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PhD Thesis

Landscape openness effect on roe deer, *Capreolus capreolus*, behavior.

Analysis on activity level, movement rate and circadian rhythm across a landscape gradient.

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Index

Abstract

This PhD Thesis is focused on the analysis of activity and movement time budgets in an intensively monitored roe deer population in an agro-ecosystem of south-west France. In this study, we analyze the effect of landscape structure on animal behaviour by studying diurnal and nocturnal activity levels and movement rates and also observing the general pattern of circadian rhythm along a landscape gradient, from strict forest habitat to open agricultural plain. This study will provide advances in current understanding of the landscape openness effect on behaviour and moreover of activity rhythms and spatial ecology of the roe deer, the most numerous large wild herbivore in Europe.

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Introduction

1.4 Landscape fragmentation.

Behavioural and ecological analysis are the basis of the preservation of wildlife and biodiversity from the effects of habitat fragmentation. Know deeply the behaviour of the species and the biological responses to biotical and abiotical factors is indeed necessary to a correct conservation and management of the wildlife, especially in areas subjected to this process. Landscape fragmentation is often resulted from the conversion of natural woodland areas to agricultural crops and open meadows devoted to livestock grazing and therefore it often provoke an increase in disturbance due to associated human activity (Cole et al. 1997; Markovchick-Nicholls et al. 2008). The fragmentation, resulting in increasing local habitat heterogeneity, involves both absolute loss of primary habitats and the reduction in size and increasing isolation of remnant habitat patches (Fig.1) (Saunders et al. 1991; Andrèn 1994; Markovchick-Nicholls et al. 2008). An habitat patch is defined as a surface on the landscape differing in appearance from its surroundings. Areas of woodlands in an agricultural landscape are examples of patches within a landscape.

This cause a decreasing, or sometimes the total elimination, of interior habitats (closed, mostly forests) and an increasing of edge habitats (opened), (Fig.2). We could define edge habitats as outermost band surrounding a patch that has an environment significantly different from the interior of a patch (interior habitat).

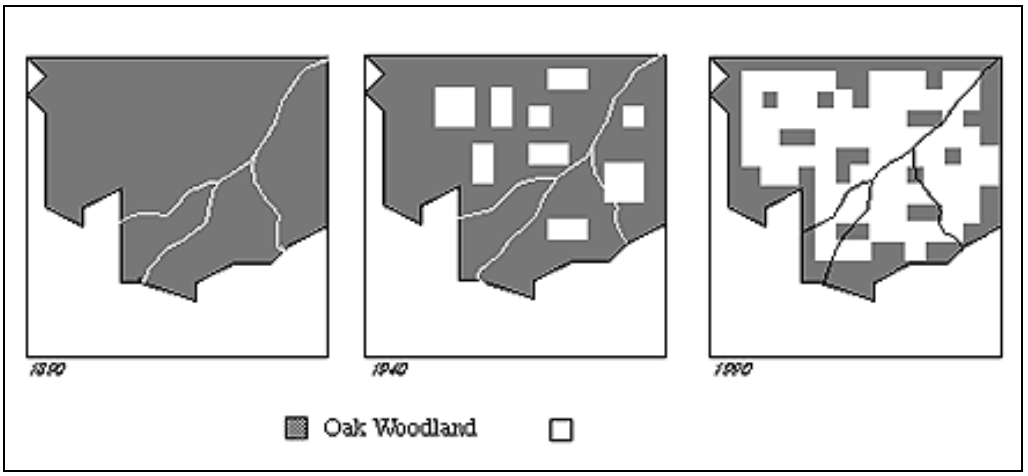
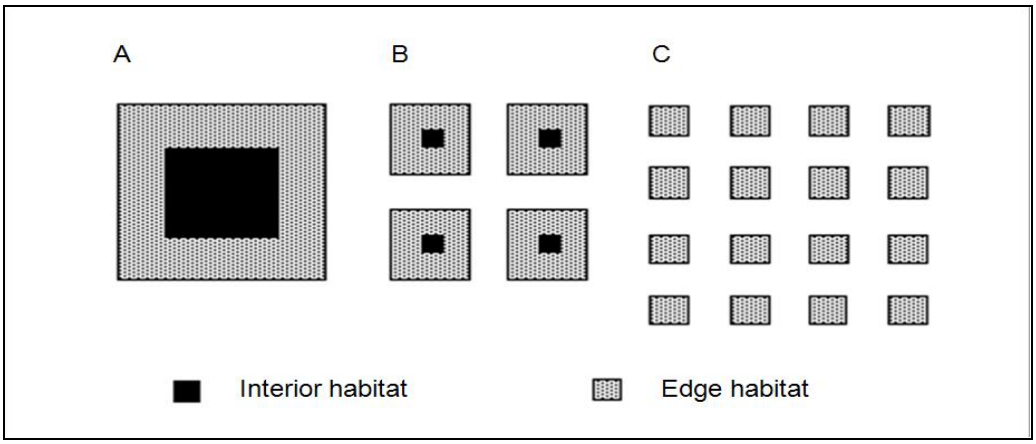


Figure1. Example of fragmentation process. Oak Woodland (in grey) showing continued habitat fragmentation over time (1890-1990) due to urbanization (in white) (Tietje and Berlund, 2000).



Fiugre2 A) Large patches provide interior habitat (in black). B) Fragmentation decreases the amount of interior habitat C) Further fragmentation increases edge habitat (in grey) at the expense of interior habitat. (Soule, 1991).

The dimension of the patches, resulted from the fragmentation process, is important indeed larger patches have more interior habitat, while smaller patches have less or no interior habitat (Fig.3).

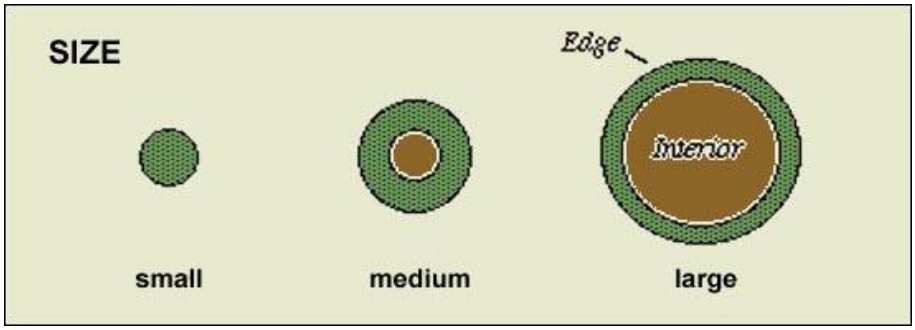


Figure 3. Patch size and dimension of edge and interior habitats (from Defenders of Wildlife, 2010).

The landscape fragmentation can potentially endanger species, populations, communities and hence entire ecosystems, resulting in biodiversity reduction (McKinney 2002; Marvier et al. 2004; Hansen et al. 2005; Olden 2006), indeed this process typically results in an increase in edge species, which are common across a landscape, and the loss of interior species, which are less common and often of conservation importance (Fig.4).

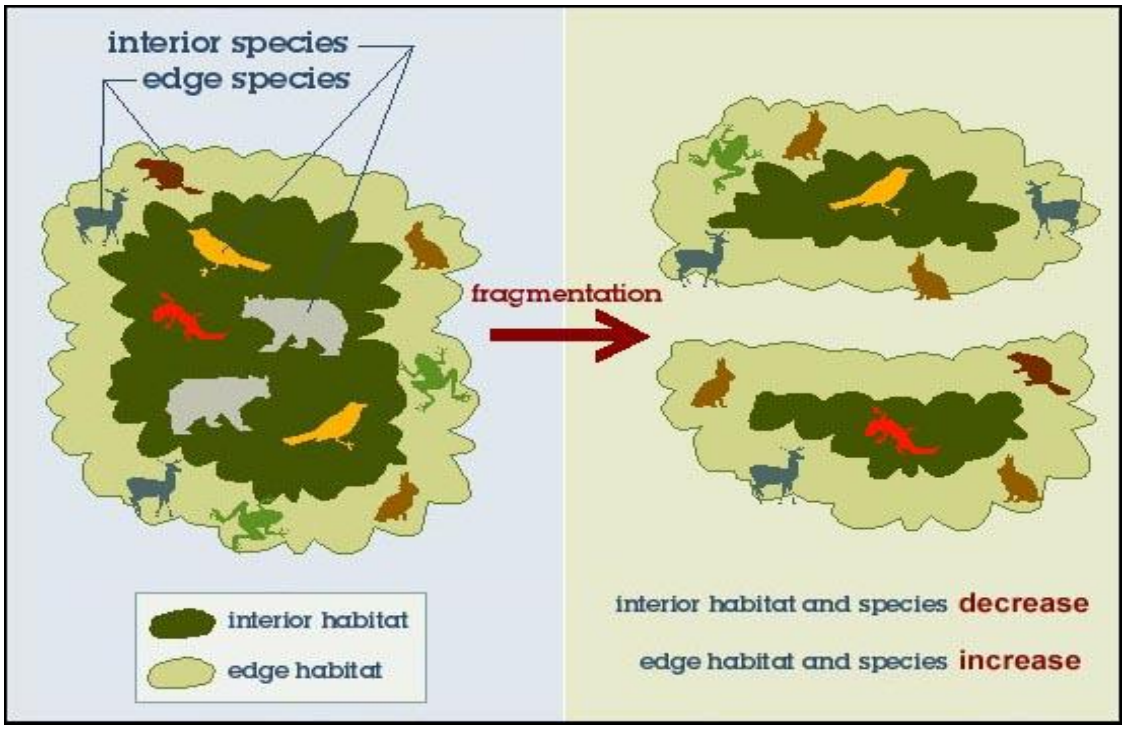


Figure 4. Effect of the landscape fragmentation on biodiversity. Interior species decrease while edge species increase, (from Defenders of Wildlife, 2010).

Moreover populations are typically more stable and sustainable and less susceptible to local extinction in large patches than small patches. A large patch often contains greater habitat and species diversity than a small patch. More importantly, large patches are more likely to maintain native species in good quality habitat, whether or not greater diversity naturally occurs or not.

For example, landscapes less than 1 hectare may support only a certain suite of species. The area may not be large enough to include a diversity of habitat patches or meet the home-range requirements of certain types of wildlife. Small, less mobile animals may be able to survive because their home-range requirements are small, however, survival of medium-sized animals is compromised over time and large animals can be rare or transient. Furthermore when the natural habitat is fragmented in isolate small areas, resident wildlife populations also become isolated and can suffer of inbreeding and restricted gene flow processes that could lead to local extinction.

Many animals require a variety of habitat patches, in close proximity, to meet their daily and seasonal needs. A deer may bed down beneath the canopy of the forest, seek cover from predators within the thickets of riparian willows, drink from a nearby stream, and leave the shelter of the trees to forage in adjacent grassland. This variety of vegetation types forms a patch-work quilt across the landscape. The size, vegetation diversity, and interconnectedness of patches that make up the landscape, determine the population size and kinds of animals found within it.

Landscape fragmentation could provoke modifications of animal behavior in terms of activity rhythm, movements and habitat use (Kie et al. 2005; Brinkman 2005; Banks et al. 2007; Rhoads et al. 2010) often associated to negative effects on animal survival. However not all the species are negatively influenced by the habitat fragmentation and the urbanization. There are species called synanthropic that live near, and benefit from, an association with humans and the somewhat artificial habitats that humans create around them. The category of synanthrope includes a large number of what humans regard as pest species and it does not include domesticated animals. Examples of synanthropic species are rodents, sparrows, pigeons and other animals. These species

received benefits, especially in terms of feeding availability, that could allow them to maximize their fitness (reproductive success) in fragmented landscape and agricultural or suburban areas.

These species are habitat generalists that may colonize and live in secondary matrix habitat because of their behavioral plasticity (Komers 1997) and ecological flexibility (Marvier et al. 2004; Olden 2006; Devictor et al. 2008; Markovchick-Nicholls et al. 2008; Crowder and Snyder 2010). Flexibility and plasticity are behavioral modifications that we can observe at individual or population level (Table 1), that allow individuals to better live in their environment. Behavioral flexibility is showed within individuals in response to environmental factors (as observed in primates, Anthes et al. 2010), while behavioral plasticity is showed among individuals or population and is the result of the interaction between genetic characteristics and the environment (as predator–induced phenotypic plasticity observed and studied in aquatic mammals, Anthes et al. 2010). A key aspect of this behavioral modifications in response to the fragmentation process is the ability to adapt activity patterns in response both to the modification of landscape structure, notably the distribution and size of secure and feeding patches (Jhonson et al. 2001; Godvik et al. 2009; Owen-Smith et al 2010), and to the increase of human disturbances (Rhoads et al. 2010).

Table 1. Overview of hierarchical levels, types, underlying mechanisms and examples of behavioral variability. Flexibility in the generic sense increases from top to bottom, (from Anthes et al. 2010).

<table>
<tr><th>Level of variability</th><th>Type of variability</th><th>Main mechanisms</th><th>Example phenomena</th></tr>
<tr><td>Among lineages</td><td>Adaptation</td><td rowspan="2">Genetic</td><td>Adaptive radiations
Lineage-specific traits
Species-specific traits</td></tr>
<tr><td>Among species</td><td>Canalisation</td><td>Species-specific traits</td></tr>
<tr><td>Among populations</td><td rowspan="2">PLASTICITY</td><td rowspan="2">Gene-environment interactions

(epi-)genetic</td><td>Local adaptation</td></tr>
<tr><td>Among individuals</td><td>Polymorphism
Personality
Predator-induced plasticity
Parental effects</td></tr>
<tr><td>Within individuals</td><td>FLEXIBILITY</td><td>Environmental</td><td>Social flexibility
Situation-dependency
(Social) Learning</td></tr>
</table>

The roe deer, *Capreolus capreolus*, that were considered as a species of closed, predominantly wooded, landscapes (Putman 1988), is one of the species that has been able to colonize a wide variety of habitats, including plantation forest, mixed forest/ farmland mosaics (Linnell et al. 1998*a*), open agricultural landscapes (Danilkin and Hewison 1996; Hewison et al. 2001) and even suburban zones (Linnell et al. 1998*a*), thanks to its behavioral plasticity and flexibility, even if it avoid areas associated with human activity and, hence, disturbance (Hewison et al. 2001; Coulon et al. 2008). So the roe deer could be an useful example of a species that has developed a behavioral adaptation in response to habitat fragmentation, especially in agricultural landscapes. Moreover the roe deer is a species wide distributed in Europe and this makes of this species a key subject to study how the landscape fragmentation could affect the animal behavior.

Very few studies deal with the effect of landscape structure on activity pattern in wildlife (Felix et al. 2007; Godvik et al. 2009; Rhoads et al. 2010), likely because of the difficulties to monitor a large number of individuals across a wide range of landscape structure. Today, the use of GPS monitoring coupled with activity captors allow to overcome this difficulty (Löettker et al. 2009; Owen-Smith et al 2010; Tomkiewicz et al. 2010).

1.5 Behavioural aspects.

1.2.5 Activity pattern.

The study of animal activity patterns is relatively an old theme of behavioural research. Of more recent interest are considerations of ecological factors affecting activity at both individual and population level. Several endogenous and exogenous factors influence the activity patterns of roe deer: anatomic structure of the digestive organs, seasonal physiological change (especially

associated with mating, gestation and lactation) and changes in quality and quantity of food (Jeppensen, 1989).

The phylogenetic affiliations seems to have the greater effect on activity time indeed the feeding style is strongly related to phylogeny and is a relatively stable evolutionary trade (Pérez-Barberíìa and Gordon, 1999). The effect of feeding type seems to be highly significant on activity levels (Mysterud, 1998) because is the major determinant of rumination time; and hence time left for the other activities seems to depend from the food quality (Cederlund 1989). However precise studies of foraging bouts are difficult to be carry on, indeed active bouts are easy to define, but an active animal can undertake a series of foraging bouts interspersed with periods of play, alertness or other non feeding behaviour (Gillingham et al. 1997).

The food intake is a central aspect to understand a herbivore's ecological relationship because acquisition of food is ultimately related to survival and reproductive output. The animals tries to maximize the energy intake and their behaviour can be a sensitive indicator of forage quality and quantity (Owen-Smith 1979). Most optimal foraging models are based on energetic considerations or constraints, assuming that behaviour should be directed primarily toward net energy gain. Foraging constraints mostly control the time budgets of ungulates (Cederlund at al. 1989; Beier and McCullough 1990) and seems that food quality, rather than abundance, affects the time spend ruminating (Cederlund et al. 1989; Owen-Smith 1994). Changes in patterns of feeding and ruminating are expected to reflect variation in the quantity and quality of available vegetation (Owen-Smith 1979). Foraging strategies vary with sex, age and physiological demand, and depend on environmental conditions and seasonality changing food resources (Bunnell and Ghillingham 1985).

The food quality affects the time spend ruminating: there is a decrease of foraging time in response to high quality food. There are difference among age-sex classes within each year time budgets. Nevertheless, the time budget in general shows similar daily activity profiles and response in terms of time allocation to variation in environmental conditions. In ungulates activity seems to be

synchronized (especially foraging and resting) (Moncorps et al. 1997) and become more polymodal in favorable range condition dependent from season with marked alternating rhythm of foraging and resting (Georgii 1981; Moncorps et al., 1997).

Foraging strategies are further constrained by such factors as the effects of dietary quality on digestion, the time available for feed and aspects of food availability relative to spatial and temporal heterogeneity in the environment (Roese et al. 1991). Moreover it is documented that activity time of ruminants changes across the year (Godvik et al. 2009; Pepin et al. 2009; Owen-Smith et al 2010; Rhoads et al. 2010) as a consequence of the annual changes in the reproductive status of individuals (Moncorps et al. 1997; Pepin et al. 2009; Rhoads et al. 2010) and is influenced by a number of factors, like temperature (Beier and McCullough 1990; Schmitz 1991; Demarchi and Bunnell 1995), daily light conditions (Beier and McCullough 1990) and predators and humans disturbance (Singer et al. 1991).

1.2.6 Circadian rhythm.

The activity pattern of deer shows peaks at dawn and dusk with in some cases higher activity at dusk (Pipia et al. 2008). These peaks of activity are typical of cervids (Cederlund 1981; Georgii 1981; Eberhardt at al. 1984; Cederlund 1989) indeed resting periods occur around midday and the two main foraging periods occur after dawn and before dusk for many ungulates (Georgii 1981; Roby and Thing 1985; Cederlund at al. 1989). The temporal organization of activity patterns is peculiar to each species, being modulated by both internal (physiological state) and external (environmental conditions) factors (Ratikainen et al. 2007). Animal life is indeed controlled by the "ciradian" rhythm. This biological rhythm has been defined as a 24-hour patterns in activity caused by endogenously controlled physical parameters (Aschoff 1966) that are influenced by daily/light conditions (Reppert and Weaver 2002; Dibner et al. 2010) and temperature (Dibner et al. 2010). All

the organisms show daily cycles of biological activities (Bell-Pedersen et al. 2005). The temporal coordination of internal biological processes, both among these processes and with external environmental cycles, is crucial for animal survival (Bell-Pedersen et al. 2005). The circadian rhythm has periodical change during the year (circannual) because of environmental stimuli defined "zeitgebers" (Aschof, 1966). Diurnal variation in light intensity is generally the most consistent and reliable of these environmental factors in mammals (Bell-Pedersen et al. 2005; Dibner et al. 2010). Factor such as seasonal variation in daylight and temperature or annual changes in the reproductive states of the individuals limit the value of time-budget comparison between seasons (Moncorps et al. 1997). It appears that climatological factors play a role in the behaviour of the roe deer. Rainfall during the dawn interval may significantly reduce deer activity while the wind may disrupt their scent-localizing abilities important in predator avoidance. Qualitative analysis of winter data indicate a negative correlation which may be related to thermoregulation. In the study of Turner (1980), if the environmental factors are included in the variance model, wind speed is not a significant factor and air temperature remain a significant negative covariable on activity level.

1.2.7 Seasonal variation in activity level and movement rate.

The data on daily active time relative to total time shows a marked annual cycle, from 40% in winter to 50% in summer (Jeppensen 1989). These daily and annual rhythms result from changes in activity bouts: minimum median active and native bout lengths were recorded during summer and maximum values during winter. In winter deer show in general a decline in activity level (Cederlund, 1981) and food intake (Ellenberg, 1978; Drozdz, 1979). The study of Jeppensen (1989) underline that in January and February the proportion of time active is generally around 40% in both sexes. After that the time active increase, but in April the activity level of males is higher than of females while in June the proportion of active time of females is higher than that of males

(Jeppensen 1989). Deer generally show lower activity during the pre-fawn phase and higher activity during the rut (Turner 1980). From September onwards the activity time in males is higher than in females (Jeppensen 1989).

Several endogenous and exogenous factors influence the activity patterns of roe deer as seasonal physiological changes, especially associated with mating gestation and lactation (Jeppensen 1989). In general gestating females energy intake increase compared to non-gestating females from 4-2 weeks prior to parturition (Ellenberg 1978; Jeppensen 1989). In the study of Jeppensen (1989), from May until September median active-inactive cycles were 27-34 minutes shorter in adult (gestating/lactating) females than in yearling females. The females of mouflon, *Ovis orientalis misimon*, decrease daily activity budget of 3-5 consecutive days in lambing period. The decrease of daily activity during lambing have a extent depth and duration and regular shape (Langbein et al. 1998). In many ungulate species the females withdraw from the herd some days prior to lambing (Bon et al. 1995). The higher level of locomotors activity during parturition, described for various ungulates in captivity, is probably the results of failure of the pregnant females to hide from the herd (Langbein at al. 1998).

Lactation may increase rumination in response to increased energetic demands and risk of predation. Direct observation on bighorn ewes, *Ovis canadensis*, shows that lactating ewes ruminated faster and have less inter-individual variability in rumination speed suggestion an energetic constraint (Blanchard 2005). Reducing the time spent chewing while grazing could allow increases in bite or vigilance rates (Blanchard 2005). The daily energetic requirements of a female ungulates may increase of 150% during peak lactation compared to maintenance. In red deer *Cervus elaphus* (Clutton-Brock at al. 1982) and bison *Bison bison* (Komers et al. 1993) lactating female spend more time foraging. Lactating females could increase food intake through a faster bit rate, as reported for bighorn sheep *Ovis canadensis* (Ruckstuhl and Festa-Bianchet 1998) or could be more selective while feeding changing the habitat selection as reporting for red deer *Cervus elaphus*

(Clutton-Brock at al. 1982). However several studies found no differences in the foraging behavior of female ungulates according to reproductive status (Pérez-barberìa and Nores 1996; Toïgo 1999).

Optimal resource utilisation theory suggests that male and female behaviour differs during mating season in a species in which access to females is disputed by males. This theory affirms that female reproductive success is determined by access to food and male reproductive success by access to mate. Red deer, *Cervus elaphus*, behaviour during the rut support this prediction. Stags spend less than 5% of the day grazing and ruminating whereas hinds spend more than 40% of their time in these activity (Clutton-Brock et al. 1982). In the moose, *Alces alces*, bulls spend less than 10% of the time feeding during rut while cows spend 50% of the time or more. During the rut the males are more active than females (Pipia et al. 2008). Indeed in this period median duration of active and inactive bouts in males is at the minimum and this cause a maximum in the number of active bouts per 24 hour (Jeppensen 1989). Bucks would be expected to spend high effort in territorial defence during rut. They spend a greater proportion of time in movement (walking and running) and in orientation (unaffected by social interaction) (Flint and Krzwiński 1997). Young males occupy large home ranges encompassing the territories of several older males. They are harassed by territorial males and as consequence they move (walking and run) more than territorial males (Bramley 1970). These findings are predictable on the basis of optimal resource utilization and in accord with the observation of Cederlund (1981) on males that recorded decrease in time spend feeding and an increase of movements (walking and running) during rut. Data on forest roe deer in eastern Poland also seems to support the optimal resource utilisation theory. During rut, does spend a greater proportion of time feeding and selecting food than bucks. Males spend more time moving (walking/running) and orientation (Flint and Krzywinski 1997).

Although there are other studies that contradicts this theory suggesting that bucks and does spend equal proportion of time in the principal activity recorded (including social interaction). During rut Turner (1979) has found no behavioural difference between sexes in the time spending orienting, searching for food items, walking, feeding and social interaction.

Probably the disagreements between the study of Flint and Krzwiński (1997) and of Turner (1979) reflects differences in behaviour between open agricultural and forest habitats. Difference in behaviour have been indeed described between roe deer inhabiting open fields and forests (Bresiński 1982; Jeppesen 1990) with the former adapting their daily feeding cycle to avoid men working in the fields, forming permanent social group and using larger home ranges. Feeding behaviour may also be affected by a greater availability of forage in cultivated areas (Turner 1979).

1.2.8 The landscape openness effect on roe deer behaviour.

The roe deer show behavioral changes in habitat use, activity patterns and movements (Kie et al. 2002; Kie et al. 2005; Felix et al. 2007; Rhoads et al. 2010) in response to environmental heterogeneity. The landscape has an effect also on social and spatial structure (Hewison et al. 1998; Lamberti et al. 2006; Pays et al. 2007; Ramanzin et al. 2007): open field roe deer use larger home ranges (Zejda and Bauerova 1990; Hewison et al. 1998; Cargnelutti et al. 2002) and may form larger social groups (Hewison et al. 1998, 2001; Pays et al. 2007) respect to deer inhabiting closed wooded landscapes. Deer tend to restrain themselves to small areas despite limited biomass of natural forage in woodlots (Mysterud 1999).

Behavioral difference due to groups dimension have been underlined by Turner (1987). During fall and winter larger groups spent more time feeding and moving and less time orienting and walking. Single animals spent significantly more time walking but les moving and they were less often seen lying. In general animals in the woodlot sector were less often seen lying in spring and summer, than animal in the field sector. In this period field animals spent less time feeding and moving and more time orienting and in social behavior. Although significant differences were found only in animals sampled within groups. Most difference in time-budget behavior between landscape were

found in fall and winter, when differences in environmental conditions, especially the amount of cover, were greatest (Turner 1987).

Also the study of Rouleau et al. (2002) on white-tailed deer underlined behavioral differences between deer that inhabiting forest and agricultural landscape. In this study the biomass of preferred forage was six time greater in the forest. Rural deer intensified the use of cultivate fields at night and ate a greater variety of plants than forest deer. It seemed that agricultural deer were adapting to the rarity of natural forage by exploiting agricultural crops (Rouleau et al. 2002). They moved at a greater speed than forest deer between June and August, likely covering longer distances is search of scarce preferred natural forage. Indeed, moving speed diverged the most between landscapes from 12:00 to 18:00, at a time when rural deer generally occupied wood-lots. Activity rate tended to be higher for rural than forest deer between July and September (Rouleau et al. 2002). Have been estimated that deer spend 95% of their activity time feeding (Beier and McCullough 1990) so it is possible to think that in this case rural deer devoted more time feeding then forest deer because of the poorer forage in rural areas (Rouleau et al. 2002).

However in general the availability and quality of food, eaten by roe deer, is higher in open areas than in wooded landscape. Cultivated plants represent a rich and abundant source of nutrients during summer (Nixon et al. 1991; Lesage et al. 2000). Population density and landscape composition affect the degree to which deer feed on cultivated plants (Nixon et al. 1991). In the study carried on by Zejda et al. (1985), in a thinly wooded area with intensive agricultural exploitation, during the growing season, rural deer had access to a smaller biomass of natural forage than forest deer, but forage availability reached the same magnitude in both landscape when adding cultivated plants. At the end of the growing season, rural deer had access to forage biomass also four time greater than that in the forest landscape, but had to move often back and forth between fields and woodlots. Field roe deer had a mainly easily digestible diet and the cycle of feeding and digesting was more rapid (Zejda et al. 1985). In the study of Zejda et al. (1985) field roe deer was active five to seven time daily in daylight time, from October to April. They was always active at

dawn and dusk so during the rest of the day they was active three to five times. Field roe deer had more periods of feeding and they relatively spent less time ruminating. In April the data showed a larger number of activity periods. The length of one bout of feeding was roughly 15 min. Males were more active than females during the daylight hours of the winter period (Zejda et al. 1985).

Human disturbance is a typically daily event in field biotopes. The disturbing effect increases the metabolism. In agricultural areas, deer may be obliged to modify their behavior in response to human disturbance associated to agricultural works. Predators and human disturbance can modify the seasonal activity patterns of animals (Singer et al. 1991; Millspaugh et al. 2000; Schneider and Wasel 2000; Vistnes and Nellemann 2001; Frid and Dill 2002; De Boer et al. 2004; Mysterud et al. 2004; Skarin et al. 2010) and in particular diurnal human disturbance can lead to greater nocturnal activity in ungulates (Georgii 1981; Langbein et al. 1997; Naugle et al. 1997; Kamler et al. 2007, Hayes and Krausman 1993; Ratikainen et al. 2007) and to a greater use of disturbed site during the night. Indeed, in many rural populations, deer spend the day in woodlots and use cultivated fields for feeding during the night (Montgomery 1963; Nixon et al. 1991). As a result of these regular forays between woodlots and fields, the movement speed and activity rate of deer living in agro-ecosystems is generally higher than that of forest populations (Rouleau et al. 2002). In some case disturbance synchronizes the activity rhythm of the whole grouping for a certain time. In the study of Langbein et al., (1997) on mouflon sheep, there was three main activity periods: dawn, dusk and hours around midnight. About 50% of daily activity happened during the night. Probably the high level of night–time activity was the results of frequent anthropogenic disturbance, especially hunting. Through the season there was a stronger temporal shift for the beginning of the activity in morning than for the end of the activity in the evening (Langbein et al. 1997).

The field roe deer behavior could be considered sign of gradual adaptation to life in open countryside characterized by an intensive agriculture. Kaluzinski (1974) considered field and forest deer to be separate ecotypes, but seems that differences in behavioral patterns between forest and field deer are the result of a phenotypic response to contrasting environmental conditions (Komers

1997), rather than genetic (Andersen et al. 1998). Hence, although some behavioral differences between roe deer populations inhabiting open field and forest have been previously documented the extent of behavioral plasticity in relation to landscape openness within a single population has not yet been investigated.

1.6 Focus questions and objectives of this thesis.

1.3. 4 How to asses animal activity/inactivity by the motion sensor? A new tool to study animal behavior through GPS collars.

The first objective of our study is to built a model able to discriminate between active and inactive behavior that we can apply in our successive analysis on roe deer behavioral differences between landscape sectors.

Usually the GPS collars are used to study animal behavior in term of spatial utilization as home range definition and movements. Know activity-inactivity on long scale time intervals is an important behavioral parameter that could allow researchers to deeper investigate animal behavior and circadian rhythms.

Roe deer show highly mixed behavior in short time intervals (as in our case of 5 minute time intervals), with active interspersed with short inactive events. We aimed to find a model to predict activity and inactivity considering that animals behavior is a mixture of active and inactive behaviors within a given short time interval. This approach is innovative as all the other models predicting activity-inactivity are built on direct observations in which the animals are purely active or inactive.

We wanted to determine what level of activity (proportion of time active) we were able to discriminate per time interval and identify the best discriminant model predicting activity-inactivity in wild roe deer.

1.3. 5 What we means as behavioral plasticity in a synanthropic species responding to landscape fragmentation process? The roe deer as example.

The overall aim of our study is to investigate the effect of habitat fragmentation expressed by landscape openness on roe deer behavior in terms of activity and movement. Habitat fragmentation is a ongoing and widespread process at a worldwide level, that can potentially endanger species. However each species react differently to this process. There are species that are able to modify their behavior to overcome this process and adapting their life to human dominated landscapes. The behavioral plasticity is the key to survive to habitat alteration and fragmentation caused by conversion of natural habitat to agricultural or suburban landscapes.

We used the roe deer as example of behavioral plasticity in response to landscape openness. We analyzed the variation of activity and movement values, across a landscape gradient from forest to agroecosystem, during the different seasons of the year.

We expected I. that activity level and movement rate increase with increasing landscape openness due to the movements between the woodlots, used as shelter during daytime, and the open agricultural areas, exploited for foraging during the night; II. that activity level and movement rate is higher during night respect to daytime over all the year, as animals tend to become more nocturnal in human-dominated landscapes, especially in the more open areas and during the hunting season and III. that behavioral pattern, and so activity and movement levels, changes across the year

following physiological and reproductive constrains determined by the roe deer biological cycle (see article 2 in results session).

1.3.6 How the landscape affect circadian rhythm in roe deer? Application of GPS data on activity level and movement (speed) to investigate the effect of landscape fragmentation on circadian rhythm.

The circadian rhythm is manifested by all the organisms and is typical of each species. Cervids are characterised by a circadian rhythm that shows two daily peaks of activity (at dawn and dusk). We have defined the roe deer as a species having a plastic behavior that allow him to adapt to fragmented landscape. To complete our investigation on landscape openness effect on roe deer behavior, we observed how the behavioral plasticity is manifested on the 24h behavioral pattern. We studied the circadian rhythm in terms of activity level and movement rate (speed) of male and females roe deer, in the different biological seasons across the year. To know how behavioral plasticity is manifested on 24h could be interesting also to discriminate between fixed and flexible traits of the circadian rhythm.

We expected I. that peaks of activity at dawn and dusk are manifested by deer of both the sexes and in both the landscape sectors because they are typical traits of cervids circadian rhythm; II. that peaks at sunrise and sunset are more marked in roe deer inhabiting open sectors; and III. that deer are more active and move more during nighttime in open areas, because they spend day in woodlots to avoid human disturbance (see article 3 in results session).

2

Materials and methods

2.1 The roe deer.

2.1.7 Habitat use.

The roe deer, *Capreolus capreolus* (Linneaus, 1758), is one of the most intensively studied mammal species (Andersen et al. 1998). It occurs in almost all of the natural habitats found in Europe (Fig.5), including deciduous, coniferous and Mediterranean forest, scrublands, moorlands and marshes, with the exception of the high alpine areas over the treeline and the most open grasslands where it is rarely present.

This species is tolerant to climatic extremes, indeed is present from the hot and dry Mediterranean forests to the cold boreal forest. It has also occupied most man-made habitats and on a fine scale habitat selection it generally prefer early successional habitat over climax habitats. An key aspect of roe deer habitat selection is the presence of escape cover from predators and humans. The roe deer could survive also in small patches of woodland or shrubs and even tall grass thanks of its small body size (Linnell et al. 1998*a*).

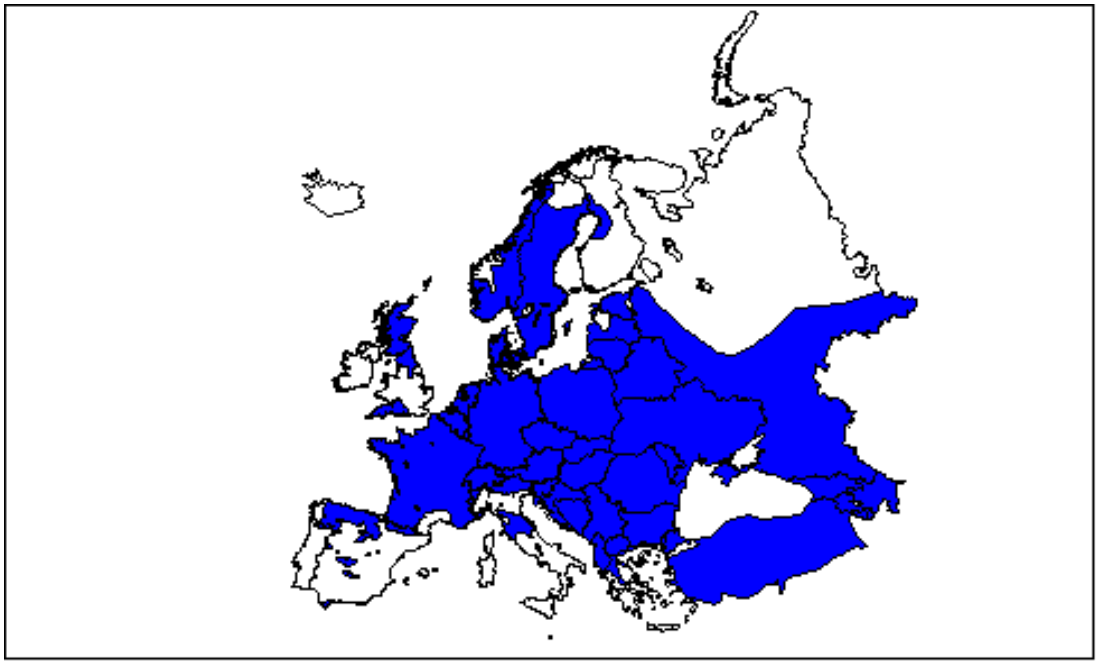


Figure 5. Roe deer paleoartic distribution (in blu) of European roe deer (from Varuzza et al., 2005). In eastern Europe the roe deer is present in Russia until the Ural mountains and in Turkey it is found in scattered populations (Andersen at al. 1998)

2.1.8 *Morphology.*

The roe deer (Fig.6) is a small deer of a light and slender build with relatively short and broad head, fairly large ears, a long neck, relatively short trunk and long limbs.

The weight of the roe deer could vary from 18 to 49 kg (Lister et al. 1998) and the mean height at shoulder is around 60-70 cm. Males are on average larger than females, but the degree of sexual dimorphism (Fig. 6) is relatively low <10% (Harris and Yalden 2008). The winter pelage is grey, with dense pithy hairs pale at the base, darkening towards the tip and with a pale subterminal band, giving an agouti-banding pattern to the pelt. The summer coat is shorter, with thinner hairs which are a bright orange-brown (Fig. 6) lacking the agouti-banding, and the skin around the forehead and the neck is thickened in males. There is a black band around the muzzle, interrupted by white narial spot below the rhinarium, and a white chin. Fawns are spotted with white upper the dorsal midline

(Lister et al. 1998). The permanent dental formula is typical of cervids, with no upper canine: i 0/3, c 0/1, p3/3, m3/3, total 32 (Lister et al. 1998).

Figure 6. Male and female European roe deer, Capreolus capreolus.

The adult males (≥ 3 years of age) have hard and stiff three-tined antlers, with the first bifurcation some distance from the relatively large burr and marked with parallel ridges which sport varied development of drop-shaped excrescences or tubercules especially on the burr (Lister et al. 1998). The roe deer antlers are short, usually <30cm and placed more or less vertical in a lyre shape (Harris and Yalden 2008). Male roe deer are exceptional among medium-sized to large cervids in that they cast their antlers in autumn (October-December) and start to grow a new set immediately during winter (Fig. 7 and 8), whereas in all other boreal cervids, antlers grow in spring and summer (Sempéré et al.1998). When the antlers begin to grow, they are covered in a thin layer of velvet fur which disappears later on after the hair's blood supply is lost (Fig. 9). Males may speed up this process by rubbing their antlers on trees.

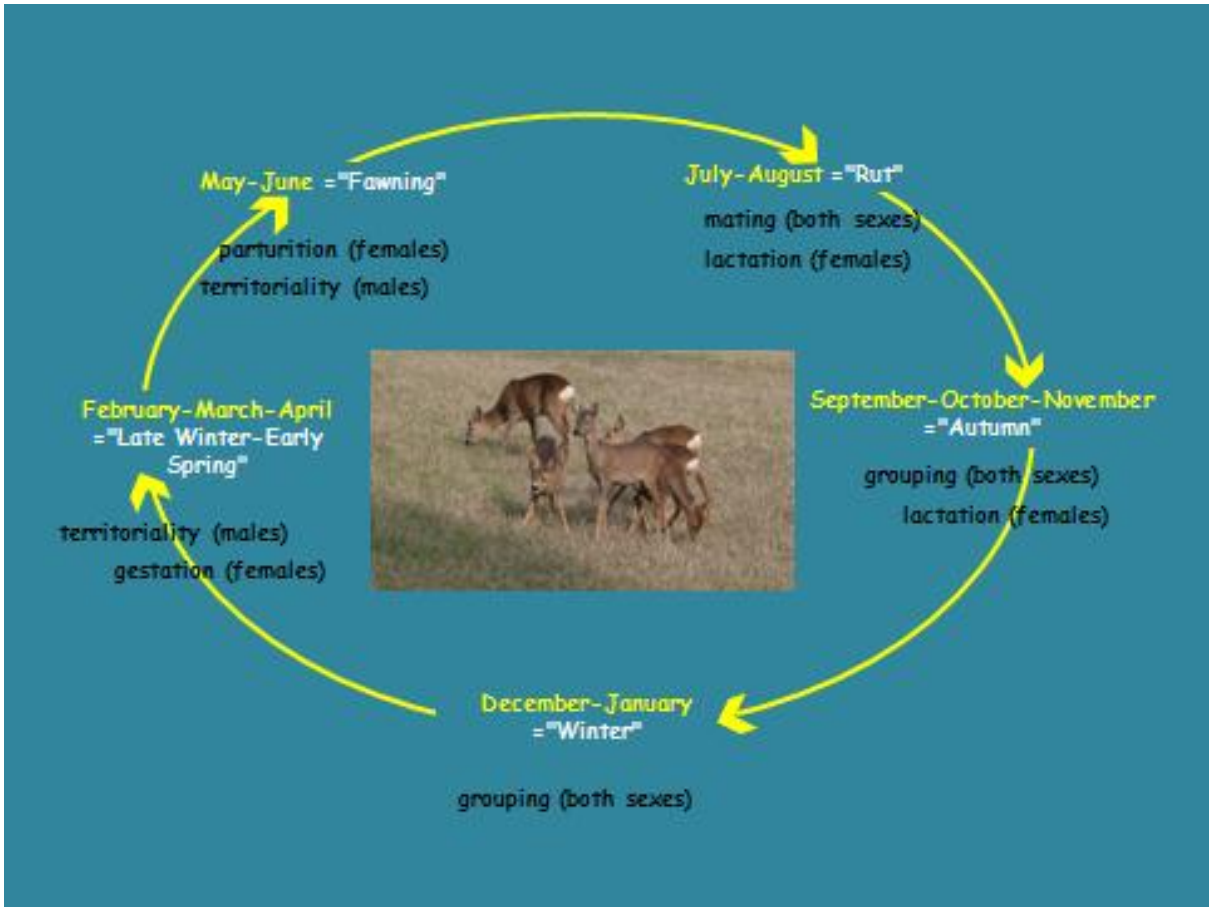


Figure 7. Roe deer biological cycle.

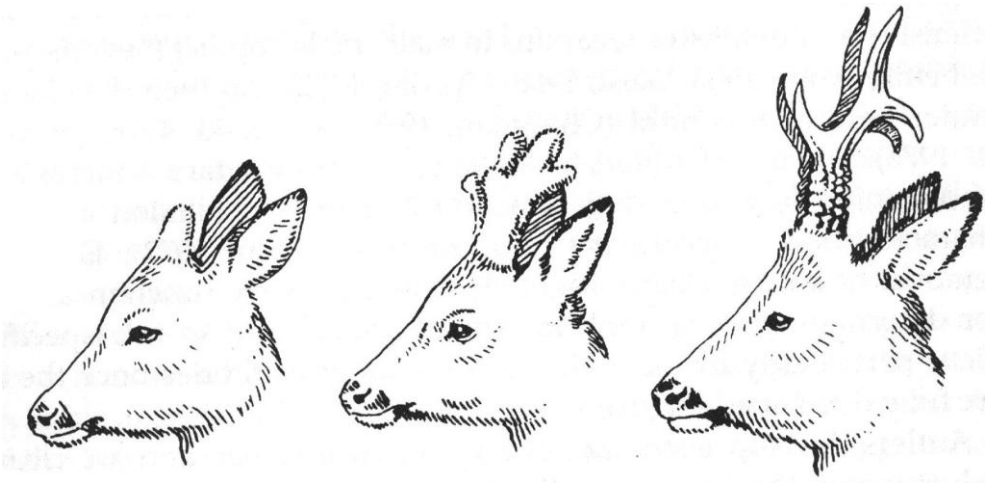


Figure 8. Antlers development in the roe deer (from Danilkin and Hewison 1996 modified). In the first (December-January) and second stage (February-March) antlers are covered by velvet. In the last stage are represented the antlers cleaned from velvet (from May onward).

Figure 9. Male roe deer that is cleaning antlers from the velvet.

The testosterone play an important role in controlling the antler cycle. The antlers have an rapid rate of growth that is maximum (mean 3 mm per day) in December-January. In February the antlers are subject to a mineralisation phase (Sempéré et al.1998) followed by the cleaning from the velvet (Fig.9) that occur in late winter-early spring (March-April). The development of the antlers (Fig.8) in male fawns start at 3-4 months when the pedicles appear and is followed by the growth of small button antlers of a few cm that may be shed around January. The first true antlers develop during late winter and early-spring in yearlings (≤ 1 year of age) as simple spikes up to 10 cm long, while subadult animals (≤ 2 years of age) has two-tined antlers (Harris and Yalden 2008).

2.1.9 Feeding behavior.

The roe deer are generalist herbivores which are capable of feed on a very wide range of plants (Table 2) including mosses, ferns, conifers, deciduous trees and shrubs, forbs, cultivated plants, grasses and sedges, and others taxonomic groups as fungi and lichens (Duncan et al. 1998).

Table 2. (Duncan et al. 1998 in Andersen at al. 1998)

Trees and shrubs	**Forbs**	**Other**
Carpinus betulus	*Chamaenerion angustifolium*	Grasses
Hedera helix	*Medicago sp.*	Fungi
Rubus sp.	*Silene sp.*	Acorns
Calluna vulgaris	*Rumex sp.*	Chestnuts
Vaccinium sp.	*Petroselinum hortense*	
Populus sp.		
Quercus sp.		
Pinus sylvestris		
Cornus sp.		
Acer pseudoplatanus		
Fraxinus excelsior	**Crops**	
Abies alba	Beetroot (leaves and rhizomes)	
Arbutus unedo	Wheat (seeds)	
Cistus salcifolius	Barley (seeds)	
Phillyrea angustifolia	Rice (seeds)	
Picea excelsia	Peas (seeds)	
Ilex aquifolium	Maize (seeds)	
Arctostaphylos uva-ursi	Oilseed rape (*Brassica*, leaves)	
Betula sp.	Potatoes (leaves)	
Rosa sp.	Honey locust (*Gleditsia*, seeds)	
Lonicera peryclymenum		
Viburnum opulus		

They use all of the plant tissues, from roots to flowers of hundreds of different vegetal species (Linnell et al. 1998*a*) and sometimes they use also woody parts of the plants. The most important part of the diet is made of forbs, woody dicotyledons and seeds. The green leaves of woody plants usually dominate the diet, and make up 40-84% of the rumen contents, except in farmland where they are replaced by seeds, roots and fruits. Forbs make up 10-42% of the diet and the graminoids

around 10% (Duncan et al. 1998). Roe deer feed on plants from the ground level up to 120cm, but they prefer to feed at intermediate level (around 75cm from the ground). The great variety in the roe deer diet shows that their feeding behaviour is highly flexible, and suggest that they can adapt their preferences/avoidances to the changes in the quality of the food available. The deer are therefore generalist but they can also be highly selective. This allows roe to harvest a diet which is of better nutritional quality than if they feed randomly on the available vegetation. Roe deer prefer plants with high soluble carbohydrate contents, especially in summer and autumn (Duncan et al. 1998) when they need more energy (reproduction and post reproduction phases). Feeding behaviour of roe deer is adapted to seasonal change of available food resources, through modifications in metabolic rate, which decline in winter (Drozdz et al. 1975; Weiner 1977). Roe deer usually feeds along edges of open areas (Tufto et al. 1996; Saïd and Servanty 2005; Van Moorter et al. 2009).

2.1.10 Reproductive behavior.

Males

Roe deer reproductive strategy is based on male territoriality, a high degree of spatial stability among adults and a weakly polygynous mating system (Hewison et al. 1998). Breeding males aggressively defend territories which overlap with or in some cases encompass one or more female home ranges (Bramley 1970). Male access to mate may be therefore dependent on the exclusion of other bucks from his territory to monopolize the female. Male territoriality is a seasonal phenomenon. Territory are established in spring and maintained over the rutting season in July and August. Territorial behaviour start often before that the antlers are cleaned and at the end of April generally all the territory holders have established their territory (Andersen at al. 1998). The territories of adult bucks during mating season have been shown to not overlap other territories at low population density, but with increasing bucks density the degree of overlap between adjacent ranges increase. However, also at high density, the core area of the territories appear to be exclusive

and of relatively constant size. Territorial defence consist in exclusion of intruders from a specific space using threat, self-adverstisment and fighting. Real combats are rare in roe deer, indeed aggressive behaviour is often ritualised in vocal and physical displays as chases and retreats, rubbing on trees and scraping activity (Hewison et al. 1998). Often adult deer (more of three years of age) are territory holder while subadult males (two years old) rarely (Andersen at al. 1998). Does may range over the territories of several bucks and the boundaries of their ranges are defined independently from those of males. Female are not territorial and at high density they can show completely range overlap (Hewison et al. 1998). Some females undergo excursions during the rut, possibly to mate with un-related males (Richard et al. 2007).

Females

The roe deer is the only member of the Artiodactyla known to use embryonic diapause as a reproductive strategy. Females roe deer show indeed a delayed implantation of five months and only one ovulation each year. For five months between the rut (July-August) and the early January the blastocysts lie dormant in the uterus without implantation and embryonic development (Andersen et al. 1998). This reproductive strategy has favourable ecological consequences leading the costly phases of the reproductive cycles of females to occur in late spring and summer where there is an higher food quality and availability (Linnell et al. 1998*b*). Most cervids of the temperate zone mating in autumn and giving birth in spring while the roe deer mates in summer and give birth in spring (Fig. 7).

Timing birth generally coincide with the period of maximal plant production, so the greater availability of good quality food can allows the lactating females to supply the energy coast of lactation. The timing of birth varies trough the latitudinal gradient and in relation to environmental characteristics of the habitats. In France birth take place in May and June. The parturitions are synchronised to provide mothers anti-predator benefits. Births are normally distributed around the mean with 80% of births fallowing within 20-30 days (Linnell et al. 1998*b*).

2.1.11Post-natal behaviour.

In the first period after the birth mothers leave their offspring hidden, but unattended, while foraging and resting at a distance. The hiding behaviour has been developed as anti predatory strategy, indeed the distance between the fawns hidden and the mother can avoid the localisation of the offspring by predators. In this way lactating does are able to forage at a distance from their hider neonates which allow them to exploit resources in habitat that carry higher risk of predation. After the end of the rut (August), hiding behaviour ends and roe deer fawns are continually associated with the doe, usually remaining within 50-100 meters (Linnell et al. 1998*b*). In April all fawns cease their association with the mother and become very mobile, making excursion out of the maternal home range. This is the beginning of the dispersal phase where the yearlings could move away from the natal home range to settlement in a new area that does not overlap that mother's home range (Linnell et al. 1998*b*). However not all the young animals disperse (Harris and Yalden 2008). The reason of dispersal behaviour are still uncertain. Some of the hypothesis are that deer disperse to avoid inbreeding and to decrease the competition for mates (in males) and for environmental resources (especially in females). Important here to say that both sexes disperse (unusual is large herbivores). It seems that the females show an "ideal-free" distribution between habitats of different nutritional quality. Dispersing females seems to distribute themselves optimally with regard to resource availability. Instead in males, adult male aggression and competition for breeding opportunities is probably the major factor determining dispersion (Linnell et al. 1998*b*, Harris and Yalden 2008).

2.1.12Social organization.

The annual social cycle of adult roe deer consist of a more or less solitary stage during summer, when females are isolated and raising fawns and while adult males are defending mating territories and a gregarious phase during late autumn and winter, where individuals of both sexes form fluid groups, whose composition changes rapidly, although membership is drawn from a limited pool of individuals (Linnell et al. 1998*b*). The roe deer is a relatively solitary animal, generally living alone or in very small groups of two-three. Small groups are often composed of an adult female with her fawns, with the possible presence of an adult male. These family units are generally stable and form the core unit of the social organisation system in roe deer (Hewison et al. 1998). Males are more solitary than females especially during the mating season when they are strict territorial. In early summer also pregnant females seek isolation to giving birth (Hewison et al. 1998). Europe, winter groups may contain more than 50 individuals whereas in mixed landscape of small fields and woodlands the groups vary from 5 to 10 individuals. Grouping may be explained in part by being an anti-predatory strategy that allows animals to decrease individual vigilance and maximise foraging time (Linnell et al. 1998*a*).

2.2 Study site and population.

This study was carried out in a mixed landscape, where human-mediated activity is widely distributed as a result of agricultural (Hewison et al. 2007) and sylvicultural practices. The study area (Fig. 10) is located in the south-west of the France (Comminges region of the Midi-Pyrénées, Aurignac canton, 43°13'N, 0°52'E) and it extends over 7500 ha (ca.). It is a hilly zone, rising to a maximum of 380 m a.s.l., with an oceanic climate (average annual temperature 11-12°C and 800

mm precipitation, mainly rain). The area is characterized by a mixed landscape of cultivated fields (about 33% of the total area), hedges (7% of the total area), meadows (34% of the total area) and small woodland patches (14% of the area with an average size of 3 ha), and a central forest of 672 ha (7% of the area) (Hewison et al. 2009). Within the study site, we identified three landscape units (Fig. 1) of contrasting habitat structure in terms of woodland extent and the relative proportions of meadows and cultivated fields. The open field sector covers 65% of the total area (1217 ha) and is composed of 12.5% woodland, 6.3% hedgerows, 33.8% meadows and 42.7% cultivated fields. The intermediate sector covers 21% of the total area (397 ha) and is composed of 35% woodland, 2.1% hedgerows, 38.5% meadows and 21.6% cultivated fields. The forest sector covers 14% of the total area (259 ha) and is composed totally of forest (Gottardi et al. submitted).

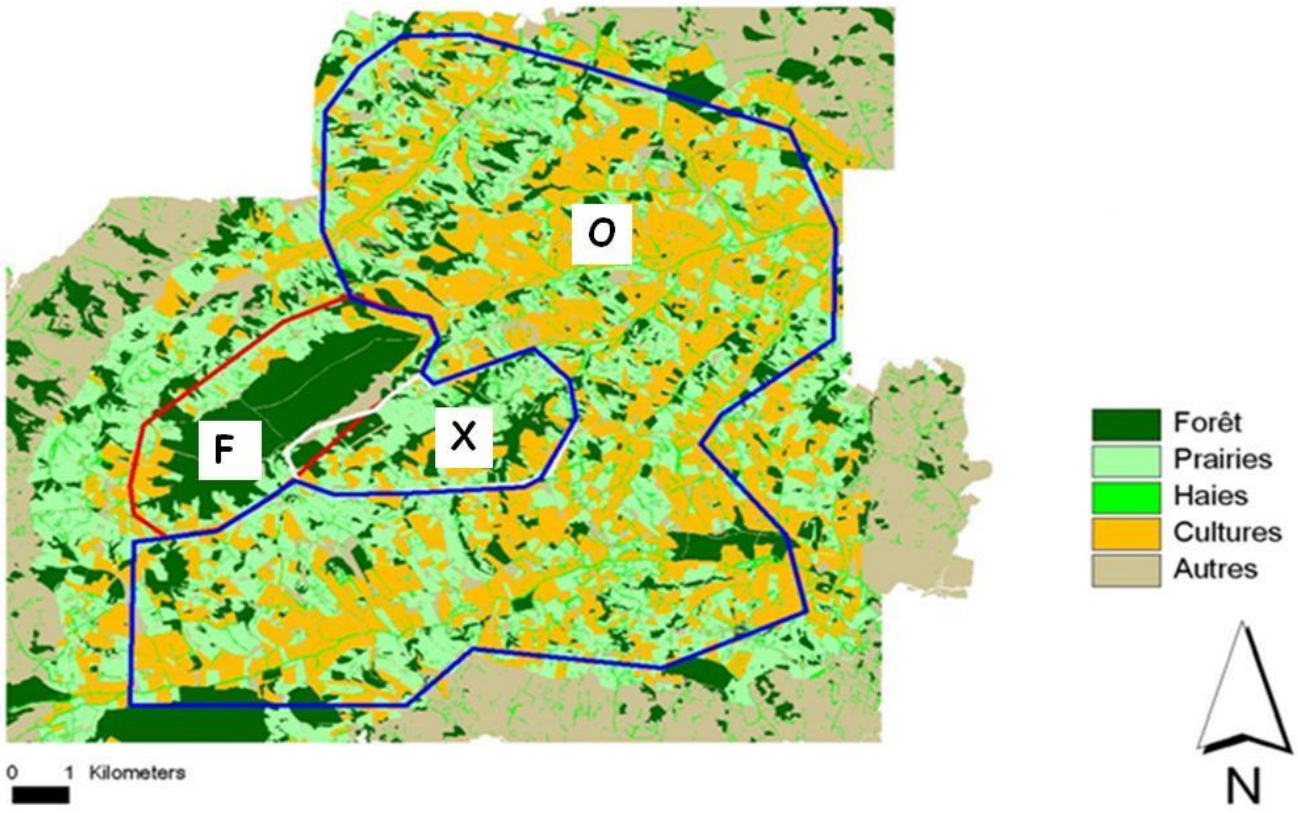
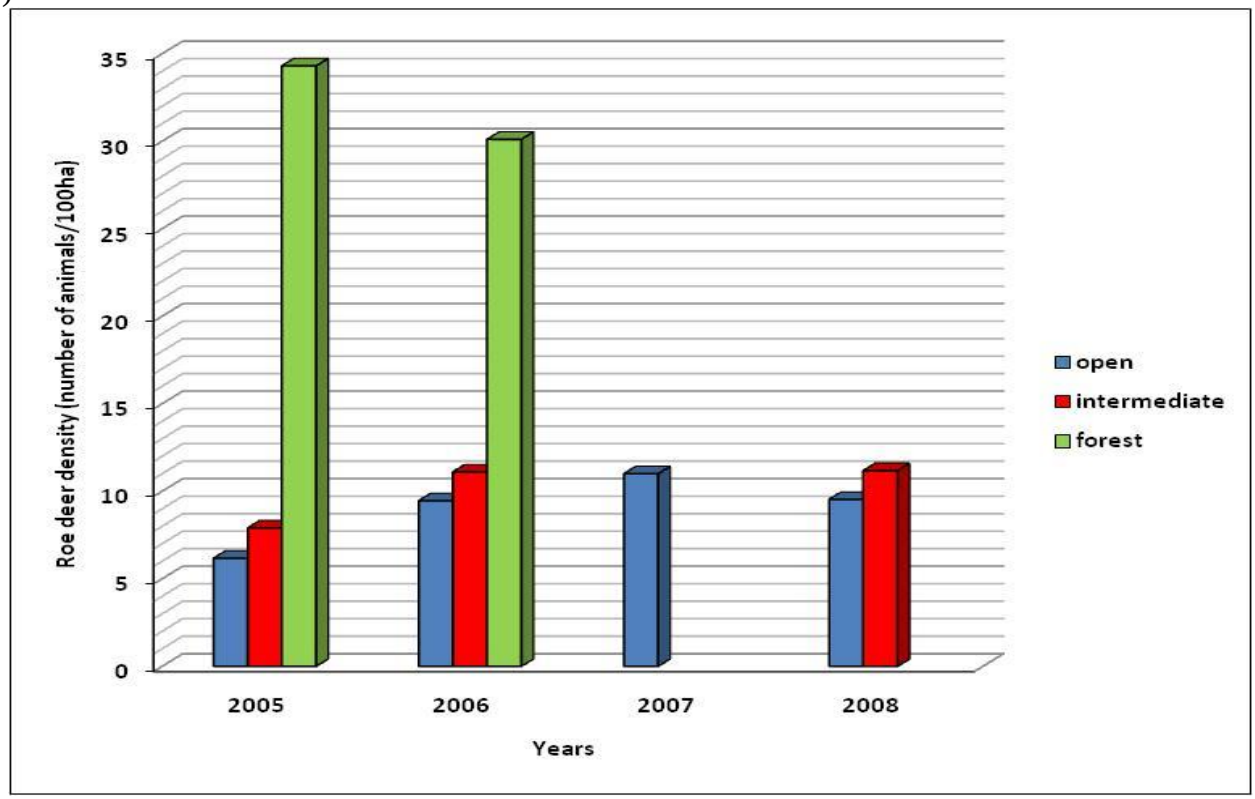


Figure10. Map (year 2007) of the study site (Aurignac, France, 43°13'N, 0°52'E) with the tree sectors classified on the basis of landscape openness parameters. F=forest (259 ha= 65% of the total area), X=intermediate sector (397 ha = 21% of the total area) and O=open fields sector (1217 ha= 14% of the total area).

The natural vegetation of the area is classified as a southwest European lowland-colline downy oak forest (Bohn et al. 2004). The open fields are cultivated mostly with wheat and barley (51%) and in minor percentage with sunflower, maize, soya, sorghum and rape (Hewison et al. 2009). Hedges contain numerous ligneous shrubs and trees (as *Quercus sp*., *Lonicera sp*., *Cornus sp*., *Prunus spinosa*, etc), grasses, sedge and forbs. The meadows have a variable species composition, with most fields dominated by *Festuca sp.*, *Dactylis glomerata* or *Agrostis capilaris* and contain also different leguminous forbs. The woodland patches are dominated by oak *Quercus sp*., often associated with hornbeam *Carpinus betulus*, while in the central forest are also present Douglas-fir *Pseudotsuga menziesii* and pine *Pinus sp*.. The understorey is dominated by brambles *Rubus sp*., butcher's broom *Ruscus aculeatus*, ivy *Hedera helix* and common honeysuckle *Lonicera peryclimenum* (Gottardi et al. submitted).

Roe deer density is not overall equal in the study site, indeed the deer density is remarkably higher in the forest respect to the intermediate and open landscapes. Deer density was estimated at around 32.20 deer/100 ha in the central forest (Fig. 11*a*) and totally 9.47 deer/100 ha in the mixed agricultural landscape of cultivated fields, hedges, meadows and woodland patches (88% of the total surface of the area). In particular in the open landscape sector deer density was estimated at 9.04 deer/100 ha and in the intermediate sector at 10.06 deer/100 ha (Fig. 11*a*). The annual estimations of population abundance indicated a relatively stable population if we consider the abundance index (total number of animal observed/km of survey) from 2005 onward (Fig. 11*b*). The censuses were carried out by standardized car transects during winter (counts of all deer seen along a 42 km circuit of the study site, repeated at dawn and dusk 6-10 times yr^{-1} between February and March). The roe deer population was hunted on a regular basis during autumn and winter (from September to January), by drive hunts with dogs and the bucks were stalked during summer (from June to August) (Hewison et al. 2009).

a)



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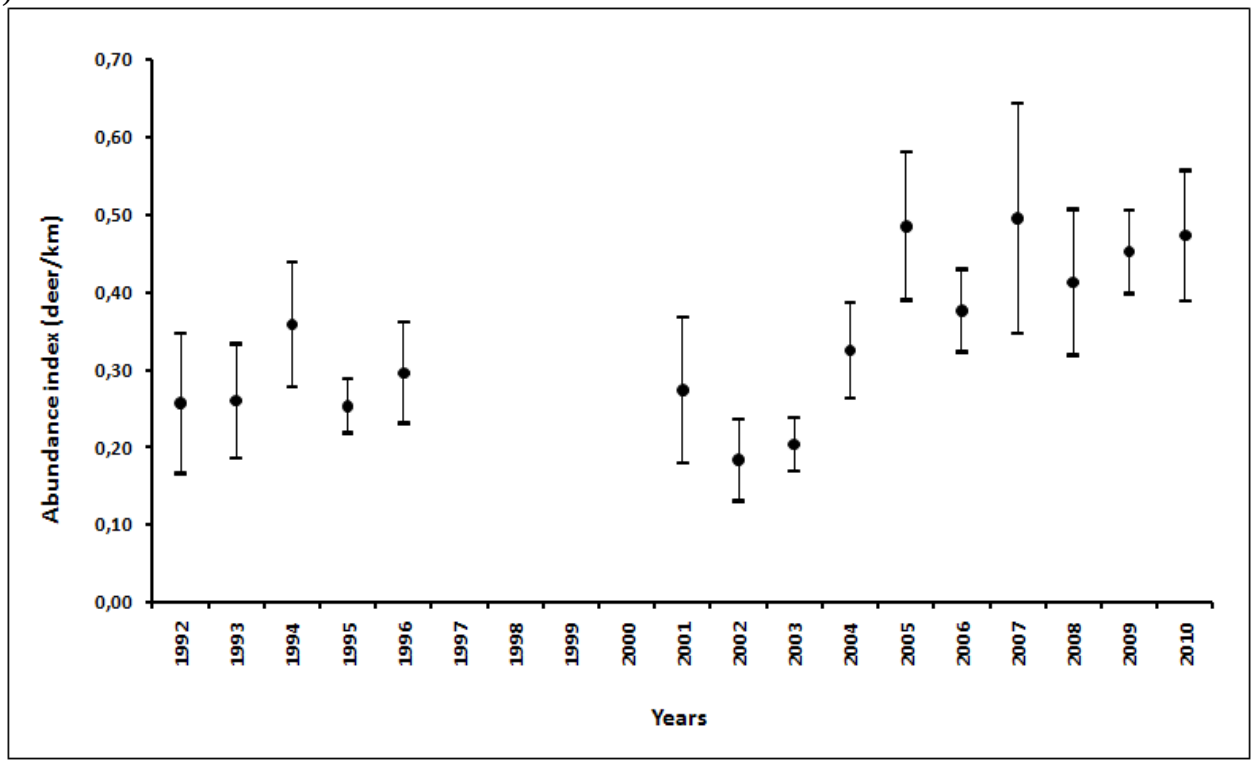


Figure 11. Estimation on roe deer population density in the study site. a) Roe deer density during the years of study (2005-2008) in the tree landscape sectors (forest, intermediate and open). b) Abundance index (number of roe deer/km of survey) from 1992 to 2010 on the whole study area. Data from 1997 to 2000 are not available.

This study was based on continuous GPS monitoring data of animals inhabiting the study area. The animals were caught and equipped with GPS collars every year during winter (December-February). Each capture area was placed in order to adequately sample across the gradient of landscape openness in the study site. Animals were caught using large-scale drives of between 30 and 100 beaters and up to 4 km of long-nets (Hewison et al. 2009). Tooth wear was used to assess age (Hewison et al. 1999) in three classes: juveniles (less than one year-old), yearlings (between one and two years-old) and adults (two years-old or more). The whole data set available was composed of 146 wild animals monitored between 2003 and 2008 (Appendix 1).

2.3 Technical informations

2.3.1 Equipment.

We used Lotek 3300 for medium-size mammals (Lotek Engineering, Inc., Newmarket, ON, Canada). The automated recording of animal behaviour offers several advantages over manual observation: measurements on more animals, for greater periods of time and less bias due to human error (Champion et al., 1997). The collars are able to provide data of activity-inactivity data through a position sensor and position (localisation by the satellites). The collar sensors provided three activity variables recorded every five minutes, a count of vertical collar movements (Y), a count of horizontal movements (X) and the proportion of time the Y sensor was in an extreme position (HD). We have used this variables to determine activity state of animals through a disciminant model (see section "The model to predict activity" below).

The 3300 collars have 12 GPS channels and an advertised precision of 35 m. Each successful fix is provided with associate information, including the date, the time, the altitude, the elapsed time

taken for the fix (max. 160 sec), the PDOP (proportional dilution of precision), the number of satellites and the fix status. The number of satellites (SATS) contacted during an attempted fix ranged between 3 and 8 (median=4) in the forest (coniferous and broad-leaved) and between 3 and 11 (median=7) in open areas. The value of PDOP is defined for each fix and describes the spatial configuration of the satellites at the moment the fix is taken (Trimble 1998). The interaction (SATS x HAB) between the number of satellites (SATS) and the habitat-period category (HAB) and the interaction ($PDOP_{res}$ x HAB) between the residual PDOP and the HAB are significant. This signify that location error varied in relation to the number of satellites contacted and with increasing residual PDOP value but in a different way in the different habitats and seasons (Cargnelutti et al., 2007). In the coniferous forest there is an higher error for a given number of satellites contacted than in the open area. Location error increase more rapidly with increasing residual PDOP for winter compared with autumn in open areas. Location error varies widely and is habitat-dependent, with the best results in open habitat and much poorer ones in forests, particularly coniferous-dominated habitats. Although localization error is correlated with both number of satellites and residual PDOP value, these parameters are poor predictors of fix quality as location error is highly variable (Cargnelutti et al., 2007). The variability of the precision could affect the movement data indeed movement/not movement is calculated started from fix errors (see the section "Statistical analysis" below and article 1 in results section). Whit high fix error an animal may be registered as moving in a single time interval while in reality he is not moving (this may be the case of the interval registered as moving but not active (see article 1 in results section).

The values of localization must be corrected (LA3L and LONL3) considering the planar visualization, the spatial analysis indeed are realized on planar maps but the fixes are identified on the globe (curve surface). The data are also corrected with a value of (LA3L and LO3C) that express the correct configuration of the satellite in relation of the passage time on the point in which the animal is located. Is a value taken by a fixed station that collect a exact fix each second. This value reduces the error of localizations. In the dataset compare also the DOPC value that join to the

PDOP value the correction done by the detection station of INRA center of Toulouse and the DELTA value that represent the correction in meters between the registered localization and the correct localization calculated through the data's corrections.

Fix status combines information on whether the fix is 2-dimensional (2D; fix based on 3 satellites only) or 3-dimensional (3D; fix based on more than 3 satellites) with an open numeric scale starting from F0 that may indicate the fix quality. We consider four categories of fix status: 2DFix-F0, 2DFx-Fn, 3DFx-F0 and 3DFx-Fn (where $n \geq 1$). Accuracy varies widely between the four categories with a median error of 36.6 m for 2DFix-F0, 20.8 m for 2DFx-Fn, 23.2m for 3DFx-F0 and 7.9m for 3DFx-Fn. There is a marked habitat related difference in fix precision. Fix location are more accurate in open areas with a median error of 7.0 m, followed by broad-leaved forest with a median error of 22.8 m and finally coniferous forest with a median error of 29.3 m (Cargnelutti et al., 2007). Indeed the open habitat is characterised by a greater proportion of the most accurate fix (type 3DFx-Fn). In addition, in broad-leaved forest there are relatively more 3DFx-Fn then in coniferous forest where there are more No Fixes and 2DFix-F0 (Cargnelutti et al., 2007). So in forest sector the incorrect classification of movement/not movement time intervals may be greater (see article 1 in results section).

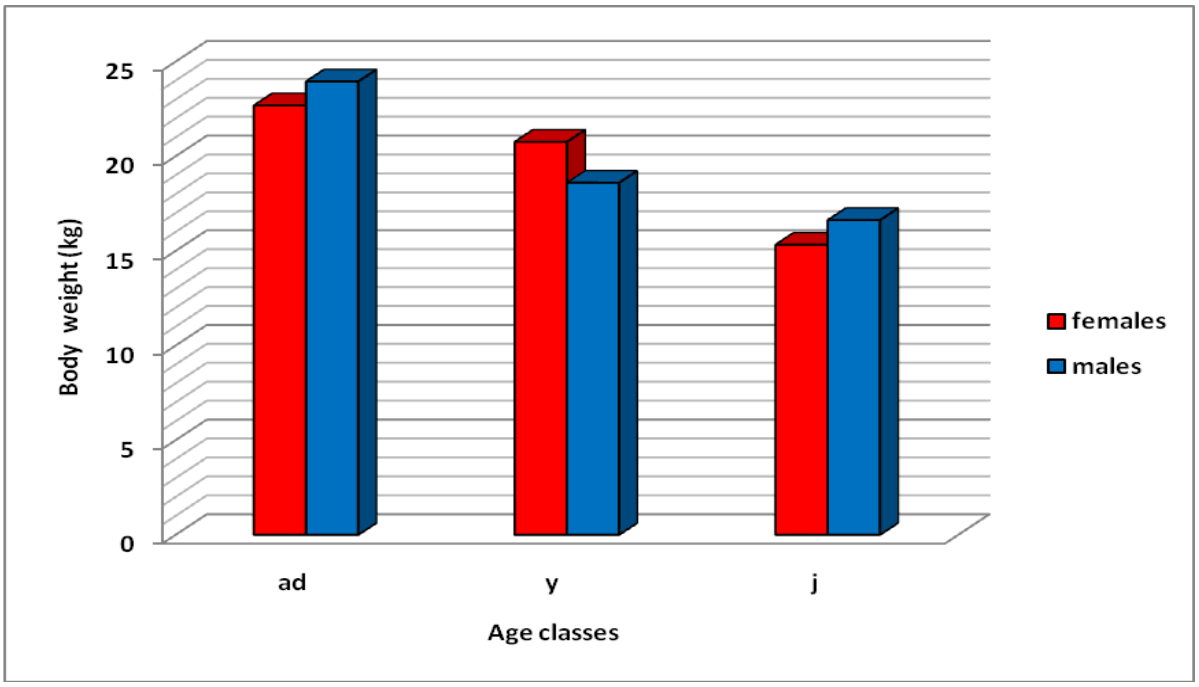
The collars are placed in order that the front side of the battery block (with Lotek stamp) faces the breast. This procedure is recommended in the Lotek manual (Lotek Wireless INC. 2002), although the reverse recommendation appears in the subsequent edition (Lotek Wireless INC. 2003). The placement of the collar should affect the HD captor values which express the percent time the head is in the down position when the Lotek stamp faces the muzzle, and the percent time with head held high when Lotek faces the breast. In our study we assume that the presence of the collar does not affect the activity of the collared animals (Hulbert et al., 1998). The 3300 collars that we use weigh 385g (Morellet et al. 2009) and the mean weight of roe deer in our study site is 22.68 kg for adult females, 23.95 kg for adult males, 20.76 kg for yearling females, 18.60 kg for yearling males and and around 16 kg for juveniles (Table 3 and Figure 12*a*). The average body weight seems to be

lower in the forest respect to the others landscape sectors (Figure 12*b*) in accord to the study of Hewison et al. 2009. Indeed roe deer body mass seems to increase along a gradient of habitat openness, with the heaviest deer occurring in the most open landscape, likely because cultivated crops provide high quality diet supplements (Hewison et al. 2009).

Table 3. Roe deer mean weights (kg) and percentages of equipment weight (GPS collar) as a proportion of animals body weight. Deer mean weights has been calculated using individual weight values in Appendix 1 (dataset 2003-2008). Data are presented divided for sex (females and males) and age: ad =adult (>2years of age), y =yearling (>1 and<2 years of age) and j=juvenile (<1yearsof age). The table shows the mean values of animal weight in the different landscape sectors (open, intermediate and forest). In the "whole study area" section are presented total mean values on all the study site, the mean weight of adults added to yearlings (total ad+y) and the mean weight values calculated on the studied animals (studied ad+y; Id a and b in Appendix1).

		Weight (kg)						**% collar weight/body mass**					
		females			**males**			**females**			**males**		
		ad	**y**	**j**	**ad**	**y**	**j**	**ad**	**y**	**j**	**ad**	**y**	**j**
Landscape sectors	**Forest**	21,16	19,33	13,55	23,18	17,80	15,16	1,82	2,01	2,94	1,67	2,16	2,58
	Intermediate	23,24	20,70	15,67	26,00	na	17,21	1,67	17,79	2,47	1,49	na	2,24
	Open	22,98	21,84	16,34	23,87	19,80	17,65	1,69	1,78	2,38	1,63	1,95	2,20
Whole study area	**Tot**	22,68	20,76	15,32	23,95	18,60	16,62	1,71	1,87	2,58	1,62	2,08	2,35
	studied ad+y	22,12		/	22,81		/	1,75		/	1,72		/

a)



b)

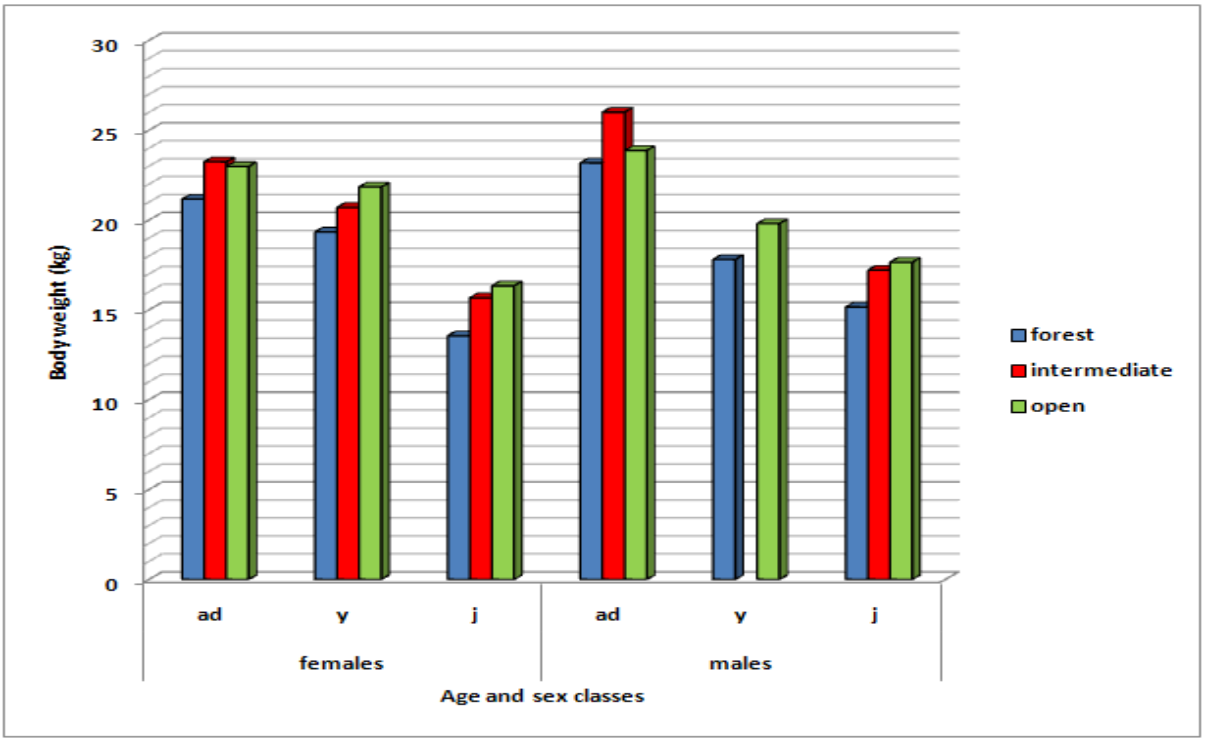


Figure 12. Roe deer body weights. Mean values of roe deer body weight (kg) in our study site (dataset 2003-2008, table 1). Age classes: ad =adult (>2years of age), y =yearling (>1 and<2 years of age) and j=juvenile (<1yearsof age). a) Between sexes comparison of body weight in the different age classes. b) Roe deer body weight in the different landscape sectors (forest, intermediate and open). The simple size is different between sex, age and landscape classes: in particular the body weight of yearling is not available for males and correspond to the value of only one individual for females in the intermediate sector.

Some studies have reported behavioural changes following the attachment of equipment at 5% of the body mass (Blanc and Brelerut, 1996; Rutter et al., 1997). In our population the mean percentage of collar weight on the body mass is always lower than 3% (see Table 3) in all the sex and age classes and in particular lower than 2% (respectively 1.75% for females and 1. 72% for males) in individuals used for the statistical analysis (Table 3). However, it is unlikely that device weight alone as a proportion of body mass (Kenward, 1987) explains the behavioural changes. Rather the method of attachment, distribution of device weight and visual impact on their associates may determine how an individual responds to the collar presence (Hulbert et al., 1998).

The study of Morellet et al. (2009) show that there is a capture effect on ranging behaviour and activity in the roe deer in the first week after release. This effect is provoked by the stress that animals suffer during capture and handling operations. Roe deer show a strategy consisting of seeking a refuge and waiting, with displacement towards a refuge and a reduction in activity level. Immediately after the capture, roe deer have been observed to be located further from the centre of their home range that normal. This abnormal displacement is more pronounced among yearlings that among fawns and adults (Morellet et al. 2009) because yearlings are generally mobile (using a larger daily and seasonal range) while adult roe deer have a high degree of spatial stability (Hewison et al. 1998). The capture effect seems to be different also between sexes in terms of spatial displacement, with males responding more than females. Females likely return quickly to their normal home range (Morellet et al. 2009) to reestablish their social ties, indeed females form family groups with their fawns and young of the previous year (Hewison et al. 1998). Moreover, there is a landscape effect on the degree of post-capture home range displacement, indeed it increase with increasing habitat openness (Morellet et al. 2009), likely because roe deer need to take shelter in a closed habitat, far from potential source of human disturbance, immediately after release. The reduced activity level observed immediately after release, associated to the temporary change in habitat use, could resulted in a reduction in food intake that may cause a nutritional stress in roe deer, in addition to the stress due to the capture (Morellet et al. 2009). However all this

behavioural modification, due to the stress of the capture, do not affect deer behaviour permanently so GPS data can be considered as reflecting the effective natural behaviour of the animals.

2.3.2 Data description.

Data from GPS (Global Position System) collars was processed using GPS-3000 Host software. The collar registered a fix of localisation at regular time intervals of 6 hours (06:00, 12:00, 18:00 and 24:00) during all the year, in the period of study (2005-2008). There were also some periods of intensive monitoring (Appendix 2) placed in different periods of the year, in particular in the more important biological periods as territoriality, parturition and mating (Fig. 7), (the days were chosen random in these periods). Each intensive monitoring period is 24 hours long (from the 12:00 of a day to the 12:00 of the following day).

In this study we considered only yearlings and adult animals monitored during the years from 2005 to 2008. We did not analyze juveniles, as they differ in their behavior from adults being hidden in the first period after the birth (about 2 months), after being strictly related to the mother following her until April when they are likely to disperse (as explained in "post-natal behavior" section of the introduction). We also removed data during the first 8 days of monitoring to avoid potential bias due to the effects of capture on behaviour (Morellet et al. 2009). Short-term behavioural alteration in terms of spatial behaviour, habitat use and overall activity, due to handling and capture, have been indeed observed in roe deer (as written above in the previous chapter). This behavioural differences have been detected during the first period of 10 days after release, but they are particular pronounced in the first 8 days (Morellet et al. 2009), so we remove data of the first 8 days of monitoring.

The data set analysed was composed of 67 animals (24 males and 43 females). Animals were monitored over a continuous time period of minimum 5 months and maximum 13 months. Within this sample, 39 animals (11 males and 28 females) inhabited the open sector, 11 animals (4 males and 7 females) inhabited the intermediate sector and 17 animals (9 males and 8 females) inhabited the forest sector (Fig.10). Activity sensor data were available for only 63 (22 males and 41 females) of the 67 animals individuals, as some collars were not equipped with these sensors.

In the current analysis, we only used data from these intensive 24 hour monitoring periods, which occurred on a total of 58 different days (Appendix 2) over the period of study (1 in December 2004, 13 in each of 2005 and 2006, 14 in the 2007 and 17 in the 2008). We divided the year in relation to the different seasons, taking into account the roe deer's biological cycle (Fig. 7) as well as hunting activity, as follows: December-January (W="Winter"), February-March-April (S="Late Winter-Early Spring"), May-June (F="Fawning"), July-August (R="Rut"), September-October-November (A="Autumn"). The "Winter" period included the data from January (the beginning of the year N) and the data from December of the previous year (N-1). Animals are drive hunted from September to January (i.e. the "Autumn" and "Winter" periods). The "Fawning" period and the "Rut" period corresponded to the reproductive season (respectively, fawn births and mating). The territoriality phase starts during the "Late Winter-Early Spring" period, generally sometime in March (Hewison et al. 1998).

2.3.3 The model to predict activity.

We performed a model to predict activity-inactivity through the position variables provided by the motion sensor of the collar. To build the model we used three tame adult roe deer (a male and two females) equipped with Lotek 3300 collars in 2005 in the INRA experimental enclosure of

Gardouch (N 43°22', E 01°40') in the South-west of France (Fig. 13). They were fed *ad libitum* with pellets and had access to natural meadow vegetation growing on the ground. They were observed from a watchtower at a maximal distance of 80 meters for 15 days (24/02/2005-10/03/2005) at different time periods spread over the day (between 7:00 to 18:00 h) (Tables 4 and 5). Animal behaviors have been recorded using the ethogram presented in the table 5.

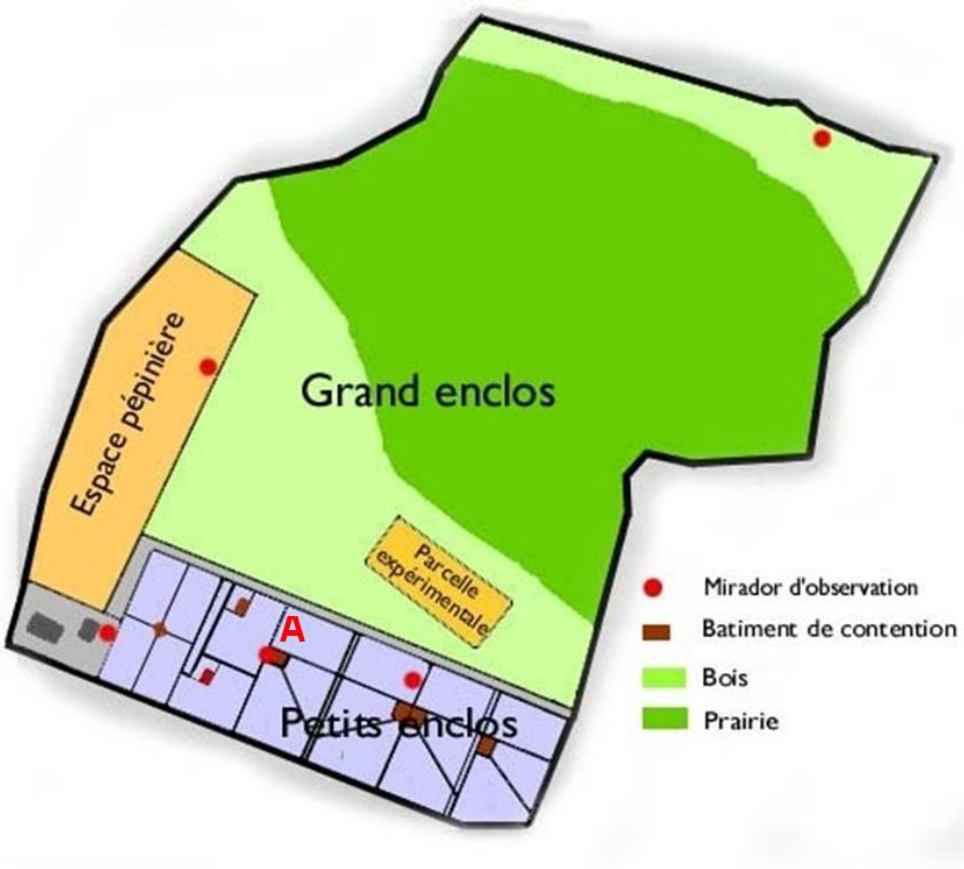


Figure 13. Plan of the enclosure of Gardouch with the observation towers (red points marked in the legend as "Mirador d'observation"). The observation tower marked with the letter "A" is the tower used for the direct observation on captive roe deer used to built the model to predict activity (article 1 in the results section). The captive deer was living in the small enclosures near the tower A.

One observer watched one animal at a time and recorded with a dictaphone the beginning of each behavior (Appendix 3). Recorded behaviors were "feeding", "standing", "bedded", "moving" and "other". Feeding, moving and others were grouped as active behaviors, while standing and bedded were considered inactive. We related observed activity of three tame roe deer with the three

variables provided by the activity sensors of their collars using discriminant analyses.

Table 4. Date and times of direct observations on captive animals in the experimental enclosure of Gardouch. Observation intervals are 5 minute lengths and they are spread over the day between 7:00 to 18:00 h. Id: Mat= female1 (collar narrower on the animal neck), Mal= female2 (collar narrow at intermediate level on the neck), Mick= male (collar less narrow on the animal neck).

id	observation intervals	Date
Mat	38	24-feb
Mat	29	25-feb
Mat	42	1-mars
Mat	45	2-mars
Mat	33	3-mar
Mat	22	4-mar
Mat	33	8-mar
Mat	37	9-mar
Mat	55	10-mar
Mal	36	24-feb
Mal	22	25-feb
Mal	47	1-mars
Mal	50	2-mars
Mal	35	03-mar
Mal	27	04-mar
Mal	39	8-mar
Mal	34	9-mar
Mal	54	10-mar
Mick	33	24-feb
Mick	20	25-feb
Mick	42	1-mars
Mick	43	2-mars
Mick	36	3-mar
Mick	33	04-mar
Mick	39	8-mar
Mick	42	9-mar
Mick	68	10-mar
TOTALS		
id	**observation intervals**	**Days**
Mat	303	9
Mal	344	9
Mick	356	9

Table 5. Ethogram used for the direct observation on captive animals, that have been used to built the model to predict roe deer activity through the collar sensor. Head high=head kept higher than the shoulder level, head at intermediate level1=head kept between the knee level and the shoulders, head at intermediate level2=head kept between the ground level and the knees and head down=head at ground level. Standing1=standing with head movements and standing2=animal completely immobile.

Behavioral classes	**Initials**	**Description**
FEEDING	ATH	feeding behavior with head high
	A I1	feeding behavior with head at intermediate level1
	A I2	feeding behavior with head at intermediate level2
	A TB	feeding behavior with head down
MOVING	M	walking with head at horizontal level
	E	walking with head at ground level
	S	behavioral stereotypy
	T	trot
	C	run
STANDING	Ar	standing1 with head at intermediate level1
	Ar TI	standing1 with head at intermediate level2
	Ar TB	standing1 with head down
	RD	standing2 with head at intermediate level1
	RD TI	standing2 with head at intermediate level2
	RD TB	standing2 with head at the ground level
BEDDED	RCTH	bedded with head at intermediate level1
	RCTB	bedded with head between the legs
OTHERS	TD	grooming standing
	TD j	grooming standing of the forelegs
	TD x	grooming standing of the antlers with the forelegs
	TC	grooming bedded
	GT	to scrape the ground
	RT	to sniff the ground
	CS	rapid general movements of body parts
	F	scrabbling the antlers
	Fr	scrabbling the antlers with head at intermediate level1 and 2
	Fr TH	scrabbling the antlers with head high
	Fr TB	scrabbling the antlers with head down

We randomly extracted 75% of the data for tame animals to build the linear discriminant models of activity per 5-min time interval as an additive function of the normalized values given by the motion sensors (Xn, Yn and HDn). We built six discriminant models based on six different rules to classify a time-interval as active or inactive. In the first model, we classified a

time interval as "active" when the animal spent at least 30% of the time in active behaviors, in the second model for at least 40% of the time active, in the third model for at least 50%, etc. The last model discriminated active intervals when at least 80% of the time was spent active. We plotted the proportion of correctly classified intervals against the time rules used to identify the best discriminant model. Then we examined the accuracy of this model to predict activity using the remaining 25% of the observations (Gottardi et al. 2010). Then we checked the consistency of the model, comparing activity-inactivity levels with movement rates, using data of 11 wild roe deer living in our study area (6 living in the forest and 5 in the open area). We determined that movement had occurred during a given 10 minute interval if the distance between successive fixes was greater than the sum of the errors associated with each of the two fixes considered (Gottardi et al. 2010). We tested the correspondence between movement (during each ten-minute interval) and predicted activity (during the corresponding two five-minute intervals) using a Kappa test of Cohen (Smeeton 1985). We considered a ten minute interval as active when the model predicted activity during at least one of the two five-minute intervals (Gottardi et al. 2010).

2.4 Statistical analysis.

We estimated rates of activity/inactivity for each 5 minute interval and movement/no movement for each 10 minute interval for each individual and for each of the 24 hour periods of intensive monitoring. To determine activity, we used the discriminant model generated from the calibration of the activity sensors by direct observation of captive animals (Gottardi et al.2010). To determine movement rates we calculated the distance between successive GPS fixes. An animal was defined as moving (Fig. 14) during a given 10 minute interval if the distance between successive fixes was greater than the sum of the errors associated with each of the two fixes considered (Gottardi et al.

2010). We calculated also the movement speed (km/h) for each 10 minute interval. Subsequently, we calculated the proportion of intervals during which an individual was active (5 minute intervals) and moved (10 minute intervals) during daylight and during night (Gottardi et al. submitted).

Figure 14. How to determine movement or not in each time interval: an animal was defined as moving during a given 10 minute interval if the distance between successive fixes was greater than the sum of the errors associated with each of the two fixes considered. At the opposite an animal was defined as not moving if the distance between successive fixes was lower or equal than the sum of the errors.

Daylight and night hours were determined according to the time of sunset and sunrise recorded on our study site coordinates (Tab 6).

Table 6. Time of sunset and sunrise recorded on our study site coordinates (sunset and sunrise timetables obtained from the Bureau des Longitudes, CNRS).

Months	**Period**	**Sunset**	**Sunrise**
December-January	Winter	05:58	18:09
February-March-April	Late Winter-Early Spring	7:17	16:37
June-July	Fawning	04: 25	19:20
July-August	Rut	04: 52	18:57
September-October-November	Autumn	06:17	17:37

Each animal was assigned to a landscape sector (Fig.10) based on the position of its home range. Animals in this study always remained within a given sector during the year's monitoring indeed adult roe deer are generally highly sedentary (Hewison et al. 1998). Home ranges (Appendix 4) were

generated and mapped using the Kernel method (Worton 1989) at the 95% isocline with ArcView® 3·02 GIS (ESRI, Redlands, California, USA).

To analyse variation in activity and movement along our landscape gradient, we performed linear mixed models (lme in the RGui v2.4.0 (http://cran.r-project.org) software, R Development Core Team (2007)), considering the proportion of intervals including activity or movement as the dependent variable, with the seasonal period, moment (day/night) and landscape sector (forest, intermediate and open) as fixed factors. We also included animal identity as a random factor to account for non-independence of data (pseudo-replication) at the individual level. We carried out the above analysis for the two sexes separately, because roe deer behavior changes across the year in a sex-specific way in relation to reproduction and physiological constraints (Andersen et al. 1998).

Finally we analyzed the variation in the animal's circadian rhythm along the landscape gradient, using movement speed values calculated each 10 minute. We performed generalised additive mixed models (gamm in the RGui v2.4.0 (http://cran.r-project.org) software, R Development Core Team (2007)), considering movement speed as the dependent variable and the landscape sector as fixed factor. Animal and day was considered as random variables. We performed one model for each seasonal period, considering the two sexes separately and we plotted the results. For this analysis we used only two landscape sectors: open and forest sectors. We classified animals belonging to intermediate sector as open sector with the exception of one individual (male) that was reclassified as belonging to the forest sector (his home range indeed overlapped more with the forest sector than the open sector). We did this to have more simply interpretable patterns of circadian rhythm. We identified activity peaks in terms of movement over the 24h and the variation in mean speed values over the seasonal periods.

3

Results and Discussion

3.1 First focus question and objective

How to asses animal activity/inactivity by the motion sensor? A new tool to study animal behavior through GPS collars.

The best discriminant model that we found, discriminated correctly 84% of the ‘‘active’’ time intervals (defined as roe deer spending at least 30% of the time active) and 97% of inactive ones, on captive animals. The model have been built through direct observation and performed very well for each animal observed, suggesting that data on more individuals would not have produced a significantly different model. We found concordance between the distribution of activity and movements on wild animals, indeed most of the inactive deer (sensors) did not exhibit movements (GPS), both in forest and open habitat deer. So we were able to consistently predict activity-inactivity also for wild roe deer.

These results have been indispensable to the successive parts of the study and to reach the objectives of this thesis. The discriminant model that we chose was indeed the base of our analysis in terms of roe deer activity and has been applied on our data as explained in the two successive chapters (article 2 and article3).

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Use of GPS activity sensors to measure active and inactive behaviours of European roe deer (*Capreolus capreolus*)

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Abstract

The aim of this study was to assess the accuracy of GPS 3300 to predict active (feeding, moving) and inactive (bedded, standing) behaviours in European roe deer. Observed activity of three tame roe deer was correlated with the three variables provided by the activity sensors of their collars (normalised for each individual) using discriminant analyses. The best model discriminated correctly 84% of the "active" time intervals (defined as roe deer spending at least 30% of the time active) and 97% of inactive ones. We tested for consistency with movements using 11 wild roe deer, six living in a forest and five in an open habitat. As expected, wild deer identified as inactive (sensors) were mostly immobile (GPS locations, 831 records of 1096), whereas deer known to be moving were mostly classified as active (493 of 758 records). The records classified as inactive but moving (24% of inactive records or 35% of moving records) can indicate short distance displacement, erroneous detection of movement, or moving without neck movements. The records classified as active but immobile (46 % of active ones, 33% of immobile ones) may represent feeding on a small patch without detectable movements.

Keywords: Activity; Feeding; Moving; Resting; Sensor; Telemetry

Introduction

GPS collars are increasingly used to study wildlife movements and habitat selection. They produce large data sets of animal locations and some measures of « activity » given by the sensors included in the collar. The knowledge of both animal locations (GPS system) and its activity (such as resting or feeding) is clearly useful for behavioural research (Cagnacci et al 2010), but also for more practical goals such as understanding the causes of sylvicultural damage or road collisions which are related to animal activity patterns.

The activity sensors included in the collars provide counts that are supposed to be linked to the behaviours exhibited by the animal. However to use such data, one should assess the correspondence between animal behaviour and the values given by activity sensors for each animal species. This requires observation of the behaviour of individuals equipped with the activity sensors to produce a statistical model predicting the dominant behaviour expressed per time unit using the independent variables provided by the sensors. Then, this model can be applied to sensor data obtained from unobserved wild animals.

In the past, several studies have been done to assess activity of many large species, often using sensors included in VHF collars (e.g. Cederlund and Lemnell 1980, Relyea et al. 1994, Maier and White 1998, Naylor and Kie 2004). More recently researchers began to use GPS collars to obtain locations of wild animals and wished to describe activity patterns using the counts provided by activity sensors often included in the collars, for example in moose *Alces alces* L. (Moen et al. 1996), red deer *Cervus elaphus* L. (Adrados et al. 2003, Löttker et al. 2009), white-tailed deer *Odocoileus virginianus* (Coulombe et al. 2006), cattle *Bos taurus* L. (Turner et al. 2000, Ganskopp 2001), mouflon *Ovis musimon* (Bourgoin et al. 2008, 2009), and brown bear *Ursus arctos* L. (Gervasi et al. 2006, Kozakai et al. 2008). However, studies comparing animal behaviours with sensor counts have shown that behaviours involving little neck movement produce similar count values, such as for standing and bedded individuals (Beier and McCullough 1988, Hansen et al.

1992) or for walking and resting animals (Ganskopp 2001, Gervasi et al. 2006). In addition, the mixture of several behaviours within a single time interval (Relyea et al. 1994) complicates the discrimination to such an extent that authors have built predictive models of activity excluding these mixed bouts (Naylor and Kie 2004, Coulombe et al. 2006, Kozakai et al. 2008, Bourgoin et al. 2008, 2009, Löttker et al. 2009). Moen et al. (1996) obtained a regression model to predict the proportion of time moose were active, but the model was not statistically significant for mixed bouts that amounted to a third of the data. To decrease the amount of mixed bouts in the data set, it is sometimes possible to reduce the time interval between records, but the number of records is limited by battery capacity. In addition, by reducing the time interval, one increases the risk of classifying short interruptions (e.g. vigilance or chewing) occurring during an active bout as inactive (Beier and McCullough 1988).

Another way to assess activity is to use movement parameters such as distance and speed between successive locations, as for example in pronghorn *Antilocapra americana* (Reynolds 1984) and in zebu cows *Bos taurus* L. (Schlecht et al. 2004). This requires information on GPS location error in order to correctly assess if the animal moved (active) or not (inactive). Due to GPS location errors, resting animals always show small distances between successive fixes and thus difficulties arise to distinguish resting from grazing with movement at a slow pace (Schlecht et al. 2004, Ganskopp and Johnson 2007).

A solution may be to combine information given by both sensors of neck movements (vertical and horizontal) and by GPS locations (distance moved) as done by Ungar et al. (2005) and Schwager et al. (2007) on cattle. The combination of these two sources of information may help distinguish between resting and grazing (both involving short distances travelled, but with high neck movement counts for grazing) and between travelling and resting (both involving few neck movements).

In this study we aimed to assess the accuracy of GPS 3300 to predict active and inactive behaviour in European roe deer (*Capreolus capreolus* L.). Firstly, we observed tame roe deer

wearing GPS collars in small enclosures to relate observed activity to collar sensor values using discriminant analyses. Roe deer have highly fractionated behaviour, with active events - feeding, searching, walking or grooming - interspersed with short inactive events - vigilant, standing with or without chewing, ruminating - in given five minute intervals (Zejda et al. 1985). We aimed to find a model to predict activity and inactivity for animals expressing normal behaviour, which is a mixture of active and inactive behaviours within a given short time interval. This approach is innovative as all the other studies we cited previously used only the observations where the animals were purely active or inactive to build their model (i.e. Coulombe et al. 2006, Bourgoin et al. 2008). We wanted to determine what level of activity (proportion of time active) we were able to discriminate per time interval. Secondly, we applied the best discriminant model to wild roe deer living in two different environments (forest and open habitat) and looked for consistency between activity and the pattern of movement obtained using GPS localisations, after taking into account location errors. Specifically, we predict that inactive deer (sensor data) will be mostly not moving (GPS data) and that moving deer (GPS data) will be mostly active (sensor data).

Materials and methods

Animals

We used three tame adult roe deer (a male and two females) equipped with Lotek 3300 collars in 2005 in the INRA experimental enclosure of Gardouch (N 43°22', E 01°40') in the South-west of France. The tame deer lived together in a 0.4 ha enclosure. They were fed *ad libitum* with pellets and had access to natural meadow vegetation growing on the ground.

We also used two data sets on wild adult roe deer caught in November 2004 and February 2007 in the South-west of France, near Aurignac (N 43°13', E 0°52') and fitted with the same type

of collars as the tame deer. The first set of individuals (3 males, 3 females, all adults) inhabited a forest area of 800 ha, while the second (4 females, 1 male) lived in a neighbouring agricultural area (open habitat) dominated by crops (56%), meadows (25%) and sparse woodland and hedgerows (15%). The study area has a mild climate (average annual temperature: 11-12 °C, average precipitation: 800 mm, mainly in the form of rain). We used the data provided by their GPS collars in winter between 1-15 December 2005 (every five minutes for the activity sensor). To assess fine scale movements, we used 24 hour-periods (between 12h00 of one day to 12h00 of the successive day) with a GPS location every ten minutes : for forest deer, on 13-14/12/2005 and, for open habitat deer, on 4-5/12/2007 and 11-12/12/2007. GPS locations provided by the collar are of four categories (2Dfix-F0, 2Dfix-Fn, 3Dfix-F0 and 3Dfix-Fn) that correspond to different levels of fix accuracy in our study area (median error = 37.6m, 20.8m, 23.2m and 7.9m respectively, see Cargnelutti et al. 2007). The distribution of the categories of fixes changes in relation to the habitat, with a higher proportion of 3DFix-Fn locations in open habitat compared with wooded habitat (Cargnelutti et al. 2007). The collars were placed in order that the front side of the battery block (with the Lotek stamp) faced the breast. This procedure was recommended in the Lotek manual (Lotek Wireless Inc. 2002), although the reverse recommendation appears in the subsequent edition (Lotek Wireless Inc. 2003). The collar sensors provided three activity variables recorded every five minutes, a count of vertical collar movements (Y), a count of horizontal movements (X) and the proportion of time the Y sensor was in an extreme position (HD). The position of the collar should affect the HD sensor values which should express the proportion of time the head was in a downward position when the Lotek stamp is facing the muzzle, and the proportion of time the head was held high when the Lotek stamp is facing the breast. Data from the GPS collars were collected using GPS-3000 Host software.

Observations

The tame roe deer were observed from a watchtower at a maximal distance of 80 meters, in winter between February 24th and March 10th 2005 at different times spread over the day (between 7:00 to 18:00 h) for a total duration of observation of 86h 05min (27h55 to 29h30 per individual). One observer watched one focal animal at a time (focal sampling) and recorded with a dictaphone the beginning of each behaviour. Recorded behaviours were "feeding", "standing", "bedded", "moving" and "other". Standing corresponded to the animal on foot, without moving its legs nor feeding, moving included walking or running animals. Other behaviours were grouped together, such as grooming, fraying, rubbing and stereotypic movement. Data from the dictaphone were transcribed to determine the proportional duration of each behaviour per five-minute time interval. Feeding, moving and others were grouped as active behaviours, while standing and bedded were considered inactive.

Data transformation

When we examined the distribution of X, Y and HD variables, we observed skewed distributions towards low values for X and Y (<20), and high values for HD (>90). We noticed a bug in the sensor data, with sometimes constant high Y-values inserted in sequences of successive low Y-values, often corresponding to bedded roe. Kozakai et al. (2008) also noticed this problem with GPS 3300S. Such sequences were unlikely because a count of collar movements may produce successive constant values only when the collar does not move (zero) or when it moves a lot (saturation of the sensor). Given their low occurrence (4.4% of the data) and their incoherent meaning, we chose to discard observations with Y values higher than 100 from the following analyses.

We noticed high between-individual variability in the range and median of the X, Y and HD variables. In the literature, it has been reported that variable tightening of the collar around the neck of the animal could induce between-individual variations of sensor counts that are not related to differences in activity levels (Moen et al. 1996, Adrados et al. 2003). In addition, between-collar

variations in the sensitivity of the sensors may also exist. Consequently we needed an individual-based model to predict activity, as was done also for red deer (Adrados et al. 2003) and for brown bears (Gervasi et al. 2006). In our case, the distribution was unimodal and both the means and the variances of X, Y and HD differed between animals, thus we used normalised variables (Xn, Yn, HDn) calculated per individual. Normalization was achieved by centering and scaling (as in Bourgoin et al. 2008) so that Xn, Yn and HDn have a mean equal to zero and a variance equal to one for each individual.

The models to predict activity

We randomly extracted 75% of the data for tame animals (n=776) to build the linear discriminant models of activity (1=active, 0=inactive) per 5-min time interval as an additive function of the Xn, Yn and HDn variables. We built six discriminant models based on six different rules to classify a time-interval as active *or* inactive. In the first model, we classified a time interval as "active" when the deer spent at least 30% of the time engaged in active behaviours. In the second model, a time interval was classified as "active" when the deer spent at least 40% of the time active, the third model for at least 50%, etc... The last model discriminated active intervals when at least 80% of the time was spent active. Because we obtained too few observations (2%) of deer active for more than 90% of a five minute interval, we did not build models to discriminate such high levels of activity We plotted the proportion of correctly classified intervals against the time rules used, and we retained the best discriminant model. We then examined the accuracy of this discriminant model to predict activity using the remaining 25% of the observations (n=259).

To build the models, we performed linear discriminant analyses (lda in the RGui v2.4.0 (http://cran.r-project.org), R Development Core Team 2007) and tested the significance of the linear combination obtained using multivariate analysis of variance. Contrary to Bourgoin et al. (2008),

we did not set prior probabilities equal between active and inactive groups because both tame and wild animals spent more time inactive than active (this study and Turner 1979) and thus the probability of being active was not equal to the probability of being inactive. We used the default procedure that considers that the probability group is equal to the observed proportions of active and inactive intervals in the training set. We used the Levene test to examine the homeogeneity of variances across active and inactive observations for Xn, Yn, HDn.

Applications to data from wild animals

We used the best discriminant model to predict activity for wild animals. First, we deleted records with Y values ≥ 100 and we normalised X, Y and HD variables using their mean and standard deviation across the 15-day period for each animal, as we had done for tame animals. Then we compared the distributions of Xn, Yn and HDn between tame and wild individuals using two-sample Kolmogorov-Smirnov tests. The null hypothesis is that values for both tame and wild animals were drawn from the same continuous distribution. Finally, we applied the discriminant model retained for tame animals to predict activity (active = 1, inactive = 0) for wild animals for each five-minute interval across the 15-day period.

We used the period of intensive GPS monitoring (a fix every 10 minutes) to evaluate movements between successive locations. We considered that the animal did not move if the distance between locations was less than the sum of the median error of the two successive GPS locations. Conversely, the animal was considered as moving if the distance between fixes was higher than the sum of errors. Because high location errors were more frequent in forest than in open habitat (more 2D fixes, Cargnelutti et al. 2007), the distance between fixes above which the animal was considered as moving was frequently higher in forest than in open habitats. Then, we tested for correspondence between movement (as indicated by the GPS location data, moving = 1, not moving = 0) during each ten-minute interval and predicted activity (from the activity sensors) during the

corresponding two five-minute intervals (active during at least one of the two five-minute intervals, or inactive during the two five-minute intervals) using a Kappa test of Cohen (Smeeton 1985).

Results

Discriminant model to predict active and inactive behaviours

We obtained 12960 records from the activity sensors for tame animals with 1035 of them (8%) corresponding to the period when we observed the behaviour of the deer directly. Tame roe deer were observed mostly inactive, with 71% of the time intervals dominated by bedded and 9% by standing behaviours, whereas 13% of them were dominated by feeding and 0.3% by moving. The variances of Xn, Yn, and HDn were not homogeneous across active and inactive observations (Levene test P<0,0001) due to higher variance for active behaviours (Figure 1).

The discriminant models correctly predicted active behaviours for 67 to 92% of the cases and inactive behaviours for 96 to 99% of the cases, depending on the time rule used to define a time interval as active (active if roe spent at least 30, 40, 50, 60, 70 or 80% of the time active, Figure 2). The sample size of active intervals markedly decreased with the increasing time rule in such a way that only 68 intervals (of 776) were defined as active for more than 80% of the time. The proportion of correct predictions for both active and inactive behaviours was higher than 90% when the time rule was 30% of the time spent active. Above this value the proportion of correct predictions for active behaviour markedly decreased with the increasing time rule, whereas the proportion of correct predictions of inactivity remained high. Thus we retained the best discriminant model that used the 30% time rule: a 5-minute time interval was defined as active when the roe deer spent at least 1.5 min active (mainly feeding and moving). With this model the prior probability of being

active (the probability of being active observed in the training set) was 25,8%. This model performed approximately similarly for each of the three animals (Figure 3), with on average 92% of the predicted active intervals that were actually observed as active and 96% of the predicted inactive intervals that were actually observed as inactive (Table 1). The discriminant model we retained was applied to the remaining 25% of the data on tame roe deer. We found that 84% of predicted active and 97% of predicted inactive time intervals were correctly predicted.

Model validation on wild animals

The distribution of Xn, Yn and HDn values (Figure 4) showed a significant difference between tame and wild deer (Kolmogorov-Smirnov tests $p<0.0001$). There were more high values for Xn and Yn, and low values for HDn, indicating more neck movements, in wild than in tame roe deer. In addition there were less low values for Xn and Yn, and high values for HDn, indicating less inactive behaviours in wild than in tame roe deer.

Using distance between locations calculated from intensive monitoring, we classified the time intervals as including movement or not. Forest roe deer moved for 36% of the time and were immobile for 55% of the time, the remaining were 9% missing locations. Open habitat roe deer spent 39% of the time moving, 59% immobile and 2% were missing locations. Using our discriminant model, we found that forest roe deer spent 40% of time active, 49% inactive and the remaining 11% being missing values. Open habitat deer spent 41% time active, 51% inactive and 8% were missing values.

The concordance between predicted activity and movement was highly significant both for forest (Kappa of Choen=0.156, $z=4.18$, $p<0.01$) and open habitat (Kappa of Choen =0.385, $z=14.1$, $p< 0.01$) roe deer. Inactive deer (activity sensor) were mostly immobile (GPS location data) (respectively 70% and 79% for forest and open habitat roe deer). Moving deer were also mostly

active, but this was less the case for forest roe deer (56% for forest and 69% for open habitat roe deer). On average, 13% of the time intervals in forest deer and 11% in open habitat deer were classified as including movement but inactive (Table 2). Missing GPS locations were more frequent during inactive time intervals compared to active ones for forest roe deer ($X^2 = 3.96$, df = 1, p = 0.047), but not for open habitat roe deer ($X^2 = 0.2974$, df = 1, p = 0.585). In addition, low quality locations (those with a high location error) were more frequent for inactive time intervals than for active ones (Forest : $X^2 = 19.41$, df = 9, p = 0.0219; Open habitat : $X^2 = 29.14$, df = 9, p = 0.001) and for immobile deer than for moving ones (Forest : $X^2 = 79.17$, df = 9, $p < 0.0001$; Open habitat : $X^2 = 73.49$, df = 9, $p < 0.0001$). Roe deer were classified both as active and immobile for 20% (forest) and 17% (open habitat) of the time (Table 2).

Discussion

We obtained a discriminant model predicting active and inactive time intervals with a very good accuracy (respectively 84% and 97% correct prediction) in the three tame animals. We acknowledge that the number of animals (3) used is very low, but this is usual in such studies due to the difficulties of raising wild species in captivity (Adrados et al. 2003, Bourgouin et al. 2008, Kozakai et al. 2008, Löttker et al. 2009). In addition the model performed very well for each animal, suggesting that data on more individuals would not have produced a significantly different model. The lower performance of the predictions for active compared to inactive behaviors can be explained by the lower sample size for active behaviors in the data set used to build the model, but also more likely by the higher variances of sensor values for active than for inactive behaviors.

Contrary to other studies that used time intervals with only purely active or inactive behaviours to develop a predictive model of activity, our model takes into account that a mixture of active and inactive behaviours usually occurs within a given five-minute interval in small ruminants such as

roe deer. Almost all the observed active 5-minute time intervals were actually a mixture of inactive standing immobile (standing, chewing, vigilance) and active bouts (feeding, moving, other), with only 1% of them being made up entirely of active behaviour for 5-minutes. This explains why the performance of the model decreases when we tried to predict increasing levels of activity. Our approach is certainly more realistic than determining activity using a cut-off value obtained with only those intervals that contain a single behaviour (20 to 50 % of the observations) as done by Coulombe et al. (2006) and Naylor and Kie (2004). Because our model discriminates active intervals based on the combination of normalised variables per individual and across several days (15-days in our study), we think it will be better adapted to other ruminant species than existing models using absolute cut-off values that do not take into account individual variability of sensor responses to neck movements. This hypothesis should be verified using other ungulate species of various sizes and feeding style which may exhibit differing activity patterns (Mysterud 1998).

We were able to consistently predict inactivity for wild roe deer, as we found concordance between the distribution of activity and movements. Most of the inactive deer (sensors) did not exhibit movements (GPS), both in forest and open habitat deer. However active behaviour was less consistently predicted, as 44 to 31% of moving deer were classified as inactive, that amounted to 12% of all time intervals. This may be explained by low model performance, because wild and tame roe deer express different behaviours, or by errors in the detection of movements. Firstly, our discriminant model was built using tame roe restricted to the small area of their enclosure and unable to fully express typical behaviour of wild roe deer that move between feeding and resting sites and forage while walking over a wide area. This is not unusual in such studies (e.g. Kozakai et al. 2008), but this kind of long-range movement may induce an "inactive-like" sensor response that we cannot detect in captivity. Indeed, behaviours involving little neck movement, such as walking and resting, may produce similarly low count values of activity sensors (Ganskopp 2001, Gervasi et al. 2006). We found that the distribution of sensor values differed between wild and tame roe deer, with more extreme values in wild deer, suggesting that high activity levels are under-sampled in

tame roe. Because in the wild data set, the model predicted active behaviours for these extreme values, this could not generate moving but inactive records. Second, because GPS location errors were higher for inactive or immobile animals, movements may have been overestimated. Other studies also suggest that GPS location error is higher for inactive animals (Graves and Waller 2006, Zweifel-Schielly and Suter 2007) because bedded animals may be masked from satellites due to obstruction by vegetation cover and the position of the collar antenna. Finally, it is also possible that moving but inactive records included short time movements lasting less than the time threshold used to predict active behaviour (> 30% of the time active) but sufficiently large to produce significant displacement.

The combination of activity data and movement data allows us to distinguish two kinds of active behaviour, one which includes movement and one which does not. Active animals which were classified as not moving were likely feeding on a small patch which may offer enough food concentrated in space to preclude the necessity for movement. Animals which were classified as active while moving may be feeding on dispersed food or travelling without feeding. Finer discrimination between walking when feeding and walking without feeding may be achieved using travel speed (Reynolds 1984, Schlecht et al. 2004), but this would require very low GPS error to precisely estimate speed and visual observation of animals to assess the range of speeds used when feeding. In the future, more sophisticated sensors placed on different parts of the body may help to discriminate between several active behaviours (Watanabe et al. 2005, Gervasi et al. 2006, Tsuda et al. 2006, Shepard et al. 2008, Wilson et al. 2008). However, in ruminants, most active time is spent feeding (Beier and McCullough 1990) and, depending on the question, discriminating active from inactive bouts may be sufficient to identify general feeding patterns.

When combining both activity and movement data for the intensive monitoring periods, we obtained missing values for 20% of the time intervals in the forest but only 9% in the open habitat. We showed that missing locations occurred more frequently for inactive behaviour in the forest, but not in the open habitat. This relates to the overall lower accuracy of GPS locations in the forest

compared to the open habitat (Cargnelutti et al. 2007, Bourgoin et al. 2009), particularly when the animal is inactive. As a consequence, resting behaviour (both inactive and immobile) was more under-sampled in the forest than in the open habitat. This bias could be corrected by assigning the mean position calculated over the entire inactive bout to missing locations, as done by Adrados et al. (2003).

Our discriminant model may be used in the future to depict activity rhythms of wild animals wearing the same type of activity sensors. This will provide a way to study the variations of activity rhythms in relation to environmental factors (nyctemeral, climate, season, habitat, food resources) and human-related parameters (tourism, hunting, dogs, livestock) that are increasingly studied topics in wild animal populations (e.g. Rouleau et al. 2002, Di Bitetti et al. 2008, Pipia et al. 2008). In addition, the combination of movement and activity data, as provided by GPS collars, offers exiting perspectives to improve the fine grained knowledge of what a wild animal does, when and where (Cagnacci et al. 2010). Given the increasing use of GPS monitoring of wild ungulates, we hope that the large amount of data it generates will be analysed following a standardised procedure, such as we propose, to allow comparative studies.

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Table 1 Discriminant analysis and MANOVA to predict active and inactive intervals in tame roe deer equipped with Lotek 3300 GPS collars.

Variables	Coefficient of linear discriminant	Group means Active (1)	Inactive (0)
Xn	0.8861	1.0216	-0.6016
Yn	0.5399	1.0294	-0.5698
HDn	-1.4583	-0.6476	0.7666

MANOVA Terms	Active (1/0)	Residuals				
Xn	374.2	225.2				
Yn	363.3	318.4				
HDn	284.1	159.9				
	DF	Pillai	Approx F	Num Df	Den Df	P
Active	1	0.78	899.26	3	741	<0.0001
Residuals	743					

Activity is observed on three roe deer during successive five-min intervals. An individuals is active (1) when spending at least 30% of five-min time interval doing active behaviours, and inactive (0) when spending more than 70% time inactive. Xn,Yn and HDn are normalised variables provided by the activity captor included in the GPS collar fitted on the three individuals.

Table 2 Consistency of activity predicted using captor data (active/inactive) and GPS data (move/not move) in wild roe deer living in two neighbouring zones (forest/open habitat)

	Active		Inactive		NA
	Move	Not move	Move	Not move	Total
Forest	144 (17%)	175 (20%)	111 (13%)	262 (30%)	172 (20%)
Field	349 (24%)	240 (17%)	154 (11%)	569 (39%)	128 (9%)

The status active and inactive is evaluated using discriminant model based on activity captor data (table 1). Movement is assessed comparing inter-fixes distances and GPS location error (see methods). We used 6 individuals in the forest and 5 individuals in the open habitat

Figures

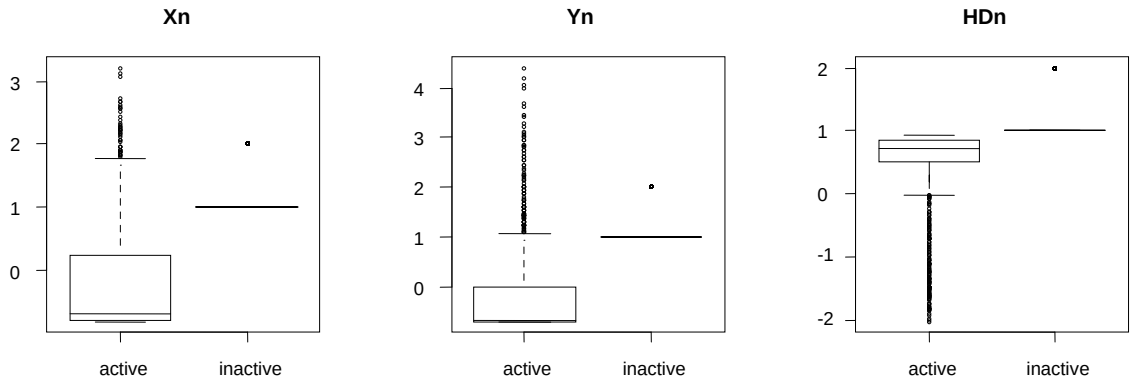

Figure 1 Boxplot of sensor variables, Xn (normalised values of horizontal collar movements), Yn (normalised values of vertical collar movements) and HDn (normalised values of the proportion of time the Y sensor was in extreme position), split between active (n=239) and inactive (n=754) observations in tame roe deer equipped with Lotek 3300 GPS collars.

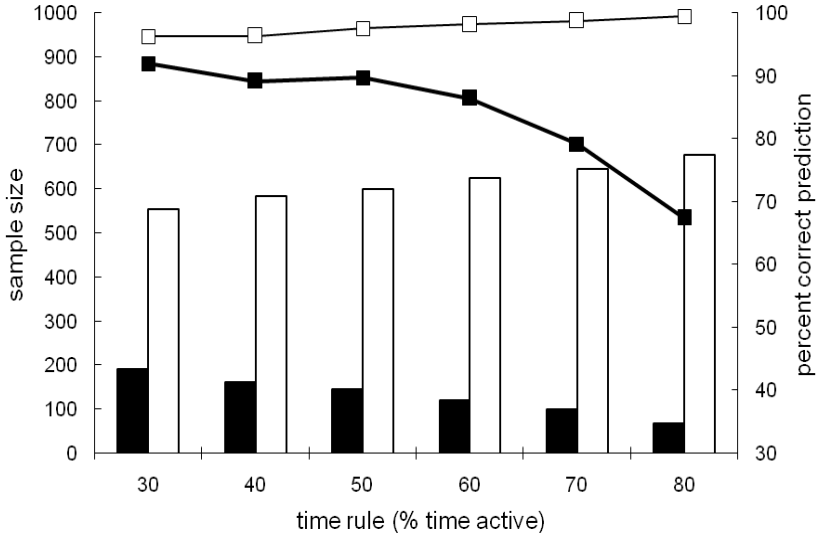

Figure 2 Proportion of correct classification of active (dark symbol) and inactive (open symbol) intervals for tame roe deer observed during five-minute time intervals (776 intervals). The histograms represent the sample sizes while the plain lines represent the proportion of correct predictions. Prediction of activity was made using discriminant functions of Xn, Yn and HDn variables provided by the activity sensor of the GPS collars (after normalisation by individual). Abscissa is the time rule used to define an interval as active. For example a time rule of 30% means that the intervals was defined as "active" if the roe were active during at least 30% of the 5-minute intervals, and "inactive" the remaining of the time

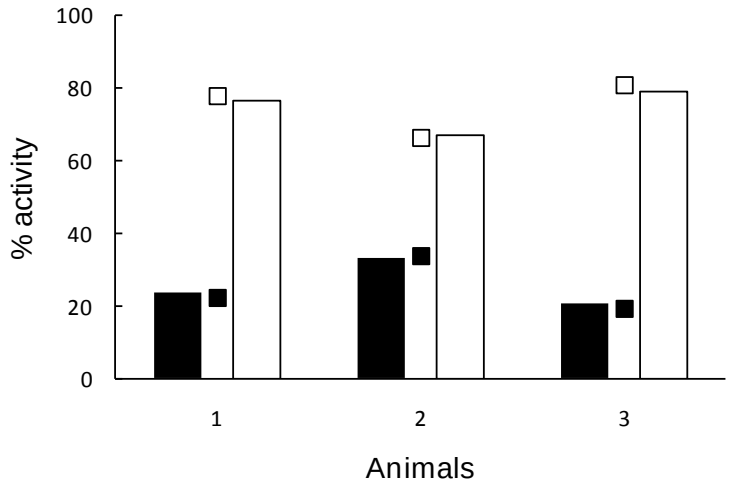

Figure 3 Proportion of intervals observed active (dark bar) and inactive (open bar) for three tame roe deer and corresponding predicted values (active : dark square, inactive : open square).

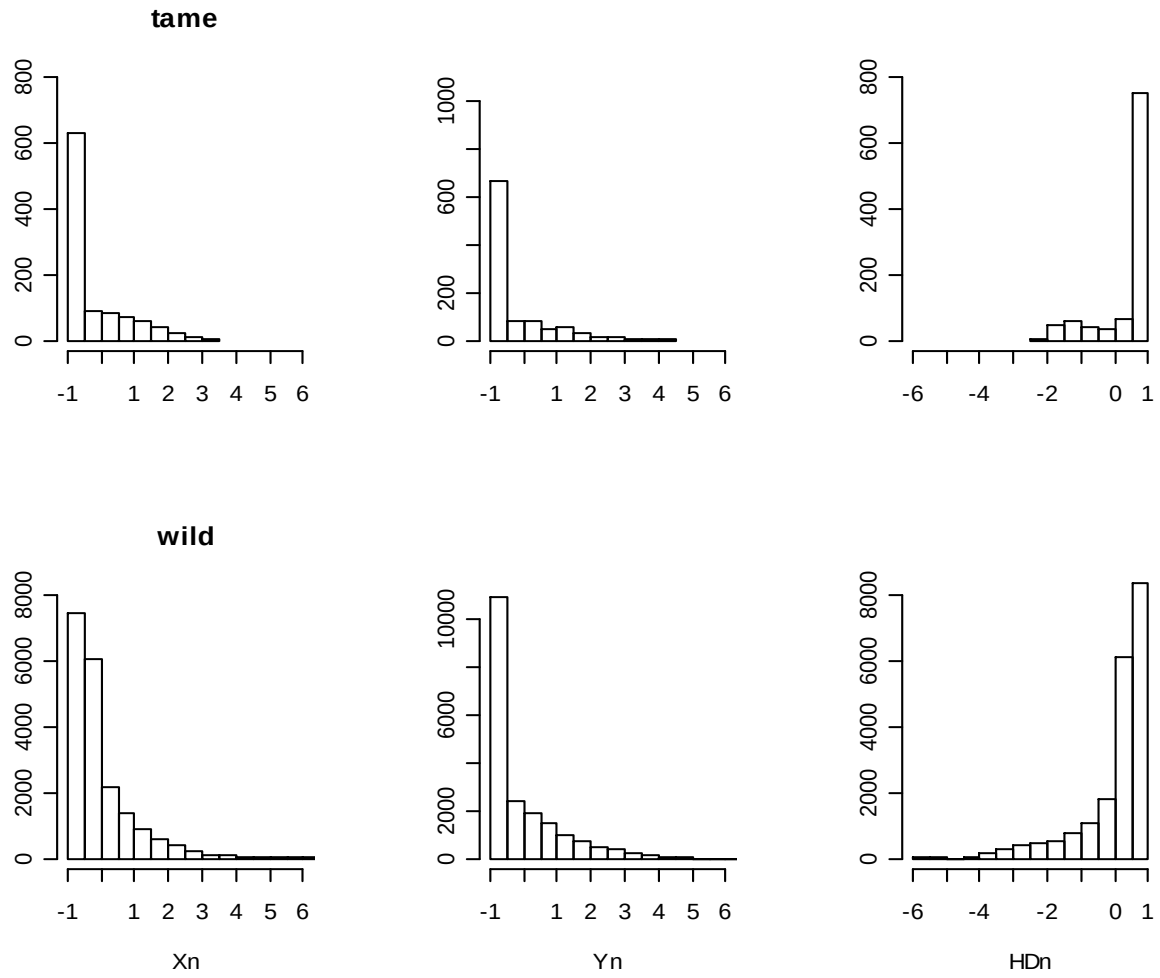

Figure 4 Distributions of Xn, Yn and HDn variables provided by the activity sensors of the GPS collars equipping three tame and 11 wild roe deer in winter. For tame roe deer, we show only the values that were used to build the discriminant model to predict activity, which were the values recorded during the days of observation of the animals.

3.2 Second focus question and objective

What we means as behavioral plasticity in a synanthropic species responding to landscape fragmentation process? The roe deer as example.

We found that landscape structure affected behavior in both the sexes but in different way across the year with several differences between seasons also refers to animal reproductive state in accord of our third hypothesis but with differences on what we expected. Our third hypothesis is partially supported indeed males showed high levels of activity and movements during the rut in accord of our expectations but at the contrary fawning does not lead to increased activity among females.

During the rut, males were more active in the most open sectors, probably linked to their search strategy for females which are more widely dispersed in this habitat. While, during winter, males deer activity and movement rates decreased along the gradient of increasing landscape openness, probably to compensate for the poorer winter food availability and quality in the forest environment. This effect of landscape openness on activity level (but not movement rate) was also significant in females, with a trend similar to that of males. Thus, this result did not support our first expectation.

Deer of both sexes were more active and moved more frequently during winter and early spring compared to the rest of the year and they were more active and moved more frequently during the night than during the day during almost all the year, likely as a response to human disturbance. This validate our second hypothesis. However we don't found a clear response to hunting at the contrary of what was expected. This suggests that deer become more nocturnal in response to the general level of non-specific disturbance, rather than because of a specific anti-predator strategy to avoid hunters.

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Variation in roe deer, *Capreolus capreolus*, activity levels and movement rates along a gradient of landscape openness

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Abstract

Natural landscapes across much of Europe have been modified extensively by man, with potentially marked impacts on wildlife behaviour. In this study, we analyze the effect of landscape structure on animal behaviour by studying activity levels and movement rates of a hunted roe deer population along a landscape gradient, from strict forest habitat to open agricultural plain. We found that landscape structure affected behavior of both male and female roe deer, but this effect differed among seasons. During winter, deer activity and movement rates decreased along the gradient of increasing landscape openness, probably to compensate for the poorer winter food availability and quality in the strict forest environment. In contrast, during the rut, males were more active in the most open sectors, probably linked to their search strategy for females which are more widely dispersed in this habitat.

We found that deer of both sexes were more active and moved more frequently during the night than during the day, likely as a response to human disturbance. Finally, deer were more active and moved more frequently during winter and early spring compared to the rest of the year. These results illustrate how spatial heterogeneity in the distribution of both food and sources of disturbance interacts with reproductive constraints to determine how deer behavior varies across fragmented landscapes.

Keywords: fragmentation; environment; habitat; plasticity; disturbance; feeding

Introduction

Landscape fragmentation, resulting in increased local habitat heterogeneity, is an ongoing and widespread process across much of Europe, with notable effects on the behaviour of animals in terms of activity rhythm, movements and habitat use (Kremsater and Bunnell 1992; Kie et al. 2002; Kie et al. 2005; Brinkman 2005; Banks et al. 2007; Rhoads et al. 2010). Habitat fragmentation involves both absolute loss of primary habitat and the reduction in size and increasing isolation of remnant habitat patches (Saunders et al. 1991; Andrèn 1994;). This process may provoke an increase in disturbance due to associated human activity (Cole et al. 1997; Markovchick-Nicholls et al. 2008) and can potentially endanger species, populations, communities and hence entire ecosystems, resulting in biodiversity reduction (World Resource Institute 1990; Marvier et al. 2004; Hansen et al. 2005). The process of landscape fragmentation has often resulted from the conversion of natural woodland areas to agricultural crops and open meadows devoted to livestock grazing during agricultural intensification. However, habitat generalists may be able to colonize and live in secondary matrix habitat because of their behavioral plasticity (*sensu* Komers 1997) and ecological flexibility (Bender et al. 1998; Kassen 2002; Marvier et al. 2004; Hansen et al. 2005; Devictor et al. 2008). A key aspect of this plasticity is the ability to adapt activity patterns in response both to the modification of landscape structure, notably the distribution and size of secure feeding patches (Jhonson et al. 2001; Godvik et al. 2009; Owen-Smith et al 2010), and to the increase in human disturbance (Rhoads et al. 2010). For example, a strictly nocturnal species can become cathemeral (irregularly active at any time of night or day, according to prevailing circumstances) as a consequence of the increasing use of matrix when the size of native habitat fragments decreases (e.g. Norris et al. 2010). Very few studies have dealt with the effect of landscape structure on activity pattern in wildlife (but see Felix et al. 2007; Godvik et al. 2009; Rhoads et al. 2010), likely because of the difficulties of monitoring a large number of individuals across a wide range of landscape structure. Today, the use of GPS monitoring coupled with activity captors has enabled us

to overcome this difficulty (Löettker et al. 2009; Owen-Smith et al 2010; Tomkiewicz et al. 2010). In this paper we study how the activity pattern of a generalist ungulate, the roe deer *Capreolus capreolus*, changes in relation to landscape structure in a fragmented European landscape.

Roe deer were previously thought of as a species of closed, predominantly wooded, landscapes (Putman 1988), foraging preferentially along habitat edges with open areas (Tufto et al. 1996; Saïd and Servanty 2005; Van Moorter et al. 2009). However, they have relatively recently colonized a wide variety of habitats, including open agricultural landscapes (Linnell et al. 1998*a*; Hewison et al. 2001), thanks to their marked behavioral plasticity, although they do avoid areas associated with human activity and, hence, disturbance (Hewison et al. 2001; Coulon et al. 2008). Roe deer populations show substantial variation in social and spatial structure in response to environmental heterogeneity (Hewison et al. 1998; Lamberti et al. 2006). Open field roe deer use larger home ranges (Hewison et al. 1998; Cargnelutti et al. 2002) and may form larger social groups, especially during winter (Hewison et al. 1998, 2001; Pays et al. 2007). Feeding behavior may also be affected by the greater availability of forage in cultivated areas (Turner 1979), with field deer adapting their daily feeding cycle to avoid farmers working in the fields. Such differences in behavioral patterns between forest and field deer are presumably the result of a phenotypic response to contrasting environmental conditions (i.e. behavioural plasticity, Komers 1997), rather than genetic (Andersen et al. 1998), although Kaluzinski (1974) considered field and forest deer to be separate ecotypes. Hence, although some behavioral differences between roe deer populations inhabiting open field and forest have been previously documented (Kaluzinski 1974; Bresiński 1982; Jeppesen 1990), the extent of behavioural plasticity in relation to landscape openness within a single population has not yet been investigated.

The temporal organization of activity patterns is peculiar to each species, being modulated by both internal (physiological state) and external (environmental conditions) factors (Ratikainen et al. 2007). The activity time-budget of ungulates changes across the year (Godvik et al. 2009; Pepin et al. 2009; Owen-Smith et al 2010; Rhoads et al. 2010), for example, in relation to seasonal variation

in daylight conditions (Beier and McCullough 1990), temperature (Beier and McCullough 1990; Schmitz 1991; Demarchi and Bunnell, 1995), and as a consequence of the annual changes in the reproductive status of individuals (Moncorps et al. 1997; Pepin et al. 2009; Rhoads et al. 2010). In ungulates inhabiting temperate and boreal areas, annual variation in activity pattern is associated with seasonal changes in the availability of food resources (roe deer, *Capreolus capreolus*, Turner 1979; red deer, *Cervus elaphus*, Godvik et al. 2009; white-tailed deer, *Odocoileus virginianus*, Beier and McCullough 1990; caribou, *Rangifer tarandus*, Roby and Thing 1985; reindeer, *Rangifer tarandus tarandus*, Skarin et al. 2010; moose, *Alces alces*, Cederlund 1989; isard, *Rupicapra pyrenaica*, Bruno and Lovari 1989). For example, the roe deer adapts to seasonal variations in forage availability through changes in metabolic rate, which declines in winter (Weiner 1977). This decline is associated with a concomitant decline in activity rate (Cederlund 1981) and food intake (Drozdz and Osiecki 1973; Drozdz 1979), such that the proportion of time a deer is active shows a marked annual cycle, from 40% in winter to 50% in summer. These annual rhythms result from changes in the frequency and length of activity bouts for these ruminants, with the shortest bout lengths recorded during summer and the longest during winter (Jeppesen 1989).

Seasonal activity patterns can be modified in the presence of predators and human disturbance (Singer et al. 1991; Mysterud et al. 2004; Skarin et al. 2010). Indeed, diurnal human disturbance can lead to greater nocturnal activity in ungulates (Georgii 1981; Langbein et al. 1997; Kamler et al. 2007), while the use of disturbed sites increases at night (Hayes and Krausman 1993; Ratikainen et al. 2007), probably because animals feel more secure during darkness (Marchinton 1967). For example, a study in South Dakota showed that hunted deer changed from being mostly diurnal to crepuscular as a consequence of the loss of escape cover due to removal of large forest tracts (Naugle et al. 1997). Agro-ecosystems in particular generally provide an environment which is subject to high levels of human disturbance. In such contexts, deer may be obliged to modify their habitat use, activity patterns and movements in order to adjust to landscape heterogeneity (Kie et al. 2002; Kie et al. 2005; Rhoads et al. 2010). For example, in many rural populations, deer spend the

day in woodlots, but use cultivated fields for feeding during the night (Montgomery 1963; Nixon et al. 1991). In addition, their centers of activity may change as crops mature (Vercauteren and Hygnstrom 1998). As a result of these regular forays between woodlots and fields, the movement speed and activity rate of deer living in agro-ecosystems is generally thought to be higher than that of forest populations (Rouleau et al. 2002), with potential consequences for the energy budgets of individual animals.

Here, we explore how roe deer activity and movement behavior varies within a single population in relation to variation in local landscape structure. We expected 1. that activity level and movement rate should increase with increasing landscape openness due to the necessity of moving between the woodlots, which provide shelter, and the more open areas, which are exploited for foraging, in fragmented landscapes; 2. that activity level and movement rate should be higher during night time than during the day throughout the year, as animals tend to forage under the cover of night in human-dominated landscapes, and that this day-night difference should be most marked in the more open areas of the landscape and during the hunting season; and 3. that reproductive considerations should constrain these patterns, such that males are more active and move more frequently during the rut, while females should be more active during fawning.

Materials and methods

Study site

The study was carried out in a fragmented agricultural landscape (Fig. 1) of 7500 ha (ca.) situated in the south-west of the France, in the Comminges region of the Midi-Pyrénées, in the Aurignac canton (43°13'N, 0°52'E). It is a hilly zone, rising to a maximum of 380 m a.s.l., with an oceanic climate (average annual temperature 11-12°C and 800 mm precipitation, mainly rain).

The study area is characterized by a mixed landscape of cultivated fields (about 33% of the total area), hedges (7% of the total area), meadows (34% of the total area) and small woodland patches (14% of the area with an average size of 3 ha), and a central forest of 672 ha (7% of the area) (Hewison et al. 2009). The natural vegetation of the area is classified as a southwest European lowland-colline downy oak forest (Bohn et al. 2004). The open fields are cultivated mostly with wheat and barley (51%), some sunflower (15%), maize (10%), soya (5%), sorghum (8%) and rape (4%) (Hewison et al. 2009). Hedges contain numerous ligneous shrubs and trees (*Prunus spinosa*, *Cornus sp*., *Lonicera sp*., *Quercus sp*., *Rubus sp*., *Rosa sp*., *Crataegus sp*. *Hedera helix*, *Ligustrum vulgare*), grasses, sedge and forbs (*Gallium sp*.). The meadows have a variable species composition, with most fields dominated by *Dactylis glomerata* and *Festuca arundinacea* or by *Festuca rubra* and *Agrostis capilaris*, and less frequently by ray gras *Lolium perenne*, *Holcus lanatus*, lucerne *Medicago sp.* and clover *Trifolium sp*. With the exception of ray grass, the meadows also contain forbs such as the leguminous *Potentilla sp.*, *Geranium sp.*, *Sanguisorba sp*., and *Taraxacum sp*.. The woodland patches are dominated by oak *Quercus spp*., often associated with hornbeam *Carpinus betulus*, while the central forest is a mixed species forest of oak, Douglas-fir *Pseudotsuga menziesii*, hornbeam *Carpinus betulus* and pine *Pinus spp*.. The understorey is dominated by brambles *Rubus spp*., butcher's broom *Ruscus aculeatus*, ivy *Hedera helix* and common honeysuckle *Lonicera peryclimenum* (Hewison et al. 2009).

Small villages and farms are distributed all along the extensive road network which covers the zone. Human-mediated activity is widely distributed across the study site as a result of agricultural and sylvicultural practices. The primary land use of the study site is pastoral for sheep and cattle grazing, with an intensification of agricultural activities during recent decades (Hewison et al. 2007).

Within this single study site, we identified three landscape units (Fig. 1) of contrasting habitat structure in terms of woodland extent and the relative proportions of meadows and cultivated fields (Hewison et al. 2009). The open field sector covers 65% of the total area (1217 ha) and is composed of 12.5% woodland (153 ha), 6.3% hedgerows (77 ha), 33.8% meadows (411 ha) and 42.7%

cultivated fields (520 ha). The intermediate sector covers 21% of the total area (397 ha) and is composed of 35% woodland (139 ha), 2.1% hedgerows (8 ha), 38.5% meadows (153 ha) and 21.6% cultivated fields (86 ha). The forest sector covers 14% of the total area (259 ha) and is composed totally of forest (Fig. 1).

Deer density in the study area was estimated for 2005 at around 4.0-7.9 deer/100 ha in the mixed agricultural landscape of cultivated fields, hedges, meadows and woodland patches (88% of the total surface of the area), while it was higher in the central forest, with a mean value of 34.3 deer/100 ha (Hewison et al. 2007). An annual index of deer abundance indicated a relatively stable population from 1992 to 2008 (unpubl. data). The roe deer population was hunted on a regular basis during autumn and winter (from September to January) by drive hunts with dogs and bucks were also stalked during summer (from June to August) (Hewison et al. 2009).

Study population and data description

Our study was based on the GPS fix and activity sensor data collected during 4 years (2005-2008) of continuous monitoring of the studied population. Animals were caught every year during winter (December-February) using large-scale drives of between 30 and 100 beaters and up to 4 km of long-nets, with each capture area placed in order to adequately sample across the gradient of landscape openness in the study site (Hewison et al. 2009). Tooth wear was used to assess age (Hewison et al. 1999) in three classes: juveniles (less than one year-old), yearlings (between one and two years-old) and adults (two years-old or more). However in this analysis we considered only yearlings and adult animals. The data set analysed was therefore composed of 67 animals (24 males and 43 females). Animals were monitored over a continuous time period of minimum 5 months and maximum 13 months. Within this sample, 39 animals (11 males and 28 females) inhabited the open sector, 11 animals (4 males and 7 females) inhabited the intermediate sector and 17 animals (9 males and 8 females) inhabited the forest sector (Fig.1).

The deer were equipped with GPS Lotek 3300 for medium-size mammals (Lotek Engineering, Inc., Newmarket, ON, Canada) which were fitted following the procedure recommended in the Lotek manual (Lotek Wireless INC. 2002). The collars provided information on activity-inactivity (through the three head-neck position sensors) and movement (through GPS location data). The activity sensors generated three variables: a count of vertical collar movements (Y), a count of horizontal movements (X) and the proportion of time the Y captor was in an extreme (head down) position (HD). Activity sensor data were available for only 63 (22 males and 41 females) of the 67 animals, as some collars were not equipped with these sensors. The activity-inactivity data were recorded every 5 minutes (the sum of movements in each plane over a 5 minute period).

GPS locations were classified into four categories corresponding to the expected values of median location error (2Dfix-F0=37.6m, 2Dfix-Fn=20.8m, 3Dfix-F0=23.2m and 3Dfix-Fn=7.9m) following extensive field tests (see Cargnelutti et al. 2007). GPS locations were programmed to be taken at regular time intervals of 6 hours (06:00, 12:00, 18:00 and 24:00) throughout the year. In addition we programmed some periods of intensive monitoring of 24 hours (from 12:00 of one day to 12:00 of the following day), taking a fix every 10 minutes, to focus on behavior during certain key periods of the year, in particular, during territoriality, mating, gestation and lactation (the days were assigned at random within these periods). In the current analysis, we only used data from these intensive 24 hour monitoring periods, which occurred on a total of 58 different days over the period of study (1 in December 2004, 13 in each of 2005 and 2006, 14 in the 2007 and 17 in the 2008). We divided the year in relation to the different seasons, taking into account the roe deer's biological cycle as well as hunting activity, as follows–: December-January (W="Winter"), February-March-April (S="Late Winter-Early Spring"), May-June (F="Fawning"), July-August (R="Rut"), September-October-November (A="Autumn"). The "Winter" period included the data from January (the beginning of the year N) and the data from December of the previous year (N-1). Animals were drive hunted from September to January (i.e. the "Autumn" and "Winter" periods). The "Fawning" period and the "Rut" period corresponded to the reproductive season (respectively, fawn births and mating). The

territoriality phase starts during the "Late Winter-Early Spring" period, generally sometime in March (Hewison et al. 1998).

Statistical analysis

We estimated rates of activity/inactivity for each 5 minute interval and movement/no movement for each 10 minute interval for each individual and for each of the 24 hour periods of intensive monitoring. To determine activity, we used a discriminant model generated from the calibration of the activity sensors by direct observation of captive animals carrying these same collars (Gottardi et al. in press). We used the three variables provided by the activity sensors of the collars (Y,X,HD) to determine activity within each 5 minute interval based on this model. This model correctly discriminated 84% of the "active" time intervals (defined as the animal spending at least 30% of the time active), and 97% of inactive ones (Gottardi et al. in press).

To determine whether an individual moved or not over a given 10 minute inter-fix interval, we calculated the distance between successive GPS fixes of that individual and compared this to instrument error (see Cargnelutti et al. 2007). That is, we determined that movement had occurred during a given 10 minute interval if the distance between successive fixes was greater than the sum of the errors associated with each of the two fixes considered (Gottardi et al. in press).

Subsequently, we calculated the proportion of intervals during which an individual was active (5 minute intervals) and moved (10 minute intervals) during daylight and during night. Daylight and night hours were determined according to the time of sunset and sunrise recorded on our study site coordinates (sunset and sunrise timetables obtained from the Bureau des Longitudes, CNRS). For a given 24 hour period, daylight was defined as from 12:00 a.m. (the start of each intensive monitoring period) to sunset plus from sunrise to 12:00 a.m. of the following day, while night was defined as from sunset to sunrise.

Each animal was assigned to a landscape sector (Fig.1) based on the position of its home range. Note that adult roe deer are generally highly sedentary (Hewison et al. 1998) and indeed animals in this study always remained within a given sector during the year's monitoring. We did not analyse juveniles, as they are likely to disperse, indeed juveniles of both sexes show a high rate of natal dispersal (Linnell et al. 1998*b*). Home ranges were generated and mapped using the Kernel method (Worton 1989) at the 95% isocline with ArcView® 3·02 GIS (ESRI, Redlands, California, USA). We used the fixed kernel method recommended by Seaman et al. (1999, 1996) which seems to be the most conservative (Bowman et al. 1997). While this method may overestimate home range size to a certain degree, the alternative, the least squares cross validation method, may introduce a marked variability to the estimates, especially at low sample size (Börger et al. 2006). We also removed data during the first 8 days of monitoring to avoid potential bias due to the effects of capture on behaviour (Morellet et al. 2009).

To analyse variation in activity and movement along our landscape gradient, we performed linear mixed models (lme in the RGui v2.4.0 (http://cran.r-project.org) software, R Development Core Team (2007)), considering the proportion of intervals including i. activity, or ii. movement as the dependent variable, with the seasonal period (5 modalities), moment (day/night) and landscape sector (3 modalities) as fixed factors. We also included animal identity as a random factor to account for non-independence of data (pseudo-replication) at the individual level. In these models, as the dependent variable was expressed as a proportion, we first performed arcsine square root transformation to achieve normality. Prior to analysis, we checked for normality (Shapiro-Wilk test) and the graphical structure of the residuals. We carried out the above analysis for the two sexes separately, because roe deer behavior changes across the year in a sex-specific way in relation to reproduction and physiological constraints (Andersen et al. 1998).

Results

i. Activity rates

a. Males

In the model analyzing the activity rate of male roe deer, the effects of the three-way interaction period*sector*moment (LR=11.76, df=32, P=0.16) was not significant. In contrast, all three of the two-way interaction terms had a significant impact on male activity rate (period*sector LR=23.23, df=24, P=0.003, sector*moment LR=9.06, df=24, P=0.01 and period*moment LR=12.26, df=24, P=0.01), suggesting that the activity rate of male roe deer varied in relation to landscape structure. During winter, there was a gradient of decreasing activity rate among males especially during the day, from the highest value in the forest sector (deer active 38% of the daily time and 44% of the night time) to the lowest in the open field sector (deer active 25% of the daily time and 38% of the night time) (Fig. 2). A marked higher activity level in the forest sector during daytime as been also observed during fawning (30% of the time active) and autumn (22% of the time active), respect to intermediate and open sectors (Fig.2). Otherwise, during the rut, day time activity was somewhat higher in the forest and in the open field sector (active 26% of the time) compared to the intermediate sector, while during the night activity level was higher in the open field sector (active 43% of the time). During autumn the activity level was lowest in the intermediate sector (active 7% of the day time and 29% of the night time) (Fig. 2). Overall, daily activity rates of males were somewhat lower during the fawning, rutting and autumn seasons compared to winter and late winter-early spring (Fig. 2). Finally, throughout the year and across the whole landscape gradient, the activity rate of males differed significantly between day and night but this difference was markedly more pronounced in the intermediate and open field sectors than in the forest sector (Fig. 3). In addition, the difference in the rate of movement between day and night appeared to be more marked during the fawning, rutting and autumn seasons (Fig. 3).

b. Females

In the model analyzing the activity level of female roe deer, the effect of the three-way interaction period*sector*moment (LR=9.46, df=32, P=0.30) was not significant. Also the two-way interaction period*sector was not significant (LR=14.48, df=24, P=0.07). In contrast, the activity level of females was significantly influenced by the two way interaction period*moment (LR=17.23, df=16, P=0.002) and sector*moment (LR=9.70, df=16, P=0.008). Thus, activity level of female roe deer was significantly related to landscape structure. Throughout the year, the activity rate of females was higher during the night than during the day (Fig. 4) with a gradient from the forest to the open sector. In the open sector the day-night difference in activity level was higher while was lower in the forest sector (Fig. 4), where during fawning day and night level of activity reached the seam mean level (30-31% time active). Activity level seemed to be lower during the fawning and rutting seasons, respect to the rest of the year (Fig. 4).

ii. Movement rates

a. Males

In the model analyzing the movement rate of male roe deer, the effect of the three-way interaction period*sector*moment (LR=15.42, df=32, P=0.051) was not significant. In contrast, all three of the two-way interaction terms had a significant impact on male movement rate. Thus, movement rate of male roe deer appeared to vary in relation to landscape structure. Daily movement rate seemed generally higher in the forest sector than in the intermediate and open field sectors (forest sector: mean 37% of the day time moving; intermediate and open field sector: mean 31%), although this difference was most pronounced during winter (period*sector interaction: LR=20.91, df=24, P=0.007, Fig. 5). The pattern for nocturnal movements was somewhat different, as males appeared to move more frequently in the intermediate sector (mean 52% of the night time moving), compared

to the forest (mean 41%) and open field sectors (mean 44%), particularly during the late-winter-early spring, fawning and rutting seasons (Fig. 6). Males moved more frequently at night than during the day, but this difference was markedly more pronounced in the intermediate and open field sectors than in the forest sector (sector*moment interaction: LR=31.09, df=24, P<0.0001) (Fig. 6). In addition, the difference in the rate of movement between day and night appeared to be more marked during the fawning, rutting and autumn seasons (period*moment: LR=17.47, df=24, P=0.002, Fig. 6). Overall, the rate of diurnal and nocturnal movements was lowest in autumn and winter, while it was highest during the rutting season and, to a lesser extent, late winter-early spring (Fig. 6).

b. Females

In the model analyzing the movement rate of female roe deer, the effect of the three-way interaction period*sector*moment (LR=12.34, df=32, P=0.14) was not significant. Similarly, neither the two-way interaction terms period*sector (LR=15.48, df=14, P=0.051) and sector*moment (LR=0.68, df=24, P=0.71), nor the main effect of sector (single effect: LR=3.18, df=14, P=0.20) had a significant impact on female movement rate. Thus, movement rate of female roe deer was not significantly related to landscape structure. In contrast, the movement rate of females was significantly influenced by the two way interaction period*moment (LR=18.64, df=18, P<0.001). That is, movement rate of females was higher during the night (mean moving 39% of the time) than during the day (mean moving 34% of the time), but this difference was particularly marked during autumn (Fig. 7). Movement rate was lower during the fawning and rutting seasons, and higher during the winter and late winter-early spring periods (Fig. 7).

Discussion

Our analysis of roe deer behavioral patterns in a spatially heterogeneous landscape revealed that deer activity and movement rates were determined by a combination of landscape structure, seasonal effects and diurnal cycles.

First, we found that, during winter (December-January), activity levels and movement rates of males decreased along the gradient of increasing landscape openness such that the highest activity levels and movement rates were observed in the strict forest environment (Figs. 2 and 5). This effect of landscape openness on activity level (but not movement rate) was also significant in females, with a trend similar to that of males (Fig. 4). Thus, this result did not support our expectation, which predicted an opposite pattern of higher activity and movement in the most open sectors because of the higher distance between landscape elements providing high quality food (open fields) and those providing shelter (woodlots) in highly fragmented areas (Nixon et al. 1991; Rouleau et al. 2002; Godvik et al. 2009). Food quality and quantity is generally poorer in the forest with respect to open areas, particularly in agro-ecosystems (Turner 1979; Andersen et al. 1998; Hewison et al. 2009), and food availability may be particularly low during late winter in the forest compared to meadows and cultivated fields where forbs and cultivated plants grow. Indeed, in our study site, we have previously shown that levels of both nitrogen and phosphorous were higher in deer faecal samples collected in the more open sectors compared to the forest environment in winter, suggesting marked spatial variation in the availability of high quality feeding habitat due to the presence of cultivated crops in the agricultural plain (Hewison et al. 2009). Thus, deer in a strict forest habitat may be obliged to increase their foraging time (activity and movements) to compensate for the lower availability and quality of food (Moncorps et al. 1997; Iason et al 2000; Skarin et al. 2010). This effect may have been particularly marked among males due to the considerable additional energetic and protein requirements of antler growth during winter (Robins 1983). However, this pattern was reversed during the rut, when males were more active and, to some extent, moved more in the more open sectors of the landscape. This is likely linked to the search for receptive females for reproduction (Kamler et al. 2007). Indeed, home range size increases with landscape openness

(Hewison et al. 1998; Cargnelutti et al. 2002) and female deer density is substantially lower in the more open sectors compared to the forest (Hewison et al. 2007). Hence, bucks in the intermediate and open landscape sectors presumably spend more time roaming over a greater surface area in search of this more dispersed reproductive resource.

Second, in support of our expectation, we found strong evidence that deer of both sexes were more active and moved more frequently during the night than during the day throughout the year (Figs. 3, 4, 6 and 7). In general, the activity pattern of cervids shows a peak at dawn and dusk (Georgii 1981; Cederlund 1989; Pepin et al. 2006; Owen-Smith et al. 2010), but in human-dominated landscapes, in the presence of diurnal human disturbance (e.g. agricultural practices), ungulates generally increase their nocturnal activity (Georgii 1981; Langbein et al. 1997; Pipia et al. 2008; Godvik et al. 2009). We also observed that this day-night difference in activity levels and movement rates was particularly marked in the intermediate and open landscape sectors (Fig. 3, 4 and 6). In more open, fragmented landscapes, deer are more vulnerable to potential threats and likely avoid disturbance by spending the day in woodlots and moving to meadows or cultivated fields to feed during night (Montgomery 1963; Nixon et al. 1991; Ager et al. 2003; Godvik et al. 2009). However, we did not find any clear evidence that the contrast in activity level or movement rate between day and night was more marked during the hunting season. This suggests that deer become more nocturnal in response to the general level of non-specific disturbance, rather than because of a specific anti-predator strategy to avoid mortality through hunting (*cf* Singer et al. 1991; Naugle et al. 1997; Neumann et al. 2009).

Third, both male and female deer seemed to be more active during winter and early spring compared to the rest of the year (Figs. 2 and 4) and females also moved more during this period (Fig. 7). Males showed high levels of activity also during the rut, especially during the night (Fig. 2) and they also moved more frequently (Figs. 5 and 6) (Cederlund and Sand 1994; Neumann et al. 2009; Pepin et al. 2009). This partially supports our expectation, in that males appear to increase their activity level and movement rate as a result of searching for mates (Flint and Krzywinski

1997; Kamler et al. 2007). However, in contrast to our expectation, fawning does not lead to increased activity among females (Fig. 4) contrary to what was observed for red deer (Clutton-brock et al. 1982) and bighorn sheep (Ruckstuhl and Festa-Bianchet 1998). Rather, it seems that the hiding behavior of roe deer fawns as their neonatal security strategy imposes a spatial constraint on the movement of adult females (Linnell at al. 1998*b*) causing females to decrease their home range size and activity during this period (Saïd et al. 2005; Rhoads et al. 2010). Indeed roe deer fawns only start to regularly follow the mother at the end of the rutting season (Linnell 1994), whereas in follower species such as bighorn the offspring follow the mother from the birth (Ruckstuhl and Festa-Bianchet 1998). We found high overall activity rates of both sexes during winter and early spring (Figs. 2 and 4). This is in contrast with other studies showing lower levels of activity in winter in roe deer (Cederlund 1981; Jeppesen 1989) and in other ungulates (Langbein et al. 1997; Maier and White 1998; Pepin et al. 2009) in relation to a general shortage of food availability and a concomitant decrease of basal metabolism (Drozdz et al. 1975; Weiner 1977). In our study area, the climate is mild and the growing season often starts in late winter, especially in meadow and cultivated field habitats (Lavalle et al 2009). Thus, food availability may not decline so drastically in winter, allowing roe deer to maintain a high level of foraging activity. This result could also indicate that deer are more active at this time in order to avoid being hunted. Indeed, hunting induces an increase in movements (Root et al. 1988; Millspaugh et al. 2000; Vieira et al. 2003) and vigilance (Jayakody 2008; Benhaiem et al. 2008), that may be especially marked in open areas (Naugle et al. 1997; Benhaiem et al. 2008; Jayakody 2008). However, we did not observe similarly high activity levels in the early part of the hunting season (September-November) (Figs. 2 and 4), suggesting that this pattern is probably due to nutritional constraints (Skarin et al. 2010) rather than hunting disturbance. Indeed, food quality and availability is generally lower during winter and early spring and highest during summer, particularly in cultivated landscapes (Nixon et al. 1991; Lesage et al. 2000), allowing deer to achieve rumen fill with good quality forage both more quickly and without the need for substantial movement (Skarin et al. 2010). This season also coincides with the

establishment phase of the territorial period for male adults that starts in February-March (Linnell and Andersen 1998; Rossi et al. 2003) and during which male movement rates generally increase (Sempéré 1979). Indeed, roe deer males are considered strongly territorial (Bramley 1970), with territory establishment and defense comprising self-advertisement, often ritualized in displays, chases and retreats, and more rarely combat (Bramley 1970; Danilkin and Hewison 1996; Hoem et al. 2007).

In conclusion, we have shown how spatial heterogeneity in the distribution of both food and sources of disturbance interacts with reproductive constraints to determine how deer behavior varies across fragmented landscapes. Further work should aim to complement the present analysis with direct observations of the time budgets of individual roe deer (feeding, vigilance, reproductive behavior, etc.) in order to elucidate in more detail the underlying mechanisms by which landscape structure influences behavioral patterns of large herbivores.

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Figures

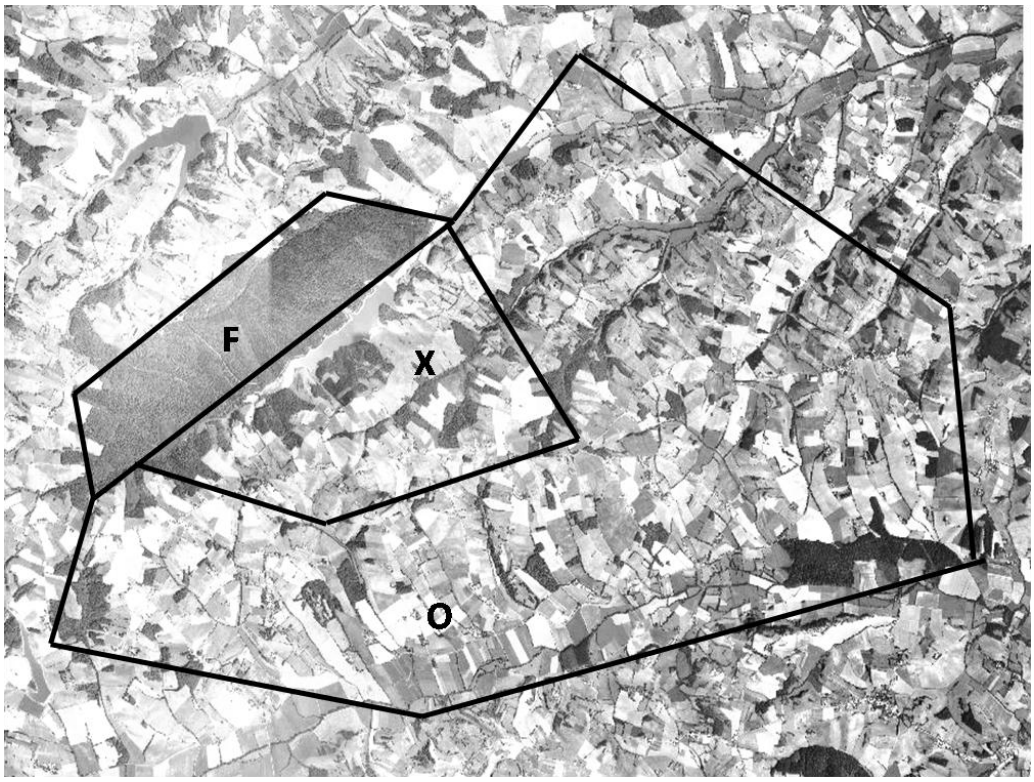
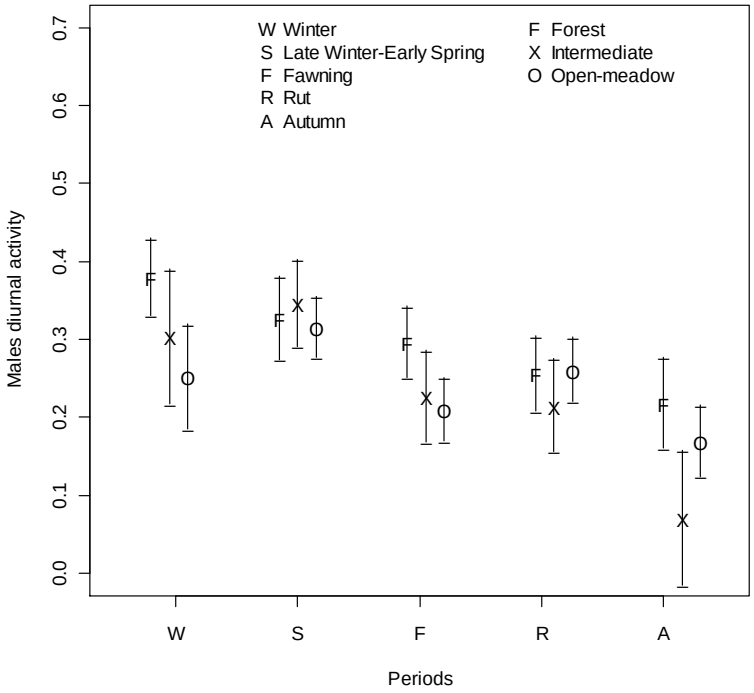


Fig. 1. Map (year 2007) of the study site (Aurignac, France, 43°13'N, 0°52'E) with the tree sectors classified on the basis of landscape openness parameters. F=forest (259 ha= 65% of the total area), X=intermediate sector (397 ha = 21% of the total area) and O=open fields sector (1217 ha= 14% of the total area)

a)



b)

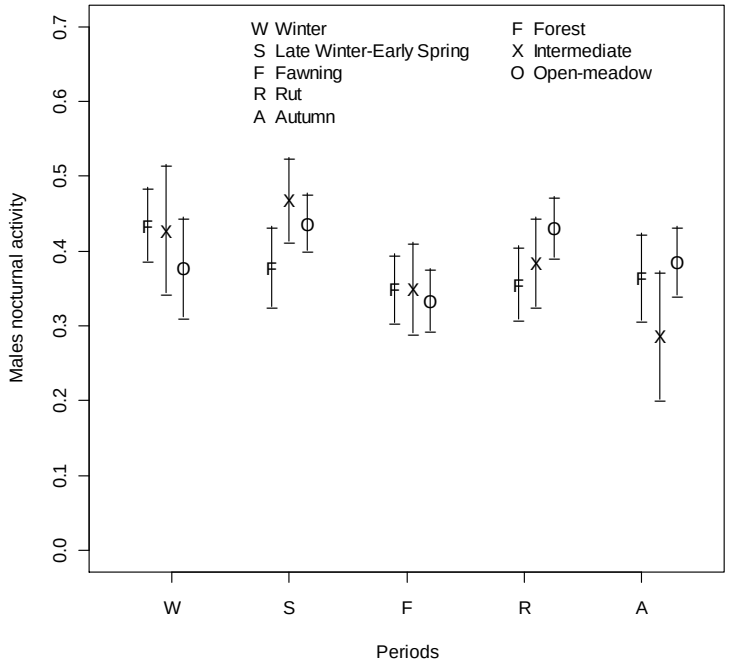
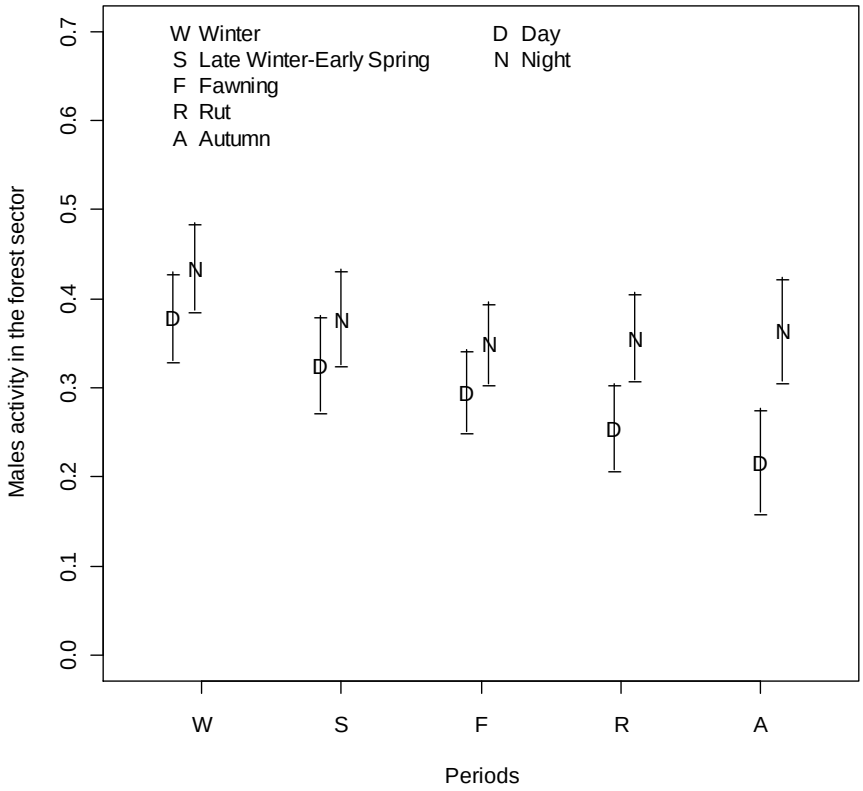


Fig. 2. Males diurnal (*a*) and nocturnal (*b*) activity (percentage of active intervals 5 min length) in the tree landscape openness sectors (forest, intermediate and open), during different biological-seasonal periods across the year: December-January (W=“Winter”), February-March-April (S=“Late Winter-Early Spring”), May-June (F=“Fawning”), July-August (R="Rut"), September-October-November (A="Autumn").

a)


W Winter
S Late Winter-Early Spring
F Fawning
R Rut
A Autumn
D Day
N Night
Males activity in the forest sector
0.0
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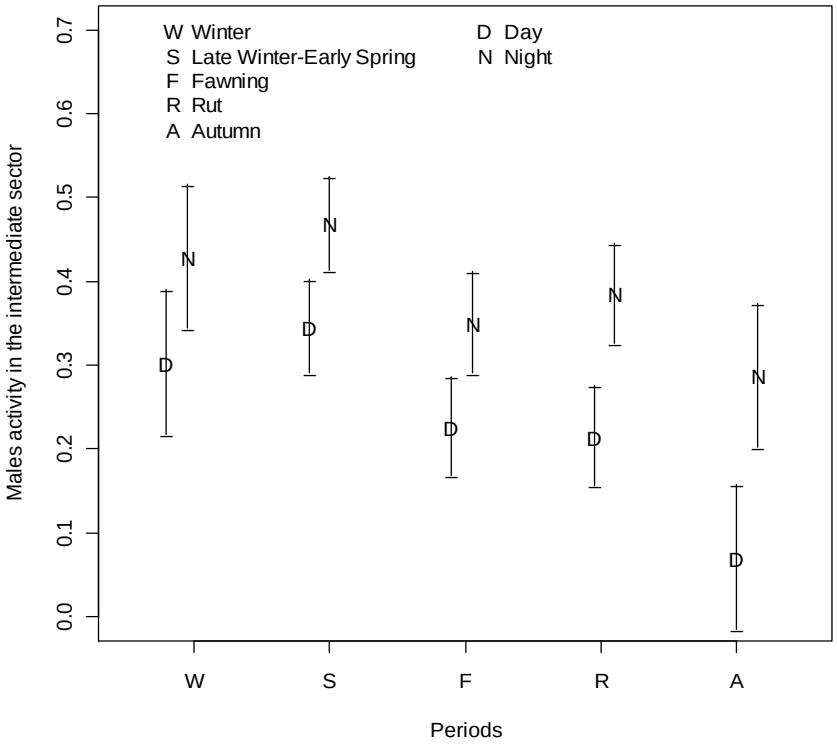
Periods

b)


W Winter
S Late Winter-Early Spring
F Fawning
R Rut
A Autumn
D Day
N Night
Males activity in the intermediate sector
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
W
S
F
R
A
Periods

c)

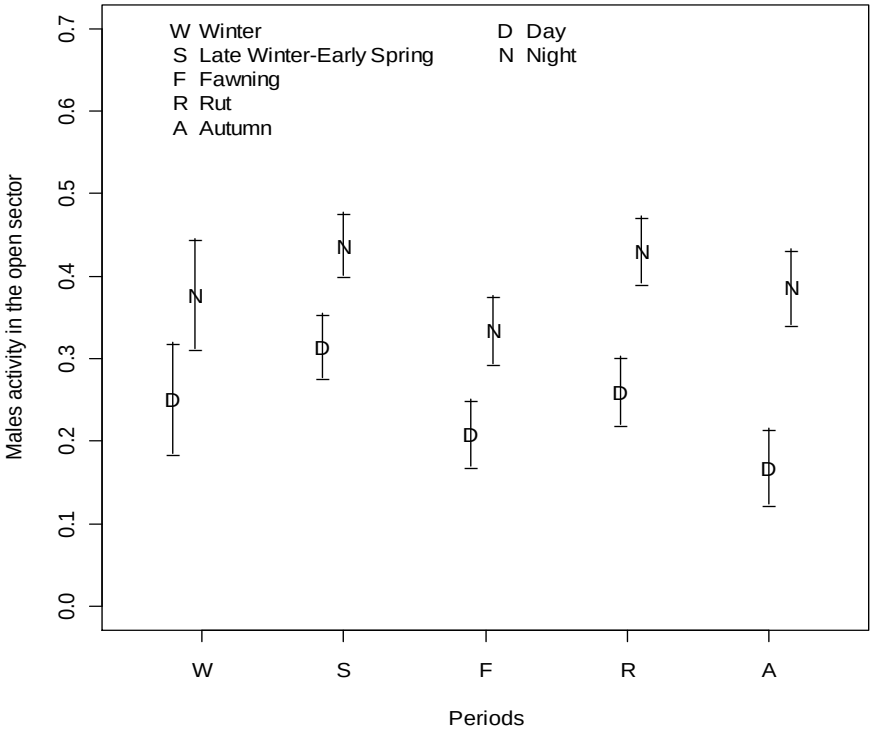
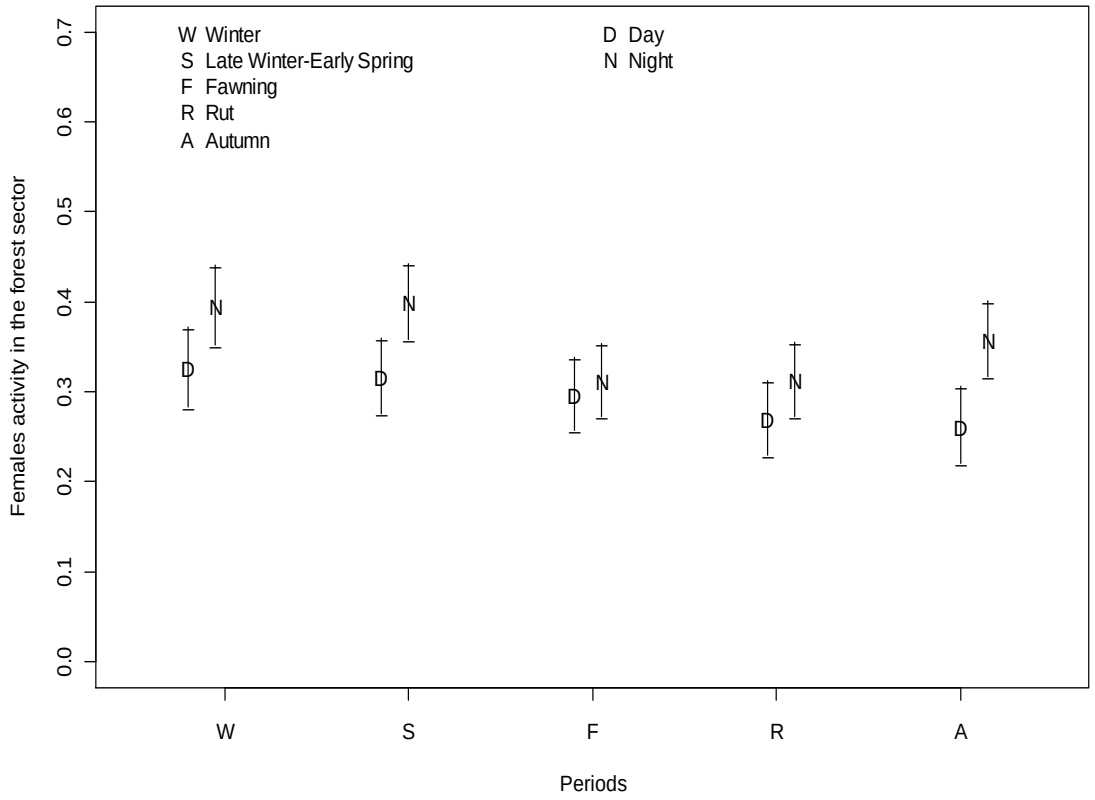
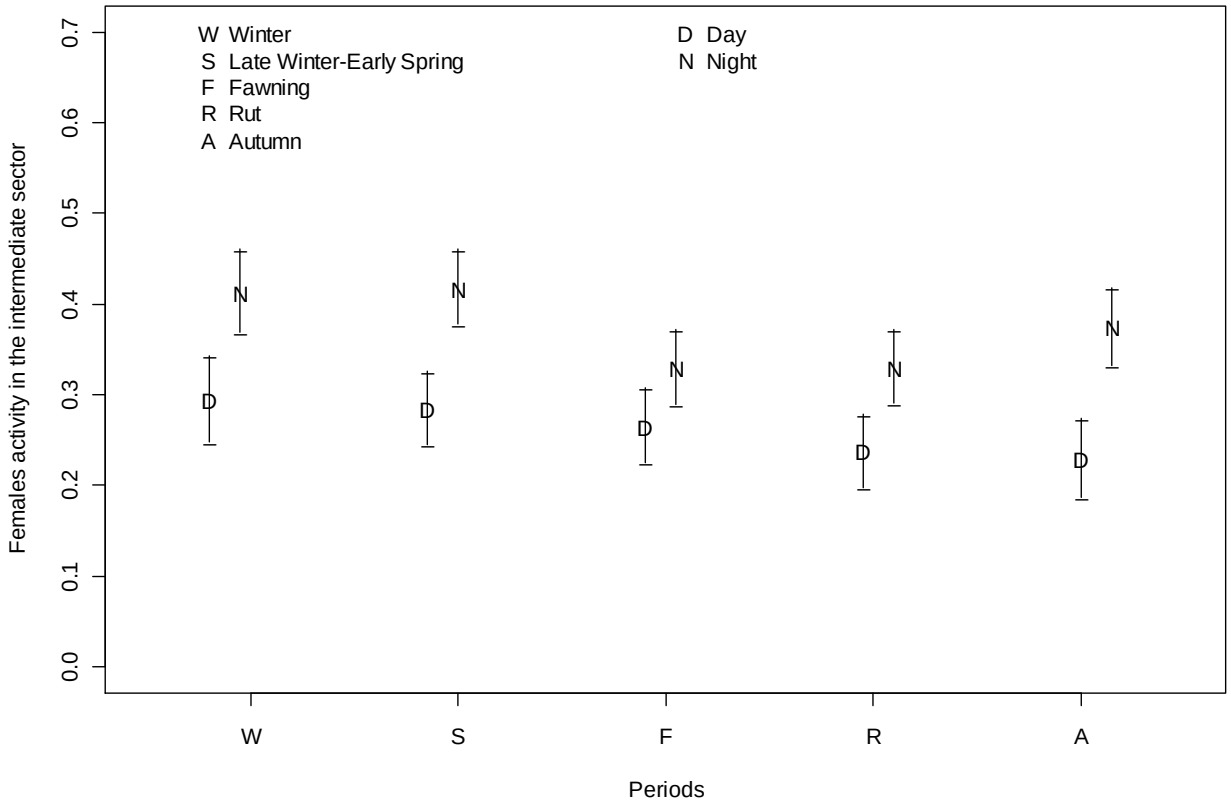


Fig. 3. Males diurnal and nocturnal activity (percentage of active intervals 5 min length) in the tree landscape sectors: forest (*a*), intermediate (*b*) and open (*c*); during different biological-seasonal periods across the year: December-January (W=“Winter”), February-March-April (S=“Late Winter-Early Spring”), May-June (F=“Fawning”), July-August (R="Rut"), September-October-November (A="Autumn").

a)


W Winter
S Late Winter-Early Spring
F Fawning
R Rut
A Autumn
D Day
N Night
Females activity in the forest sector
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
W
S
F
R
A
Periods

b)


W Winter
S Late Winter-Early Spring
F Fawning
R Rut
A Autumn
D Day
N Night
Females activity in the intermediate sector
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
W
S
F
R
A
Periods

c)

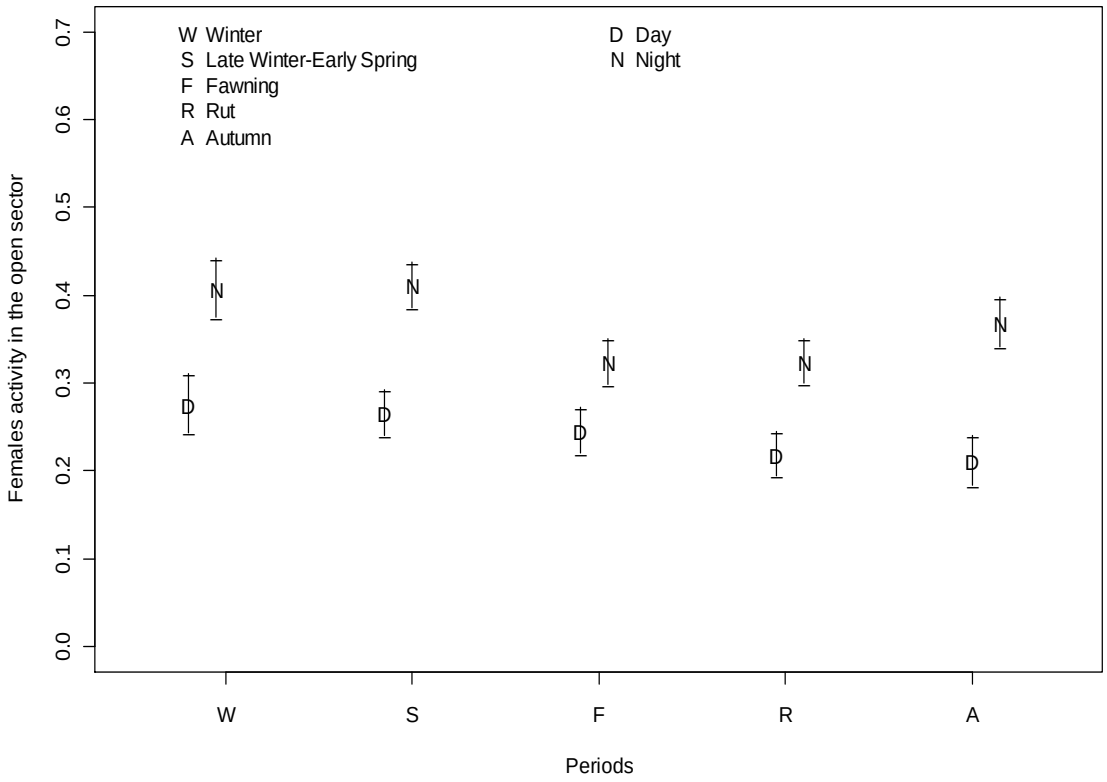
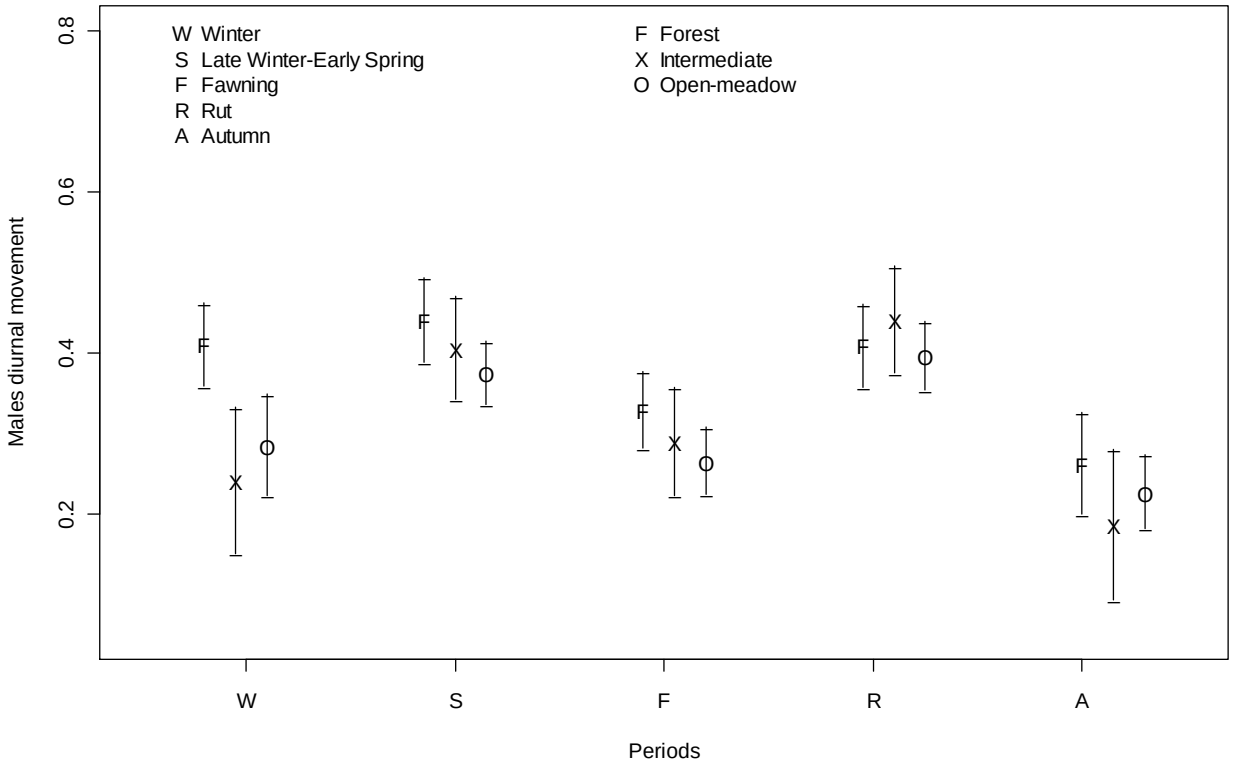


Fig. 4. Females diurnal and nocturnal activity (percentage of active intervals 5 min length) in the tree landscape sectors: forest (*a*), intermediate (*b*) and open (*c*); during different biological-seasonal periods across the year: December-January (W="Winter"), February-March-April (S="Late Winter-Early Spring"), May-June (F="Fawning"), July-August (R="Rut"), September-October-November (A="Autumn").

a)



b)

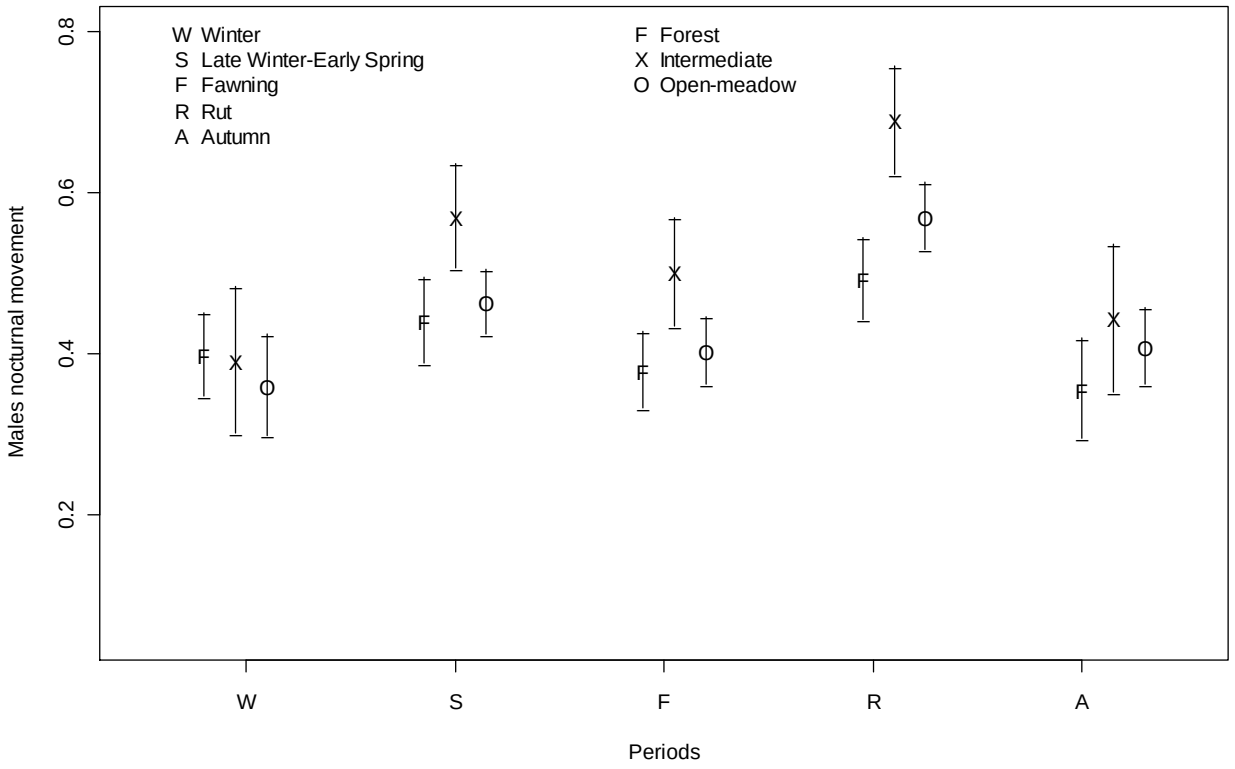
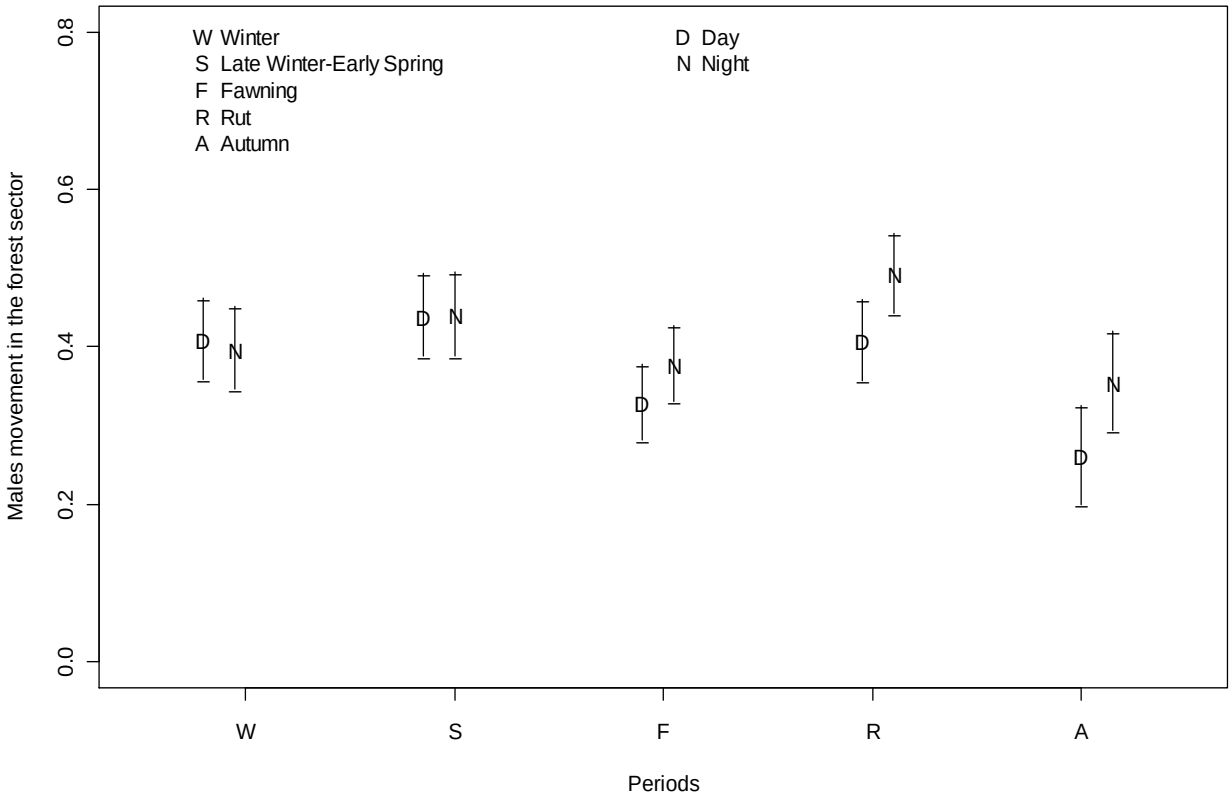


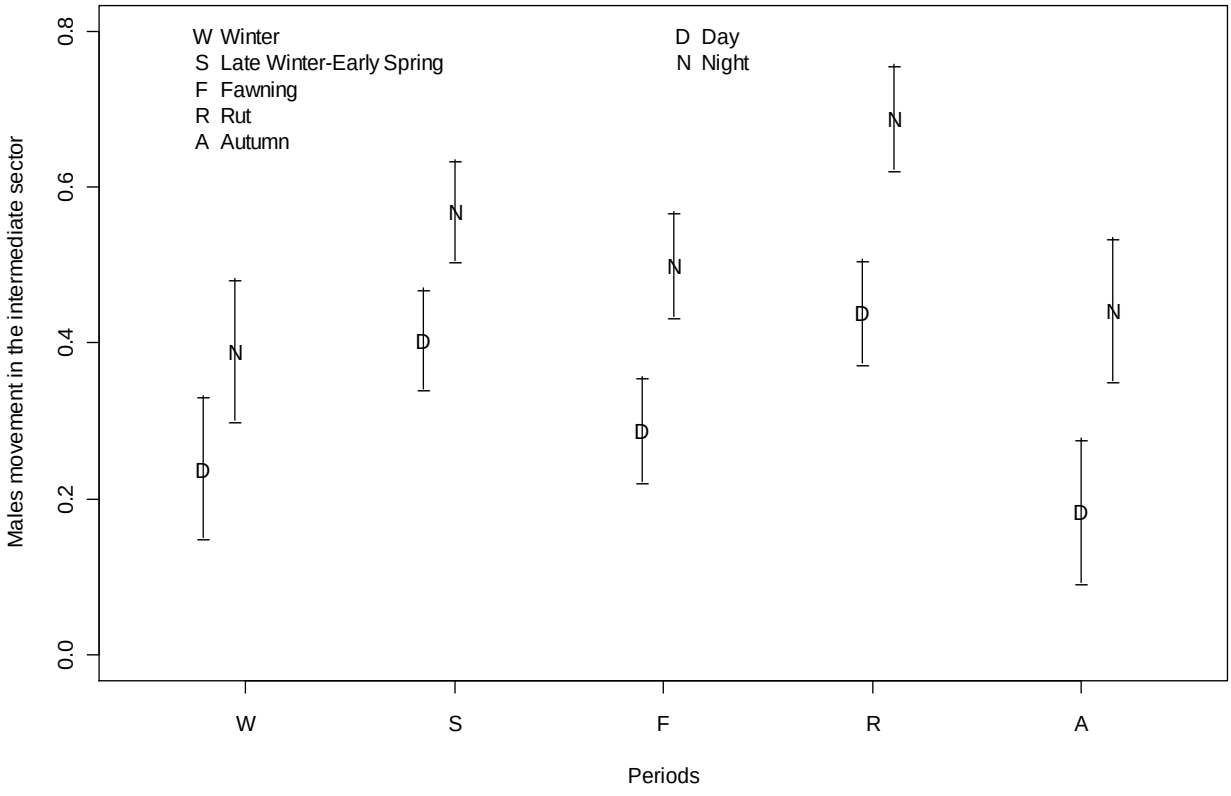
Fig. 5. Males diurnal (*a*) and nocturnal (*b*) movement (percentage of movement intervals 10 min length) in the tree landscape openness sectors (forest, intermediate and open), during different

biological-seasonal periods across the year: December-January (W=“Winter”), February-March-April (S=“Late Winter-Early Spring”), May-June (F=“Fawning”), July-August (R="Rut"), September-October-November (A="Autumn").

a)


W Winter
S Late Winter-Early Spring
F Fawning
R Rut
A Autumn
D Day
N Night
Males movement in the forest sector
0.0
0.2
0.4
0.6
0.8
W
S
F
R
A
Periods

b)


W Winter
S Late Winter-Early Spring
F Fawning
R Rut
A Autumn
D Day
N Night
Males movement in the intermediate sector
0.0
0.2
0.4
0.6
0.8
W
S
F
R
A
Periods

c)

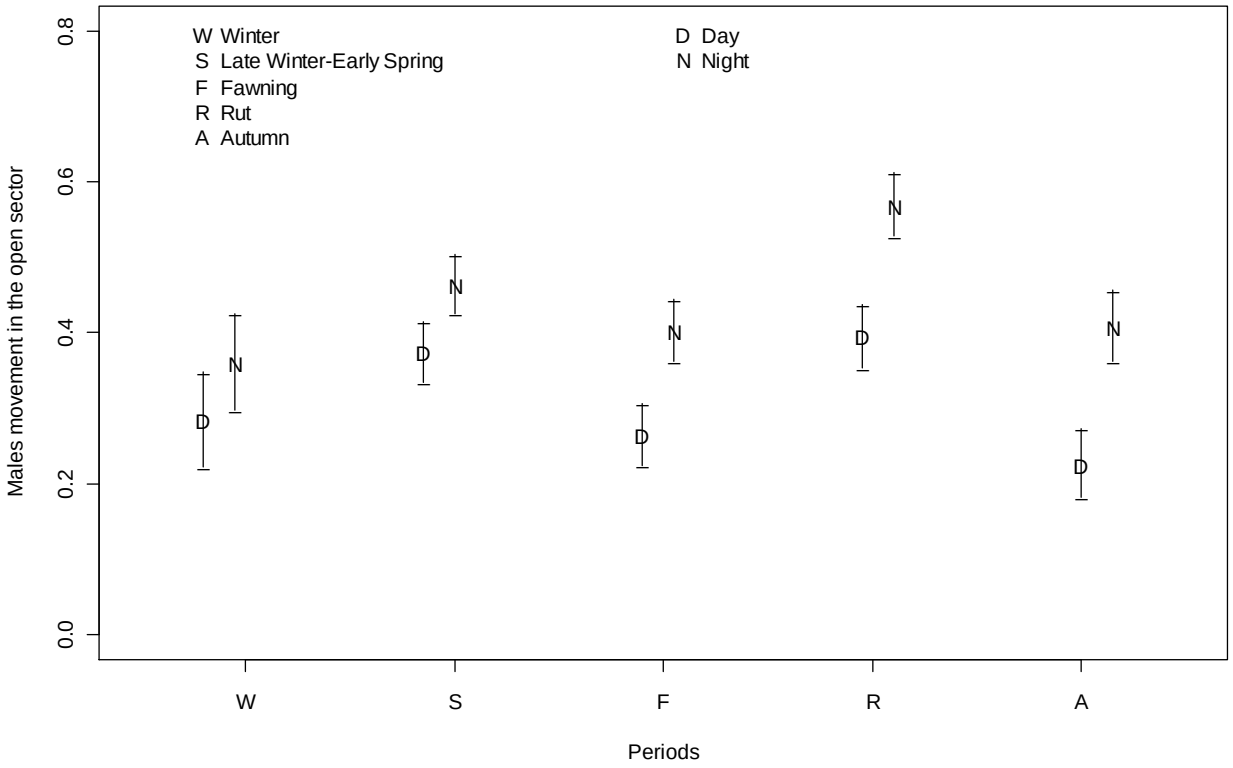


Fig. 6. Males diurnal and nocturnal movement (percentage of movement intervals 10 min length) in the tree landscape sectors: forest (*a*), intermediate (*b*) and open (*c*); during different biological-seasonal periods across the year: December-January (W="Winter"), February-March-April (S="Late Winter-Early Spring"), May-June (F="Fawning"), July-August (R="Rut"), September-October-November (A="Autumn").

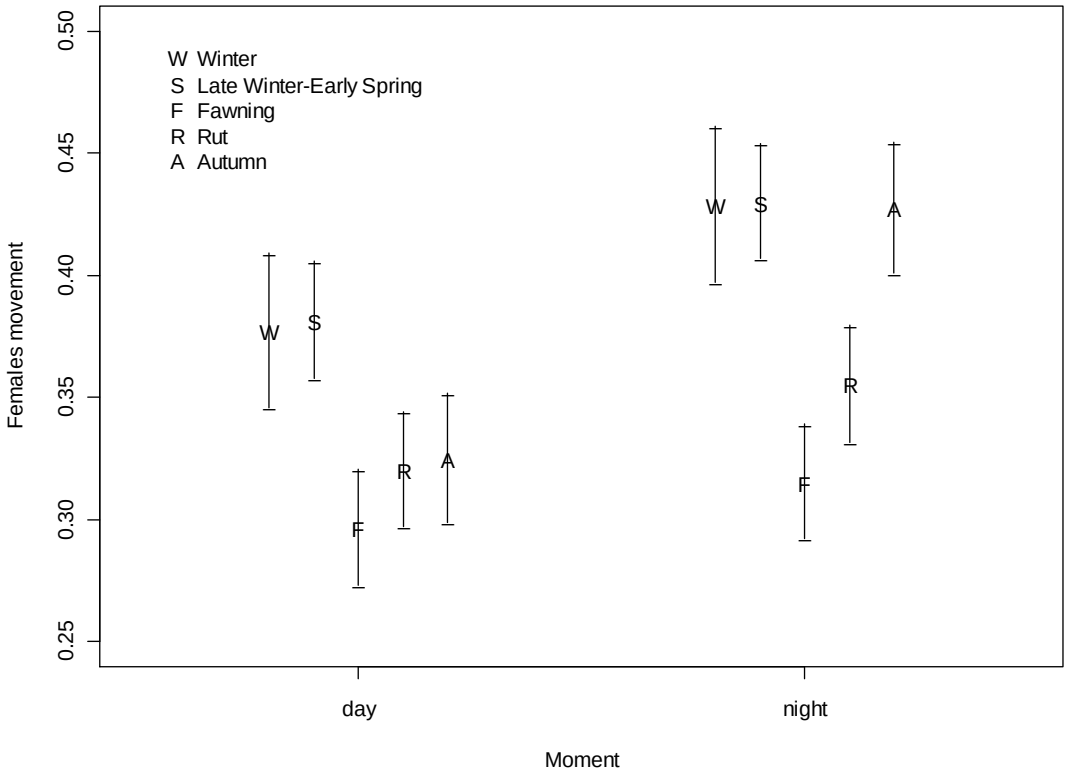


Fig. 7. Females day-night movement (percentage of movement intervals 10 min length) during different biological-seasonal periods across the year: December-January (W="Winter"), February-March-April (S="Late Winter-Early Spring"), May-June (F="Fawning"), July-August (R="Rut"), September-October-November (A="Autumn").

3.3 Third focus question and objective

How the landscape affect circadian rhythm in roe deer? Application of GPS data on activity level and movement (speed) to investigate the effect of landscape fragmentation on circadian rhythm.

Our analysis of roe deer circadian rhythm confirmed that deer activity and movement rates were determined by a combination of landscape structure, seasonal effects and diurnal cycles

As we expected the circadian rhythm of activity showed peaks at sunrise and sunset in deer of both the sexes and in both the landscape sectors.

Deer showed high activity values during nighttime, as expected, in both the landscape sectors with often a secondary peak around midnight. However the higher nocturnal activity level was not clearly more marked in the open sector. The high nocturnal level of activity was probably due to diurnal human disturbance in the open sector and to the poorer food availability and quality in the forest sector.

The high diurnal movement speed observed during autumn in both the sexes could indicate that animals run to avoid hunters during the day. However the rest of the hunting season did not confirm the presence of an hunting effect on 24h behavioral pattern. This suggests that modifications of the circadian rhythm are due to general level of non-specific disturbance, rather than because of a specific anti-predator strategy to avoid mortality through hunting.

Roe deer inhabiting the open sectors showed more marked movement peaks at dawn and dusk probably as consequence of the forays between woodlots using during day and fields at night.

Circadian rhythm of ore deer seems to be characterize both by species-specific fixed traits (as peaks at dawn and dusk) and by behavioral flexibility and plasticity in relation to environmental characteristics.

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Abstract

Animal life is controlled by circadian rhythm that changes during the year in relation to seasonal environmental characteristics. The landscape fragmentation process has modified many natural landscapes increasing human disturbance. In this study, we analyze the effect of landscape structure on the ore deer circadian rhythm, comparing data of deer inhabiting forest and open habitat.

The circadian rhythm of activity showed peaks at sunrise and sunset in both the landscape sectors. Deer showed high activity values during nighttime with often a secondary peak around midnight. This was probably due to diurnal human disturbance in the open sector and to the feeding strategies in forest deer especially during winter. Movement peaks at dawn and dusk were more marked in roe deer inhabiting open sectors, likely as consequence of a regular forays between woodlots and fields as disturbance avoidance strategy. Circadian rhythm of ore deer seems to be characterize both by species-specific fixed traits (as peaks at dawn and dusk) and by behavioral flexibility and plasticity in relation to environmental characteristics. With this work we have confirmed that spatial heterogeneity in the distribution of both human disturbance and resources interacts with reproductive constraints to determine behavioral differences across different landscapes. Further work should aim to investigate behavioral synchrony in deer inhabiting different environments to confirm our results.

Keywords: fragmentation; environment; habitat; activity; movement; plasticity; disturbance; feeding; GPS collar

Introduction

The organization of biological activities into daily cycles is universal in organisms (Bell-Pedersen et al. 2005). Animal life is indeed controlled by the "ciradian" rhythm. This biological rhythm has been defined as a 24-hour patterns in activity caused by endogenously controlled physical parameters (Aschoff 1966) that are influenced by daily/light conditions (Reppert and Weaver 2002; Dibner et al. 2010) and temperature (Dibner et al. 2010). The temporal coordination of internal biological processes, both among these processes and with external environmental cycles, is crucial for animal survival (Bell-Pedersen et al. 2005). The circadian rhythm has periodical change during the year (circannual) because of environmental stimuli defined "zeitgebers" (Aschof 1966). Diurnal variation in light intensity is generally the most consistent and reliable of these environmental factors in mammals (Bell-Pedersen et al. 2005; Dibner et al. 2010).

The temporal organization of activity patterns is peculiar to each species, being modulated by both external (environmental conditions) and internal (physiological state) factors (Ratikainen et al. 2007). The typical circadian rhythm of cervids is characterised by two daily peaks of activity at dawn and dusk (Cederlund 1981; Eberhardt at al. 1984; Cederlund 1989), that correspond to the two main foraging periods for many ungulates while resting periods occur around midday (Georgii 1981; Roby and Thing 1985; Pépin and N'Da 1991).

In ruminants, is documented that activity time change across the year (Godvik et al. 2009; Owen-Smith et al 2010) as consequence of the annual changes in the reproductive status of individuals (Pepin et al. 2009; Rhoads et al. 2010) and is influenced by temperature (Schmitz 1991; Demarchi and Bunnell 1995), time of sunset and sunrise (Beier and McCullough 1990) and disturbance by predators and humans (Mysterud et al. 2004; Skarin et al. 2010). In ungulates inhabiting temperate areas, annual variation in activity pattern is associated with seasonal changes in the availability of food resources (roe deer, *Capreolus capreolus*, Turner 1979; red deer, *Cervus elaphus*, Godvik et al. 2009; white-tailed deer, *Odocoileus virginianus*, Beier and McCullough 1990). The annual rhythm of activity results from changes in activity bouts: minimum active bout lengths were

recorded during summer and maximum values during winter (Jeppesen 1989). In spring has been registered a greater number of active bouts and value of daily activity time, probably due to the increased food quality, faster digestion and the high energetic requirements due to reproduction (Bourgoin et al., 2008).

Roe deer annual life cycle could be divided in five mainly seasonal-biological periods: December-January, February-March-April, May-June, July-August, September-October-November. The period of February-March-April corresponded to the beginning of the territoriality phase that starts usually in March (Hewison et al. 1998). Roe deer males are considered strongly territorial (Bramley 1970). Territory establishment and defense includes self-advertisement often ritualized in displays and more rarely combat (Danilkin and Hewison 1996; Hoem et al. 2007). Territory are established in spring and maintained over the rutting season in July and August. The periods of May-June corresponded to the fawning period. Most cervids of the temperate zone giving birth in spring and mating in autumn while the roe deer mates in summer. Females roe deer show a delayed implantation of five months between the rut (July-August) and the early January in which the blastocysts lie dormant in the uterus without implantation and embryonic development (Andersen et al. 1998). Hunted population are usually hunted in autumn (September-October-November) and winter (December-January). The roe deer is a relatively solitary animal, generally living alone or in very small family groups of two-three composed by an adult female with her fawns, with the possible presence of an adult male (Hewison et al. 1998). During late autumn and winter individuals of both sexes form fluid groups, whose composition changes rapidly, although membership is drawn from a limited pool of individuals (Linnell et al. 1998*a*).

The study of animal activity patterns is relatively an old theme of behavioral research. Of more recent interest are considerations of ecological factors affecting activity at both individual and population level (Gottardi et al. submitted). Very few studies have dealt with the effect of landscape structure on activity pattern in wildlife (Felix et al. 2007; Godvik et al. 2009; Rhoads et al. 2010), likely because of wildlife monitoring difficulties. Roe deer behavioral patterns in a spatially

heterogeneous landscape is determined by a combination of landscape structure, seasonal effects and diurnal cycles (Gottardi et al. submitted). Today, the use of activity captors integrated in GPS collars allows progresses in wildlife monitoring (Löettker et al. 2009; Owen-Smith et al 2010; Tomkiewicz et al. 2010). New studies on the effect of landscape structure on activity pattern in wildlife are necessary to analyze and better understand the effect of the mainly process that has modified natural habitat: the landscape fragmentation.

Landscape fragmentation, resulting in increased local habitat heterogeneity and disturbance due to associated human activity (Cole et al. 1997; Markovchick-Nicholls et al. 2008), is an ongoing and widespread process across much of Europe. It is often resulted from the conversion of natural woodland areas to agricultural crops and open meadows devoted to livestock grazing. This process can potentially endanger species, populations and communities, resulting in biodiversity reduction (World Resource Institute 1990; Marvier et al. 2004; Hansen et al. 2005) by both absolute loss of primary habitat and increasing isolation and reduction in size of remnant habitat patches (Saunders et al. 1991; Andrèn 1994). Landscape fragmentation has notable effects on animal behaviour of in terms of activity rhythm, movements and habitat use (Kie et al. 2005; Brinkman 2005; Banks et al. 2007; Rhoads et al. 2010). However, habitat generalists may be able to colonize and live in secondary matrix habitat because of their ecological flexibility (Marvier et al. 2004; Hansen et al. 2005; Devictor et al. 2008) and behavioral plasticity (Komers 1997; Anthes et al. 2010). A key aspect of this plasticity is the ability to adapt activity patterns in response to increase in human disturbance (Rhoads et al. 2010) and the modification of landscape structure (Jhonson et al. 2001; Godvik et al. 2009; Owen-Smith et al 2010).

Here, we explore how the circadian rhythm of a generalist ungulate, the roe deer *Capreolus capreolus*, change in relation to variation in local landscape structure. Previous studies has underlined that activity level and movement rate varies within a single population in relation to habitat openness in this species (Gottardi et al. submitted). Landscape structure affected behavior of both male and female roe deer, but this effect differed among seasons. During winter, deer activity

and movement rates decreased along the gradient of increasing landscape openness, probably to compensate for the poorer winter food availability and quality in the strict forest environment (Gottardi et al. submitted). Likely most difference in time-budget behavior between landscapes are found in winter because the differences in environmental conditions, especially the amount of cover, are greatest (Turner 1987). In contrast, during the rut, males were more active in the most open sectors, probably linked to their search strategy for females which are more widely dispersed in this habitat (Gottardi et al. submitted).

In fragmented landscapes associated with high human disturbance, ungulates often increase the nighttime activity (Georgii, 1981; Hayes and Krausman 1993; Langbein et al. 1997) and movement, as found in our previous study (Gottardi et al. submitted). It have been already observed that many rural deer spent the day in woodlots and used cultivated fields during the night (Montgomery 1963; Nixon et al. 1991; Rouleau et al., 2002).

Although some observation on circadian rhythm in roe deer populations inhabiting open field and forest have been previously done (Zejda et al. 1985; Rouleau et al. 2002; Pipia et al. 2008), specific studies aiming to find possible modifications on ungulates circadian rhythm due to the landscape openness effect has never be done. In the study of Rouleau et al. (2002) the circadian activity pattern of roe deer inhabiting open and forest habitat seemed to not differ showing peaks of activity at dawn and dusk. In some cases field deer has been observed to show an higher activity level at dusk (Pipia et al. 2008). In the study carried on by Zejda et al. (1985), in a thinly wooded area with intensive agricultural exploitation, field roe deer was active five to seven time daily in daylight time, from October to April. They was always active at dawn and dusk so during the rest of the day they was active three to five times (Zejda et al. 1985).

In this study, we analyze the effect of landscape structure on roe deer circadian rhythm by studying activity levels and movement rates on 24h in strict forest habitat and open agricultural plain. We expected 1. that both forest and open habitat deer show peaks of activity at dawn and dusk; 2. that

activity and movement peaks at dawn and dusk are more marked in roe deer inhabiting open sectors; and 3. that deer are more active and move more during nighttime especially in open areas.

Materials and methods

Study site

This study study was carried out in the south-west of the France (Comminges region of the Midi-Pyrénées) in the Aurignac canton (43°13'N, 0°52'E). The study area has a surface of 7500 ha (ca.) and is situated in a hilly zone, rising to a maximum of 380 m a.s.l., with an oceanic climate (average annual precipitation 800 mm mainly in form of rain and average annual temperature 11-12°C). The area is characterized by a fragmented agricultural landscape with a central forest of 672 ha (7% of the total area) surrounded by a mixed open landscape with small woodland patches with an average size of 3 ha (14% of the total area), hedges (7% of the total area), meadows (34% of the total area) and cultivated fields (33% of the total area) (Hewison et al. 2009). Human presence is widely distributed across the study site as a result of sylvicultural and agricultural practices. Farms and small villages are placed all along the extensive road network which covers the zone (Gottardi et al. submitted).

The natural vegetation of the area is classified as a southwest European lowland-colline downy oak forest (Bohn et al. 2004). The central forest is mixed, composed by oak, Douglas-fir *Pseudotsuga menziesii*, hornbeam *Carpinus betulus* and pine *Pinus spp*.. The understorey is dominated by brambles *Rubus spp*., butcher's broom *Ruscus aculeatus*, ivy *Hedera helix* and common honeysuckle *Lonicera peryclimenum*. The woodland patches are dominated by oak *Quercus spp*., often associated with hornbeam *Carpinus betulus*. Hedges contain trees and ligneous shrubs (*Prunus spinosa*, *Cornus sp*., *Lonicera sp*., *Quercus sp*., *Rubus sp*., *Rosa sp*., *Crataegus sp*. *Hedera helix, Ligustrum vulgare*), grasses, sedge and forbs (*Gallium sp*.) (Hewison et al. 2009). The

meadows are most dominated by *Dactylis glomerata* and *Festuca arundinacea* or by *Festuca rubra* and *Agrostis capilaris*, and less frequently by ray gras *Lolium perenne*, *Holcus lanatus*, lucerne *Medicago sp.* and clover *Trifolium sp*. They contain also forbs such as the leguminous *Potentilla sp., Geranium sp., Sanguisorba sp*., and *Taraxacum sp*. but not when they are dominated by ray grass. The open fields are cultivated mostly with wheat and barley (51%), some sunflower (15%), maize (10%), soya (5%), sorghum (8%) and rape (4%) (Hewison et al. 2009).

Within the study site, we identified two landscape units: the forest and the open sectors. The forest sector covers 14% of the total area (259 ha) and is composed totally of forest (153 ha). The open sector covers 86% of the total area (1614 ha) and is composed of 18.1% woodland (292 ha), 5.3% hedgerows (85 ha), 35% meadows (564 ha) and 37.5% cultivated fields (606 ha).

The roe deer population was hunted on a regular basis from September to January by drive hunts with dogs and bucks were also stalked during summer (from June to August) (Hewison et al. 2009). An annual index of deer abundance indicated a relatively stable population from 1992 to 2008 (unpubl. data). Deer density in the study area was estimated for 2005 at around 4.0-7.9 deer/100 ha (Hewison et al. 2007).

Study population and data description

Our study was based on activity sensor data and GPS data collected during 4 years (2005-2008) of continuous monitoring of the studied population. The data set analysed was composed of 67 animals (24 males and 43 females), of these 17 animals (10 males and 8 females) inhabited the forest sector and 50 animals (14 males and 35 females) inhabited the open sector (Fig. 1). Animals were caught every year during winter (December-February) using large-scale drives of between 30 and 100 beaters and up to 4 km of long-nets (Hewison et al. 2009) and they were monitored over a continuous time period of maximum 13 months and minimum 5 months. In our analysis we considered only yearlings and adult animals. Tooth wear was used to assess age (Hewison et al.

1999) in three classes: juveniles (less than one year-old), yearlings (between one and two years-old) and adults (two years-old or more).

The roe deer were equipped with GPS Lotek 3300 for medium-size mammals (Lotek Engineering, Inc., Newmarket, ON, Canada) which were fitted following the procedure recommended in the Lotek manual (Lotek Wireless INC. 2002). Activity sensor data were available for only 62 (21 males and 41 females) of the 67 animals individuals, as some collars were not equipped with these sensors (Gottardi et al. submitted). The activity-inactivity data were recorded every 5 minutes (the sum of movements in each plane over a 5 minute period). The collars provided information on activity-inactivity through the three head-neck position sensors that generated three variables: a count of vertical collar movements (Y), the proportion of time the Y captor was in an extreme (head down) position (HD) and a count of horizontal movements (X).

Movement data are collected through GPS location data (fixes). GPS locations were taken at regular time intervals of 6 hours (06:00, 12:00, 18:00 and 24:00) throughout the year and at regular time intervals of 10 minutes during some periods of intensive monitoring of 24 hours (from 12:00 of one day to 12:00 of the following day). Intensive monitoring periods are randomly placed within the year and they cover all the biological periods of the roe deer annual life cycle, (especially territoriality, gestation, lactation and mating).

In the current analysis for both activity and movement, we only used data from these intensive 24 hour monitoring periods, which occurred on a total of 58 different days over the period of study (1 in December 2004, 13 in each of 2005 and 2006, 14 in the 2007 and 17 in the 2008) (Gottardi et al. submitted). The first period included the data from January (the beginning of the year N) and the data from December of the previous year (N-1). We also data during the first 8 days of monitoring to avoid potential bias due to the effects of capture on behaviour (Morellet et al. 2009).

Statistical analysis

Each animal was assigned to a landscape sector (forest or open sector) based on the position of its home range. Home ranges were generated and mapped using the Kernel method (Worton 1989) at the 95% isocline with ArcView® 3·02 GIS (ESRI, Redlands, California, USA). We used the fixed kernel method recommended by Seaman et al. (1999, 1996) which seems to be the best comparing to the alternative method, the least squares cross validation method, that may introduce a marked variability to the estimates, especially at low simple size (Börger et al. 2006). Adult roe deer are generally highly sedentary (Hewison et al. 1998) and indeed animals remained within a given sector during the year's monitoring (Gottardi et al. submitted). We did not analyse juveniles of both sexes, as they show a high rate of natal dispersal (Linnell et al. 1998*b*). We also removed data during the first 8 days of monitoring to avoid potential bias due to the effects of capture on behaviour (Morellet et al. 2009).

We estimated activity/inactivity for each 5 minute interval and the movement speed for each 10 minute interval for each individual and for each of the 24 hour periods of intensive monitoring. We used the three variables provided by the activity sensors of the collars (Y,X,HD) to determine activity within each 5 minute interval using a discriminant model (Gottardi et al. 2010) previously built to determitate active/inactive status. This model was generated from the calibration of the activity sensors by direct observation of captive animals carrying the same collars used in this study. The model correctly discriminated 84% of the "active" time intervals (defined as the animal spending at least 30% of the time active), and 97% of inactive ones (Gottardi et al. 2010).

We calculated the movement speed (km/h) on 24h monitoring. We calculated at individual level, the distance travelled between successive GPS fixes (see Cargnelutti et al. 2007; Gottardi et al. 2010) and then transformed the speed (km/10minutes) in km/h.

We divided the year in 5 periods in relation to the different seasons and we performed our analysis for each period independently, because behavior change across the year in relation to life cycle. We token into account the following periods: December-January (grouping in both sexes), February-March-April (territoriality in males and gestation in females), May-June (territoriality in males and

parturition in females), July-August (mating in both sexes and lactation in females), September-October-November (grouping in both sexes and lactation in females). Animals were drive hunted from September to January. We considered male and females in two separate sex group doing independently the analysis because their behaviour differ within each biological period.

To analyse variation in activity and movement speed during the 24 hours in the two sectors of landscape openness, we performed generalized additive mixed models (gamm in the RGui v2.4.0 (http://cran.r-project.org) software, R Development Core Team (2007)), considering i. activity, or ii. movement speed as the dependent variable. We also included as random factors animal identity, to account for non-independence of data (pseudo-replication) at the individual level and the day of monitoring. In the model used to analyse activity cycle the dependent variable was expressed as binomial value (1 as active 5 minute interval and 0 as inactive interval). While in the model used to analyse movement speed we performed logarithmic transformation (log(movement speed)) to achieve normality. Prior to analysis, we checked for normality the graphical structure of the residuals.

At last we displayed through graphical figures the circadian rhythm of activity and movement (speed), in the different biological-seasonal periods located across the year, of deer inhabiting forest and open sectors. Sunrise and sunset were determined using the timetables obtained from the Bureau des Longitudes, CNRS on our study site coordinates.

Results

i. Activity

a. Males

Circadian rhythm of activity showed peaks at dawn and dusk but with some difference between seasons. During winter (December-January) males forest deer showed one clear and high peak of activity at sunrise and two secondary peaks before midnight and at sunrise (fig. 2). Activity levels weakly differed between this two secondary peaks of activity indeed the values remained high from before midnight to around midday. Males open field deer showed low activity during day and high activity levels during night; activity level decreased after sunrise and increased before sunset reaching at dawn and dusk the maximum levels. During late winter-early spring period (February-April) males forest and open field deer showed peak of activity at sunrise and at sunset (fig. 5) but not highly or well definite at exception of the peak at sunset of deer inhabiting open field sector. Males forest deer showed in this period two additional peaks of activity: one around midday and one before midnight. In males inhabiting open field sector we observed a peak of activity that started around midnight and went on until sunrise. During fawning period (May-June) we observed a very similar circadian rhythm in both the landscape sector with peaks of activity at dawn and dusk (more marked in the forest habitat) and a third peak of activity around midnight. Activity levels were higher during nighttimes respect to daytime, especially in open habitat. Males open habitat roe deer showed a secondary weak peak of activity after midday (around 14:00). Also during rutting period (July-August) males forest and open habitat roe deer showed a very similar circadian rhythm (fig. 8) with low activity during the day and high activity during nighttimes. Activity level decreased after sunrise, reaching the lower values around midday and increased reaching the highest values at sunset. Activity values remained high during all the night (between the sunset to the sunrise of the successive day) but however was observed weak peaks at dawn and dusk. During rutting period (July-August) and autumn (September-November) (fig.3) males forest and open habitat roe deer showed a very similar circadian rhythm with low activity during the day and high activity during nighttimes. In both this periods activity level decreased after sunrise, reaching the lower values around midday and increased reaching the highest values at sunset. Activity values remained high during all the night (between the sunset to the sunrise of the successive day) but

however was observed weak peaks at dawn and dusk. A secondary weak peaks was observed around midnight in both the environments.

Movement peaks at dawn and dusk were not more marked in males roe deer inhabiting open sectors.

We observed a generalized higher activity level during night respect to daytime over all the year and in both the landscape sectors.

The activity peak corresponding to sunset was sometime somewhat more marked but not preferentially in the open field habitat respect to forest. As example it was more marked in open field landscape during winter-early spring period (February-April) but extremely more marked in forest landscape during winter (December-January) (figs. 2 and5).

b. Females

Circadian rhythm of activity showed peaks at dawn and dusk but with some difference between seasons. During winter (December-January) females roe deer showed peaks at dawn and dusk and some other peaks. Females forest deer showed a third activity peak around midnight while females open field habitat deer showed two additional peaks during night one before and one after midnight. Females open field deer showed also a marked peak of activity around midday while forest deer only a weak increase of activity in this part of the day. During late winter-early spring period (February-April) females forest and open field deer showed a peak of activity at sunset. Females forest deer showed only one peak of activity while females inhabiting the open habitat showed two secondary peaks one at sunrise and one around midnight. Open field deer showed high activity levels over all the night. During fawning period (May-June) we observed more pronounced peaks of activity in females forest deer (fig.6). However also females open field deer showed peaks at dawn and dusk with a third peak around midnight. In females inhabiting open field landscape, activity level was high during all the night. Females of the forest sector showed a weak peak of activity

around midday. During rutting period (July-August) forest and open habitat females roe deer showed high activity level during the night with a peak around midnight particularly high in female forest deer. Activity peaks at dawn and dusk were showed by females of both the landscape but they were higher in forest habitat. Females inhabiting both the sectors showed a secondary weak peak during daytime (in the morning in forest deer and around midnight in open landscape). During autumn (September-November) forest and open habitat roe deer showed a peak at sunset but only females inhabiting the open landscape showed the peak at sunrise. Females inhabiting the forest showed high activity during the night and decreasing activity after sunrise but they did not show a clear peak at dusk. Females of the open habitat showed a third peak of activity around midnight and one smaller around midday.

We observed a generalized higher activity level during night respect to daytime over all the year and in both the landscape sectors. During winter period (December-January), differently to the other periods, nightly activity level did not remained high over all the night but deceased after sunset and before sunrise reaching the daytime lowest levels. We observed the same thing in the circadian rhythm of females inhabiting the forest during fawning (May-June) (fig.6).

Also in females the activity peak corresponding to sunset was sometime somewhat more marked but not preferentially in the open field habitat respect to forest. As for males as example it was more marked in open field landscape during winter-early spring period (February-April) but more marked in forest landscape during winter (December-January).

ii. Movement speed

a. Males

Circadian rhythm of movement speed showed in general peaks at dawn and dusk but with some difference between seasons. During winter (December-January) males forest deer showed only one

peak at sunrise (no peak at sunset) and decreasing movement speed during the day with a minimum level after the sunset. Males open field deer showed in this period three peaks of activity one at sunrise (not highly pronounced), one (the highest) around midday and the last after sunset. During late winter-early spring period (February-April) both males forest and open field deer showed peaks at dawn and dusk both with a delay from the mean time of sunrise and sunset of this period. Males inhabiting open field sector showed a third peak of movement speed around midnight. During fawning period (May-June) both males forest and open field deer showed peaks at sunrise and sunset. The movement speed peak at sunset in open field deer is particularly high. Male deer inhabiting open field sector showed also changes in activity speed tendency during daytime but with low values. During rutting period (July-August) only males open field deer showed peaks at dawn and dusk. They showed also an additive peak around midnight and movement speed remained high during all the night. Data on males forest deer did not permit to show a pattern of movement speed in this period. During autumn period (September-November) both males forest and open field deer showed peaks at dawn and dusk but in both the landscapes movement speed remained high during all the daytime respect to nighttimes (fig.4). Movement speed in higher during the morning in open field deer and during the afternoon in forest deer.

Movement peaks at dawn and dusk were overall more marked in males roe deer inhabiting open sectors especially during winter (December-January) and summer (July-August) periods.

b. Females

Circadian rhythm of movement speed showed in general peaks at dawn and dusk but with some difference between seasons. During winter period (December-January) both females forest and open field deer showed peaks at sunrise and sunset. They showed in addition some secondary peaks. Females forest deer showed a third peak of movement speed after midnight and females open field deer two additional peaks during nighttimes, one before and one after midnight. Females inhabiting

the open field deer showed in addition a weak secondary peak around midday. During late winter-early spring period (February-April) only females open field deer showed peaks at dawn and dusk. They showed also a secondary weak peak around midnight. Data on forest deer did not permit to show a pattern of movement speed in this period. During fawning period (May-June) (fig.7) females forest deer showed clear peaks at dawn and dusk while females open field deer showed a peak at sunset and an increasing movement speed through nighttimes (after midnight). From the sunset onward during daytime, movement speed remained high and weakly increased. During rutting season (July-August) movement speed of females of both landscape sectors did not show clearly peaks at dawn and dusk. Females forest deer showed increasing movement speed during daytime that reaches maximum levels around midday and showed decreasing values during nighttimes until the sunrise. Females inhabiting open field sector showed high movement speed during daytime with a weak peak at sunset and another around midday, a third peak of activity was observed around midnight. During autumn period (September-November) both females forest and open field deer showed peaks at sunrise and sunset, but peaks showed by females forest deer are weak. Females open field deer showed clear and strong peaks at dawn and dusk with a secondary weak peak around midnight and another (very weak) around midday.

Movement peaks at dawn and dusk were overall more marked in females roe deer inhabiting open sectors especially during late winter-early spring period (February-April) and autumn (September-November).

Movement speed in females seemed to be generally higher during the day over all the year and in both the landscape sectors.

Discussion

Our analysis of roe deer circadian rhythm confirmed that deer activity and movement rates were determined by a combination of landscape structure, seasonal effects and diurnal cycles (Gottardi et al. submitted).

Both forest and open habitat deer showed in general peaks of activity at dawn and dusk as expected, with some difference between seasons and sexes.

During winter (December-January) (Fig. 2) the activity level in male forest deer is particularly high at sunset and activity showed high levels also during the daytime (in the morning). Has been previously observed that during winter activity levels of males decreased along a gradient of increasing landscape openness from the strict forest environment to the open field habitat (Gottardi et al. submitted). Deer inhabiting a strict forest habitat may be obliged to increase their foraging time to compensate for the lower availability and quality of food respect to agro-ecosystems (Iason et al 2000; Hewison et al. 2009; Skarin et al. 2010). This effect may have been particularly marked among males due to the considerable additional energetic and protein requirements of antler growth during winter (Robins 1983). We think that this pattern is probably due to nutritional constraints (Skarin et al. 2010) rather than hunting disturbance indeed during the first part of the hunting season (September-November) we did not notice the same pattern. During autumn, the circadian rhythm of activity was the same for both the landscape sectors and was characterized by low activity during the day, peaks of activity at dawn and dusk and high activity level during the night with a third peak around midnight (Fig.3) in both sexes. This result may indicate a behavioral response to hunting by decreasing activity during day and concentrate feeding during nighttime. Predators and human disturbance can affect deer activity patterns (Singer et al. 1991; Mysterud et al. 2004; Skarin et al. 2010) and in particular, diurnal human disturbance, can lead to greater nocturnal activity in ungulates (Kamler et al. 2007; Pipia et al. 2008; Godvik et al. 2009). Hunting generally induces an increase in movements (Millspaugh et al. 2000; Vieira et al. 2003) and vigilance, that may be especially marked in open areas (Benhaiem et al. 2008; Jayakody 2008). In our case we observed high movement speed during daytime respect to nighttime (Fig. 4) during autumn in both the sexes

this could indicate that animals run to avoid hunters during the day. However this is not confirmed during the rest of the hunting season (December-January) when only males inhabiting open landscape sector showed high diurnal movement speed (during the afternoon). This could maybe indicate that the hunting effect is stronger at the beginning of the hunting season while in late winter nutritional constraints have the greater effect on roe deer behavior (Skarin et al. 2010) rather than hunting disturbance (Gottardi et al. submitted).

The circadian rhythm observed in males during late winter-early spring period (February-April) seems to validate the winter nutritional constraints effect in forest landscape. Indeed, in male forest deer, activity level was high during the night and the circadian rhythm showed a diurnal peak of activity (reaching the nocturnal level of activity) around midday (Fig. 5) while open field deer did not show diurnal activity. However, the higher diurnal activity level observed in forest deer, may be also the consequence of the higher roe deer density of the forest habitat. For male adults, this season coincides with the territories establishment that starts in February-March (Linnell and Andersen 1998; Rossi et al. 2003). In our study area deer density is around six time greater in forest habitat respect to open agricultural landscape (Hewison et al. 2007). The elevate level of deer density could increase the manifestation of territorial behavior in forest deer, in the first phases of territories establishment.

During fawning period (May-June) females roe deer showed peaks at dawn and dusk, more marked in forest sector (Fig. 6). Open field females showed also a peak of activity around midnight (Fig. 6) and in general high activity level over all the night while at the contrary forest females showed low activity level during night. The high nighttime activity level, in accord of what already described for winter and autumn periods, may be de consequence of human disturbance. Indeed nocturnal activity increase with increasing human disturbance in ungulates (Kamler et al. 2007; Pipia et al. 2008; Godvik et al. 2009) and during spring the intensification of the agricultural works increase human disturbance in open field landscape. The relatively high movement speed showed in females inhabiting open habitat during the day (Fig. 7) may probably indicate an higher level of stress and

short fast movements around the place in which they leaved their offspring hidden. Indeed fawns hiding behavior as neonatal antipredatory strategy imposes a spatial constraint on adult females (Linnell at al. 1998*b*) causing females to decrease their activity and home range size during this period (Saïd et al. 2005; Rhoads et al. 2010). In our study area, as already observed in Gottardi et al. (submitted) fawning does not lead to increased activity among females contrary to what was observed in other ungulates (Clutton-brock et al. 1982; Ruckstuhl and Festa-Bianchet 1998).

During rut (July-August) males roe deer showed high activity level during all the night (Fig. 8) with increasing activity around midnight. We observed the same pattern in the circadian rhythm of the movement speed although we had not results for forest sector. The circadian rhythm of males roe deer is in accord of what expected in this period for the species indeed males are expected to increase their activity level and movement rate as a result of searching for mates (Flint and Krzywinski 1997; Kamler et al. 2007) especially during nighttime (Neumann et al. 2009; Pepin et al. 2009; Gottardi et al. submitted). Looking at Fig. 8 we noticed that activity peak at sunset was more marked in the open sector. Our previous study (Gottardi et al. submitted) showed that levels and movement rates of males increased along the gradient of increasing landscape openness, likely because home range size increases with landscape openness (Hewison et al. 1998; Cargnelutti et al. 2002) and female deer density is substantially lower in the open sector (Hewison et al. 2007). Hence, bucks in the open landscape sector presumably spend more time roaming over a greater surface area in search of this more dispersed reproductive resource (Gottardi et al. submitted).

Peaks of activity were not more marked in the open landscape despite our expectation. The activity peak corresponding to sunset was sometime somewhat more marked but not preferentially in the open field habitat respect to forest. Peaks at dawn and dusk were manifested in both the landscape sectors with not remarkably difference generalizable across the year, probably because peaks of activity at dawn and dusk in the circadian rhythm of cervids (Cederlund 1981; Eberhardt at al. 1984; Cederlund 1989) are strongly controlled by light conditions and physiological state than by landscape characteristics and disturbance level.

The circadian rhythm of activity showed often a secondary peak around midnight or in general a higher value of activity during nighttime respect to daytime. This was probably due to disturbance that occur during the day in the open sector and maybe due to the feeding strategies in forest deer because, having less food available respect to cultivated areas (Turner 1979), they must to spend more time searching food. This confirm the results of our previous work done on the same population where deer of both sexes were observed to be more active and more mobile during the night than during the day, likely as a response to human disturbance (Gottardi el al. submitted). Roe deer were previously thought of as a species of closed, predominantly wooded, landscapes (Putman 1988) and they have relatively recently colonized open agricultural landscapes (Linnell et al. 1998*a*; Hewison et al. 2001) thanks to their marked behavioral plasticity, but they do avoid areas associated with human activity and, hence, disturbance (Hewison et al. 2001; Coulon et al. 2008). In presence on human disturbance the use of disturbed sites increases at night (Hayes and Krausman 1993; Ratikainen et al. 2007), probably because animals feel more secure during darkness (Marchinton and Jeter 1967). We did not find any clear evidence that the higher activity during night was more marked during the hunting season (September-January). So, in accord of our previous study (see Gottardi et al. submitted), roe deer seems to become more nocturnal in response to the a general level of non-specific disturbance, rather than because of a specific hunting response as anti-predator strategy (Naugle et al. 1997; Neumann et al. 2009). In our work we observed that nighttime peaks were more marked in open sector as we can attend as response to a greater disturbance level and a lower level of cover. Deer could indeed became mostly crepuscular as a consequence of the loss of escape cover (Naugle et al. 1997). In agro-ecosystems deer may be obliged to adjust their behavior in response to landscape heterogeneity (Kie et al. 2002; Kie et al. 2005; Rhoads et al. 2010).

Also the circadian rhythm of movement speed showed in peaks at dawn and dusk with some difference between seasons and sexes. Movement peaks at dawn and dusk were more marked in roe deer inhabiting open sectors. In our previous study on landscape effects on roe deer behavior we observed that day-night difference in activity levels and movement rates was particularly marked in

the intermediate and open landscape sectors (Gottardi et al. submitted). In many rural populations, deer spend the day in woodlots, but use cultivated fields for feeding during the night (Nixon et al. 1991; Ager et al. 2003; Godvik et al. 2009). As a result of these regular forays between woodlots and fields, the movement speed of deer living in agro-ecosystems is generally thought to be higher than that of forest populations (Rouleau et al. 2002).

However circadian rhythm of movement speed is less clear than those of activity level in forest area, maybe due to a greater individual difference of animals inhabiting the forest sector that should be investigated in further analysis.

Circadian rhythm of ore deer seems to be characterize both by species-specific fixed traits (as peaks at dawn and dusk) and by behavioral flexibility and plasticity (as observed during the night). With this work we have confirmed our previous results on landscape openness effect: spatial heterogeneity in the distribution of both human disturbance and resources interacts with reproductive constraints to determine how deer behavior varies across fragmented landscapes. However until now, we have not investigate behavioral differences at individual level. The degree of behavioral synchronization could vary between landscape sector and this could mask some environmental effects and homogenize the results between different habitats. Further work should aim to investigate on individual differences and behavioral synchrony in deer inhabiting different landscapes to confirm our results.

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Figures

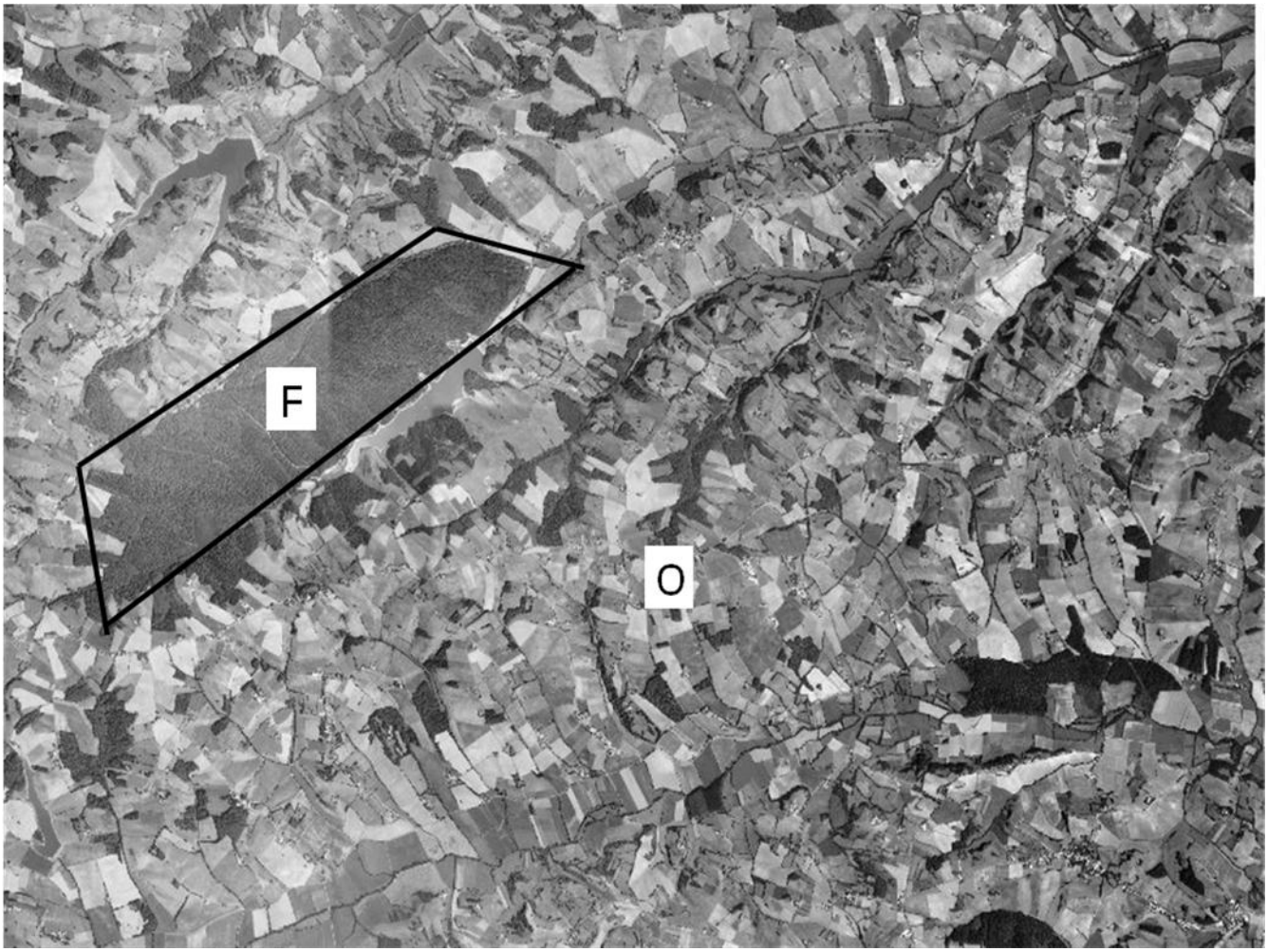

Fig. 1. Map (year 2007) of the study site (Aurignac, France, 43°13’N, 0°52’E) with the tree sectors classified on the basis of landscape openness parameters. F=forest (259 ha= 65% of the total area) and O=open fields sector (1614 ha= 35% of the total area)

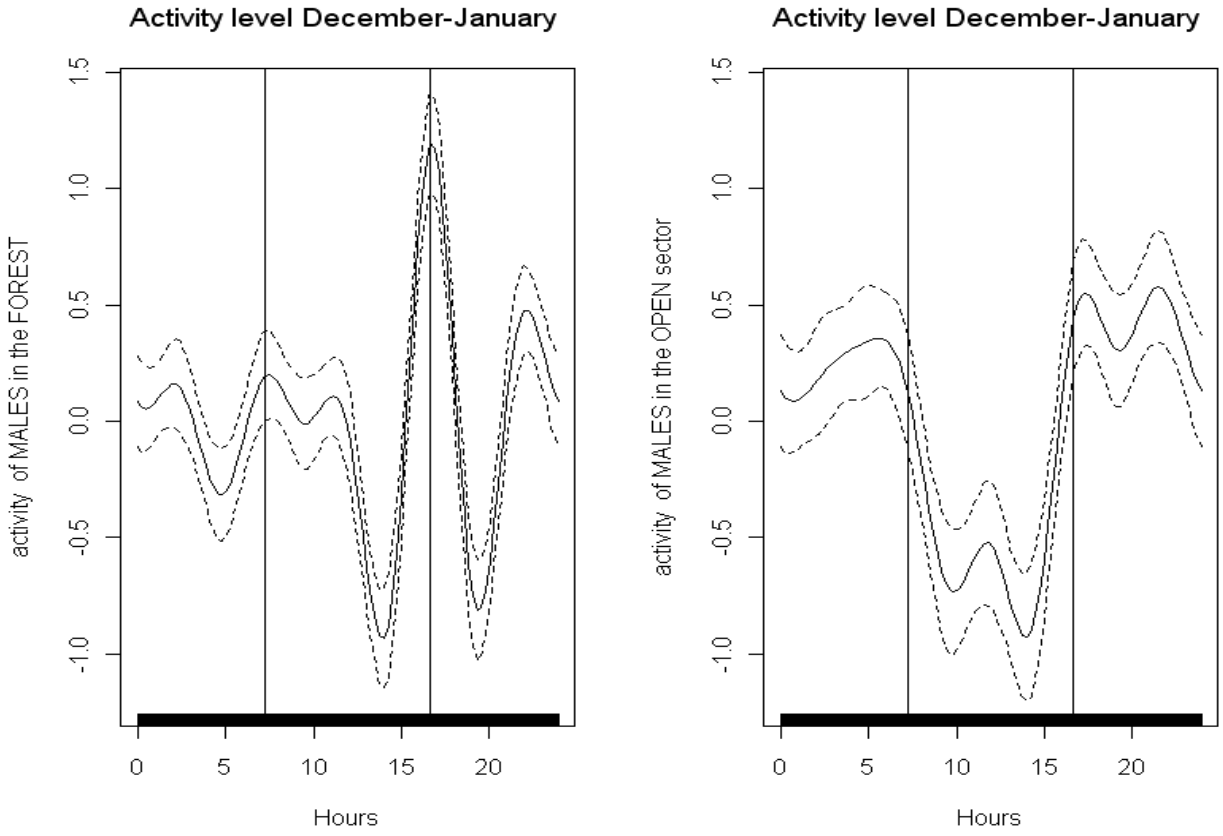

Figure 2. Males activity in winter (December-January)

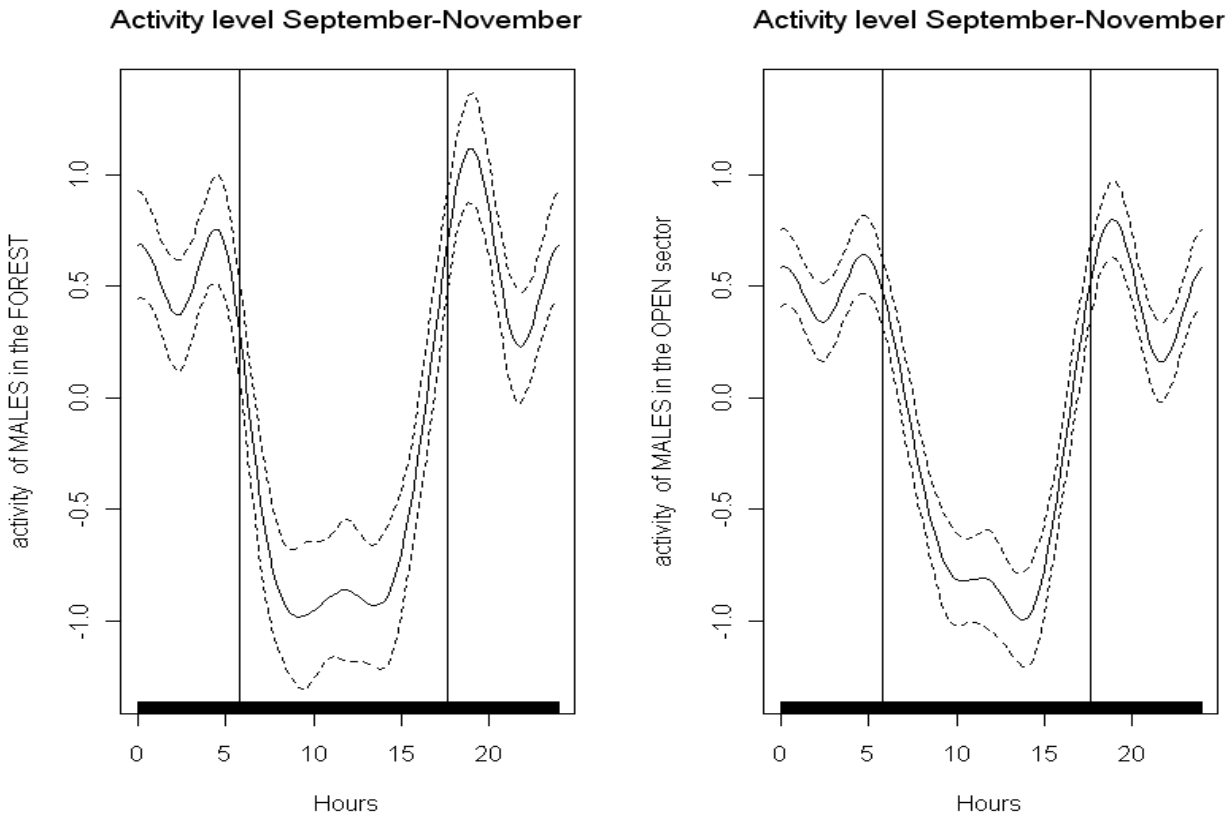

Figure 3. Males activity in autumn (September-November)

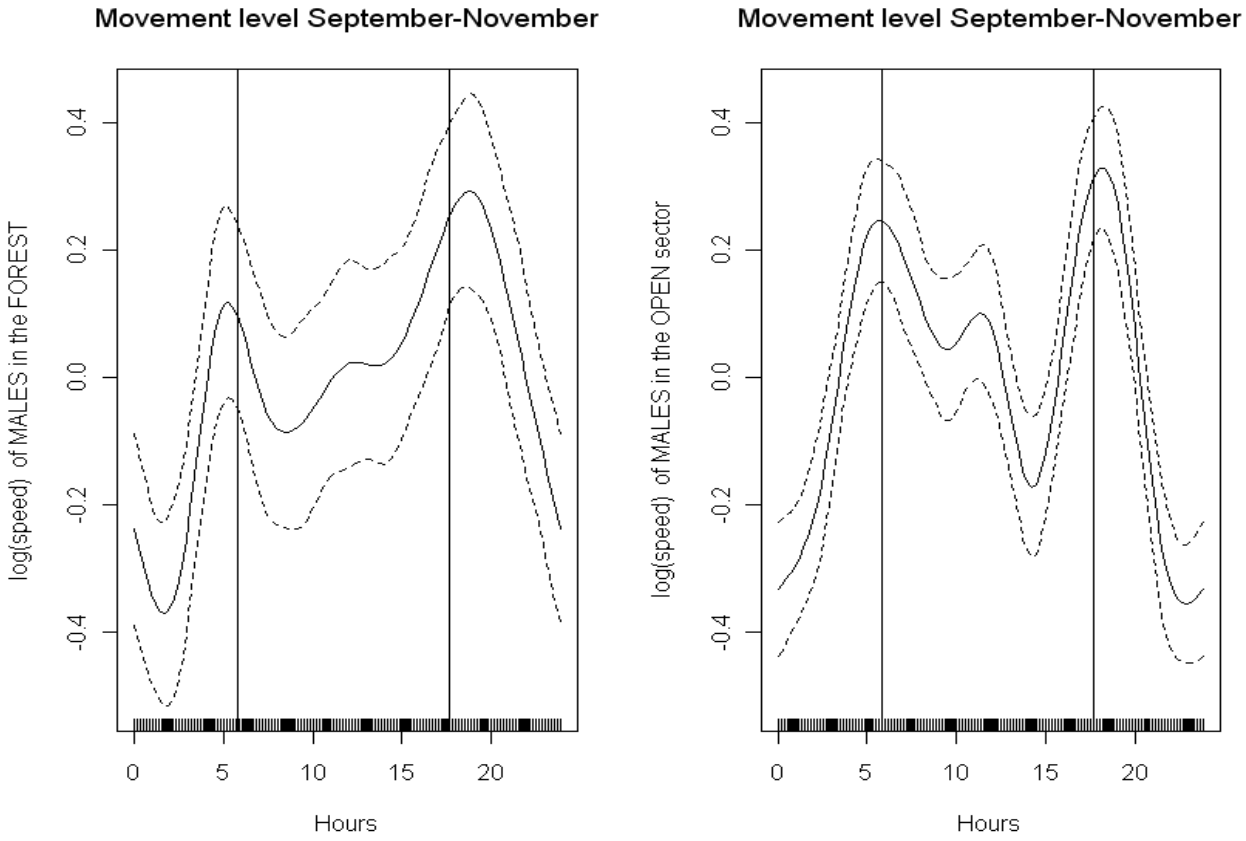

Figure 4. Males movement speed in autumn (September-November)

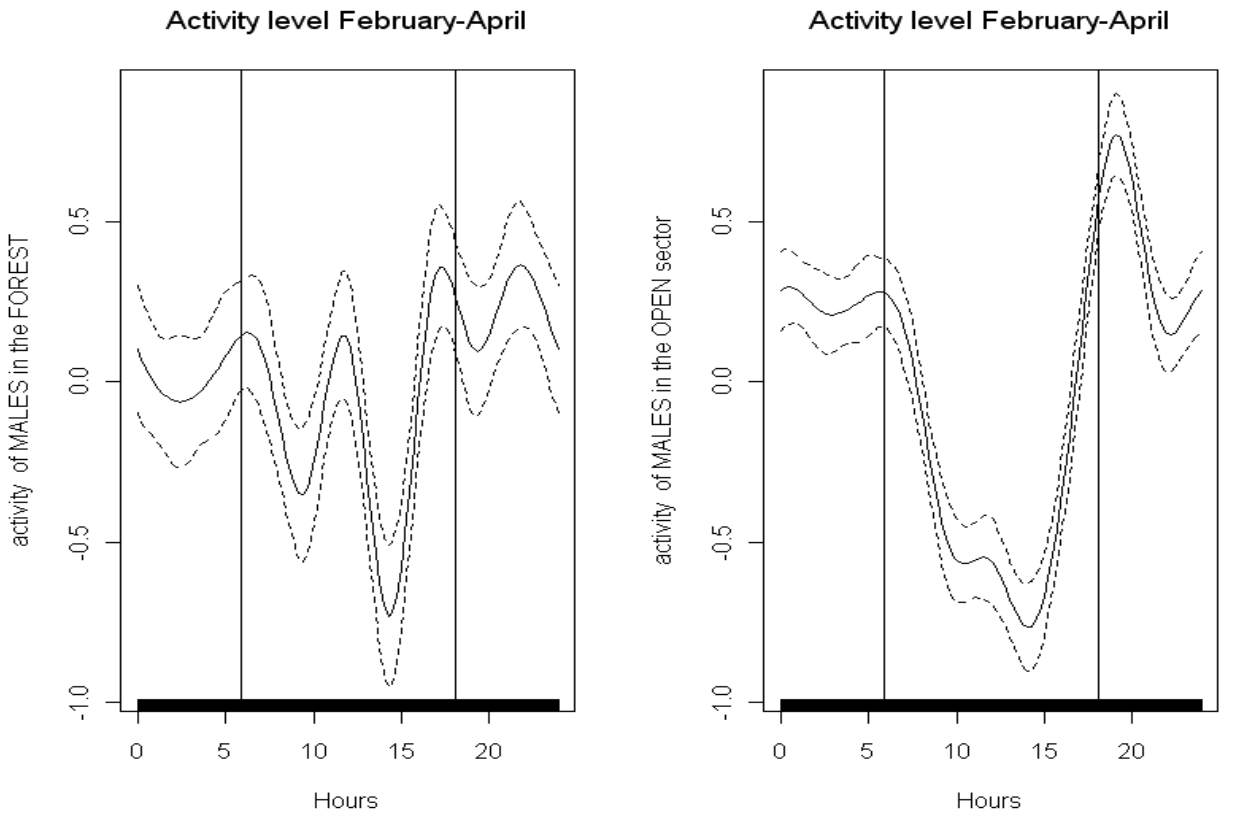

Figure 5. Males activity during late winter-early spring period (February-April)

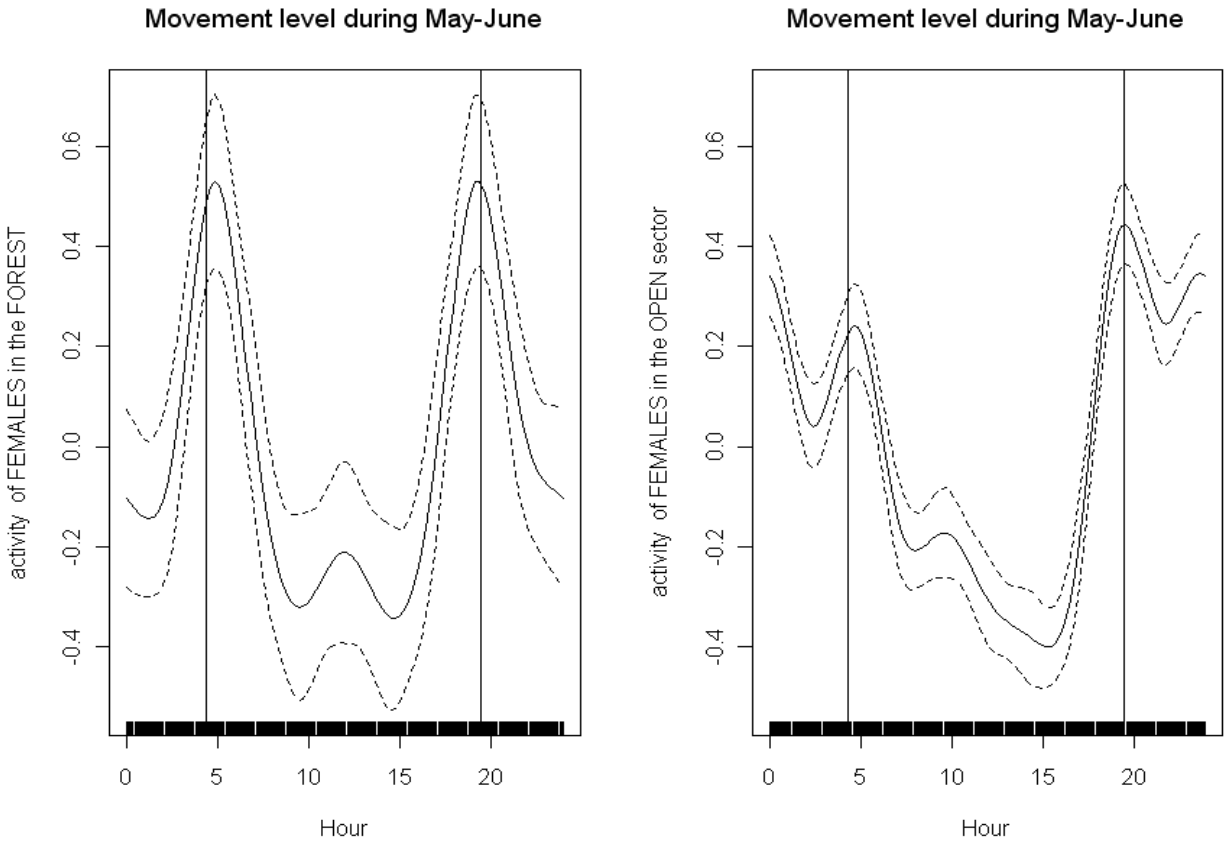

Figure 6. Females activity during fawning period (May-June)

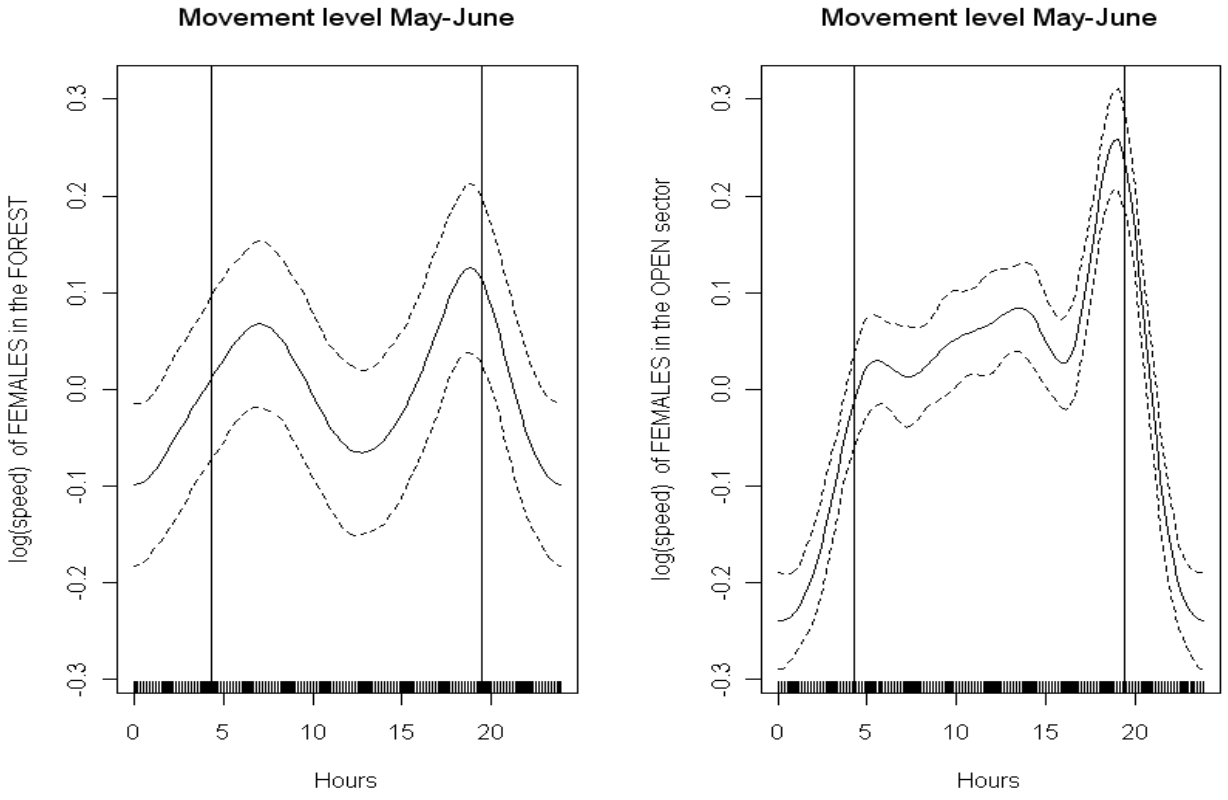

Figure 7. Females movement speed during fawning period (May-June)

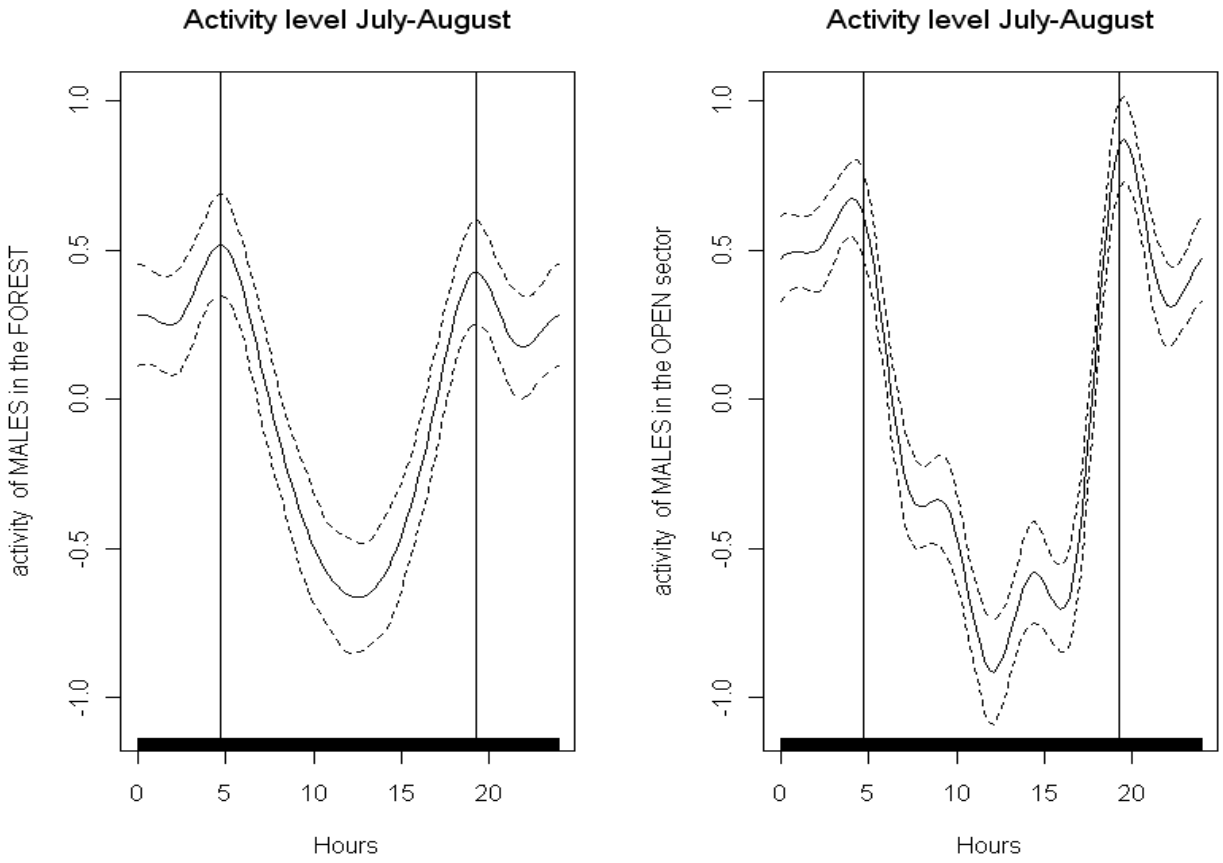

Figure 8. Males activity during rutting period (July-August)

4

Conclusions

Usually the GPS collars are used to study animal behavior in term of spatial utilization as home range definition and movements (mainly daily movements and migrations). This study respond to an ecological question but provide also technical progress and advice about how to utilize GPS data in ecological studies based on animal behavior investigations.

Know activity-inactivity on long scale time intervals is an important behavioral parameter that could allow researchers to deeper investigate animal behavior and circadian rhythms. The use of the model that we performed could allow researchers to know activity-inactivity without direct observation and on a wide dataset. Data on activity-inactivity measured by the motion sensor of the collar could add more information to position data. Utilization of both movement and activity data could indeed allow a deeper discrimination between behavioral classes otherwise impossible without direct observation: active while not movement could means for example feeding or vigilance, active while movement could means walking or running and absence of activity and movement means lying or standing. We performed this discriminant model on roe deer so it could likely be applied with good success to others ungulates but need to be verified and supported to direct observation and maybe modified if applied to other animals. However this could be a good start to develop similar model adapting to study activity-inactivity on other species.

We found that landscape structure had an affected on male and females roe deer behavior but differently in relation to season and sex. In particular deer activity and movement rates decreased along the gradient of increasing landscape openness during winter, probably to compensate for the

poorer winter food availability and quality in the strict forest environment. In contrast, during the rut, males were more active in the most open sectors, probably because females are widely dispersed in this habitat. Deer of both sexes were more active and moved more frequently during nighttime almost all the year, probably in response to human disturbance. Deer showed activity peaks at dawn and dusk in both the landscape sectors with often a secondary peak of activity around midnight or in general a higher value of activity during nighttime respect to daytime probably due to disturbance that occur during the day in the open sector and maybe due to feeding reasons for forest deer because they have less quality food available.

In conclusion we can affirm that deer behavior varies across fragmented landscapes because of the landscape openness effect that result in spatial heterogeneity in the distribution of both resources and disturbance. Further work should aim to complet the present analysis in order to elucidate in more detail the mechanisms by which landscape structure influences behavioral patterns of large herbivores. Further knowledge should indeed be developed in the study of the behavioral responses at individual level, evaluating the degree of behavioral synchronization between individuals. Furthermore other studies should aim to discriminate in more details the identification of behavioral classes through remote sensing.

This thesis represent an useful pilot study on behavioral plasticity mechanism and a start point to deeper investigate the behavioral responses of synanthropic species to fragmentation process, that could help to understand the mechanisms that drove adaptation and behavioral evolution.

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Appendix

Appendix 1.

The whole dataset available 2003-2008. Id: a and b =collared roe deer used in our analysis (a =activity and movement data available; b =only movement data available), c =others animals collared in the study area but not used for the statistical analysis. Animal =identity number of each animal; sex: f =female and m =male; age: ad =adult (>2years of age), y =yearling (>1 and<2 years of age) and j=juvenile (<1yearsof age); sector (=landscape sector): open; intermediate and forest; start monitoring =data of beginning of monitoring (capture and handling); end monitoring =data of end of the monitoring (collar lost, collar without battery or animal death); days =total number of days of monitoring; months=total number of months of monitoring; weight =animal body weight (kg) measured during the handling operations.

Id	animal	sex	age	sector	start monitoring	end monitoring	days	months	weight (kg)
c	7	f	ad	forest	18/12/2002	24/08/2003	248	8.3	21.50
c	11	m	ad	forest	18/12/2002	01/10/2003	287	9.6	24.40
c	21	f	y	forest	18/12/2002	16/09/2003	272	9.1	19.40
c	48	m	j	forest	18/12/2002	03/10/2003	288	9.6	15.90
c	52	f	ad	forest	18/12/2002	17/01/2003	30	1	21.40
c	58	f	j	forest	18/12/2002	11/10/2003	296	9.9	13.90
c	62	m	j	forest	18/12/2002	06/10/2003	291	9.7	14.70
c	64	f	j	forest	18/12/2002	26/05/2003	161	5.4	9.60
c	66	f	j	forest	18/12/2002	23/09/2003	275	9.2	15.60
c	68	m	j	forest	18/12/2002	04/05/2003	139	4.6	13.50
c	70	f	j	open	18/12/2002	06/11/2003	323	10.8	16.70
c	74	m	ad	forest	18/12/2002	04/10/2003	289	9.6	24.10
c	80	m	ad	open	28/01/2003	30/12/2003	336	11.2	26.00
c	84	m	ad	open	12/02/2003	14/01/2004	335	11.2	24.10
c	86	m	ad	open	12/02/2003	18/08/2003	187	6.2	24.20
c	45	f	ad	open	18/02/2003	31/01/2004	347	11.6	25.70
c	47	f	ad	open	18/02/2003	02/03/2004	378	12.6	24.50
c	88	m	ad	open	18/02/2003	29/02/2004	376	12.5	21.80
c	90	f	ad	open	18/02/2003	22/03/2004	398	13.3	25.00
c	93	m	ad	open	18/02/2003	12/02/2004	359	12	21.40
c	94	f	j	open	18/02/2003	23/03/2004	399	13.3	17.60
c	96	f	ad	open	11/03/2003	19/01/2004	314	10.5	21.80
c	42	f	ad	intermediate	14/03/2003	18/01/2004	310	10.3	24.30
c	100	f	ad	intermediate	14/03/2003	17/04/2003	34	1	27.10
c	102	f	ad	open	27/11/2003	03/12/2003	6	/	21.20
c	104	m	ad	open	27/11/2003	01/12/2004	369	12.3	26.20

c	106	m	j	open	27/11/2003	11/10/2004	319	10.6	19.90
c	108	m	ad	open	27/11/2003	01/12/2003	4	/	24.40
c	110	m	j	open	02/12/2003	30/11/2004	364	12.1	18.90
c	112	f	j	open	11/12/2003	29/11/2004	354	12	18.20
c	114	f	ad	open	11/12/2003	27/03/2004	107	3.6	24.90
c	116	f	y	open	11/12/2003	30/10/2004	324	10.8	22.60
c	118	m	j	open	11/12/2003	30/07/2004	232	8	16.60
c	132	m	j	forest	05/02/2004	13/08/2004	190	6	13.30
c	134	m	j	forest	05/02/2004	13/08/2004	190	6	18.00
c	130	f	j	forest	08/02/2004	07/10/2004	242	8	11.80
a	19	f	ad	forest	25/11/2004	28/10/2005	337	11	20.00
a	166	m	ad	forest	25/11/2004	01/09/2005	280	9	23.30
a	168	m	ad	forest	25/11/2004	24/10/2005	333	11	24.60
c	170	m	j	forest	25/11/2004	27/10/2005	336	11	15.70
c	172	m	j	forest	25/11/2004	28/10/2005	337	11	17.60
c	174	m	j	forest	25/11/2004	27/10/2005	336	11	14.80
a	176	f	ad	forest	25/11/2004	27/10/2005	336	11	20.70
c	178	f	ad	forest	25/11/2004	15/01/2005	51	/	21.20
c	180	m	j	forest	25/11/2004	27/10/2005	336	11	16.40
a	182	m	ad	forest	25/11/2004	27/11/2005	367	12	22.30
a	184	f	y	forest	25/11/2004	29/10/2005	338	11	21.70
c	188	f	j	forest	25/11/2004	25/03/2005	120	4	13.90
a	10_05	f	ad	forest	25/11/2004	27/10/2005	336	11	21.60
a	132_05	m	y	forest	25/11/2004	31/05/2005	187	6	17.30
c	62_05	m	ad	forest	25/11/2004	29/01/2005	65	/	20.80
a	7_05	f	ad	forest	25/11/2004	27/10/2005	336	11	22.80
c	164	f	j	forest	26/11/2004	27/10/2005	335	11	17.10
a	152	m	y	open	06/01/2005	30/12/2005	358	12	20.90
c	114_05	f	ad	open	06/01/2005	07/01/2005	1	/	26.20
a	142	f	y	intermediate	13/01/2005	31/12/2005	352	12	20.70
c	154	f	ad	intermediate	13/01/2005	04/02/2005	22	/	24.80
c	156	f	j	intermediate	13/01/2005	07/01/2006	359	12	16.70
c	158	m	j	intermediate	13/01/2005	17/05/2005	124	4	17.40
a	160_05	m	ad	intermediate	13/01/2005	01/09/2005	231	8	24.90
a	144	f	ad	intermediate	20/01/2005	07/01/2006	346	12	21.60
a	146	m	ad	intermediate	20/01/2005	13/09/2005	236	8	25.60
c	190	f	j	intermediate	20/01/2005	20/07/2005	181	6	16.40
c	148	f	ad	open	27/01/2005	28/01/2005	1	/	20.80
a	150	f	ad	open	27/01/2005	02/12/2005	309	10	19.00
a	194	m	y	open	27/01/2005	09/11/2005	286	10	18.70
c	104_05	m	ad	open	27/01/2005	17/02/2005	21	/	26.50
a	196	f	ad	open	03/02/2005	08/12/2005	308	10	22.90
b	198	m	ad	open	03/02/2005	04/03/2006	394	13	18.20
a	200	f	ad	open	03/02/2005	01/12/2005	301	10	24.60
b	202	f	ad	open	03/02/2005	02/02/2006	364	13	20.10

a	94_05	f	ad	open	03/02/2005	08/12/2005	308	10	22.20
a	206	m	ad	open	09/02/2005	27/10/2005	260	9	25.40
c	210	f	j	open	09/02/2005	04/02/2006	360	12	16.40
a	212	f	ad	open	09/02/2005	14/12/2005	308	10	26.70
a	217	f	ad	forest	24/11/2005	26/10/2006	336	11.2	19.70
a	219	m	ad	forest	24/11/2005	10/07/2006	228	7.6	22.20
a	221	f	ad	forest	24/11/2005	22/07/2006	240	8.1	20.40
a	228	m	ad	forest	24/11/2005	26/10/2006	336	11.2	21.80
a	230	m	ad	forest	24/11/2005	26/10/2006	336	11.2	25.10
c	232	f	y	forest	24/11/2005	26/10/2006	336	11.2	16.90
a	234	f	ad	forest	24/11/2005	26/10/2006	336	11.2	22.30
a	238	m	y	forest	24/11/2005	26/10/2006	336	11.2	18.40
a	3	m	ad	open	05/01/2006	07/12/2006	336	11.2	24.40
a	260	f	ad	open	05/01/2006	07/12/2006	336	11.2	21.80
a	248	m	ad	intermediate	12/01/2006	14/12/2006	336	11.2	24.80
a	250	m	ad	intermediate	12/01/2006	14/12/2006	336	11.2	28.70
a	252	f	ad	intermediate	12/01/2006	14/12/2006	336	11.2	20.90
a	256	f	ad	intermediate	12/01/2006	14/12/2006	336	11.2	24.40
a	258	f	ad	intermediate	12/01/2006	14/12/2006	336	11.2	20.30
a	264	f	ad	open	19/01/2006	21/12/2006	336	11.2	23.20
a	266	f	ad	open	19/01/2006	21/12/2006	336	11.2	23.70
a	268	m	ad	open	19/01/2006	30/12/2006	345	11.5	20.60
c	280	m	j	open	19/01/2006	22/12/2006	337	11.2	19.10
a	282	m	ad	open	26/01/2006	06/01/2007	345	11.5	22.90
c	284	m	j	open	26/01/2006	15/09/2006	232	7.7	17.80
a	286	m	ad	open	26/01/2006	06/01/2007	345	11.5	24.20
a	47_06	f	ad	open	26/01/2006	22/12/2006	330	11	25.60
a	290	m	ad	open	02/02/2006	06/01/2007	338	11.3	23.70
b	302	m	ad	open	02/02/2006	22/12/2006	323	10.8	24.90
a	306	f	y	open	02/02/2006	22/12/2006	323	10.8	20.50
a	318	f	ad	open	11/01/2007	13/12/2007	336	11.2	17.90
c	320	f	j	open	11/01/2007	13/12/2007	336	11.2	16.10
a	322	f	ad	open	11/01/2007	13/12/2007	336	11.2	22.10
a	328	f	ad	open	11/01/2007	13/12/2007	336	11.2	20.70
c	332	m	j	intermediate	18/01/2007	28/06/2007	161	5.4	17.20
c	334	m	j	intermediate	18/01/2007	21/12/2007	337	11.2	17.70
c	338	m	j	open	01/02/2007	21/12/2007	323	10.8	16.70
a	340	f	ad	open	01/02/2007	21/12/2007	323	10.8	22.00
c	342	f	j	open	01/02/2007	13/12/2007	315	10.5	16.60
c	344	f	j	open	01/02/2007	21/12/2007	323	10.8	15.20
a	346	f	y	open	01/02/2007	21/12/2007	323	10.8	22.80
c	212_07	f	ad	open	01/02/2007	20/09/2007	231	7.7	27.50
c	352	m	j	open	08/02/2007	21/12/2007	316	10.5	18.90
b	356	f	ad	open	08/02/2007	21/12/2007	316	10.5	22.80
a	358	m	ad	open	08/02/2007	21/12/2007	316	10.5	26.90

a	360	f	ad	open	08/02/2007	18/07/2007	160	5.3	23.10
a	362	f	ad	open	08/02/2007	10/01/2008	336	11.2	24.10
a	364	f	ad	open	08/02/2007	19/12/2007	313	10.5	22.00
a	366	f	ad	open	08/02/2007	20/12/2007	315	10.5	22.50
c	368	f	j	open	08/02/2007	13/12/2007	308	10.3	16.30
a	202_07	f	ad	open	08/02/2007	20/12/2007	315	10.5	19.70
c	350	m	j	open	09/02/2007	21/12/2007	315	10.5	17.90
c	378	m	j	forest	06/12/2007	04/12/2008	364	12.1	11.70
b	382	m	y	forest	06/12/2007	05/09/2008	274	9.1	17.70
c	384	f	j	forest	06/12/2007	23/02/2008	79	2.6	11.10
c	386	f	j	forest	06/12/2007	01/08/2008	239	8	15.40
a	390	f	ad	open	10/01/2008	11/12/2008	336	11.2	23.70
a	402	f	ad	open	10/01/2008	11/12/2008	336	11.2	22.30
c	406	f	j	open	10/01/2008	11/12/2008	336	11.2	18.10
c	412	m	j	open	10/01/2008	11/12/2008	336	11.2	14.30
c	392	m	j	intermediate	17/01/2008	12/12/2008	330	11	16.52
a	394	f	ad	intermediate	17/01/2008	12/12/2008	330	11	21.36
c	396	f	j	intermediate	24/01/2008	12/12/2008	323	10.8	13.90
a	414	f	ad	intermediate	24/01/2008	12/12/2008	323	10.8	24.40
a	418	f	ad	open	31/01/2008	12/12/2008	316	10.5	19.65
a	424	f	ad	open	31/01/2008	12/12/2009	316	10.5	26.80
a	426	f	y	open	31/01/2008	12/12/2008	316	10.5	21.46
c	430	f	j	open	31/01/2008	10/02/2008	10	0.3	14.86
a	432	f	ad	open	07/02/2008	12/12/2008	309	10.3	24.50
c	434	m	j	open	07/02/2008	08/01/2009	336	11.2	16.00
c	436	m	j	open	07/02/2008	08/01/2009	336	11.2	17.20
c	438	f	j	open	07/02/2008	08/01/2009	336	11.2	13.20
c	442	m	j	open	07/02/2008	08/01/2009	336	11.2	18.50
c	444	f	j	open	07/02/2008	22/01/2009	350	11.7	15.00
c	446	f	j	open	07/02/2008	20/08/2008	195	6.5	18.10

Appendix 2.

Date of intensive monitoring and roe deer biological periods during the year: December-January ="Winter", February-March-April ="Late Winter-Early Spring", May-June ="Fawning", July-August ="Rut", September-October-November ="Autumn". Data of 2004 (December) has been analysed with data of the beginning of 2005 (January), indeed they are part of the same biological period (W="Winter"). For each period is added a key behavior of males or females: grouping (both sexes), territoriality (males), gestation, parturition and lactation (females) and mating (in particular refers to males for territoriality and between males competition).

Year	**Month**	**Days**	**Period**	**Behaviour**
2005	December	2004dec16-17	Winter	grouping
2005	January	2005jan27-28	Winter	grouping
2005	February	2005feb17-18	Late Winter-Early Spring	territoriality/gestation
2005	March	2005mar17-18	Late Winter-Early Spring	territoriality/gestation
2005	April	2005apr21-22	Late Winter-Early Spring	territoriality/gestation
2005	June	2005june09-10	Fawning	territoriality/parturition
2005	June	2005june16-17	Fawning	territoriality/parturition
2005	July	2005july28-29	Rut	mating/lactation
2005	July	2005july28-29	Rut	mating/lactation
2005	August	2005aug11-12	Rut	mating/lactation
2005	August	2005aug11-12	Rut	mating/lactation
2005	October	2005oct06-07	Autumn	grouping/lactation
2005	October	2005oct13-14	Autumn	grouping/lactation
2006	December	2005dec13-14	Winter	grouping
2006	January	2006jan24-25	Winter	grouping
2006	February	2006feb14-15	Late Winter-Early Spring	territoriality/gestation
2006	March	2006mar14-15	Late Winter-Early Spring	territoriality/gestation
2006	April	2006apr18-19	Late Winter-Early Spring	territoriality/gestation
2006	May	2006may09-10	Fawning	territoriality/parturition
2006	June	2006june06-07	Fawning	territoriality/parturition
2006	June	2006june13-14	Fawning	territoriality/parturition
2006	July	2006july25-26	Rut	mating/lactation
2006	August	2006aug01-02	Rut	mating/lactation
2006	August	2006aug08-09	Rut	mating/lactation
2007	December	2007dec04-05	Winter	grouping
2007	January	2007jan29-30	Winter	grouping
2007	February	2007feb20-21	Late Winter-Early Spring	territoriality/gestation
2007	March	2007mar14-15	Late Winter-Early Spring	territoriality/gestation
2007	April	2007apr17-18	Late Winter-Early Spring	territoriality/gestation
2007	May	2007may08-09	Fawning	territoriality/parturition
2007	June	2007june05-06	Fawning	territoriality/parturition
2007	June	2007june12-13	Fawning	territoriality/parturition
2007	July	2007july24-25	Rut	mating/lactation
2007	August	2007aug01-02	Rut	mating/lactation

2007	August	2007aug07-08	Rut	mating/lactation
2007	September	2007sept11-12	Autumn	grouping/lactation
2007	October	2007oct02-03	Autumn	grouping/lactation
2008	December	2008dec01-02	Winter	grouping
2008	January	2008jan29-30	Winter	grouping
2008	February	2008feb20-21	Late Winter-Early Spring	territoriality/gestation
2008	March	2008mar12-13	Late Winter-Early Spring	territoriality/gestation
2008	April	2008apr15-16	Late Winter-Early Spring	territoriality/gestation
2008	May	2008may07-08	Fawning	territoriality/parturition
2008	June	2008june05-06	Fawning	territoriality/parturition
2008	June	2008june12-13	Fawning	territoriality/parturition
2008	July	2008july23-24	Rut	mating/lactation
2008	July	2008july23-24	Rut	mating/lactation
2008	July	2008july30-31	Rut	mating/lactation
2008	August	2008aug04-05	Rut	mating/lactation
2008	August	2008aug04-05	Rut	mating/lactation
2008	August	2008aug12-13	Rut	mating/lactation
2008	August	2008aug12-13	Rut	mating/lactation
2008	August	2008aug28-29	Rut	mating/lactation
2008	September	2008sept10-11	Autumn	grouping/lactation
2008	October	2008oct07-08	Autumn	grouping/lactation
2008	November	2008nov27-28	Autumn	grouping/lactation

Appendix 3.

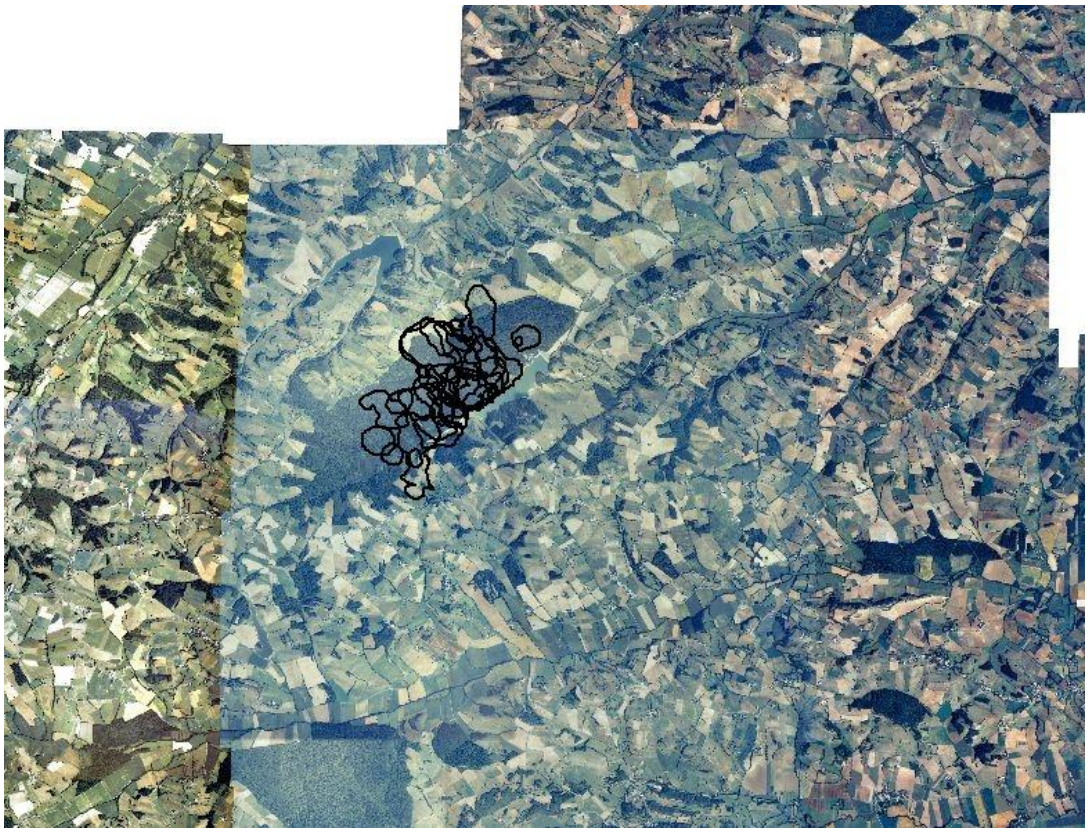
Example of schedule used to recorded direct observation on captive roe deer behavior. Part of the schedule completed by the watcher. X, Y and %h.D are the variable of the motion sensor on the collar. On the left there are the behaviors registered in the ethogram (see table 5). The values express the %time of the behavioral expression within each single time interval (5minute length).

					Données brutes			ATH	ATN	ATB	ATB	DEP	DEP	DEP	DEP	DEP	IMTN	IMTB	IMTB	RTN	RTB	RTB	CTN	CTB	AUT	AUT	AUT	AU	AU	AU
Collier	GPS	hre	Jour	J	X	Y	% h.D	A TH	A I1	A I2	A TB	M	S	E	T	C	Ar	Ar TI2	Ar TB	RD	RD TI	RD TB	RCTN	RCTB	TD	TD J	TD x	TC	CT	RT
Mat	9.05.00	110	24-feb	8	15	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	9.10.00	111	24-feb	8	5	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	9.15.00	112	24-feb	8	7	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	9.20.00	113	24-feb	8	1	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	9.25.00	114	24-feb	8	1	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,07	0,93	0	0	0	0	0	0
Mat	9.30.00	115	24-feb	8	2	0	69,3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,64	0,36	0	0	0	0	0	0
Mat	9.35.00	116	24-feb	8	0	1	7,3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Mat	9.40.00	117	24-feb	8	11	1	91,3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,92	0,077	0	0	0	0,003	0	0
Mat	9.45.00	116	24-feb	8	3	7	19,3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,247	0,55	0	0	0	0,203	0	0
Mat	9.50.00	119	24-feb	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Mat	9.55.00	120	24-feb	8	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Mat	10.00.00	121	24-feb	8	63	8	98	0	0	0	0	0,083	0	0	0	0	0	0	0	0,53	0	0	0,35	0	0,037	0	0	0	0	0
Mat	10.05.00	122	24-feb	8	163	39	78	0	0	0	0,173	0,22	0	0,017	0	0	0,23	0	0,09	0,243	0	0	0	0	0,027	0	0	0	0	0
Mat	10.10.00	123	24-feb	8	115	57	57,3	0	0	0	0,277	0,15	0	0	0	0	0,18	0	0,08	0,213	0	0	0,05	0	0,05	0	0	0	0	0
Mat	10.15.00	124	24-feb	8	4	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,99	0	0	0	0	0,01	0	0
Mat	10.20.00	125	24-feb	8	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	10.25.00	126	24-feb	8	2	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	10.30.00	127	24-feb	8	3	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	10.35.00	128	24-feb	8	5	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	10.40.00	129	24-feb	8	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	10.45.00	130	24-feb	8	0	128	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	10.50.00	131	24-feb	8	1	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	10.55.00	132	24-feb	8	2	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	13.30.00	163	24-feb	8	195	49	92,7	0,02	0	0	0,01	0,307	0,063	0	0,013	0	0,423	0	0	0,147	0	0	0	0	0	0	0	0	0	0
Mat	13.35.00	164	24-feb	8	66	6	93,3	0	0	0	0,023	0,027	0	0	0	0	0,097	0	0	0,05	0	0	0,777	0	0	0	0	0	0,027	0
Mat	13.40.00	165	24-feb	8	8	0	98,7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	13.45.00	166	24-feb	8	10	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	13.50.00	167	24-feb	8	10	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0,26	0	0	0,74	0	0	0	0	0	0	0
Mat	13.55.00	168	24-feb	8	67	30	87,3	0	0	0	0,1	0,033	0	0	0	0	0,057	0	0	0,76	0	0	0	0	0,05	0	0	0	0	0
Mat	14.00.00	169	24-feb	8	56	6	87,3	0	0	0	0,123	0	0	0	0	0	0,017	0	0,027	0,797	0	0	0	0	0,037	0	0	0	0	0
Mat	14.05.00	170	24-feb	8	125	23	88,7	0	0	0	0,077	0,217	0	0	0,043	0	0,193	0	0	0,437	0	0	0	0	0	0	0	0	0	0,033
Mat	14.10.00	171	24-feb	8	145	45	39,3	0	0	0	0,603	0,183	0	0,027	0	0	0,113	0	0	0,073	0	0	0	0	0	0	0	0	0	0
Mat	14.15.00	172	24-feb	8	109	17	75,3	0	0	0	0,223	0,317	0	0	0	0	0,413	0	0	0,02	0	0	0	0	0,02	0	0	0	0	0
Mat	14.20.00	173	24-feb	8	151	55	70,7	0	0	0	0,233	0,263	0	0	0	0	0,087	0	0	0	0	0	0,367	0	0	0	0	0	0,037	0
Mat	14.25.00	174	24-feb	8	2	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	14.30.00	175	24-feb	8	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	14.35.00	176	24-feb	8	6	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	14.40.00	177	24-feb	8	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	7.15.00	88	25-feb	9	220	58	81,3	0,123	0,093	0	0,01	0,053	0	0,017	0	0	0,507	0	0,043	0,13	0	0	0	0	0,023	0	0	0	0	0
Mat	7.20.00	89	25-feb	9	167	32	89,3	0,097	0,01	0	0,08	0,157	0	0	0	0	0,267	0	0	0,363	0	0	0	0	0,027	0	0	0	0	0
Mat	7.25.00	90	25-feb	9	12	64	92,7	0	0	0	0,01	0,34	0	0,017	0	0	0,393	0	0	0,19	0	0	0	0	0,05	0	0	0	0	0
Mat	7.30.00	91	25-feb	9	88	8	90	0	0	0	0,087	0,023	0	0	0	0	0,2	0	0,017	0,37	0	0	0	0	0,303	0	0	0	0	0
Mat	7.35.00	92	25-feb	9	191	36	75,3	0	0	0	0,207	0,26	0	0,01	0	0	0,153	0	0,013	0,35	0	0	0	0	0	0	0	0	0	0
Mat	7.40.00	93	25-feb	9	64	6	80,7	0	0	0	0,173	0,13	0	0	0	0	0,13	0	0	0,48	0	0	0	0	0,087	0	0	0	0	0
Mat	7.45.00	94	25-feb	9	180	10	20,7	0	0	0	0,783	0,037	0	0,033	0	0	0,11	0	0	0,013	0	0	0	0	0,023	0	0	0	0	0
Mat	7.50.00	95	25-feb	9	107	11	8,7	0	0	0	0,913	0	0	0	0	0	0,04	0	0	0,047	0	0	0	0	0	0	0	0	0	0
Mat	7.55.00	96	25-feb	9	57	136	16	0	0	0	0,84	0	0	0,03	0	0	0,05	0	0	0,06	0	0	0	0	0,02	0	0	0	0	0
Mat	8.00.00	97	25-feb	9	39	11	84	0	0	0	0,09	0	0	0	0	0	0,027	0	0,02	0	0	0	0,803	0	0	0	0	0,023	0,037	0
Mat	8.05.00	98	25-feb	9	1	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	8.10.00	99	25-feb	9	4	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	8.15.00	100	25-feb	9	11	6	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,493	0,067	0	0	0	0,44	0	0
Mat	8.20.00	101	25-feb	9	6	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,983	0,017	0	0	0	0	0	0
Mat	8.25.00	102	25-feb	9	0	128	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mat	8.30.00	103	25-feb	9	8	0	100	0,00	0,00	0	0	0	0	0	0	0	0	0	0	0	0	0	0,647	0,077	0	0	0	0,277	0	0
Mat	8.35.00	104	25-feb	9	14	0	100	0	0	0	0	0,047	0	0	0	0	0	0	0	0,027	0	0	0,88	0	0	0	0	0,047	0	0
Mat	8.40.00	105	25-feb	9	195	46	91,3	0,167	0	0	0,01	0,2	0	0	0	0	0,403	0	0	0,15	0	0	0	0	0,057	0,013	0	0	0	0
Mat	8.45.00	106	25-feb	9	56	140	82	0,023	0	0	0,167	0,07	0	0,017	0	0	0,13	0	0	0,593	0	0	0	0	0	0	0	0	0	0
Mat	9.05.00	110	25-feb	9	5	2	98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,927	0	0	0	0	0,073	0	0
Mat	9.10.00	111	25-feb	9	7	6	99,3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,8	0	0	0	0	0,2	0	0
Mat	9.15.00	112	25-feb	9	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Appendix 4.

Home ranges of roe deer inhabiting: a) forest, b) intermediate and c) open sectors (years 2005-2008).

a)



b)

c)