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Avoidance behaviour of wild ungulates to roads: its effects on spatial distribution, habitat use and activity patterns

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“The Road goes ever on and on

Down from the door where it began.

Now far ahead the Road has gone,

And I must follow, if I can,

Pursuing it with eager feet,

Until it joins some larger way

Where many paths and errands meet.

And whither then? I cannot say”

J.R.R. Tolkien

Resumo

Sabe-se que as actividades antropogénicas afectam a vida selvagem de várias formas, muitas delas não inteiramente estudadas. As estradas já são consideradas parte da paisagem e representam do ponto de vista ecológico, uma forma de conflito entre o Homem e a vida selvagem. Este projecto decorreu na Serra da Lousã, pertencente à região Centro de Portugal, e tem como objectivo perceber de que modo a rede rodoviária da região, influencia o comportamento das populações de veado face às estradas, bem como a sua distribuição espacial, uso do habitat e padrões comportamentais.

Foram usados dois métodos de campo complementares para avaliar os efeitos das estradas na população de veados: contagem de amostras fecais ao longo de transectos lineares com amostragem de distância e armadilhas fotográficas. Os pontos de amostragem para ambos os métodos foram definidos num desenho amostral estratificado, com base no tipo de habitat e tipo de estrada. Dois tipos principais de habitat foram considerados, os matos, que representam áreas abertas; e florestas, que representam áreas fechadas. Em relação às estradas, foram considerados dois tipos principais com base no pavimento, estradas pavimentadas (asfalto e gravilha) e estradas não pavimentadas (geralmente de terra batida).

Os nossos resultados evidenciam um padrão de actividade crepuscular e nocturno, sugerindo que o uso das áreas mais expostas a perturbações antropogénicas é usado fora dos períodos de maior actividade humana, enquanto que áreas fechadas têm um uso contínuo ao longo do dia. Relativamente aos resultados obtidos através da contagem de excrementos, verificou-se uma densidade similar em ambos os tipos de estrada (pavimentados e não pavimentados) mas uma densidade diferente entre os tipos de habitat. Os matos apresentaram o dobro da densidade das áreas florestais, o que demonstra uma clara preferência do veado por estas áreas. Considerando os grupos de amostras fecais em relação á distância á estrada foi possível verificar que tanto o tipo de estrada como o habitat influenciam a sua distribuição. Em concordância com a nossa hipótese, verificou-se que o veado apresenta um comportamento de evitamento, principalmente em áreas de florestas com estradas pavimentadas, nos primeiros 20 metros após a estrada, e nas áreas de matos com estradas não pavimentadas, nos 10m iniciais. Na presença de perturbação antropogénica, a população de veado da Serra da Lousã, ajusta o seu comportamento e uso de habitat, optando por transitar para habitats com maior refúgio, neste caso as florestas, nas alturas de maior actividade humana. Assim, o veado parece evidenciar evitamento quer espacial quer temporal em resposta às estradas e às pressões antropogénicas a estas associadas.

Palavras-chave: *Cervus elaphus*; comportamento de evitamento; estradas; uso de habitat; padrões de actividade

Abstract

Anthropogenic activities are known to affect wildlife in multiple ways, wihich many are not fully studied. Roads are already considered part of landscape and represent from the ecological point of view, a form of conflict between man and wildlife. This project elapsed in Lousã Mountain, belonging to the center region of Portugal, and aims to understand how the road network in the region influences the behaviour of red deer populations in relation to roads, as well as their spatial, use of habitat and activity patterns.

Two complementary field methods were used to evaluate the effects of roads in the deer population: counting faecal samples along linear transects with distance sampling and camera-traps. The sampling points for both methods were defined in a stratified sample design, based on the type of habitat and type of road. Two major habitat types were considered, the shrublands that represent open areas and forests that represent closed areas. In relation to roads, two main types were considered based on pavement, paved roads (asphalt and gravel) and unpaved roads (usually of dirt).

Our results evidence a pattern of crepuscular and nocturnal activity, suggesting that the use of areas most exposed to anthropogenic disturbances are used outside periods of higher human activity, while enclosed areas are in continuous use throughout the day. Regarding the results obtained by pellet-counts, there was a similar density in both types of road (paved and unpaved) but a different density between habitat types. The shrublands showed twice the density of the forest areas, which shows a clear preference of the red deer in these areas. Considering the groups of faecal samples in relation to the distance to the road, it was possible to verify that both the type of road and the habitat influence its distribution. In agreement with our hypothesis, it was verified that the red deer shows avoidance behaviour, mainly in areas of forests with paved roads, in the first 20 meters after the road, and in the areas of shrublands with unpaved roads, in the initial 10m. In the presence of anthropogenic disturbance, the red deer population of the Lousã Mountain adjust their behaviour and habitat use, choosing to move to habitats with greater refuge, in this case forests, at heights of greater human activity. Thus, red deer seems to evidence both spatial and temporal avoidance in response to the roads and the associated anthropogenic pressures.

Keywords: *Cervus elaphus*; avoidance behaviour; roads; habitat use; activity patterns

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Chapter 1

General introduction

Ecology and Behaviour of Wild Ungulates

"Ungulate" means "having hoofs". The ungulate group consists of medium sized and large mammals that are classified into two main orders, Artiodactyla (e.g., donkeys, camels, pigs, hippopotamus, peccaries, deer, musk deer, bovids, giraffes) also known by even-toed ungulates, and Perissodactyla (e.g., horses, zebras, tapirs, rhinoceroses) also known by odd-toed ungulates (Graves,1984; Vanpé, 2007).

The even-toed ungulates are the most successful group of large herbivores on earth, inhabiting and being native to almost all continents except Antarctica and Oceania. There are three well-established suborders Tylopoda (camels) Suiformes (pigs and peccaries) and Ruminantia, the ruminants (cattle, goats, sheep, deer, and antelope). In this project we will study in more detail the Cervidae family, belonging to the Ruminatia suborder.

The populations of ungulates have increased in the last century worldwide, and in Europe was not an exception (Gill, 2000; Fuller & Gill, 2001; Reimoser, 2003; Côté et al., 2004; Pépin et al., 2006). Ungulates are considered high natural resources, being an important source of economic revenue due to hunting, cultural through photographs, recreational activities, besides its ecological value as integral part of biodiversity (Cederlund et al., 1998; Vanpé, 2007). Ungulates are generally considered animals with a high behavioural plasticity due to their ability to inhabit in vast variety of habitats (Salazar, 2009; Podgórski et al., 2013; Linnell et al., 1998) from European woodlands of deciduous and, coniferous trees to Mediterranean forests, shrublands, grasslands and sometimes even making use of open agricultural areas (Zejda, 1978; Danilkin & Hewison, 1996; Alves, 2013). In a very general way, it was assumed that ungulates prefer more enclosed habitats, giving them protection during the day, even with low levels of high quality food, moving to open areas with more quantity, quality and variety of food at night (Bjørneraas et al., 2011; Bonnot et al., 2013). This suggests that habitat selection would be made with the focus on food and cover (Borkowski, 2004). The temporal component is also important when studying wildlife, since depending on the season the demand for food will depend on its availability, resulting in a temporal effect on habitat selection (Gebert & Verheyden-Tixier, 2001; Alves, 2013).

Many ungulates show a wide variation in sexual dimorphism such in body size, with males being larger and heavier than females (Loison et al., 1999), and/or in the presence of secondary sexual characters, like antlers that in most species only males possesses it (Peixoto, 2014) or upward curving canines that form tusks in males of some species (Graves, 1984). Some ungulates are polygamous species (i.e. a male may breed with several females; Vanpé, 2007) that present a slightly gregarious behaviour, characterized by a sexual segregation outside the breeding season, with matriarchal societies and solitary males (Alves et al., 2013). The females become lonelier and reduce their home range when they are almost giving birth, then returning to small groups composed of females with their offspring (Kurz & Marchinton, 1972). In the case of females, spatial displacement and habitat choice will depend on the reproductive cycle, since after give birth their priority will be to provide food and protection to the offspring, guaranteeing their survival (Main, 2008; Van Beest et al., 2011). Ungulate reproductive females and their offspring form closed social bonds that appear to provide the optimum environment for rapid development and learning, achieved throughout optimal levels of stimulation by the maternal care activity and by behavioural patterns (Lent, 1974). Ungulates are particularly responsive to movement in the visual field, to any predator, human or anthropogenic disturbance and so maternal-offspring relationship is of great importance to the basic formation of the behavioural development of the newborn, since they learn from their mother how to react to adversity (Lent, 1974; James, 1959).

Habitat Use and Spatial Distribution

As for most mammals, the main elements necessary for habitat selection by ungulates are food and cover (Borkowski, 2004). The distribution of ungulates is somewhat conditioned by the habitat (Theuerkauf & Rouys, 2008) and in turn the habitat selection can be influenced by the risk of predation (Lima, 1998; Brown et al., 1999; Zollner and Lima, 1999). Nowadays, since humans have eliminated most of the large carnivores in the ecosystem (Ripple & Beschta, 2004), human presence (not only hunting) is interpreted by ungulates as a predation risk (Frid and Dill, 2002). In a predator-prey relationship, the selection of habitat by prey species will be done taking into account the basic needs of the animals as foraging, breeding and protection, avoiding predators (Werner and Anholt, 1993). Prey species make use of the habitat according to the risk of predation, which means that even if a particular place has higher quality of food preys prefer to avoid it in a way that reduces their risk to predators (Ripple & Beschta, 2004). In environments that provide open and closed habitats, the ungulates have two different approaches, use the closed areas to safely feed and protect or use the open areas in a vigilant way that gives them greater line of sight to see if a predator is near (Kie, 1999). As evidenced by Jiang et al. (2008) in China, roe deer (*Capreolus pygargus bedfordi*) and red deer (*Cervus elaphus* *xanthopygus*) made use of the habitat that was most distant from humans, maintaining a distance of about 3 km from human settlements, 1.5 km from logging sites and 3 km agriculture fields. Nevertheless, a spatial separation between these two species was observed in relation to the human settlements, due to the fact that roe deer is a smaller animal and because of that it is less noticed and more easily covered, when the distances to settlements of red deer were almost the double of those of roe deer (Jiang et al., 2008).

An inherent feature of a landscape is its spatial heterogeneity, which can be defined as the complexity and variability in the space of the properties of an ecosystem (Li and Reynolds, 1994). To understand how this heterogeneity affects the distribution of animals is to understand how they interpret and respond to the spatial variation of their environment (Buechner, 1989; Turner et al.,1989; Wiens, 1989, Wiens and Milne, 1989).

The ungulates are good models for the study of spatial heterogeneity, among other factors that may affect the spatial distribution of the animals, since the most part of them are large herbivores that require temporally and spatially diverse habitat elements, such as food and cover, thus having an impact on vegetation composition and other ecological communities, and being important ecological indicators (Molvar et al., 1993; Wallis de Vries, 1995; Hanley, 1996; Hobbs, 1996). The animals move in the environment, looking for food, shelter, mates among other daily activities creating an area called home range (Burt, 1943). The home range therefore depends on several natural and unnatural factors. The natural ones are for example the physical constitution of the animal, the sex and the age, whereas the unnatural are anthropogenic factors. Anthropogenic factors such as roads can affect habitat use and thus directly affecting the home range size and consequently the spatial distribution (Jerina, 2012).

A study carried out in the Lousã Mountain, Portugal (Alves et al., 2014), Portugal, showed spatial and temporal patterns in the habitat used by a wild species of ungulates, the red deer (*Cervus elaphus*). The authors pointed to the importance of food and cover in the spatial use of the habitat and the balance that red deer did between these two components depending on their need at each particular time. It was also showed that the red deer's temporal and spatial use of habitat was made according to the proximity to the water, ecotones and topographic features of the mountainous region where the study was conducted. The shrubland was the preferred habitat of this species, regardless of sex, age and season (Alves, 2013; Alves et al., 2014).

Ecological effects of roads on wildlife

The development of a worldwide network of roads and associated traffic has had a major ecological impact, especially on wildlife (Laurance et al., 2014), and this fact has attracted many conservation biologists to focus on a discipline called *road ecology* (Trombulak & Frissell, 2000)

"A road is an open way for the passage of vehicles and ecology is the study of the interactions between organisms and the environment. Therefore road ecology explores and addresses the relationship between the natural environment and the road system." (Forman et al., 2003)

Roads are already considered part of the landscape and represent, from an ecological point of view, a form of conflict between humans and wildlife. Not only the roads but all that comes from it are disturbing factors. The "road-effect zone" is a concept that defines the area as far as the ecological effects of the road are felt, from chemical pollutants, noise, light, habitat modification and others (Forman & Deblinger, 2000). Associated with the roads is also the traffic, and both can be felt individually in an ecosystem. The impact that roads have on the habitat start as soon as the construction begins, due to the machines, noise, pollution and human presence, directly affecting the habitat and wildlife present there. Previous studies were done in order to understand the impacts of these infrastructures on the ecosystem. From the moment a road starts to be build the whole area used for this purpose is removed and damaged, leading to habitat loss and degradation. In association, an easier access is created to a zone that was not accustomed to having the human presence and allied to this factor comes the anthropogenic development of a previous natural area, that loses its natural and wild aspect and characteristics, and soon stops serving to the wild. The barrier effect and mortality of wildlife are somewhat associated (van der Ree et al., 2015). In a presence of a road, paved or not, the animal has two hypotheses: to cross it or to avoid it (Forman et al., 2003; Grilo et al., 2012). If the animal wants to avoid it, it will return to the other path, being subject to less variability of resources, inhibition of possible seasonal migrations and reduction of gene transmission because it reduces the probability of finding new intraspecific ones (van der Ree et al., 2015). If the animal crosses the road (considering traffic unlike previous point) or continues its course and faces a new habitat either dies or gets injured due to collision with vehicles (Figure 1). Avoid or to be attracted, two antonyms commonly related to this anthropogenic factor. The animal can avoid the road due to the degradation of habitat, noise, pollution, pavement and traffic or the animal is attracted to this infrastructure as in the case of some reptiles that seeking heat on the surface of the road, or ghouls that feed of the animals that die on the roads or yet herbivores looking for plants that grow on the edge (van der Ree et al., 2015). In some cases, contrary to the usual, there are some animals adapted to a highly modified environment that make use of these linear structures to move easily along the landscape (Seabrook & Dettmann, 1996) such as the red fox (*Vulpes vulpes*), feral cat (*Felis catus*), and dingo (*Canis familiaris dingo*) (Bennett, 1991).

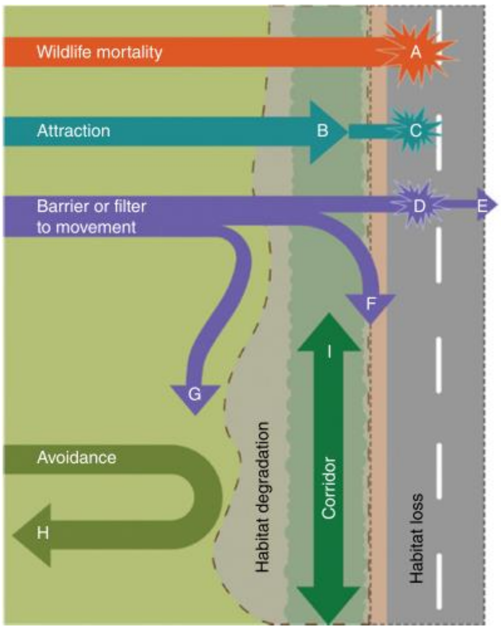

Figure 1 Ecological effects of roads; (A) animal mortality due to collisions with vehicles; (B), the animal is attracted to the road and may die (C); some animals want to cross the road and may die (D) or are succeed (E); others are dissuaded and remain on the edge (F); or stay in the degraded habitat area (G); finally there are species that avoid the roads and the “road-effect zone” (H). Adapted from van der Ree et al., (2015).

Therefore, in a summarized way, roads can have three distinct effects on wildlife, negative, positive or neutral, depending on the species or ecosystem (Figure 2). Negative in the case of affecting the fitness at individual level, decrease the population of a certain species, or leading to loss and damage in the ecosystem; positive when results in an increase in the number of individuals of a species or on the individual's fitness; or neutral if there is no significant change at the individual level or in the ecosystem (Saunders et al., 1991, Cushman, 2006).

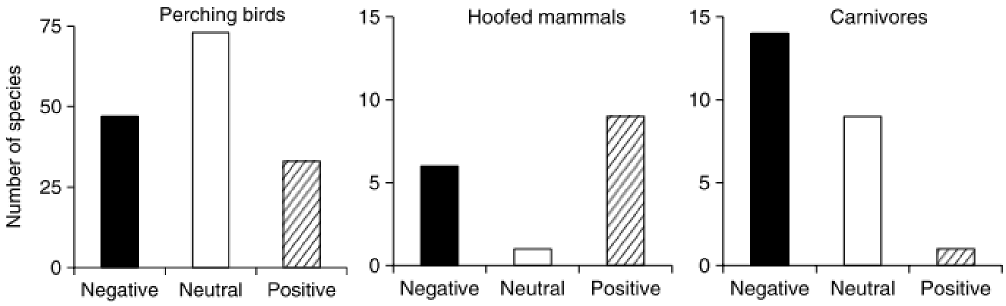

Figure 2 Number of species showing average neutral, positive and negative effects of roads on their population abundance for birds and mammals, respectively. Adapted from Rytwinski and Fahrig (2015).

Avoidance Behaviour to Roads

Taking into account the impact that roads have on an ecosystem previously described, there is one in particular in which this project will focus more specifically, the avoidance behaviour. Roads do not only change a landscape, do not only disturb an ecosystem, it changes behavioural patterns in wildlife (Jaeger et al., 2005; McGregor, Bender & Fahrig, 2008).

Avoidance behaviour, in a general way, can occur due to different factors inherent to roads, such as: surface avoidance, avoidance to traffic and its associates (light, chemical pollution, noise) and avoidance to vehicles (being able to perceive the vehicle and not being hit). Animals that avoid roads due to pavement have a lower risk of mortality because they never cross the road, avoiding collisions, on the other hand, get reduced habitat and become possibly isolated from better essential resources and, increasing the risk of extinction. Finally, animals that avoid collision with vehicles do the crosses when the traffic volume is lower, even if there is a risk of mortality by collision with vehicles the cross can also be successful (Rytwinski and Fahrig, 2015). The volume of traffic and all its associated to it is one of the major factors leading to habitat degradation (Forman et al., 2003). Studies have shown that amphibians, reptiles, birds and mammals (carnivorous and herbivorous) are affected by the volume of traffic (Fahrig et al., 1995; Clarke et al., 1998; Carr & Fahrig, 2001; Hels & Buchwald, 2001; Kuitunen et al., 2003; Mazerolle 2004; Seiler 2005; Roe et al., 2006; Colino-Rabanal et al., 2011). In areas close to roads depending on the animal and traffic volume can be manifested avoidance behaviour between 50 to 2800 meters (da Rosa & Bager, 2013).
There are species that are more susceptible than others to the impact caused by roads, and even within the same species there are factors that cause the behavioural

response not to be the same, as age, sex and reproductive status. The seasons, the climate and the characteristics of the road itself (such as the pavement) are factors that will also influence an individual behavioural response (Fahrig et al., 1995; Andrews et al., 2008; van der Ree et al., 2015). Species which do not exhibit avoidance behaviour in relation to roads or traffic have a high probability of dying by collision, unlike species that exhibit avoidance behaviour (Jaeger and Fahrig, 2004). Groups with large numbers of individuals represent greater security. The time an animal expends in being vigilant decreases with the increase of the size of the group where it is, as if each one was being vigilant in turn (Delm, 1990; Lima, 1995; Roberts, 1996). By reducing alertness, the animal may have more time for other activities such as foraging (Lima and Dill, 1990; Treves, 2000). Offspring also require a lot of time from the progenitors, most of the time the females with calves are on alert to protect them and have less time to look for food, shelter or other essential resource (Elgar, 1989). In 2001, Vistnes & Nellemann carried out a study on semi-domesticated reindeer to understand if there was avoidance behaviour to cabins, roads and power lines during calving. They performed transects of 20 km in length and 2-3 km in width parallel to the roads and depending on the viability of the terrain, recording all groups of reindeer that were observable and classified according to age and sex (i.e., males, females, calves, or yearlings). Of all reindeer, 77% were observed > 4 km from both the tourist resort and the separate power line. That area covered 45% of the area studied. The avoidance behaviour was much more pronounced for maternal females in relation to the tourist resort, which may suggest a behavioural adaptation in order to protect the offspring from possible predators or disturbances (Bergerud & Page, 1987). Males were more tolerant of surrounding disturbances than females (Dau &Cameron, 1986; Murphy &Curatolo, 1987; Nellemann & Cameron, 1996) but still females, calves, males and yearlings all avoided the 0-4 km areas from sources of disturbance (Vistnes &Nellemann, 2001).

According to Rytwinski & Fahrig (2015), there are few quantitative studies on avoidance behaviour in relation to roads and it is not known if the absence of animals in areas with high road density is due to avoidance behaviour, or if the absence of animals in these areas is due to vehicle collision mortality. They also say that even if you observe an animal's behavioural pattern on roadways, the hesitation to cross it may be either because of traffic or because of the road itself, not being able to know for sure whether it is an avoidance behaviour, unless the animal chooses to cross the road only when the level of road traffic is lower, and thus we can say that it is an avoidance behaviour (Rytwinski & Fahrig, 2015). As in the case of a project carried out by Brody and Pelton in 1989, that involved the study of the effect of roads on the patterns of black bears displacement in North America. The animals were captured, the radio collars were placed and the variation of the displacements in the area of residence was observed through ground triangulation and sometimes aerial homing (Brody, 1984). They were able to realize that the bears avoided crossing highways due to the high volume of traffic but smaller roads don´t appear to be a problem to road-crossing. They conclude that the frequency with which they crossed the roads had nothing to do with the age or sex. The bears did not limit their movements due to the roads, but they could change the home range according to areas with less traffic if the present ones had more road density, to minimize the risks associated with traffic (Brody and Pelton 1989). Another study also detected greater avoidance behaviour of an ungulate in areas near the roads during the day that decreased at night due to the decrease in traffic volume (Meisingset et al., 2013). The avoidance behaviour may be more accentuated by the increase in road traffic and this in turn may differ daily, weekly and seasonally (Rowland et al., 2000; Dodd et al., 2007; Gagnon et al., 2007b).

Why wild ungulates?

Ungulates need to move around the environment in order to find the resources essential for their survival and genetic transfer. These displacements can reach several kilometres and are made according to the seasonal availability of the resources required. Inevitably, the animals end up crossing linear infrastructures and a conflict arises between them. This disorder may limit the movement of animals and lead to death by collision with vehicles, endangering both animals as well as humans. The ungulates are mostly herbivores and therefore eat plants and thus help in the recycling of nutrients, in the diversify the plants in grasslands and serve as food for carnivorous. Being large and medium-sized animals, they are often related to collision accidents with vehicles (Cramer et al., 2015). In 1996, more than 500 humans died from this type of accident with ungulates (Groot-Bruinderink & Hazebroek, 1996).

It is important to realize how animals move in fragmented environments by roads, how they react to this type of infrastructure, and what can be altered so that solutions can be found to keep wildlife and humans safe. Thus, ungulates are a good model species for this project because they are very susceptible to human disturbances (Stankowich, 2008), including roads and their its associated effects (Alexander, Waters & Paquet, 2005; Ito et al., 2013).

Red deer – *Cervus elaphus*

In Portugal, this species was almost extinct in the late nineteenth century, due to overexploitation, degradation and fragmentation of the habitat. Due to reintroduction programs as well as the natural dispersion of populations, this problem has been overcome. Nowadays, it is possible to observe populations of red deer a little throughout Portugal (Salazar, 2009; Alves, 2013).

Figure 3 Red deer distribution in Portugal (Adapted from Salazar, 2009)

This reintroduction occurred between 1995 and 1999 in the Lousã Mountain with the release of 96 animals (32 males and 64 females), aiming to improve the natural patrimony of a typical Mediterranean landscape (Alves, 2013).

Red deer have the ability to inhabit different habitats and are therefore considered a species of high plasticity, from woodlands at temperate climates (Bobek, Boyce & Kosobucka, 1984; Theuerkauf & Rouys, 2008; Alves, 2013) to shrublands and grasslands in Mediterranean zones (Soriguer et al., 1994; Garín, 2000; Alves, 2013). It is a highly sexual body size dimorphic ungulate with a, polygamous mating system (Clutton-Brock, 1989). Usually described as a non-territorial, red deer may present territoriality depending on the availability of resources (Carranza, Alvarez & Redondo, 1990). It is a species with a well-defined life cycle and with well-established periods of birth and reproduction, and thus they present a temporal and seasonal effect on habitat selection. The demand for essential resources changes according to the phase of the life cycle in which they are what can constitute a spatial gradient in the selection of the habitat (Alves, 2013).

Having a matriarchal society outside the breeding period, males live segregated from females adopting a solitary behaviour, while females are normally observed aggregated to sub-adult females (Alves et al., 2014). This dispersion strategy of the males causes them to seek and occupy new territories increasing the population range (Clutton-Brock, Guinness & Albon, 1982; Bonnet & Klein 1991; Soriguer et al., 1994). Males and females present two different reproductive strategies, while males ensure a good physical condition, females excel at the survival of offspring (Clutton-Brock, Guinness & Albon, 1982; Main & du Toit, 2005).

Aims

The main objective of this project is to see if there is avoidance behaviour by the wild ungulates to the roads, In particular by red deer. In the presence of an ecological effect of roads, we intended to understand how it will influence the spatial distribution, habitat use and activity patterns of red deer in the Lousã Mountain. The ungulates are mostly large animals and therefore have a fairly wide distribution in the environment, with crepuscular activity, so the hours of greater human movement do not match the typical activity patterns of these animals. Notwithstanding, red deer may be susceptible to road effects. As so, this study also focused on understands the behavioural patterns of red deer in areas near by roads, aiming to determine possible behavioural changes as result of it.

Chapter 2

Avoidance behaviour of red deer to roads: its effects on spatial distribution, habitat use and activity patterns

Introduction

The ecological impact of roads, of different types like paved, unpaved, forestry roads, agricultural paths or highways have been studied for different wildlife species, and many have already been identified (e.g. Forman & Alexander, 1998; Forman et al., 2003). Among the disturbances caused by roads to wildlife identified, the most relevant are the destruction of the habitat caused by roads construction, fragmentation of habitats, chemical and physical changes in the environment, collision mortality between wildlife and vehicles and changes in animal behaviour (Coffin, 2007). Changes in animal behaviour inflicted by roads can lead them to learn to avoid it (e.g. Reijnen & Foppen, 2006; Roedenbeck & Voser, 2008). Although avoidance behaviour can be a good strategy employed by animal to reduce the risk of collision and mortality rate, it also has negative effects to wild population, since it increases the barrier effect and diminish the genetic and individual exchange between habitats fragmented by roads (Holderegger and Di Giulio, 2010).

Large herbivores need to move along the landscape to find food, water, shelter, and mates, this happens with both ungulates that migrate for long distances and to the ones that remain as local residents. These movements can sometimes reach many kilometres, making inevitable the animals to encounter roads (Cramer et al., 2015).
Roads are transport infrastructures and from here arise several disturbances associated as vehicles, noise, light, hikers and hunters which may affect wildlife at the habitat level, population level or at individual level, affecting animal activity and behaviour (Fahrig and Rytwinski, 2009; Forman and Alexander, 1998; Trombulak and Frissell, 2000). This can cause temporary or permanent avoidance of areas adjacent to roads disturbance, making them to choose areas more isolated and with greater coverage to increase protection (Jerina, 2006; Waller and Servheen, 2005).

Roads can have distinct effects on animals, from attraction, neutral or avoidance. It may seem strange that there is an attraction to an anthropogenic disturbance like roads are, but what happens is that roadside vegetation may be nutritionally beneficial resulting in attraction towards roads by several species of grazers, such as deer species (Finder et al.,1999). Avoidance levels can be different depending on traffic density. The deer show their behavioural patterns rather concisely, being further away from the roads and nearby areas during the day, and approaching more to these at night (Ager et al., 2003; Wisdom et al., 2005; Gagnon et al., 2007*a, b*). In previous studies it was verified that the greater frequency in crossing roads happened during the night in the winter and in autumn, when traffic and human disturbances are less frequent, revealing that avoidance behaviour and the choice to not cross or cross the road are related to these two factors (Gagnon et al., 2007b, Laurian et al., 2008). It has also been suggested that in some cases, depending on the habitat, females tend to cross more than males (Meisingset et al., 2013), males are more sensitive to this disturbance than females (McCorquodale, 2003, Dodd et al., 2007) and spend more time being vigilant in the presence of road traffic (Clair and Forrest, 2009).

Wild animals when disturbed in their habitat need to adjust their behaviour to remain safe (Lima & Dill, 1990), and they alternate their behavioural patterns to avoid predation (Caro et al., 2004).

The human presence and its activities can be considered as risk of predation by wild animals, since both induce similar trade-offs, altering individual investment by adopting an anti-predator tactic (Frid & Dill, 2002). Therefore, roads may be perceived as predation risk, so wild animals will behave as if they were facing a predator, and as consequence to adopt the same protective behaviour (Lima & Dill 1990, Roberts, 1996, Papouchis et al., 2001, Fernandez-Juricic & Schroeder, 2003). Due to the absence of their natural predators, red deer *Cervus elaphus* in the Lousã Mountain, face the risk of predation or disturbance only by humans and abandoned dogs, that act as non-natural predators (Alves, 2013), so any behavioural changes are due to anthropogenic activities, such as recreational activities (e.g., mountain biking, trekking and hunting), or even more frequently by the use of roads infrastructures.

The main aim of this study is to understand if the effects of roads on red deer population at the Lousã Mountain. If any type of ecological effect is observed, we intend to understand if and how it affects the spatial distribution, habitat use and activity pattern of the red deer population in our study area. Red deer is the larger mammal in Lousã Mountain having thus a wide geographical distribution and moving along the landscape. These displacements sometimes lead to the encounter with roads and here arise the conflicts between animal and anthropogenic disturbance. In this study area we have two types of roads, paved and unpaved, and two types of habitat, forests and shrublands. We expect forests to be used as shelters and as crossing areas, while due to nutritional variety and food abundance, shrublands will tend to be preferred. We expect differences between sexes, once that males and females live more of their time segregated. Regarding road type, it is expected a more pronounced avoidance of paved roads in comparison to unpaved roads due to pavement, paved roads may cause pavement avoidance; traffic, traffic tends to be higher in paved roads; and vehicles speed, vehicles move at higher speeds in paved roads making more noise and pollution.

Methods

Study Area

The Lousã Mountain (Serra da Lousã) is the westernmost region of the Cordilheira Central of Portugal (40°3'N, 8°15'W). This region presents the typical Mediterranean climate, with hot and dry summers and windy and rainy winters, usually without snow (Archibold, 1995; Alves et al., 2014). Due to slope, aspect and altitude, normal characteristics of a mountainous topography, climatic differences are present in the study area. Temperatures range from -4.1 ° C to 35.9 ° C, precipitation is around 827 mm, but can reach 1600 mm at higher altitudes. Altitude ranges from 100m to 1205m above the sea level, within deep valleys and round (Alves, 2013).

This mountainous region has mixed habitats composed manly by coniferous forests, broadleaf trees and the typical large Mediterranean shrublands. The most common species of the coniferous forests in this area are pine trees (e.g. *Pinus pinaster*, *Pinus sylvestris*, *Pinus nigra*), Douglas fir (*Pseudotsuga menziesii*) and Mexican cypress (*Cupressus lusitanica*). Broadleaf forests are composed by *Quercus* sp., *Castanea sativa*,and *Prunus lusitanica* The shrublands are mainly composed by heathers (*Erica* spp. and *Calluna vulgaris*), gorses (*Ulex* spp.) and “carqueja” (*Pterospartum tridentatum*). It can also be observed in the lower altitudinal areas of the Lousã Mountain eucalypts forests (mainly *Eucaluptus globulus*) (Alves et al.,2013A) and agricultural fields annual irrigated crops, such as potatoes, vegetables and maize, and non-irrigated crops like rye, wheat and oats, sometimes associated with olive and fruit trees (Alves, 2013).

Concerning fauna, the study area encompasses a variety of species such as birds like *Circus pygargus* and *Caprimulgus europaeus*, amphibians like *Chioglossa lusitanica* and *Rana iberica* and reptiles like *Vipera latastei* and *Lacerta schreiberi*. Regarding carnivores, *Vulpes vulpes*, *Genetta genetta*, *Mustela putorius* and *Martes foina* inhabit in this region. Besides the studied species, the study area also has wild populations of roe deer *Capreolus capreolus* and wild boar *Sus scrofa*. No natural predators are present, but some abandoned dogs may act as non-natural predators, predating principally young, sub-adults and adult females (Alves, 2013).

In this mountainous region there is a vast road network, although there is only one major asphalt road that crosses it (EN236). The number of smaller roads, paved with gravel or non-paved, such as forestry roads, windfarm road infrastructures, and firebreaks is quite high (Alves, 2013). The central region presents in general a low volume of traffic, but the surrounding areas are more affected by this disturbance, presenting greater traffic volume, both at the beginning of the day and at the end (Alves, 2013)

Field methods and sampling design

To analyse the effects of roads in the red deer population, two complementary field methods were applied: faecal pellets counts along line transects with distance sampling and camera-traps. The sampling points for both methods were defined in a stratified sampling design, based on habitat type and road type. Based on land cover of the study area, and on previous results on the habitat used by the studied population (Alves el. al., 2014), two major habitat types were considered, the shrublands which represent open areas, and forests which represent closed areas. Regarding roads, two major road types were considered based on its pavement: paved roads, roads paved with asphalt or gravel, usually with 5m to 10m of width; and unpaved roads, which are in general dirt roads with 2m to 5m of width. Besides the type of pavement, there are other characteristics associated with the road type that may influence a potential avoidance behaviour, namely traffic volume, vehicle speed and hour of human activity. As so, paved roads have a higher traffic volume, leading to higher disturbance due noise, higher vehicle speed and higher human movement in the first hours of the working day (8h to 10h) and at the end of the working day (17h -20h). In the opposite, unpaved roads are usually used by forestry workers, having for that reason very low traffic, slow speed from the vehicles, with no peaks in its use.

In total, 30 sampling points were defined in the central region of the Lousã Mountain, distributed as 7 in forest paved roads, 10 in forest unpaved roads, 6 in shrubland paved roads and 7 in shrubland unpaved roads. At each sampling point, two perpendicular faecal pellet counts along linear transects with distance sampling and one camera-trap were made from October to November, 2017, representing the post-rut season (Alves et al., 2014).

Regarding activity pattern study, five Bestok camera-traps (12MB resolution) were used to monitor red deer behavioural patterns near to roads. The cameras were recording for 1 week in each of the 30 sampling points mentioned above, taking 3 photos and a 30 seconds video every time its activated by motion sensor, recording date and hour. The surveyed period was the same has the one mentioned for pellet counts. The cameras were placed at 50m to 60m from surveyed road, at 1.10m height, to capture red deer behaviour and activity 24h/day for 7 days.

For each animal recorded by the camera-traps, sex, age class, group composition and behaviour was registered. The behaviours recorded were classified as feeding, alert state, walking, running and laying (Table 1) and were only determined, when the photos or video quality provided sufficient visibility.

Table 1: Ethogram of red deer behaviours.

Behaviour	Description
Feeding	Consumption of any plant material. Usually the animal has the head down.
Alert state	Standing in a state of attention with his head held up in response to some stimulus from the environment. It is characterized by the sudden interruption of a previous activity.
Walking	Moving at a constant rate from one point to another.
Running	Moving at a fast rate from one point to another.
Laying	Lying down while not engaged in any other behaviour. Includes sleeping and resting.

The faecal pellet counts along linear transects with distance sampling were performed following Mayle et al. (1999), in a total of 59 transects of 200m of length, perpendicular to the sampling roads, consisting in two per sampling point (except in one case that was not logistically feasible). Along each transect, all the pellet groups detected were registered and its linear distance to the sampling point (transect starting point) and perpendicular distances to the centre of line transect were recorded.

This method was applied to determine the spatial distribution of red deer in relation to the surveyed roads, and understand their habitat use. Faecal pellets are very useful, since they have a low decay rate (581 ± 55 days; see Alves et al., 2013a for further details), are deposited at regular intervals due to the high defecation rate of red deer (25 pellet groups per day; Mitchell, 1984), and are not affected by differences in the daily habitat use

Since the only other deer species present at Lousã is roe deer *Capreolus capreolus*, the pellets of both deer species are easily distinguishable, not causing any misidentification issues.

Data analysis

Data obtained from the observation of camera-traps photos was analysed in terms of behavioural activity patterns that were estimated by fitting kernel density functions (Ridout and Linkie, 2009) to temporal activity patterns of red deer males and females, for each combination of road type and habitat.

Regarding pellet counts dataset, each transect was subdivided into segments of 10m, and the total number of pellets per segment used as dependent variable. A generalized additive mixed model (GAMM) with zero-inflated Poisson distribution was fitted to examine the effects of distance to road, road type and habitat on the number of pellet groups. Since detection probability (0.428±0.01) of pellets in the two surveyed habitats was not statistically different ($t = 0.305$; $df = 881$; $p = 0.761$), no estimation of the real number of pellet groups was necessary.

P values lower than 0.05 were considered significant. The results are expressed as mean ± standard error (SE), unless otherwise stated. The statistical analyses were performed using R 3.2.0 (R Core Team 2014), using package “overlap” (Meredith & Ridout, 2016) to calculate kernel density functions, and package “mgcv” (Wood, 2006) to perform GAMM.

Results

Activity patterns of red deer

From October to December 2017, a total of 128 (32 males and 96 females) adult red deer, were recorded by the camera-traps (5 cameras per week, in 5 different points and rotated weekly to survey the 30 sampling points).

The general activity patterns of red deer showed multimodal peaks in activity (Fig. 4). In this period, both males and females showed significant peaks in activity throughout the daytime and night-time (Fig. 4).

The comparison of the activity patterns observed per road type and habitat revealed differences on the periods of activity (Fig. 4). When evaluating the activity in open areas of shrublands, it is notorious that red deer concentrate their activity during night, avoiding the peaks of human movement (that mostly occur from 8:00h to 10:00h and from 17:00h to 20:00h). In forest areas, the activity seems more even distributed along the day.

Regarding the road type, when animals are in the forest areas, they tend to avoid the vicinity of paved roads between the hours of 6:00h to 12:00h and again between 18:00h to 23:00h. When roads are unpaved there is almost constant use by both sexes, with males being more nocturnal, and more active between 1:00h and 8:00h, while females are active around 6:00h increasing their activity until 12:00h. Is also clear that males decrease their activity around 16:00h returning to be more active around 0:00h.

In shrubland the periods of activity of both sexes are quite demarcated, coinciding in a general way. Once again males tend to be more active in the night time when they are near paved roads existing two significant periods of activity between 18:00h and 4:00h and 8:00h and 12:00h. Females tend to be more active in these conditions than males, with a breakdown of activity between 12:00h and 17:00h. Near unpaved roads, males tend to be more active between 6:00h and 12:00 and again between 17:00h and 1:00h. Regarding females the results show two peaks between 4:00h and 10:00h and again between 16:00h and 21:00h.

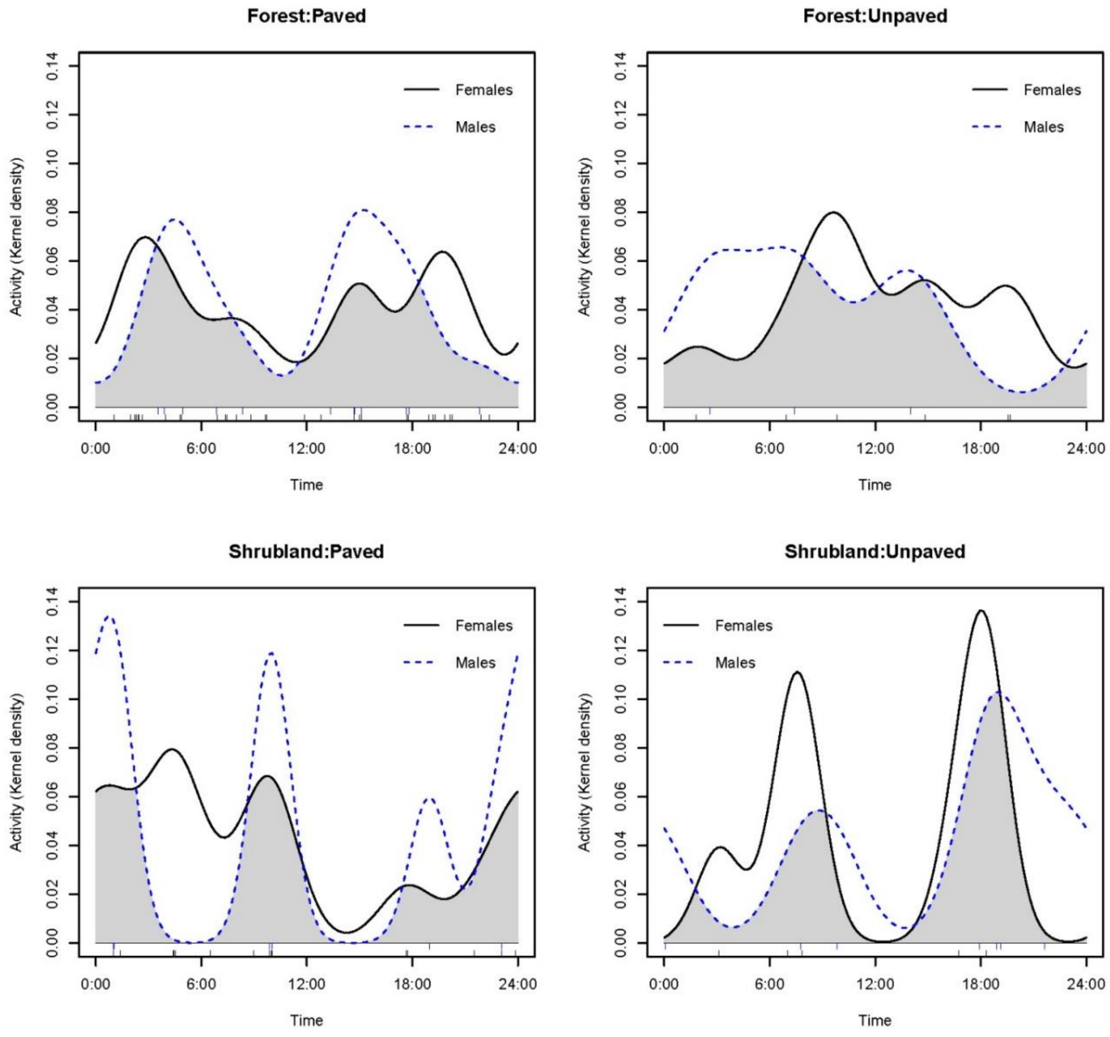

Figure 4 Activity patterns of red deer males (dashed blue line) and females (solid black line) in Lousã Mountain, for each road and habitat type.

Road effects on red deer pellet counts

Regarding the density of pellet groups, we found a similar density in the both types of roads (paved and unpaved), but different between habitat types (Table 2). Shrublands present a density two times higher than forest areas (Table 2).

Table 2: Density of pellets (number of pellets per linear meter) per road and habitat type

	Forest	*Shrubland*
Paved	0.049	0.109
Unpaved	0.048	0.120

Concerning the number of pellet groups in relation to the distance to the road, is possible to verify that both road type and habitat have an influence on the pattern of pellet distribution in relation to the distance to road (Fig. 5). In forest habitats with paved roads, a non-linear pattern was obtained, characterized by an avoidance until 20m of road, followed by an attraction and afterwards, being these patterns significant different from uniform distribution (χ=14.155, P=0.044). Similar pattern was obtained in shrubland with unpaved roads (χ=14.737, P=0.019) (Fig. 5). In forest with unpaved roads and shrublands with paved roads, an almost linear response was verified in relation to the distance to road with an approximated uniform distribution (Forest:Unpaved - χ=2.471, P=0.429; Shrubland:Paved - χ=6.214, P=0.102), but with opposite trends (Fig. 5).

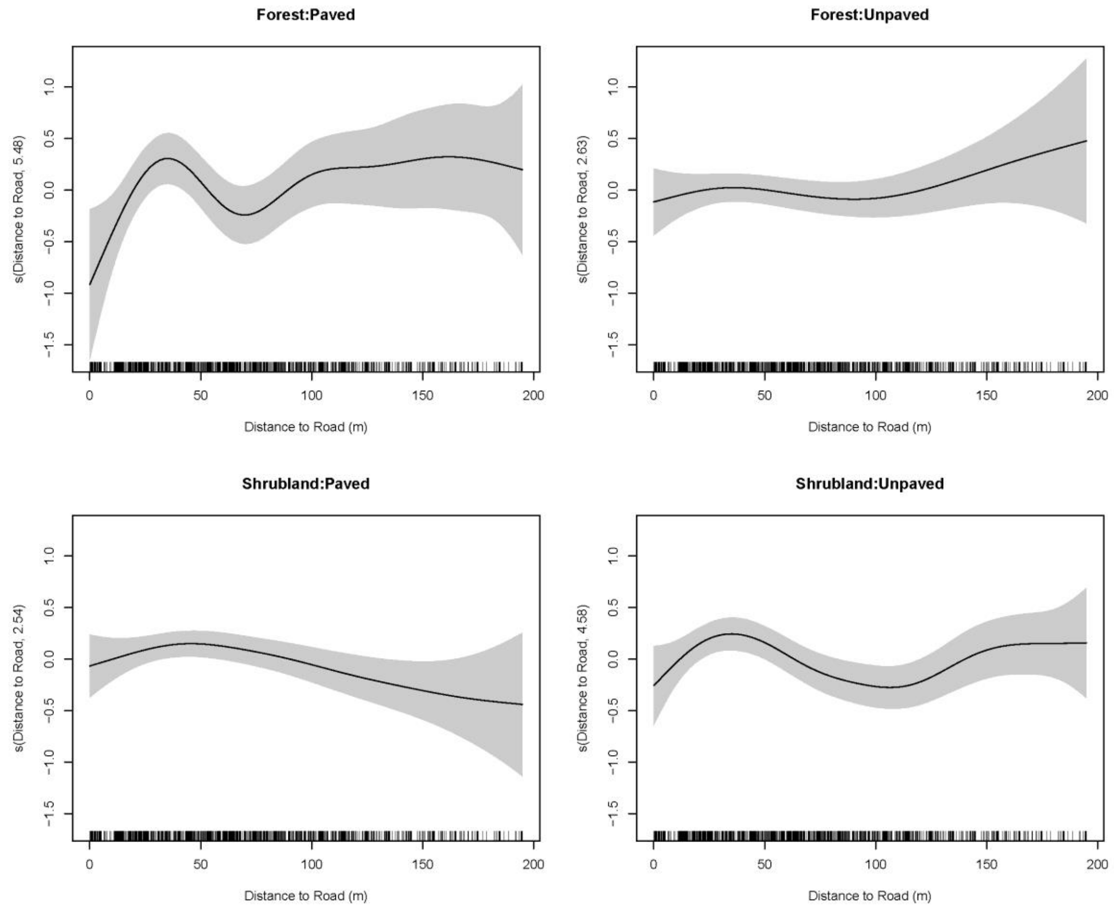

Figure 5 Estimated effect of the distance to roads on the number of red deer pellet groups for each road and habitat type.

Discussion

Our results demonstrated an effect of roads and habitat on the behaviour patterns of red deer. As expected, we obtained a non-random use of habitat, i.e. a selection of the space according to land cover and type of road. Shrubland is the habitat type preferred by red deer, as also documented in another study realized in 2013, in this same region (Alves et al., 2014). Contrary to our predictions, red deer did not exhibit strong sexual differences in their activity patterns. Being a species that lives segregated more than 80% of the time during the year (Clutton-Brock et al., 1987; Alves et al., 2014), a difference in preference and occupation would be expected, but it is not strongly verified from our results. This can be justified by the surveyed period, that was right after rut season, in a period during which males and females are still aggregated or random distributed (Alves et al., 2014), and for that reason with more synchronized activities.

It is possible to observe the occasional increase of activity and displacement at specific times, such as those coincident with sunrise and sunset, characterizing the crepuscular habits of red deer. Crepuscular habit is presented as a behavioural strategy to avoid elevated temperatures and predators (Cederlund et al., 1989; Beier and McCullough, 1990; Pépin et al., 2006; Loe et al., 2007). In this study the effect of the roads may promote a similar response to the ones verified in the presence of predators (Frid and Dill, 2002), since human disturbance is the major pressure felt by the animals.

As previously verified in the study about habitat use and selection made in this population (Alves et al., 2014), our results once again indicate a clear preference of red deer by shrubland areas, in comparison to forest areas. This goes in agreement with the results reported in other studies, where red deer tend to prefer habitats that provide simultaneously food and cover (Borkowski 2004). Given the variety and quality of food in the open areas of this region and since the vegetation has a height between 0.5 and 2 meters, both food and cover are assured (Alves et. al., 2014). Despite the obvious preference for shrublands, it is the forest that is used continuously throughout the day, while in the open areas it is possible to observe very distinctively peaks of activity, in the forest the use is almost continuous with significant oscillations when near paved roads which no longer occurs when animals are nearby unpaved ones.

Analysing pellet distribution along the distance to road in forests with unpaved roads, was not possible to denote a of the roads on the number of pellets, neither on animal behaviour. However, is also this combination of habitat and road type the least used one in terms of landscape features by red deer. Contrary to previous studies in other red deer populations, which indicated that red deer preferred closed environments (McShea et al., 2001; Jiang, Zhang & Ma 2008), the present study is in agreement to the previous one, and both clear support that red deer in the Lousã Mountain have a preference by shrublands.

In forests with paved roads an avoidance was verified in the initial meters from the road. This can be explained by avoidance of pavement, traffic avoidance (the paved road facilitates access to any means of transport and has higher density traffic) or pollution avoidance (sound or chemical) (Jaeger et al., 2005). Our results are in agreement with a study about impalas, in which the impalas avoided the proximity (up to 10 m) of paved roads and the unpaved ones would have no effect on the spatial distribution of the animals (Mulero-Pázmány et al., 2015).

Evaluating both activity analysis and pellet-counts, we realized that although forests are used in the same way throughout the day, there are no significant preferences for any specific time or period, these areas are probably used as transition and refuge areas, and that near paved roads the animals tend to avoid the vicinity to the road for the protection to be effective.

It has already been mentioned that there is a preference of this red deer population for shrublands, and the results obtained relating the two variables, habitat and type of road, are more significant than the previous one. By the analysis of the number of pellet groups the difference in the density found in shrublands and forests is the double. This habitat preference may be related to its great quality and food abundance typical of the Mediterranean regions (e.g. Carranza et al. 1991; Garín 2000; Lovari et al. 2007; this study). Our results for paved roads in shrubland areas showed that there is no avoidance, this can be explained because in the open areas although the vegetation has a considerable size and can be used as shelter for the animals, they are still more exposed than when are in forest areas. As so, animals tend to use these areas when human activity or anthropogenic disturbances is lower or absent, as evidenced by the activity patterns. Dawn, dusk and night are the periods of the day when the animal's activity is greater; soon arriving at midday there is a sharp descent that may reflect the transition of the animals to another type of habitat, since results showed that forests are used continuously throughout the day. The mountainous landscape is not flat and it is necessary to take into account topographic features like slope when studying animal distribution (Stage & Salas 2007). This fact leads us to realize that the activity patterns verified in shrublands with paved roads may be due to the slope, since the animals are less exposed and therefore are not the target of any threat, remaining more time in the preferred habitat. In shrublands with unpaved roads, different trends were obtained. In relation to the activity, the use of these areas is slightly smaller than the previous one, being mostly used in the period of dusk and night. Unpaved roads in this region are secondary roads, rarely used and with low traffic (less than one car/hour) (Alves, 2013). Despite the preference for shrublands and the insignificant traffic that exists in this type of roads, it is noticeable a slight avoidance in the first meters after the road, as well as, the animal activity is reduced during the day and increasing from the dusk to night. This fact can be explained by the road-effect zone. The road-effect zone is considered the band next to the edge of the road that is highly asymmetric, due to nature's directional flows and the spatial patterns of each side of the road (Forman and Deblinger, 2000). In this study refers to the zone just after the road where plants may become more unpalatable due to dust (Trombulak & Frissel, 2000), that may come from the passage of cars or by strong winds. This avoidance may therefore be due to habitat loss, that can be direct where habitat is removed to build roads and their verges, or indirect, where habitat quality close to roads is reduced or damaged due to emissions from traffic such as, noise, vibrations, light or dust (Mader, 1984; Reijnen et al., 1995; Forman & Alexander 1998; Kaseloo, 2005).

In conclusion, we found that, in general, the behavioural pattern depends on the combination of the road and habitat type. We observed a preference for shrubland in relation to forest, since shrubland offers simultaneously food and cover to the red deer population of Lousã Mountain. Although males and females have been found in same type of habitat with no significant differences, the activity pattern is slightly different between both sexes. Avoidance behaviour was observed but not related exclusively to road type but to the type of road inserted in a given habitat. The combinations of unpaved roads in shrubland as well as paved roads in the forest were the most significant landscapes, evidencing an avoidance of the first 10-30 meters after the road side. According to the activity of the animals, a crepuscular habit was observed, as previously documented (Cederlund et al., 1989; Beier and McCullough, 1990; Pépin et al., 2006; Loe et al., 2007), using the forests continuously throughout the day as opposed to great peaks of activity on shrubs at lower human activity.

Chapter 3
General conclusions

Conclusions

The main goal of this study was to perceive the impact of paved and unpaved roads and type of habitat on red deer behaviour, and its effect on animal's spatial distribution, habitat use and activity patterns.

We expected a negative effect of the roads, which was confirmed. As expected, paved roads have a greater effect on avoidance behaviour by red deer, since from paved roads result higher traffic, higher probability of vehicle speed, noise and pollution, and the surface itself can cause inhibition. The avoidance of unpaved roads in shrublands may correspond to the degradation of the surrounding habitat since these roads are often used for recreational activities such as mountain biking and four-wheel motorcycle and/or wood-cutters with tractors that damage the vegetation of the roadsides. The observed avoidance can be related to the loss of habitat indirectly related to the roads although the roads are not directly the cause of this avoidance.

The activity patterns do not present significant differences between the sexes; both use the forests continuously throughout the day preferring the shrublands given their variety and quality of food. Males tend to have a more nocturnal activity whereas females are more active in the twilight periods. Shrublands were heavily used, however more when there is a lower human pressure.

The present study highlights the problematic of the influence of anthropogenic disturbances and impact in wildlife populations. Thus, additional studies are essential to improve the current knowledge, and to better understand the impact of human disturbances on wildlife, and how this can affect the ecology, conservation, evolution and management of the species.

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