A multi-patch use of the habitat: testing the First-Passage Time analysis on roe deer Capreolus capreolus paths

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A multi-patch use of the habitat: testing the First-Passage Time analysis on roe deer *Capreolus capreolus* paths

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A heterogeneous environment includes several levels of resource aggregation. Individuals do not respond to this heterogeneity in the same way and their responses depend on the scale at which they perceive it, and they develop different foraging tactics accordingly. The development of methods to analyse animal movements has enabled the study of foraging tactics at several scales. Nevertheless, applied to large vertebrates, these methods have generally been used at large scales, such as for migration trips or for the study of marine patches several kilometres large. In our study, we applied a recent method, the First-Passage Time analysis, based on a measure of the foraging effort along the path, to a much finer scale, i.e. < 500 m. We used 30 daily paths of highly sedentary roe deer *Capreolus capreolus* females. We modified the initial method, developed by Fauchald & Tveraa (2003), to detect a multi-patch use of the habitat. First-Passage Time analysis results showed that most of the female roe deer exploited their home range as a patchy resource, ranging within 1-5 areas of intensive use in their home range. These areas were identified as the most attractive sites within the roe deer female home range. Moreover, this method allowed us to rank the attractive areas according to the time spent in each area. Coupled with habitat selection analysis to identify what makes these areas attractive, the First-Passage Time analysis should offer a suitable tool for landscape ecology and management.

Key words: area-restricted search, Capreolus capreolus, First-Passage Time Analysis, roe deer, spatial heterogeneity

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Animals live in a patchy and hierarchically structured environment. Resources are aggregated and habitat complexity is generally reflected by this aggregation at different scales, lower levels nesting into upper levels (Kotliar & Wiens 1990). According to the scale, resources differ in density, turnover and predictability (Wu & Louks 1995, Fauchald 1999, Fauchald et al. 2000). The spatial and temporal distribution of a resource has a dominant influence on the searching efficiency and behaviour of a predator (Bell 1990). Hierarchical organisation of resource aggregation thus induces both a differential perception of the habitat by predators according to the scale, and a modification of their search behaviour (Fauchald 1999). Animals will change their movement patterns in relation to changes in the spatial distribution of resources (Fritz et al. 2003). According to the Optimal Foraging Theory, when resources are distributed in patches, a consumer should increase its intake rate in a high-resource density patch (Stephens & Krebs 1986), slowing down its speed and increasing its turning rate. Kareiva & Odell (1987) defined this concentration of consumer activity within an area of interest as an 'Area-Restricted Search' behaviour (ARS). In fact, animal movement trajectories should result from the interaction between animal decisions and landscape properties (Morales et al. 2005).

Movement patterns of animals have mainly been analysed using point distribution and path trajectories (Turchin 1998). Two main but different ways have been used to study vertebrate movements: studies based on random walks (Mårell et al. 2002) or on fractal dimension (Nams 2005). Correlated random walks have been used to model random movements with a certain degree of directionality (Kareiva & Shigesada 1983, Bergman et al. 2000), whereas the fractal dimension measures a path tortuosity. The tortuosity of foraging paths represents animal reactions to landscape heterogeneity in which animals translate environmental stimuli into movements (Crist et al. 1992, With 1994). Our understanding of these relationships and processes has heavily relied on studies of small organisms or insects for which the monitoring of movement and the manipulation of the microlandscapes are feasible (e.g. Crist et al. 1992, With 1994, With et al. 1999). However, the monitoring of foraging paths of large animals has recently been developed (e.g. Gross et al. 1995, Etzenhouser et al. 1998, Viswanathan et al. 1999, Johnson et al. 2002, Mårell et al. 2002, Fauchald & Tveraa 2003, Fritz et al. 2003). The methods developed in these studies are mainly based on the shift between displacement patterns to define spatial scale changes. The study of trajectories allows the understanding of how the habitat heterogeneity affects foraging efficiency of the predators, and how they react to changes in the spatial structure of resources.

In a recent study, Fauchald & Tveraa (2003) used variation in the search effort to assess at which scale consumers interact with their environment. The 'First-Passage Time' (FPT) analysis, developed by Fauchald & Tveraa (2003), estimates the search effort, measuring the time spent by a predator to cross a circle of a given radius and so, highlights the part of the path where it adopts an ARS behaviour. The FPT analysis provides an estimation of the scale at which a consumer perceives resource by determining the exploited patch size (Fauchald & Tveraa 2003).

Determination of the perception scale of resource by an animal is important in understanding exploitation tactics, and this perception often differs from our own (Levin 1992). Like most of the studies on large animal movements (e.g. Bascompte & Vilà 1997, Viswanathan et al. 1999, Bergman et al. 2000, Johnson et al. 2002, Mårell et al. 2002, Fritz et al. 2003, Austin et al. 2004), FPT analysis was performed on seabirds with high travelling abilities, making long foraging trips in low predictable resource habitats (Fauchald & Tveraa 2003, 2006, Pinaud & Weimerskirch 2005, 2007). However, Frair et al. (2005) and Bailey & Thompson (2006) also performed FPT at a smaller scale; on a large ungulate (elk *Cervus elaphus*) living in a more restricted home range and on groups of bottlenose dolphins *Tursiops truncatus* in a small surface area, respectively. In our study, we also attempted to apply the FPT analysis at a finer scale than in Fauchald & Tveraa (2003) and Pinaud & Weimerskirch (2005) in order to investigate the structure of daily paths of roe deer *Capreolus capreolus*.

It has been assumed that herbivores generally feed at sites with high food quality and/or quantity, following qualitative predictions from Optimal Foraging Theory (e.g. Stephens & Krebs 1986). These predictions are supported by feeding-patch selection by deer, which has been shown to be related to nutrient content and plant biomass (Wilmshurst & Fryxell 1995). Effects of habitat quality on roe deer population dynamics are quite well understood (Pettorelli et al. 2001, 2002, 2003a,b), but less so on the individual use of space (Mysterud et al. 1999). Though many studies on roe deer have been performed on the relationship between environmental factors and home-range variation (Tufto et al. 1996, Mysterud et al. 1999, Saïd et al. 2005, Saïd & Servanty 2005), very few studies have investigated the heterogeneous use of the habitat within the home range.

In our paper, we used data from roe deer females equipped with GPS collars to investigate the structure of their movements throughout a day, using FPT analysis. Roe deer are known to have quite fixed and restricted home ranges (Strandgaard 1972, Liberg et al. 1998). It is thus particularly challenging to determine how roe deer may perceive or define the spatial organisation of their resource in their daily environment and the impact of environmental structure on their movements.

The aim of our study was to see if roe deer perceive their habitat as heterogeneous. We hypothesised that 1) in a heterogeneous environment roe deer will use areas where they will increase their search for palatable plants and slow down their speed to increase their intake rate (Fauchald & Tveraa 2003); 2) roe deer will use several ARS throughout the day as this species presents several activity phases with two main peaks at dawn and dusk (Bubenik 1960, Maublanc et al. 1991).

Methods

Study area

Our study was carried out in the Chizé reserve (Fig. 1). The Chizé reserve is an enclosed forest of 2,614 ha in western France (46°05'N, 0°25'W). The elevation varies between 47 and 101 m a.s.l. and the oceanic climate is characterised by mild winters and hot and dry summers. The Chizé forest includes three habitats contrasting in quality: an oak *Quercus* spp. forest with resource-rich coppices dominated by hornbeam *Carpinus betulus* in the northeastern part, an oak forest with coppices of medium quality dominated by Montpellier maple *Acer monspessulanum* in the northwestern part, and a poor beech *Fagus sylvatica* forest in the southern part (Pettorelli et al. 2003a, Saïd & Servanty 2005; see Fig. 1). The roe deer population at Chizé was estimated from Capture-Mark-Recapture methods to be approximately 400 adults in 2003 and 450 in 2004 (e.g. Gaillard et al. 1992, 1993, Pettorelli et al. 2002, 2003b; J-M. Gaillard, unpubl. data).

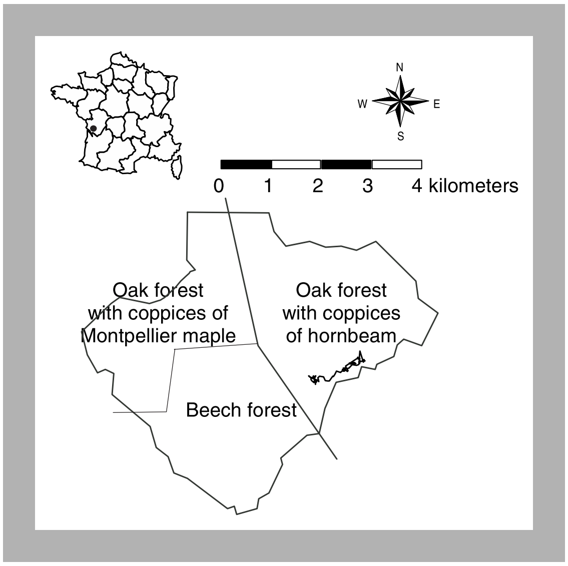

Figure 1. Spatial representation of the Chizé reserve, an enclosed forest covering 2,614 ha in western France. A daily path of a female roe deer in 2003 is represented in the eastern part of the reserve.

Data collection

Does were equipped with Lotek's GPS_3300 radio collars (Lotek Wireless, Fish & Wildlife Monitoring). These collars, weighing 285 g, provided information on GPS positioning in differential mode (i.e. latitude, longitude, date and time) at preprogrammed intervals, fixed quality (DOP = dilution of precision) and ambient temperature. We scheduled collars programming one location every five minutes during 24 hours for 1-3 days per month. In September-December 2003, two females were equipped with GPS collars. In January-February 2004, another seven does were collared, in addition to the two previously equipped females. Data location and data activity were recovered during the capture campaign in January-February 2004 and 2005. We obtained 15 daily paths with one point every five minutes from September 2003 to January 2004 and 15 daily paths during May-November 2004 (Fig. 2).

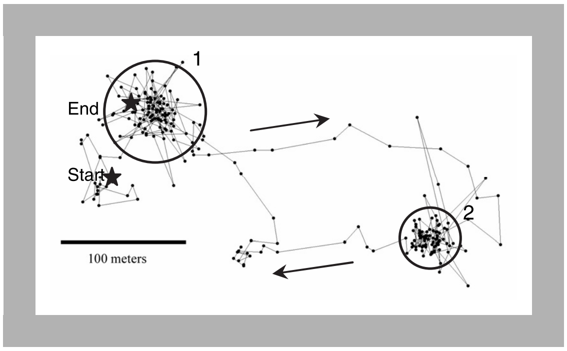

Figure 2. Example of a path on which several areas were detected for female 35 on 24 November 2003. The numbers beside the circle correspond to the detection order of the areas. The circle 1 is a first class circle and the circle 2 a second class circle. The arrows indicate the direction of the walk.

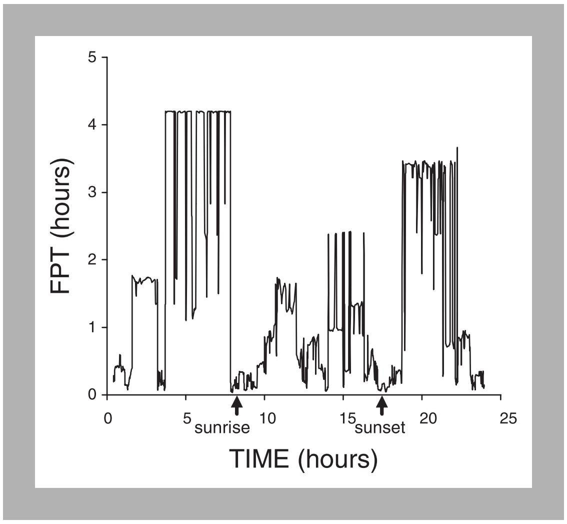

Figure 3. Example of First-Passage Time (FPT) all along the path for the scale assessed by the analysis (here 50 m for female 35 on 30 December 2003). The high and constant FPT near dawn corresponds to the most intensive Area-Restricted Search (ARS) behaviour. A second FPT near dusk, lower, seems to indicate a multi-patch use of the environment throughout the day.

First-Passage Time analysis

The First-Passage Time method

To detect one or several ARS, we performed an FPT analysis on our data, following the method of Fauchald & Tveraa (2003), and using the software R (version 2.1.0; R Development Core Team 2005; Ihaka & Gentleman 1996) distributed under the GNU General Public License. The First-Passage Time (FPT) corresponds to the time needed by an animal to cross a circle of a given radius r. In order to perform the analysis, we assumed linear path with a constant speed between locations (e.g. Kareiva & Shigesada 1983) and completed inter-location path by points spaced every 5 m as 90% of the path segments were longer than 5 m. FPT was calculated at each point of individual paths for a given radius r, the location corresponding to the centre of the circle. We determined this measure of time for r ranging within 5-400 m, as locations were spaced every 5 m maximum and as the mean radius of the roe deer home range in the Chizé Forest is about 300 m. The radius where the highest peak of variance in FPT is observed corresponds to the spatial scale (radius) of the area where the individual concentrates its search effort. We thus calculated the variance in FPT given by Var[log t(r)], S(r), for each radius, and plotted it against the radius to obtain the spatial scale corresponding to the peak in S(r), of the globality of individual path. Spatial scale was confirmed when the plot of the FPT against time for the radius for which S(r) was maximum showed intensive search pattern, that is a high and constant FPT (see Fauchald & Tveraa 2003; Fig. 3). Then, the intensive search area which corresponds to an ARS was identified on a path as the circle with the longest FPT for the determined spatial scale.

Multi-patch detection

Using the FPT analysis, we detected the area where the search effort was the highest. Moreover, the circle radius gave us an estimation of the size of the exploited patch. However, the majority of our paths were clearly composed of more than one ARS (see Figs. 2 and 3). The scale used to estimate the size of the main exploited patch cannot be applied to the other ARS. Indeed, these ARS do not necessarily have the same radius as the one with the highest FPT. In order to assess the scale of these ARS, we needed to remove the effect of the main ARS. We therefore modified the original process described by Fauchald & Tveraa (2003) and programmed by Pinaud & Weimerskirch (2005), to detect other potential ARS (program available by contacting the authors). Part of the path included in the first determined FPT circle was removed and replaced by a segment that individuals cover in five minutes, as if the point before and after the ARS were really two successive points in the path. We then corrected the time of the locations following the removed part of the path. FPT analysis was finally performed on the modified path, and we repeated the analysis until we obtained no more potential ARS (Fig. 4).

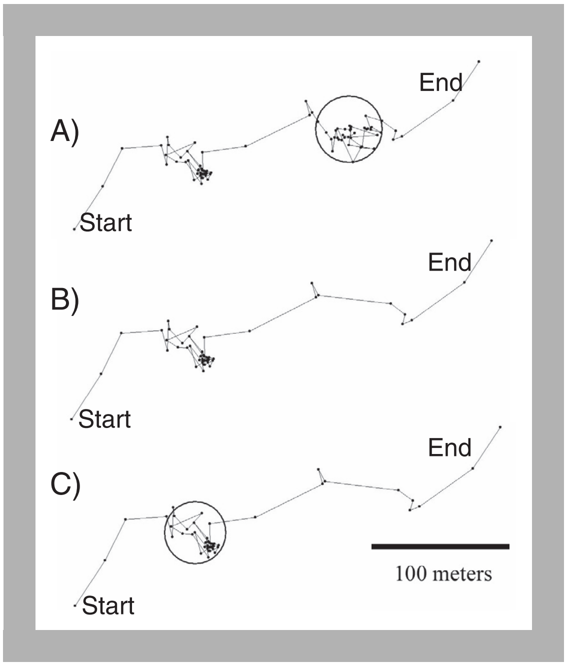

Figure 4. Example of detection of a second area: (A) a first circle was detected after the FPT analysis was performed; (B) part of the path inside the first detected circle was removed and replaced by a segment which the individual covered in five minutes; (C) FPT analysis was performed again and the second area was detected.

ARS validation

All circles for which the FPT plotted against time did not show any intensive search pattern were removed. Remaining circles were resorted: circles overlapping previously detected ARS and circles with radius of <25 m (GPS error calculated for Chizé forest = 25.56 ± 33.99 m) were removed, especially in order to minimise the bias induced by the positioning error of the GPS. Finally, circles with a mean speed displacement higher than the mean speed in the whole path were eliminated. Indeed, when applying the method in order to detect other ARS, the substitution of previously detected circles by a straight line covered in five minutes sometimes produced a bias in the detection. The identified parts of the path correspond to the parts where individuals spend more time and slow down their speed according to the ARS behaviour. As these parts of the path were substituted by a segment covered in five minutes, the mean speed displacement along the path increased. A new ARS was detected where individuals moved slower than of the whole new generated path. However, the speed of the new generated path was higher than the speed of the original path. The difference between the mean speed inside the ARS and the mean speed of the original path was smaller than with the generated path where the FPT method was applied. In extreme cases, the speed inside the ARS was even higher than the speed of the original path, and animals moved faster in the detected circle than in the whole original path that was not congruent with the definition of the ARS. Consequently, such circles were not taken into account. In order to identify these circles, we estimated the individual's mean speed in the ARS and compared it with the speed that the deer could have during the same time period. Given that the part of the path included in the circle is composed of n segments with associated speed, we randomly drew n segments, with replacement, of the whole path and estimated the mean speed. We performed this 100,000 times to obtain a mean speed distribution over the path. If the mean speed in the ARS was higher than the median value of the distribution, we did not take the corresponding circle into account. At last, the selected ARS were divided into three classes to assess whether the ARS differed according to the detection order: class 1, the first detected ARS; class 2, the second detected ARS; and class 3, the last ARS.

Statistical analysis

To test the effect of female identity, year, month, class of circle and circle radius as a covariable on the FPT in the circle, we fitted mixed linear models ('lme' function in the 'nlme' R package; Laird & Ware 1982, Pinheiro & Bates 2000, Pinheiro et al. 2005) with the FPT in the circle, the year (2003 or 2004) as a two-modality fixed factor, the month (May, August, September, November and December) as a five-modality fixed factor, the class of circle (1, 2 or 3) as a three-modality fixed factor, and the females identity as random factor.

We did the same with the log-transformed FPT divided by the circle surface (FPT/m^2). This measurement represents the utilisation intensity of an area. We fitted mixed linear models with log(FPT/m), year, month, class of circle (1, 2 or 3) as fixed factors, and only the females identity as random factor. We tested the random effect with a Restricted Maximum Likelihood (REML) procedure and the fixed effect with a Maximum Likelihood (ML) procedure (Vaida & Blanchard 2005). To select the best model, we used the Akaike Information Criterion (AIC; Burnham & Anderson 1998), and we retained the model with the lowest AIC value. When the difference between two models was <2, we retained the

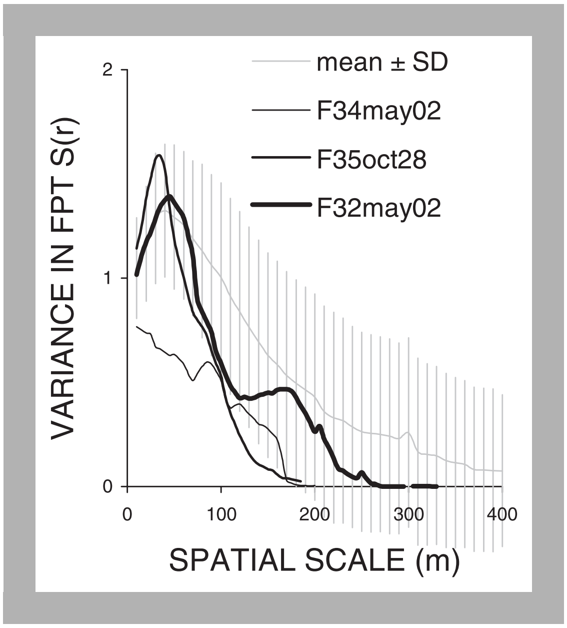

Figure 5. Mean variance in First-Passage Time (FPT) S(r) against the radius r of all paths showing ARS and example for three paths. The peak in S(r) corresponds to the used spatial scale. The female roe deer F34 did not express ARS in May 2004 (according to Pinaud & Weimerskirch 2005).

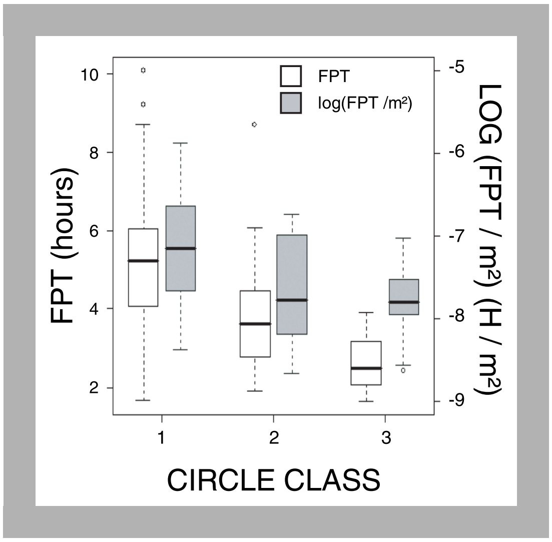

Figure 7. First-Passage Time (FPT; in hours) and Mean log(First-Passage Time/Surface Unit; log(FPT/m^2) according to the circle classes. The FPT decreased with the detection order (class 1 vs class 2: df = 38, t-value = -4.897, P < 0.001; class 1 vs class 3: df = 38, t = -5.035, P < 0.001; class 2 vs class 3: df = 38, t = -1.289, P = 0.205). The log(FPT/m^2) decreased with the detection order (class 1 vs class 2: df = 38, t = -6.039, P < 0.001; class 1 vs class 3: df = 38, t = -7.017, P < 0.001; class 2 vs class 3: df = 38, t = -2.432, P = 0.020).

simplest model according to the parsimony rules (Burnham & Anderson 1998). We checked the normality of residuals of our selected models for FPT (Shapiro-Wilk test: W = 0.994, P = 0.94) and log (FPT/m^2) (Shapiro-Wilk test: W = 0.991, P = 0.77). For each model, the standard deviation of the random factor Female Id and the residuals were: Female Id SD = 0.852, Residual SD = 0.994, and Female Id SD = 0.517, Residual SD = 0.330, respectively.

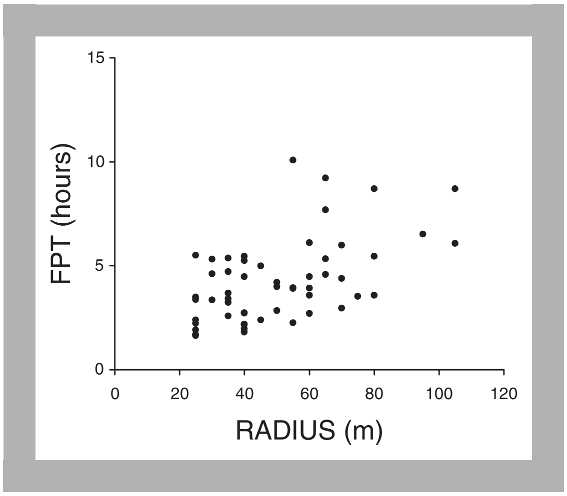

Figure 6. First-Passage Time (FPT; in hours) as a function of the corresponding radius (in m) of detected areas.

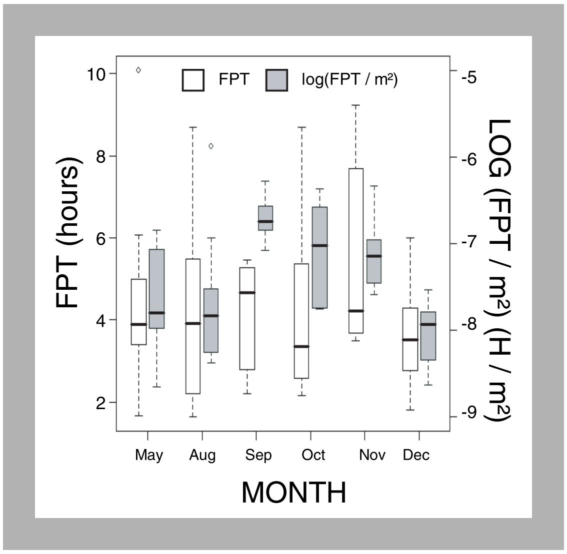

Figure 8. First-Passage Time (FPT; in hours) and Mean log(First-Passage Time/Surface Unit; log(FPT/m^2) according to month.

Table 1. Results of the mixed linear models for the First-Passage Time (FPT) and for the log-transformed First-Passage Time ($\log(FPT/m^2)$ divided by the circle area of female roe deer paths in Chizé forest, with the female identity as random factor.

Tested models	Random factor	Fixed effect	Number of parameters	Δ AIC
FPT	Female	Month	2	52.65
		Year	2	48.58
		Constant	1	46.54
		Circle class + Month	3	39.13
		Circle class + Year	3	34.56
		Circle class	2	32.57
		Radius	2	29.61
		Radius + Circle class + Year	4	7.34
		Radius + Circle class	3	6.02
		Radius + Circle class + Month	4	0
$\log(FPT/m^2)$	Female	Year	2	41.61
		Year + Circle class	3	31.67
		Circle class	2	29.99
		Month	2	15.28
		Month + Circle class	3	0

Results

Over the 30 analysed paths, 24 (13 in autumn/winter, 11 in spring/summer) presented a peak of the relative variance S(r) (Fig. 5) with a radius that seemed to correspond to an ARS. There was a total of 55 ARS detected (Class 1 = 23, Class 2 = 20, Class 3 = 12), ranging within 1-5 ARS per path (mean = 2.2, SE = 0.96; see Fig. 3). Radius of the detected circles ranged within 25-105 m (mean = 50.1, SE = 20.47m), and the FPT ranged within 1 hour 38 minutes - 10 hours 5 minutes (mean = 4 hours 13 minutes, SE = 1 hour 59 minutes). The best mixed linear model for the First-Passage Time included ARS radius (Fig. 6), circle class (Fig. 7) and month (Fig. 8), as well as the female ID (Tables 1 and 2; AIC = 189.96). We observed a positive relationship between the FPT and the ARS radius (slope = 0.052; see Fig. 6).

For $\log(FPT/m^2)$, the best mixed linear model included circle class (see Fig. 7), month (see Fig. 8) and female ID (see Tables 1 and 2; AIC = 75.36). Moreover, the result showed that $\log(FPT/m^2)$ was negatively correlated with circle class: the use of the patches by the females was more intensive in the first detected ARS than in the second and the third ones (see Fig. 7).

Discussion

Using the First-Passage Time (FPT) analysis (Fauchald & Tveraa 2003), we detected at least one Area-Restricted Search behaviour (*sensu* Kareiva & Odell 1987) on most of the paths. Our study highlighted the existence of a second scale of landscape use which was finer than the home-range scale for the roe deer (0.8 ha vs 24.5 ha for home range in Chizé forest; Saïd & Servanty 2005). Many authors showed that certain portions within the home range are more frequently used than others (Adams &

Table 2. Estimates for the mixed linear models selected in Table 1 for the First-Passage Time (FPT) and for the log-transformed First-Passage Time ($\log(FPT/m^2)$ divided by the circle area of female roe deer paths in Chizé forest, with the female identity as random factor. Standard deviation of random factors for each model are: Female Identify SD = 0.852, Residual SD = 0.994, and: Female Identify SD = 0.517, Residual SD = 0.330, respectively.

Tested models	Response variable	Explanatory variables	Value	SE	DF	t	P
FPT	Radius + Circle class + Month	(Intercept)	+1.42	0.762	38	+1.864	0.070
		Radius	+0.08	0.010	38	+7.539	<0.001
		Circle class 2	-1.66	0.339	38	-4.895	<0.001
		Circle class 3	-2.24	0.444	38	-5.032	<0.001
		May	-0.42	0.622	38	-0.674	0.505
		August	+0.06	0.719	38	+0.081	0.936
		October	+0.24	0.784	38	+0.303	0.764
		November	+0.50	0.804	38	+0.621	0.539
		December	-1.67	0.732	38	-2.274	0.029
$\log(FPT/m^2)$	Circle class + Month	(Intercept)	-7.18	0.251	39	-28.626	<0.001
		Circle class 2	-0.46	0.111	39	-4.178	<0.001
		Circle class 3	-0.50	0.146	39	-3.418	0.002
		May	-0.37	0.238	39	-1.562	0.126
		August	+0.42	0.248	39	+1.706	0.096
		October	+0.15	0.279	39	+0.523	0.604
		November	+0.03	0.287	39	+0.121	0.905
		December	-0.78	0.259	39	-3.017	0.005

Davis 1967, Dixon & Chapman 1980, Springer 1982, MacDonald & Courtenay 1996). These areas of concentrated use by resident animals, loosely termed core areas, commonly include nest sites, daytime roost sites, refuges, and regions with the most dependable food sources (Burt 1943, Kaufmann 1962, Ford 1983).

Methods such as harmonic mean (Dixon & Chapman 1980) or bivariate models (Koeppl et al. 1975) were used to estimate core areas based on the cumulative proportion of an animal's location and the related increase of the area estimated by these locations within the total home range. We decided to use the FPT method, because it allows identifying smaller sectors where animals spend more time using ARS than does the core area method. Although the limited accuracy of the GPS collars did not allow us to explore nested levels of resource aggregation, our study highlights a patchy exploitation of their home range by the roe deer females. A large proportion of their activity is concentrated in restricted parts of their environment. In our study, we focused on the third scale of habitat selection defined by Johnson (1980; Fig. 9) but more accurate data are needed to highlight and define the finest scale (i.e. selection of food item inside the feeding site).

The modification of the original method in order to detect further ARS along the path allowed us to highlight a multi-patch use of the home range at a daily level in roe deer females for 20 out the 24 paths. One major methodological questions associated with the use of our modified version of the FPT is obviously when to stop running the iterative analysis, i.e. how many patches make biological sense or can truly be distinguished with some statistical power. We chose to rely on a very simple and repeatable methodological rule to set our limit: we stopped when the size of the ARS circles fell below the accuracy of the GPS measures (i.e. below 25 m). There certainly are other decision rules, for instance for animals showing a very high selection for one or two patches, and for which the addition of another three minute circle, although significant, may not make much biological sense. We never had to question ourselves about this on our roe deer data, probably because our decision rule fell nicely within the scales at which roe deer make decisions about patch choices. However, we encourage users of this modified method to adapt the decisions rules to their equipment but more so to the biology of their studied animals.

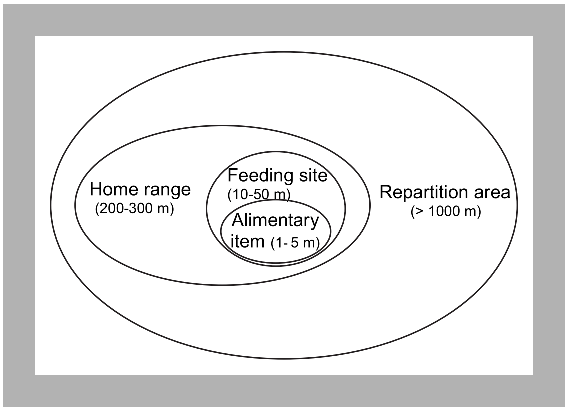

Figure 9. The four scales of habitat selection in the case of roe deer defined by Johnson (1980), with radius in metres. The first scale corresponds to the selection of the repartition area of the species; the second scale corresponds to the selection of the home range; the third scale corresponds to the selection of the feeding sites inside the home range; and the last scale corresponds to the selection of the alimentary items inside the feeding site.

In our study, we used the FPT value and the FPT by surface unit. The first one represents the time an individual stayed in the patch and gives us the time it spent foraging. The second one represents the exploitation effort of an individual in a patch. It indicates the intensity with which an individual foraged in the patch. We found a continuum in the FPT between the circle classes: animals spent more time in circles of first class than in circles of second and third classes. However, this result can be directly linked to the way our extension of the FPT method works. Indeed, as the method focuses on the ARS where the FPT is the maximum, the first detected ARS is systematically the one with the highest FPT, the second detected ARS is the one with the second highest FPT and so on. Nevertheless, the exploitation intensity ($\log(FPT/m^2)$) of the patch really differs between circle classes. The time spent in an ARS of a given radius is higher in circles of the first class than in circles of the two other classes. Thus, the detection order seems to reflect an order of preference in the use of patches within the home range, and roe deer should spend more time in the most valuable patch.

There could be another way to interpret differences between circle classes. They could reflect a spatial discrimination of different behaviours (e.g. resting and feeding activities) that imply different constraints and resources, or environmental features. In Fauchald & Tveraa (2003, 2006) and Pinaud & Weimerskirch (2005), studied paths were foraging trips. They performed the FPT analysis on the Antarctic petrel *Thalassoica antarctica* and the yellow-nosed albatross *Thalassarche carteri*, respectively, during the breeding period. In Pinaud & Weimerskirch (2007), the analysis was also performed on seven breeding species of Procellariforms. During the breeding period, the two species displayed a central-place forager behaviour (Ashmole 1971): they made a long foraging trip of several days after they left the colony, and then come back. Birds thus have to maximise their energy gain, spending most of their trip in the food patch so that their activity within the ARS is mainly related to foraging. In our study, like in the study of Frair et al. (2005), roe deer path did not seem to be typically displaying central-place foraging as starting point hours were chosen arbitrarily and the path remained all the day including feeding and resting activity for which roe deer look for different structures of vegetation (Mysterud & Øtsbye 1995). Frair et al. (2005) worked at a large temporal scale using elk paths taken over several months with a two hour inter-location interval. They used the FPT analysis to define three scales of movements (inter-patch relocations, foraging displacements and resting movements). In our study, we used daily paths, working at a finer temporal scale with a five minute inter-location interval. Performing the FPT analysis on paths with locations every five minutes gives us sharp information on the animal movement and allows us to highlight a succession of used patches at the scale of the day. These patches can also be characterised by activity data, as GPS collars can be used in combination with activity sensors (e.g. Adrados et al. 2003, Frair et al. 2005). The use of such tools to identify activity within FPT circles will provide means to assess whether animals display a multi-patch use of the environment because of the resource patch heterogeneity, versus a spatial discrimination between different behaviours (e.g. resting vs feeding sites).

The patch use behaviour reported in our study corresponds, in the case of a food search strategy, to the animal's perceptions of the resource aggregation, and it is probably related to the habitat heterogeneity. This habitat heterogeneity, natural or due to human disturbance, drives ecological processes (Fortin & Agrawal 2005). Understanding the link between these processes and the heterogeneity of the environment is a key question for management and landscape ecology (Wiens et al. 1993). Coupling a Geographic Information System with the FPT analysis would allow us to characterise areas of interest (e.g. ARS for feeding and resting site) in terms of environmental features (such as topography, vegetal cover, thermic cover and vegetation quality) according to animal activity. FPT analyses should offer a suitable tool to be incorporated in habitat selection analysis in order to improve identification of the environmental features that make a habitat attractive to animals. Fine approaches as FPT analysis enable us to highlight the response of species to habitat heterogeneity at very small scales. The study of this behavioural response allows for comprehensive assessment of the consequences of management decisions on population dynamics and then to orientate these decisions to improve the management of these populations and their habitats.

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