year in a 2700 ha forest). Hunting is the most important factor driving changes in deer abundance in the study site. Climatic factors such as summer droughts and winter severity likely contribute to some changes although we lack quantitative information on the effect of climatic factors on population growth in either roe deer or red deer. Bonenfant et al. (2002) found no relationship between weather and red deer body mass, as expected from the mild climatic condition of the study area. The low density leads to limited competition between deer species. Moreover, the recent increase of food resources generated by the Lothar hurricane in 1999 could have contributed to decrease interspecific competition by improving roe deer condition (Duncan et al. 1998, Widmer et al. 2004). We focused on static interactions (i.e. spatial locations used by females

of the two species during a given period) and we did not consider dynamic interactions (i.e. use of the same places but not at the same time, Doncaster 1990). Niche partitioning among species has been traditionally evaluated along three niche dimensions: dietary differences, spatial separation, and temporal avoidance (Stewart et al. 2002, 2003). As we did not consider temporal avoidance, we cannot discard the possibility of a competition on the temporal rather than on the spatial dimension between females of the two deer species at La Petite Pierre. The spatial distribution of large herbivores is dynamic and is related to resources and landscape physiography (Frank 1998). Further studies are thus required to develop a null model approach that includes the temporal dimension of the interaction.

The simple use of measures of spatial overlap is useless to identify a potential competition between sympatric species because there is no functional link between the degree of spatial overlap and the intensity of competition. The application of null model analysis offers a suitable tool to assess the occurrence of competitive interactions by providing explicitly formulated testable hypotheses, as shown in the present work. However, elaborating null models is far from an easy task and has been controversial, mainly because there are many ways of generating a random expectation (Schoener 1982). The debate has focused on the construction of null models. Indeed, whether testing null models is predisposed to type II error (i.e. incorrectly accepting a false null hypothesis, Colwell and Winkler 1984) or type I error (i.e. incorrectly rejecting a true null hypothesis, Wilson 1995) remains unknown. However, although null models can be biased to some extent, they are worth being considered by population ecologists for analysing spatial interactions among species. In the state of art of our current knowledge about assessing competitive interactions between sympatric populations, population ecologists lack a suitable tool. Null model analysis, a common method considered as useful for revealing spatial coexistence patterns (or the lack thereof) in natural communities (Gotelli 2001), are also likely to be helpful for revealing spatial competition (or the lack thereof) between sympatric populations, as the present study demonstrated. The implementation of the null model analysis in population ecology studies might in addition contribute to fill the gap between population ecology and community ecology. By doing that, future research will be likely to provide lacking answers to the questions about what shapes ecological assemblages at different spatial scales. As well discussed by Ricklefs (2004: 4–6), we crucially need ‘means of rejecting hypotheses about the ways in which the available niche varies among, or is divided among, species’ as well as ‘realistic models of the regulation of diversity’. As exemplified in our case study, the consideration of species-specific peculiarities (e.g. sedentary habits, movement patterns, habitat preference) is a first step towards such realistic models. To conclude, we encourage population ecologists to use this null model analysis in spatial studies to get a better understanding of the complex patterns of interactions among species.

Acknowledgements – The Petite Pierre National Reserve has been managed by the Office National de la Chasse et de la Faune Sauvage and the Office National des Forêts. This study was financed by the

Office National de la Chasse et de la Faune Sauvage. We are grateful to the wildlife technicians (Julien Séré, Erwin Schmitt, Abdelkader Larbi, Monique Hamann) the foresters (Romain Gaudry, Hubert Holveck, Philippe Mortz, Eric Muller and Eric Krauser), the 67 Départemental Services and the many volunteers for their help in the capture of deer. We thank Catherine Carter for revising the English manuscript.

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Appendix 1

Equations used in the randomization procedure. PHR computes the volume under the utilization distribution of the animal j that is inside the home range of the animal i (i.e. the probability to find the red deer j in the home range of a roe deer i , Fieberg and Kochanny 2005), GOI (global overlap index) corresponds to the mean of PHR.

$$PHR_{i,j} = \iint_{A_i} UD_j(x,y) dx dy$$

$$GOI = \frac{\sum PHR_{i,j}}{n}$$

Appendix 2

Distribution of 1000 values of (a) PHR expected under the hypothesis of similar space use and (b) random distribution of female roe deer in relation to female red deer. This distribution is compared with the observed values (i.e. global overlap index GOI, which corresponds to the mean PHR). GOI is interpreted as the probability to find a red deer in a roe deer home range.

