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ENVIRONMENTAL AND HUMAN FACTORS AFFECTING SPATIAL BEHAVIOUR AND DETECTABILITY OF ROE DEER (*Capreolus capreolus*): INFLUENCE ON POPULATION ESTIMATE

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Paolo Bongi ENVIRONMENTAL AND HUMAN FACTORS AFFECTING SPATIAL BEHAVIOUR AND DETECTABILITY OF ROE DEER: INFLUENCE ON POPULATION ESTIMATE tesi di dottorato in BIOLOGIA AMBIENTALE 21 CICLO UNIVERSITA DEGLI STUDI DI SASSARI

INDEX

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INTRODUCTION

This thesis consist of three main parts dealing with some crucial aspects concerning the determination of roe deer (*Capreolus capreolus*) population abundance. In the first part I evaluate the census methods actually used in Italy and in Europe, to estimate roe deer density, and I evaluate the applicability and accuracy of each method considered. In the second part I considered some anthropic factors that can influence the roe deer spatial behaviour and consequently the census results. Finally in the third part I analyse some ecological variable that have influence on roe deer behaviour and I consider the deer in prey-predator system.

Density estimate is based on possibility to detect animals, and consequently to know their behaviour can be useful to increase the possibility of observations. In fact many factors can influence a spatial modification and to induce deer to use environment safe. Therefore this choice may affect the result of census, given that increase the difficulty to detected a roe deer in a dense vegetation.

The aim of this thesis is to compute different census methods and to put in light how factors are linked to density estimate, causing a influence on roe deer spatial behaviour.

In the last decades the increase of roe deer population was recorded in many European countries (Gortázar et al. 2000, Cargnelutti et al. 2002, Acevedo et al. 2005, Ward et al. 2005, Milner et al. 2006). As consequence of this increasing it is an increasing of ungulate-human conflict. Particularly, two different opinion are expressed on this problem. On one side the hunters would to maintain or increase the population size for better hunting bag (Whittaker et al. 2001). On the other side the damage to forest and farming were increased (Gill, 1992), the diseases linked to wild ungulate were widespread (Simpson, 2002), the ungulate-vehicle collision increased too (Groot Bruinderink & Hazebroek, 1996). So this component of people is favourable to a decrease of roe deer abundance. Therefore it is necessary to know very well the population size of ungulate hunted. Given that a sustainable use of wildlife strongly depends on the monitoring of population status and trends, and the definition of appropriate harvesting quotas, a scientist approach to estimate density is request. Several methods are used in management choice: drive census (Staines and Ratcliffe

1987); line transect (Buckland et al., 1993), pellet group count (Putman, 1984) and mark-resighting of radiotagged individuals (Minta & Mangel, 1989, Neal et al., 1993). However we must consider the applicability of census methods in relationship of different environment, of different period and in reference to different ecological characteristic. Nevertheless it necessary to consider different survey techniques in terms of accuracy and precision of results (Jachmann and Bell 1984; Koster and Hart 1988; Knott and Venter 1990; Jachmann 1991; Klinger et al. 1992; Mandujano and Gallina 1995; Peel and Bothma 1995). Given such scenario the main aim of the *first part* of this thesis is to evaluate different census methods and to identify the method with best accuracy and applicability (**Chapter 1**). This data are very important, both from a management and scientist point of view. In fact a good knowledge of population density can permit adequate shooting plan to satisfy hunter exigencies and to preserve deer population. First of all it is necessary to individuate the best method to calculate density in relationship environmental characteristics. So, I compare densities estimate, obtained with six different census methods, to understand which method have a good applicability, accuracy, and which method give an underestimate of population size.

In fact data on population density, obtained using different census methods, gave discordant results. Therefore a census result can be conditioned by several factors. Human activities can modify the spatial behaviour of roe deer and to compromise the detectability. As consequence of that, we could recorded a variation in density estimate. It appears that human activities influence the distribution of large animals (Blom et al. 2004). Wild ungulates exhibited different responses to human disturbance, whereby their behavior and physiology were modified (Cederna and Lovari 1985, Jeppesen 1987b, Jeppesen 1987a, Weisenberger et al. 1996). Both predation risk and human harassment may evoke different responses in wild ungulates according to sex or age classes. The *second part* of this thesis is to analyze different human activities that can influence movement of roe deer. Particularly we take into account the hunting activities and forest work, like cutting tree.

Hunting was recognized and studied as a crucial factor that can modify the animal behaviour. Several authors argued that hunting was able to shape the fright behavior in response to humans in birds, (Madsen 1985, Madsen and Fox 1995) and ungulate (Dorrance et al. 1975, Shultz and Bailey 1978, McLaren and Green 1985, Jeppesen 1987b). Colman et al. (2001) tested the flight distance in rein-deer (*Rangifer tarandus*) and did not find any evidence of it, while, as regards roe deer (*Capreolus capreolus*), those living in hunting areas seemed to fear man more than those living in areas where hunting was not practiced (de Boer et al. 2004). Certain traditional modes of hunting which are practiced in central and southern Europe entail the use of dogs to hunt preys. We tested if roe deer showed a different behavior in relation to different hunting activities (**Chapter 2**). Especially we test if roe deer modify their spatial behavior and increase the use of protected areas during the stalking season as a consequence of a direct hunting pressure; if hunting with dogs induces roe deer to find refuge in protected areas, even though they are not the target prey species of this hunting practice, and finally if different sex and age classes are affected to a similar degree by the hunting harassment as a consequence of similar body sizes. All this aspect have a considerable effect on density estimate.

Moreover the relationship between roe deer and forest is studied to understand if deer prefer some kind of habitat. Furthermore in the last few decades the relationships between wild ungulates and forest ecosystems were deeply investigated (Jorritsma et al. 1999, Reimoser et al. 1999, Sipe & Bazzaz 2001, Partl et al. 2002, Horsley et al. 2003). Even because silvicltural systems, that conserve the natural processes and functions within the forest ecosystem and tend towards sustainable forest management, became more and more common. Coppice system is mostly under private ownership, which controls two thirds of total forest area of Apennines. The coppice areas are mainly concentrated in the sub-mountainous vegetation belt. Oaks and chestnut represent the most common tree species of these areas. On the contrary, high forest system prevails in public ownership, which is largely present in the upper mountainous belt, dominated by beech forests. Both environments are of high importance for ungulates (Jedrzejewska & Jedrzejewsky 1998) and represent one of the most suitable habitats for roe deer, which are the more common ungulate species (Apollonio 2004b). The use of coppice area by roe deer is possible to quantify in terms of browsing pressure. Moreover with analysis on spatial behaviour it is possible to determinate the time spent inside to this area. The **Chapter 3** put in evidence these aspects. Considering that the coppice area are rich from trophic point of view and very dense, for ore deer became really a favourable environment. Therefore if a roe deer lying in a coppice wood it is difficult to observe its. Then if we want to organize a census based on direct observation of deer, it is necessary to consider the presence/absence of coppice area in our monitoring area.

Finally in the *third part* of this thesis I consider the ecological variable, like disturbing factor on density estimate.

Roe deer is important also on prey-predator relationship. In fact, even if the wolf is a predator with a highly diversified diet (Voigt et al. 1976; Salvador and Abad 1987; Spaulding, Krausman and Ballard 1998), where wild ungulates are abundant, the wolf feeds mostly on them (Jedrzejewski et al. 1992; Meriggi and Lovari 1996). Thus, in most Eurasian countries, wolves coexist with a wild ungulate community made up by only a few species. In these contexts, their foraging behaviour may be shaped more strongly by the population dynamics of their prey. On the other side, the predator can be see like a regulator factor of prey communities. The "green world hypothesis" (Hairston et al. 1960) and the hypothesis of exploitation ecosystems (Oksanen et al. 1981, Fretwell 1987, Oksanen & Oksanen 2000) both predict a strong limitation of herbivore populations by predators (top-down control). By contrast, the so called "plant self-defense hypothesis" (Murdoch 1966) predicts that herbivores are limited by the availability of ingestible plant material (bottom-up control). Surely the prey in presence of a natural predator change their behaviour.

In our study area a wolf pack are present, then it has been possible to study the relationships between forest productivity, prey densities and the effects of predation (**Chapter 4**). Moreover we considered the hunting harvest and investigate the different preferences of wolves and hunters for ungulate age classes. This results are important to underline the antipredator behaviour exhibit by roe deer. Mammalian females exhibit complex behaviour patterns during pregnancy, parturition and lactation that are all directed towards the survival of their young (Svare, 1981). The presence of fawns may influence social organization of lactating females (Schwede, Hendrichs & Wemmer, 1993; Bertrand et al., 1996; Tufto, Andersen & Linnell, 1996), as well as may evoke a diverse activity budget or foraging behaviour (Kohlmann, Müller & Alkon, 1996; Langbein, Streich & Scheibe, 1998; Ruckstuhl & Festa-Bianchet, 1998) or induce space use modifications (Berger, 1991; Green, 1992a; Tufto et al., 1996; Boschi and Nievergelt, 2003; Ciuti et al., 2006; Grignolio et al., 2007). In regards to space use, researchers reported that during birth and lactation the female is likely either to enlarge her home range (*Capra pyrenaica* Escos and Alados, 1992; *Capreolus capreolus* Tufto et al., 1996; Boschi and Nievergelt, 2003) or to reduce it (*Odocoileus virginianus* Schwede et al., 1993; *Dama dama* Ciuti et al., 2006; *Capra ibex* Grignolio et al., 2007). In response to the high risk of predation for neonates and the associated substantial loss in lifetime productivity (Bergerud, 1971; Garrot, Bartman & White, 1985; Smith, 1986), ungulates have evolved an array of characteristic maternal-neonate strategies represented by the "hiding-to-following" spectrum (Geist, 1971; Lent, 1974; Leuthold, 1977; Rudge, 1970; Walther, 1968). Roe deer is considered one of the most marked hider species, given that fawns of this cervid lie concealed for prolonged periods during lactation waiting for mother's milk (Linnell et al. 1998).

Therefore the aim of **Chapter 5** is to investigate if the roe deer mother during fawning period use different habitat, more safety, then more dense, respect to female without fawn. This notice, linked to knowledge of percentage of pregnant female could give some information about the results of census performed during fawning season.

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First Part

METHODS USED IN THE ESTIMATION OF ROE DEER POPULATION DENSITY

Chapter 1

HOW TO COUNT ROE DEER? A COMPARISON BETWEEN SIX CENSUS METHODS.

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HOW TO COUNT ROE DEER?
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Introduction

Numbers or range of ungulates species or subspecies have been increased and stabilised in many countries over the last decades (Gortázar et al. 2000, Cargnelutti et al. 2002, Acevedo et al. 2005, Ward et al. 2005, Milner et al. 2006, Apollonio et al. in prep.). This increase have been favoured by several factors, as a reduction of livestock and abandonment of agricultural practices (Acevedo et al. 2006). Many studies, performed in north Europe, showed that roe deer preferred to live in forest environment or in ecotone zone (Gill et al. 1996; Guibert, 1997, Melis et al. in prep.). The habitat structure had a strong influence on movement and home range size of roe deer (Vincent and Bideau, 1985). Another important factor that facilitated the roe deer population increase, was the regulation of exploitation and control of poaching (Gortázar et al. 2000).

As a consequence this lead to an increase of ungulate-human conflict. Hunters supported, in fact, the ungulate population increase (Whittaker et al. 2001) but in so

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doing, damages to forest and farming were increased (Gill, 1992), diseases linked to wild ungulate were widespread (Simpson, 2002), ungulate-vehicle collision increased too (Groot Bruinderink & Hazebroek, 1996). Then estimation of abundance is a recurrent problem in the study of population dynamics. The information on population abundance is also crucial to scientific management of wildlife. To estimate the density, the accuracy of a method is an important consideration (Huapeng et al., 1997). Many methods are used to investigate wildlife population abundance also in relationship to environment characteristics. Direct observations are used in open habitats (Focardi et al. 2002, Smart et al. 2004,) while in cover habitat indirect method are used and could be fecal count (Putman 1984), vocalization (Reby et al. 1998) trackway counts (Mayle et al. 2000) or biological index (Vincent et al. 1991, Whipple et al. 1994, Maillard et al. 2001, Morellet et al. 2007).

Some study suggest that in case of large animals the estimate of the population density could be particularly difficult, given that often they are secretive, crepusoclar in behaviour and frequent areas of cover such as woodlands (Mayle et al., 2000). In the other side to know the population density is most important for several factors. It is important for scientist knowledge, to foresee and to prevent the damages, and to perform a good management in game species.

The most common cervid both in Italy and in Europe, is roe deer. Furthermore roe deer is a game species and hunting quotas are determined on a shooting plan based on census data.

Several census methods are used in current management: drive census (Staines and Ratcliffe 1987); line transect (Buckland et al., 1993), pellet group count (Putman, 1984) and mark-resighting of radiotagged individuals (Minta & Mangel, 1989, Neal et al., 1993).

Sustainable use of wildlife strongly depends on the monitoring of population status and trends, Kremen et al. (1994), because this lead to the definition of appropriate harvesting quotas. Many techniques have been adopted to improve monitoring of large terrestrial mammal populations (Norton-Griffiths 1978; review from Van Hensbergen and White 1995). These survey techniques have often been compared in terms of accuracy and precision of results (Jachmann and Bell 1984; Koster and Hart 1988; Knott and Venter 1990; Jachmann 1991; Klinger et al. 1992; Mandujano and Gallina 1995; Peel and Bothma 1995), including the undercounting bias in aerial survey (see reviews from Caughley 1974; Hone1988; East 1998; Jachmann 2002).

Another important aspect is the cost effectiveness (Van Hensbergen and White 1995; Reilly and Reilly 2003) and the effort to organize the census (Hochachka et al. 2000; Walsh et al. 2001; Gaidet-Drapier et al. 2006).

In this paper we reported on a study conducted in a fragmented area, with wood cover and agricultural areas, where six methods are tested. The aim of the study is to put in evidence the accuracy and the applicability of each method. The methods used are: drive census, line transect, pellet group count, observation by advantage point, block count, night census with spotlight.

Methods

Study area

The study was performed in a fragmented landscape in Pisa province, Italy (43°19'N, 10°39'E). The study site include an area of 1200 ha were hunting was forbidden. Considering the movement of roe deer a buffer zone was used and the total area was 2000 ha. The climate is sub-Mediterranean, with mild winter and warm and dry summers. The agriculture has an high pressure on the environment and the major part of field is cultivate with corn. The woods were present, with oak (*Quercus cerris*, *Quercus pubescens*, *Quercus ilex*), ash (*Fraxinus* spp.) and juniper (*Juniperus axicedrus* var. communis). The understory was very dense; the most important species were bramble (*Rubus ulmifolius*), butcher's broom (*Ruscus aculeatus*) and blackthorn (*Prunus spinosa*).

Methods

We used six census methods: 1) drive census; 2) direct observation from advantage point; 3) line transect; 4) block count; 5) spotlight census; 6) pellet group count.

Drive census

We performed drive census in six random sample areas. Those areas represented the 20,26% of total cover area (more than 10%, as suggest in Meriggi et al., 1989). The battues were organized in early April in two days of work, with a number of operators proportional to size of battues areas (Staines and Ratcliffe, 1987). In our case the battuers density was 16 person each 1km^2. The battues started at 7 a.m. and it concluded before 12 a.m.

Data analysis was based on average density per each area and on total average. This value represented estimate density of roe deer present in the area.

Line transect

The transects had been choice more rectilinear as possible and the length was 1 km. On the study area was superimposed a grid of 20 squares, each with 1km per side. The point of beginning and the direction were choose in random way inside of each square. Every animal that were detected was recorded. The distance from the observer to the deer was measured and compass bearings were taken to determine the angle between deer and transect. The distance between deer an observer was measured with a telemeter Leica LRF 1200 Scan (Solms, Germany) (range 15-110 m: precision ± 1m / ± 0.1%). Software DISTANCE 4.0 was used to analyse the data and obtained a density estimate (Thomas et al., 2004). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using simple polynomial, cosine and hermite polynomial adjustment terms, fitted sequentially. The best models was selected basing on Akaike's Information criterion (AIC) (Akaike, 1974). For population density we reported coefficient of variation (CV) and confidence interval obtained on bootstrap distribution.

Pellet group count

The pellet group count methods was used in connection with the plot sampling method. Above all study area we created a grid constituted of 20 square, each with 1km per side. In each square we selected in random way (EPA 2002, Barabesi, 2003), a point that represented the centre of a plot with radius of 5m (plot's area equal to 78,5 m^2). The plot was visited and all pellets presents were removed. After 10 days, during a second visit, each pellets group laying down by roe deer were counted. We recorded the number of roe deer pellet groups containing at least 10 pellets (Mitchell et al., 1985). After to have estimated the pellets number on total study area with following formula we estimated the roe deer abundance a consequent density (Mayle et al., 1999).

$$\text{roe deer number} = \frac{\text{pellet group number}}{\text{time period (n° days) between two visit} * \text{defecation rate}}$$

Moreover to evaluated the variance of method linked to mobility of animal we individuated 5 plot that we monitored for 5 consecutive time.

The censuses were performed in spring and in autumn 2006.

Observation from vantage points

A number of point for observation was individuated in study area. The points were choosen in order to the maximise visibility and to cover the major part of open areas. The surface observed from each point was known and we avoided overlapping between sector observed. All observer recorded data at the same time: one operator for each observation point were note. So it was not possible to assume an approach from draw. The model we choose was very simple and it assume that the number of deer detected on the area is forming a random binomial variable (v.c.) with parameter equal to the proportion of census area. Then, the number of deer present in total area was estimate with the method of maximum verisimilitude (Borchers et al., 2002).

Censuses were replaced in different days, both in spring and in autumn. For each replicate the density, the variance estimate at confidence interval at 0,95 were calculated used quantili of log-normal distribution (Borchers et al., 2002).

Block count

We choose six bordering, not overlapping, areas on the study site where was easy to pass trough. The surface of each area was calculated. Each area was monitored at the same time from six observers and each roe deer detected was counted. The total census area was 44% of study area. Given that the areas were not random choosen, the density estimate was not calculate with an approach based on draw, but it was necessary to use an approach based on model. Because it was possible assume that every deer present in the area was counted, and it was possible exclude double count, we considered this approach like a plot sampling.

The model was very simple and it assume that the number of deer detected on the area is forming a random binomial variable (v.c.) with parameter equal to the proportion of census area. Then, the number of deer present in total area was estimate trough out the method of maximum verisimilitude (Borchers et al., 2002).

The census operations were repeated in different days, both in spring and in autumn. Each time the density, the variance estimate at confidence interval at 0,95 was calculated used quantili of log-normal distribution (Borchers et al., 2002).

Spotlight transect counts

Roe deer were counted along two transect 10 km each one (400 m on each side of an observer) illuminated using a 150-W spotlight on a 4-wheel-drive vehicle travelling 10km/hr. The transect area surveyed was 8 km^2, then 80% of study area. The count was performed in may and the operations were replaced in different near day . Also for this method, like for the other direct methods, we used a simple model. The model assume that all deer inside to illuminated surface was counted and using a random binomial variable (v.c.) with parameter equal to the proportion of census area. Then, the number of deer present in total area was estimate trough out the method of maximum verisimilitude (Borchers et al., 2002).

The census was replaced in different days, both in spring and in autumn. For all replicate time the density, and the variance estimate at confidence interval at 0,95 were calculated used quantili of log-normal distribution (Borchers et al., 2002).

Results

Using the methods based on direct observation, we evaluated the minimum number of live animals and consequently roe deer density. The accuracy of other methods had been considered of reference to this value density.

Observation from advantage points

During spring 2006 the observers made the census based on contemporary observations from vantage points. The area monitored was 7,98 km2, that corresponded to 71% of total open area and to 39,21% of total study area. The results are shown in table A1, appendix A. The maximum number of deer counted was 33, and allowed to estimate a density of 4,20 roe deer in 1km^2 (Tab. 1).

The total results of different session of census with observations from vantage points, are shown in table A2.

Table 1. Results of observation form advantage points census, obtained from the two sessions.

Session	*Roe deer detected*	*Surface monitored (km^2)*	*Density estimate ($deer/km^2$)*	*Variance estimate*
Spring	**33**	**7,84**	**4,20**	**0,33**
Autumn	**72**	**7,84**	**14,95**	**2,36**

Censuses were replaced also in autumn season. The maximum number of roe deer detected and counted was 72 allowed and gave an estimate of a density of 14,95 deer per km^2 (Tab. 1). In table A3, are shown the density estimate, the variance estimate and the variation coefficient obtained with autumn data.

Drive census

The results of drive census are shown in table A4.

The variance estimate was obtained from sample variance divided to number of battues areas.

Confidence interval was based on quantili of normal distribution.

Data analysis based on density estimate for each battue area. The average of each density was calculated and referred to areas like battues areas

Variance estimate was obtained with sampling variance divide number of battues areas.

During spring census a total of 27 roe deer was detected in battues areas, and a density of 18,51 deer per km^2 was calculated. The roe deer number, the surface monitored and the density estimate are shown in table 2.

Table 2. Results of drive census obtained in different season.

Session	*Roe deer detected*	*Surface monitored (km^2)*	*Density estimate ($deer/km^2$)*	*Variance estimate*
Spring	**27**	**1,45**	**18,51**	**1,44**
Autumn	**29**	**1,45**	**20,80**	**9,43**

In autumn, in the same areas, was counted 29 roe deer and consequently the density increase and was estimated as 20,80 deer per km^2 (Tab. 2).

Even if the density estimate was higher in autumn than in spring, it's necessary to underline the different variance estimate. In spring we calculated a variance of 1,44, while in autumn the variance was 9,43 at the same interval confidence.

The total results of autumnal drive census are shown in table A5.

Line transect

During spring line transect the total number of roe deer contact was 24; in 20 cases we measured the distance from their transect (minimum distance 0m; maximum distance 320,80m). We considered the density value estimated by 4 models calculate by means of DISTANCE software and after we selected the best model, evaluating AIC. The minimum value of AIC was for the model key-uniform with cosine adjustment, and it showed in Table A6.

There was variation in the AIC values for the model (Table A6). The truncation of the 50% of the distance corresponded to a distance of 157,96 m. The detection function of selected model and the histogram of the distance are reported in figure A1.

The summary results of spring are shown in table 3.

Table 3. Results census with line transect, obtained in different season.

Session	*Roe deer detected*	*Total length of transect (km)*	*Density estimate (deer/km^2)*	*Coefficient of variation*
Spring	**24**	**20**	**1,74**	**0,46**
Autumn	**26**	**20**	**5,05**	**0,58**

The same operations were replaced in autumn, from 3 October to 19 December 2006.

The total number of distances from the transect recorded was 12 for 26 roe deer (minimum distance 33,86m; maximum distance 170,77m) (Tab. 3).

The density value increase, and the best model was still key-uniform. The total results are shown in Table A7. The histogram of detection function are shown in figure A2.

In autumn season the truncation of the 50% of the distance corresponded to a distance of 69,36m.

Pellet group count

The monitoring of total plots was done from 28 April to 19 June 2006.

The distribution of frequency of pellet group number recorded in the plots and the synthesis index were showed in table A8 and A9 respectively.

We considered a defecation rate equal to 17-23 pellet group per day for density estimate.

For each value we calculated the density and the results were shown in table A10.

The confidence interval was 0,95, based on quantili of normal distribution.

The summary results of pellet group count performed in spring are shown in table 4.

Table 4. Results of pellet group counts, obtained in different season.

Session	*Surface monitored (m^2)*	*Density estimate (deer/km^2)*	*Coefficient of variation*	*Defecation rate*
Spring	**1570**	**13,84**	**0,81**	**23**
Autumn	**1570**	**8,30**	**0,73**	**23**

On the basis of this results we assumed at least a density of 13,84 deer per km^2.

During autumn season the monitoring of plots was done from 6 October to 27 November 2006.

The distribution of frequency of pellet group number recorded in the plots and the synthesis index were showed in table A11 and A12 respectively.

The results of fall census are shown in table A13.

The result of autumnal census with pellet group counts is summarized in table 4.

To compare the results obtained used pellets groups count method with other census methods, we considered the maximum number of defecation rate, and consequently the minimum density value.

Spotlight census

The spotlight census was performed in may by two team that contemporary monitored the transect. The census was repeated to investigate the variance of the method.

In spring 20 roe deer were detected during census and a density of 1,25 deer per km^2 was estimate (Tab.5)

Table 5. Results of census with spotlight count, obtained in different season.

Session	*Roe deer detected*	*Total length of transect (km)*	*Density estimate (deer/km^2)*	*Variance estimate*
Spring	**20**	**20**	**1,25**	**0,02**
Autumn	**37**	**20**	**2,30**	**0,07**

The number of roe deer counted in each session are shown in table A14. While table A15 showed the density estimate, the variance estimate and the extreme of confidence interval at 0,95.

An increase of density value was recorded during autumn. In fact 37 roe deer were detected a the density was estimate as 2,30 deer per km^2 (Tab. 5).

Also during autumn the census was repeated to test the variance and the results are shown in table A16 and A17, respectively.

To evaluate the variability of the method, linked to animal behaviour, we considered 25 dataset obtained with replicateof track. The frequency distribution of density estimate, both for spring and for autumn census, was showed in figure A and A respectively.

Block count census

During spring season, between 13 and 22 may 2006, six sector were monitored contemporary by different operators. Every deer that was present in the zone was detected and recorded. Each sector was monitored five time to investigate the variability of the method.

A maximum of 23 roe deer was counted and a density value of 2,55 deer per km^2 was estimated (Tab. 6).

The number of roe deer detected in each sector and each time are shown in table A18, while in table A19 the density estimate, the variance estimate and the extremes of confidence interval at 0,95 are shown.

Table 6. Results of block count census, obtained in different season.

Session	*Roe deer detected*	*Surface monitored (km^2)*	*Density estimate ($deer/km^2$)*	*Variance estimate*
Spring	**23**	**8,85**	**2,55**	**0,16**
Autumn	**45**	**8,85**	**5,05**	**0,11**

The census repeated in autumn. Also with this method we recorded an increase of density. 45 roe deer were counted and a density estimate of 5,05 deer per km^2 was calculated (Tab. 6).

The number of roe deer detected in each sector and each time, during autumn season, are shown in table A20, while in table A21 the density estimate, the variance estimate and the extremes of confidence interval at 0,95 are shown.

Comparison between six methods

The densities estimated with each method are evaluated in reference to minimum number alive, obtained with observation from vantage points. In fact 33 roe deer were detected in spring, contemporary by 20 operators. Then a minimum density of 4,20 deer per km^2 was estimated. Starting from this value, the other methods were evaluated. Line transect, spotlight count and block count, gave an underestimate of density, while the density estimated with drive census and pellet group count was higher than density calculated with observation (Fig. 5).

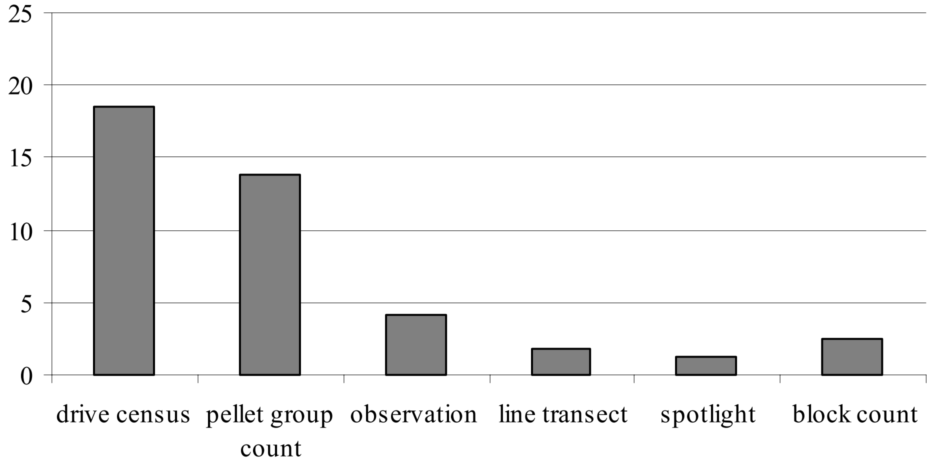

Figure 5. Comparison between density estimate with six census method, during spring.

Also in autumn we considered the minimum number alive, starting from density of observation (14,95 deer per km2). In autumn also the pellet group count showed a underestimate of density, while the drive census give an acceptable result.

Therefore, excluding the pellet group count, other methods, in autumn allowed to estimate an increase of density. the results are shown in figure 6.

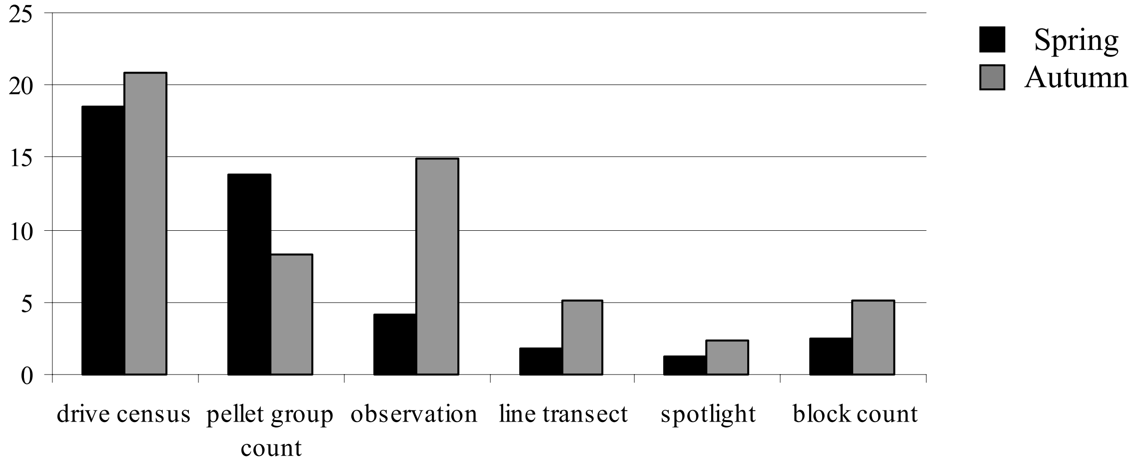

Figure 5. Comparison between density estimate with six census method in different season.

Discussion

We compared six different methods of estimating roe deer population size in a fragmented environment. We used methods for open and for wodded area. We performed the census during: spring and autumn. On the basis of the minimum number alive, determined on number of roe deer counted contemporary in open areas, we evaluated the density estimated with other methods. Moreover we evaluated the density estimate in reference to different season.

Using 20 point for observations (1 point for each km^2), we counted during spring census a total of 33 roe deer, that means a density of 4,20 deer peer km^2 in whole study area for spring census, and 72 roe deer detected in autumn, that means a density of 14,95 deer per km^2 in whole study area.

Considering that the 71% of open areas was monitored, it was reasonable to use this density to evaluate the accuracy of other method.

Three methods underestimate population size. In fact the density estimated with line transect, spotlight count and block count, had lower value than observations from vantage points. Instead drive census and pellet group counts gave a density value higher than observations from vantage points.

All methods, less pellet group counts, evidenced an increase during autumn. During autumn the vegetation is less dense than in spring, and deer are more detectable. This aspect is favourable to census methods based on direct observations and made at dawn and dusk, when roe deer are in full activity. At least we have to take into account human disturbance. In fact hunting as with dogs started, roe deer shift their home range inside to the protected area (Bongi et al. submitted).

In both season, the method that gave a lower value of density, were line transect and spotlight count. Nocturnal surveys of mammals often use established tracks and roads as transects (Smart et al. 2004; Ward et al. 2004; Vincent et al. 2007). Then roe deer could not detected because they move away from observer before detection or because avoid roads (Ward et al. 2004).

Line transect posed as major difficulty is to identification of detection function.

Our data showed a variation in encounter rate in relationship to seasonality. On the contrary to Focardi et al. (2002), autumn-winter season is more favourable period for line transect than spring-summer. Also because our study area is most fragmentised and there is a seasonality in vegetation density. Moreover our data showed a seasonal variation of sighting distance. During springtime the maximum distance was higher than in autumn. In this season the female are pregnant and near to the fawning season and they use safe environment more characterised by dense vegetation (Bongi et al. 2008). The buck are going to start the establishment of the territory live, winter groups and are more secretive and spend more time in the territory. As a consequence detectability is lower, especially at major distances and the density estimate become lower.

The block count performed in sectors with special reference to open spaces, gave results close to line transect and spotlight census. In this case, it is to consider also the time spent to investigate the block. In fact a 6 km trails was walked to monitor this sector. As a start the block were at dawn and few hour before dusk or near to dusk, and census lasted 3 hour, roe deer were allowed to move from open to cover area, compromising their detectability. In fact a low density is obtained with this method.

The only indirect method that we used was pellet group counts. An index can be a valid assay for trends in abundance of wildlife populations only if the relationship between the count index, pellets in our case, and true density does not chenas (Pollock et al., 2002, Bart et al. 2005, Lancia et al. 2005). In the case of roe deer this is probably true. Pellet equation to calculate density is another aspect of discussion (McKelvey et al. 2002; Murray et al. 2002) we used equation following Pisani et al. (2002) based on simple random sampling without replacement, usually referred as SRSWOR. Our data showed a density estimate higher than density obtained with observations from advantage points, and with a low C.V., both in spring and in autumn (Tab. A10 and A13 respectively).

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Appendix A

Observation from advantage points

Table A1. Data of census, and characteristic of advantage points.

Date	*Number of point used*	*Surface (kmq) monitored*	*Roe deer recorded*
01/06/2006 - dusk	20	7,84 (39,21%)	24
02/06/2006 - dawn	20	7,84 (39,21%)	31
02/06/2006 - dusk	20	7,84 (39,21%)	23
03/06/2006 - dawn	20	7,84 (39,21%)	33
03/06/2006 - dusk	20	7,84 (39,21%)	27

Table A2. Density estimate, variance estimate, variation coefficient, and confidence intervals at 0,95, obtained with data on spring census.

Date	*Density estimate (per km^2)*	*Variance estimate*	*C.V.*	*mim.*	*max.*
01/06/2006 - dusk	3,05	0,24	0,16	2,24	4,16
02/06/2006 - dawn	3,95	0,31	0,14	3,01	5,19
02/06/2006 - dusk	2,90	0,22	0,16	2,11	3,99
03/06/2006 - dawn	4,20	0,33	0,14	3,22	5,48
03/06/2006 - dusk	3,40	0,26	0,15	2,53	4,56

Table A3. Density estimate, variance estimate, variation coefficient, and confidence intervals at 0,95, obtained with data on autumnal census.

Date	*Density estimate (per km^2)*	*Variance estimate*	*C.V.*	*mim.*	*max.*
18/10/06 - dusk	5,45	0,42	0,12	4,32	6,87
18/10/06 - dawn	3,95	0,25	0,13	3,09	5,05
19/10/06 - dawn	14,95	2,36	0,10	12,23	18,27
20/10/06 - dawn	9,35	1,48	0,13	7,26	12,05
20/10/06 - dusk	6,75	0,52	0,11	5,48	8,32

Drive census

Table A4. Density estimate, variance estimate, C.V. estimate obtained during spring drive census

Desnity estimate (per km^2)	18,51
Variance estimate	1,44
C.V.	0,06
Confidence interval at 0,95	
min.	16,16
max.	20,86

Table A5. Density estimate, variance estimate, C.V. estimate obtained during autumn drive census

Desnity estimate (per km^2)	20,80
Variance estimate	9,43
C.V	0,15
Confidence interval at 0,95	
min.	14,78
max.	26,81

Line transect

Table A6. Density estimate with different model using DISTANCE software, for spring line transect census

Model						**Confidence interval**		**Confidence interval based on Bootstrap**	
Key	*Num. of parameter*	*% distance deleted*	*AIC*	*Density estimate per km^2*	*C.V.*	*min.*	*max.*	*min.*	*max.*
Half-normal	1	0	232,80	1,96	0,40	0,90	4,25	1,01	3,78
		10	201,52	2,06	0,38	0,98	4,31	1,05	3,78
		20	176,94	2,01	0,38	0,95	4,22	1,05	3,52
		30	152,70	1,84	0,42	0,81	4,16	0,95	3,81
		40	128,79	1,65	0,49	0,64	4,24	0,97	3,61
		50	103,25	1,74	0,54	0,61	4,93	0,92	3,64
Uniform	**0**	0	230,83	1,87	0,30	1,02	3,44	0,94	3,74
		10	199,52	2,06	0,30	1,12	3,78	1,01	3,56
		20	174,94	2,01	0,29	1,11	3,64	1,06	3,62
		30	150,70	1,84	0,32	0,95	3,54	0,91	3,50
		40	126,79	1,65	0,38	0,77	3,54	0,89	3,57
		50	**101,25**	**1,74**	**0,46**	**0,70**	**4,31**	**0,84**	**3,41**
Negative exponential	1	0	232,82	1,96	0,49	0,76	5,05	1,00	4,21
		10	201,52	2,06	0,47	0,83	5,13	0,97	3,87
		20	176,94	2,01	0,48	0,79	5,12	1,03	4,20
		30	152,70	1,84	0,53	0,67	5,08	1,02	4,15
		40	128,79	1,68	0,60	0,54	5,23	0,80	4,01
		50	103,25	1,74	0,65	0,51	5,95	0,78	4,54
Hazard	2	0	234,45	2,01	0,33	1,03	3,90	1,01	4,13
		10	203,52	2,06	0,30	1,12	3,78	1,01	3,87
		20	178,94	2,01	0,29	1,11	3,64	0,98	4,55
		30	154,70	1,84	0,32	0,95	3,54	1,03	5,15
		40	130,79	1,65	0,38	0,77	3,54	0,89	20,29
		50	105,25	1,74	0,46	0,70	4,31	0,76	30,31

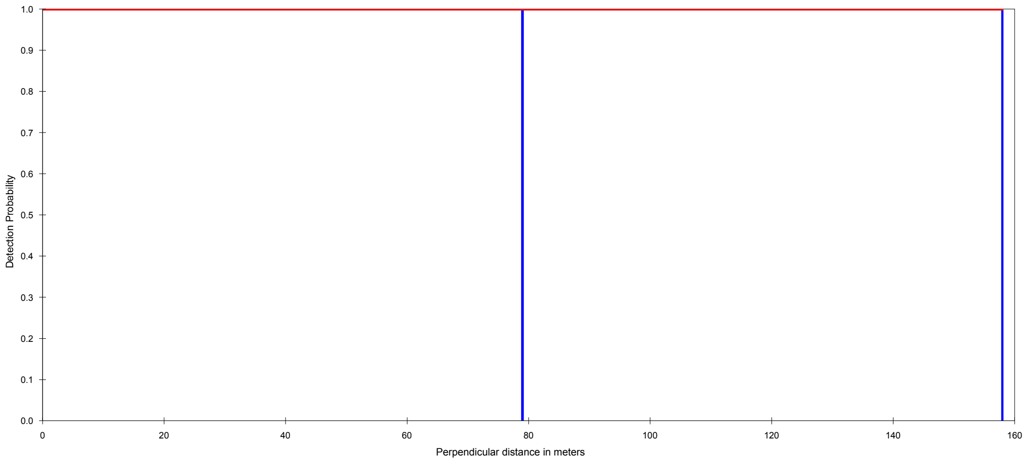

Figure A1 Histogram of distance recorded in line transect during spring and detection function. Model considered: key-uniform with cosine adjustament (DISTANCE output, truncation: 50%)

Table A7. Density estimate with different model using DISTANCE software, for autumn line transect census

Model						**Confidence interval**		**Confidence interval based on Bootstrap**	
Key	*Num. of parameter*	*% distance deleted*	*AIC*	*Density estimate per km^2*	*C.V.*	*min.*	*max.*	*min.*	*max.*
Half-normal	1	0	125,36	4,07	0,50	1,56	10,62	1,63	9,36
		10	110,45	4,70	0,51	1,76	12,57	1,61	10,27
		20	99,02	4,89	0,54	1,73	13,80	1,61	11,53
		30	75,74	5,23	0,61	1,64	16,68	1,81	12,62
		40	63,65	4,90	0,61	1,54	15,53	1,60	11,90
		50	52,87	5,05	0,64	1,52	16,78	1,60	11,53
Uniform	**0**	0	123,37	3,95	0,36	1,91	8,16	1,32	9,09
		10	108,45	4,70	0,39	2,16	10,24	1,76	10,12
		20	97,02	4,89	0,40	2,21	10,79	1,60	11,17
		30	73,73	5,23	0,46	2,13	12,84	1,76	12,34
		40	61,65	4,89	0,50	1,84	13,05	1,76	11,90
		50	**50,87**	**5,05**	**0,58**	**1,67**	**15,28**	**1,60**	**11,90**
Negative exponential	1	0	125,37	3,95	0,72	1,02	15,34	1,56	9,72
		10	110,45	4,70	0,72	1,21	18,21	1,60	9,81
		20	99,02	4,89	0,77	1,14	20,91	1,63	11,32
		30	75,74	5,23	0,85	1,07	25,53	1,81	11,90
		40	63,65	4,90	0,80	1,10	21,82	1,60	11,96
		50	52,87	5,05	0,79	1,17	21,81	1,53	11,18
Hazard	2	0	127,24	4,29	0,48	1,70	10,82	1,58	10,08
		10	112,45	4,70	0,39	2,16	10,24	1,61	10,47
		20	101,02	4,89	0,40	2,21	10,79	1,76	12,26
		30	77,73	5,23	0,46	2,13	12,84	1,81	11,53
		40	65,65	4,89	0,50	1,84	13,05	1,56	11,53
		50	54,87	5,05	0,58	1,67	15,28	1,81	11,71

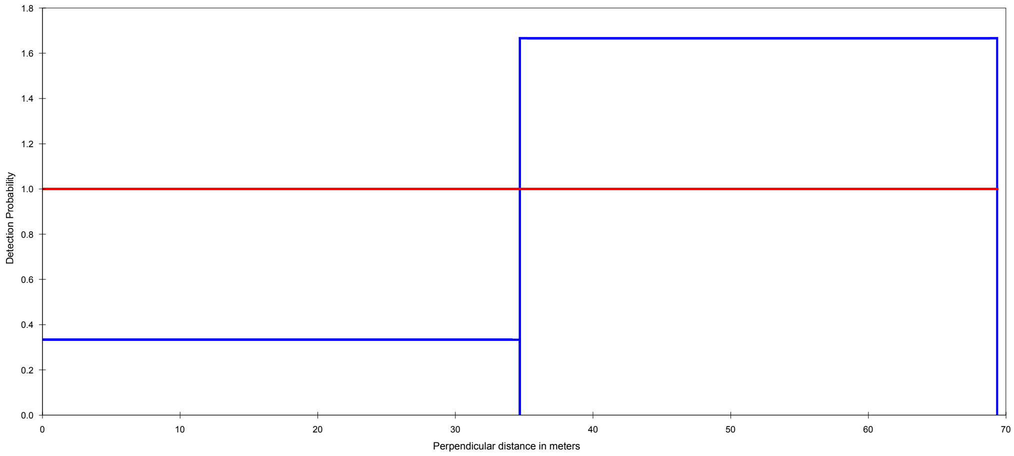

Figure A2. Histogram of distance recorded in line transect during autumn and detection function. Model considered: key-uniform with cosine adjustment (DISTANCE output, truncation: 50%)

Pellet group counts

Table A8. The distribution of frequency of pellet group number in the plots during spring.

Pellet number	frequency
0	18
1	1
4	1
total	20

Table A9. Synthesis index of distribution of pellet number, recorded in spring.

Total of pellet	5
Average of pellet per plot	0,25
Variance	0,79
C.V.	3,55

Table A10. Density estimate of roe deer (per km^2), coefficient of variation and confidence interval at 0,95, obtained with spring pellet group count.

Defecation rate	17	18	19	20	21	22	23
Density (per km^2)	18,72	17,68	16,75	15,92	15,16	14,47	13,84
C.V.	0,81	0,81	0,81	0,81	0,81	0,81	0,81
Confidence interval at 0,95:							
min.	0,00	0,00	0,00	0,00	0,00	0,00	0,00
max.	48,61	45,91	43,49	41,32	39,35	37,56	35,93

Table A11. The distribution of frequency of pellet group number in the plots, during autumn.

Pellet number	frequency
0	18
1	1
2	1
total	20

Table A12. Synthesis index of distribution of pellet number, recorded in autumn.

Total pellet	3
Average pellet per plot	0,15
Variance	0,23
C.V.	3,18

Table A13. Density estimate of roe deer (per km^2), coefficient of variation and confidence interval at 0,95, obtained with autumn pellet group count.

Defecation rate	17	18	19	20	21	22	23
Density (per km^2)	11,23	10,61	10,05	9,55	9,09	8,68	8,30
C.V.	0,73	0,73	0,73	0,73	0,73	0,73	0,73
Confidence interval at 0,95:							
min.	0,00	0,00	0,00	0,00	0,00	0,00	0,00
max.	27,30	25,78	24,42	23,20	22,10	21,09	20,18

Spotlight census

Table A14. Number of roe deer counted in each spring-session during spotlight census.

Date	***Roe deer counted*** *deer counted in track 1*	*deer counted in track 2*	*total deer counted*
14-15/05/06	7	8	15
15-16/05/06	9	4	13
30-31/05/06	12	8	20
16-17/06/06	5	9	14
21-22/06/07	4	2	6
average	7,40	6,20	13,60

Table A15. Density estimate, variance estimate, coefficient of variation and extreme of confidence interval at 0,95 obtained with replace during spring spotlight census.

Date	*Density estimate per Km^2*	*Variance estimate*	*C.V.*	*min.*	*max.*
14-15/05/06	0,90	0,01	0,12	0,71	1,13
15-16/05/06	0,80	0,01	0,13	0,63	1,02
30-31/05/06	1,25	0,02	0,10	1,03	1,52
16-17/06/06	0,85	0,01	0,12	0,67	1,08
21-22/06/07	0,35	0,00	0,19	0,24	0,51

Table A16. Number of roe deer counted in each autumn-session during spotlight census.

Date	***Roe deer counted*** *deer counted in track 1*	*deer counted in track 2*	*total deer counted*
10/10/2006	28	9	37
11/10/2006	23	14	37
12/10/2006	18	5	23
16/10/2006	27	8	35
17/10/2006	21	2	23
average	23,40	7,60	31,00

Table A17. Density estimate, variance estimate, coefficient of variation and extreme of confidence interval at 0,95 obtained with replace during autumn spotlight census.

Date	*Density estimate per Km^2*	*Variance estimate*	*C.V.*	*min.*	*max.*
10/10/2006	2,30	0,03	0,07	1,99	2,66
11/10/2006	2,30	0,03	0,07	1,99	2,66
12/10/2006	1,40	0,02	0,09	1,16	1,68
16/10/2006	2,15	0,03	0,08	1,85	2,50
17/10/2006	1,40	0,02	0,09	1,16	1,68

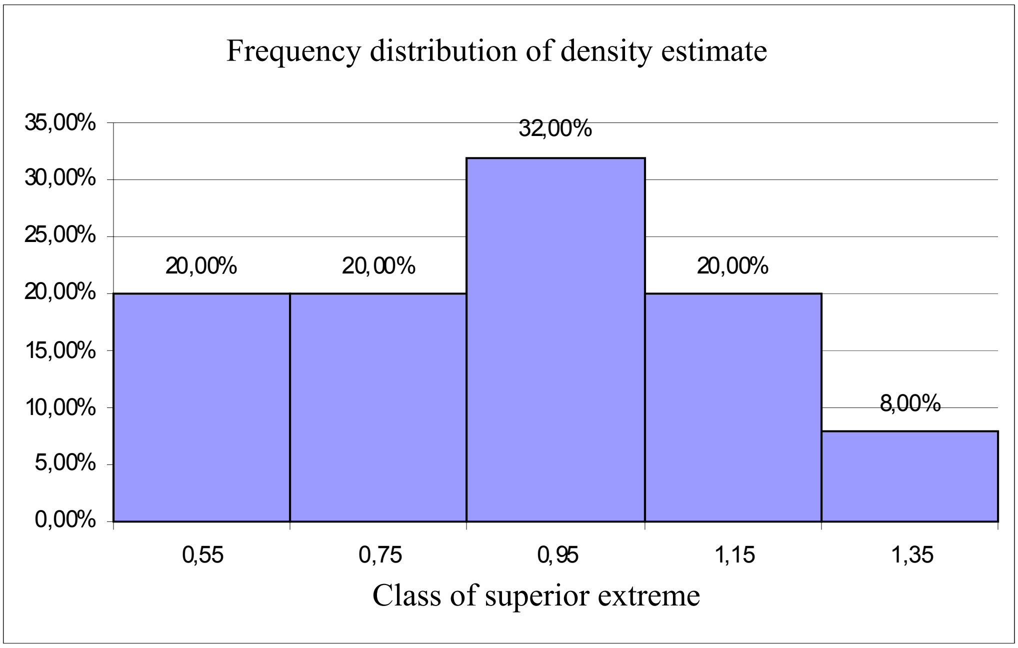

Figure A3. Frequency distribution of density estimate with replace of spotlight-track during spring

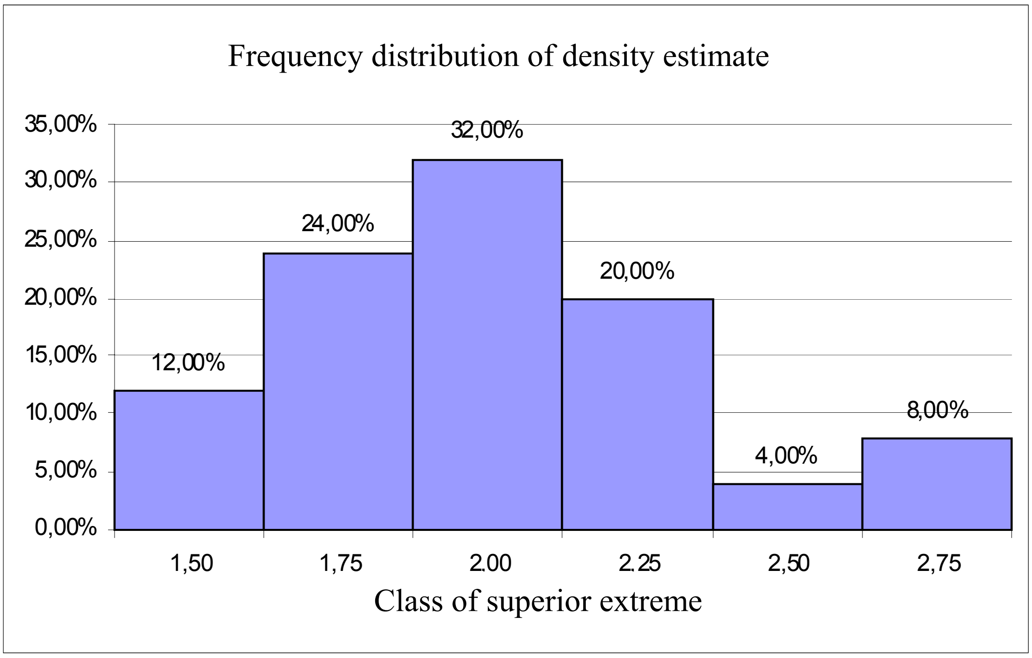

Figure A4. Frequency distribution of density estimate with replace of spotlight-track during autumn

Block count

Table A18. Roe deer detected in each sector and in different days during spring census.
The surface (km^2) of each sector are shown.

Sector monitored	*Date* *13/05/06 dusk*	*14/05/06 dawn*	*14/05/06 dusk*	*21/05/06 dusk*	*22/05/06 dawn*
	Roe deer counted in each sector				
1 (1,24 km^2)	3	1	2	3	0
2 (1,14 km^2)	2	1	4	2	5
3 (1,08 km^2)	0	4	1	1	1
4 (1,55 km^2)	4	3	9	3	5
5 (1,77 km^2)	8	7	4	2	4
6 (2,07 km^2)	0	1	3	0	2
Total deer counted	**17**	**17**	**23**	**11**	**17**

Table A19. Density estimate, variance estimate and extremis of confidence interval at 0,95 obtained with spring observations.

Date	*Density estimate per Km^2*	*Variance estimate*	*C.V.*	*min.*	*max.*
13/05/06 dusk	1,90	0,12	0,18	1,33	2,71
14/05/06 dawn	1,90	0,12	0,18	1,33	2,71
14/05/06 dusk	2,55	0,16	0,16	1,88	3,46
21/05/06 dusk	1,20	0,08	0,23	0,77	1,87
22/05/06 dawn	1,90	0,12	0,18	1,33	2,71

Table A20. Roe deer detected in each sector and in different days during autumn census.

The surface (km^2) of each sector are shown.

	Date				
Sector monitored	*03/12/06 dusk*	*04/12/06 dawn*	*05/12/06 dawn*	*07/12/06 dusk*	*11/12/06 dawn*
	Roe deer counted in each sector				
1 (1,24 kmq)	4	6	7	2	5
2 (1,14 kmq)	5	9	6	6	1
3 (1,08 kmq)	6	4	20	8	0
4 (1,55 kmq)	8	3	2	3	2
5 (1,77 kmq)	4	1	5	3	3
6 (2,07 kmq)	10	5	5	4	4
Total deer counted	**37**	**28**	**45**	**26**	**15**

Table A21. Density estimate, variance estimate and extremis of confidence interval at 0,95 obtained with autumn observations.

Date	*Density estimate per Km^2*	*Variance estimate*	*C.V.*	*min.*	*max.*
03/12/06 dusk	4,15	0,26	0,12	3,26	5,28
04/12/06 dawn	3,15	0,20	0,14	2,39	4,15
05/12/06 dawn	5,05	0,32	0,11	4,06	6,28
07/12/06 dusk	2,90	0,18	0,15	2,18	3,87
11/12/06 dawn	1,65	0,10	0,20	1,13	2,41

Second Part

HOW HUMAN FACTORS MAY AFFTEC ROE DEER SPATIAL BEHAVIOUR AND, CONSEQUENTLY, CENSUS METHODS

Chapter 2

ROE DEER BEHAVIORAL MODIFICATIONS IN RELATION TO DIFFERENT HUNTING PRACTICES: A DIFFERENTIAL RESPONSE ACCORDING TO SEX AND AGE CLASSES.

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(*Manuscript*)

Abstract

Despite the crucial importance of hunting, poor information is currently available on the biological effects of hunting on prey population and particularly on prey behavior. Researchers used to focus on the hunting effects on the specific target prey, and only recently have they expanded their analyses to include the indirect effects of hunting. As a consequence, there is still a lack of information about the effects of hunting on non-target prey species. In our study area (Apennine Mountains, in Central Italy), different hunting practices such as roe deer stalking, wild boar hunting, and small game hunting were allowed during different periods of the year. We analyzed how roe deer adapted their spatial behavior during hunting season and we focused on their response to different hunting practices, in particular on the differences among individuals belonging to different age and sex classes. We captured roe deer (24 males and 33 females), marked them by means of VHF radiocollars and collected spatial behavior data in an intensive area of about 30.000 ha. In the center of the intensive area, a strictly protected 3000 ha-wide area (Oasi Alpe di Catenaia, OAC) is located where hunting is permanently banned. Surprisingly, roe deer stalking did not seem to affect the spatial behavior of this species. In fact, the percentage of time the radio-collared animals spent outside of the protected area did not diminish when deer stalking was practiced. On the contrary, hunting with dogs (wild boar and small game hunting) seemed to affect roe deer spatial behavior in view of the fact that roe deer increased the use of the habitat within OAC. Moreover, males and females showed a similar response to the harassment caused by hunting with dogs, even though with different magnitudes: females were more receptive and showed a higher use of the protected area than males. Being this the case, hunting with dogs seemed to induce a sexual spatial segregation on a large time scale in roe deer, even though roe deer is thought to be slightly sexually dimorphic and is not known to exhibit sexual segregation. Furthermore, we found a significant behavioral difference among age classes too: at times when hunting with dogs was allowed, sub-adult (2-3 yr.) and adult (more than 3 y.r.) roe deer had larger percentages of fixes outside OAC when compared to young roe deer (1 y.r.). In conclusion, even though roe deer was not the target of hunting with dogs, this mode of hunting strongly modified their spatial behavior, as it was able to evoke a differential response within the species. Responses varied according to age and sex classes: this aspect should be further investigated for its management implications.

Introduction

It is well established that outdoor activities generally affect wildlife and certain activities can actually have severe effects on it. Overall, it appears that human activities negatively influence the distribution of large animals (Blom et al. 2004). Enggist-Düblin and Ingold (2003) showed that, in order to correctly assess different forms of wildlife harassment, it is important to analyze, not only the flight distance, but also other behaviors such as the home range modifications and the feeding behavior. Wild ungulates exhibited different responses to human disturbance, whereby their behavior and physiology were modified (Cederna and Lovari 1985, Jeppesen 1987b, Jeppesen 1987a, Weisenberger et al. 1996). Both predation risk and human harassment may evoke different responses in wild ungulates according to sex or age classes. As regards fallow deer (*Dama dama*), males and females exhibited different behaviors in response to human disturbance, particularly in terms of flight distance (Recarte et al. 1998). In order to assess the magnitude of disturbance it is thus important not only to analyze the usual display of antipredator behavior (i.e. flight or alert), but also to address its consequences on life history and population dynamics.

Hunting was recognized and studied as a crucial factor in the biological and cultural evolution of men (Klein 1989), whereas conversely poor information is currently available on the biological effects of hunting on prey populations and in particular on prey behavior. What is better understood is the role of humans in the extinction of large vertebrates. In fact, like the ruminants, also some large vertebrate species were shown to be affected by hunting as regards their behavior and in particular their spatial and antipredator behavior. Several authors argued that hunting was able to shape the fright behavior in response to humans in birds, (Madsen 1985, Madsen and Fox 1995) and ungulate (Dorrance et al. 1975, Shultz and Bailey 1978, McLaren and Green 1985, Jeppesen 1987b), even though only in the last years such a response has been tested empirically and heterogeneous findings have been obtained. Colman et al. (2001) tested the flight distance in rein-deer (*Rangifer tarandus*) and did not find any evidence of it, while, as regards roe deer (*Capreolus capreolus*), those living in hunting areas seemed to fear man more than those living in areas where hunting was not practiced (de Boer et al. 2004).

Since the requirements for the existence of an animal can be located within its home range, the study of spatial behavior of animals being affected by human harassment can help explain how they respond to disturbance and in general to modifications within their environment (Apollonio et al. 2005).

The findings of a study on 12 native populations of mountain goats (*Oreamnos americanus*) suggested that hunting had negative effects on the population dynamics of some herds (Gonzalez Voyer et al. 2003). However, the same study also pointed out that other factors are likely to prevent or delay the population recovery after the end of the harvest. More accurate analyses on the modifications of behavior, life history, and population dynamics which are connected to hunting should be carried out . In particular, it is important to consider the indirect and sometimes neglected consequences of hunting. For instance, hunting was found to be correlated to the autumn peak in deer-vehicle collisions because it contributed to the increased movement rates of white-tailed deer (*Odocoileus virginianus*) (Etter et al. 2002), in particular immediately after the opening of the firearm-hunting season (Sudharsan et al. 2006). Kilgo (1998) evidenced how hunting modified home range size and habitat selection of white-tailed deer and how such effects also influenced the predator-prey dynamics (Florida panther, *Felis concolor coryi*). Although in the last years researcher have expanded their analyses to include the indirect effects of hunting, there is still a lack of information about the effects of hunting on the species which are not directly hunted.

Certain traditional modes of hunting which are practiced in central and southern Europe entail the use of dogs to hunt preys. Several authors analyzed the influence of hunting with dogs on prey behavior. In a study on red deer (*Cervus elaphus*) Jeppesen (1987b) recorded two behavioral modifications in response to hunting with dogs. Accordingly, he distinguished the immediate escape, which occurs at the beginning of the disturbance, from the late escape, occurring at the end of the disturbance. The latter reaction was showed by both the animals being pursued and those not being pursued by the dogs. The presence of hunting dogs also modified habitat selection (individuals spent more time in densely vegetated areas) and stimulated strictly nocturnal habits in ungulates (Swenson 1982, Kufeld et al. 1988, Kilgo et al. 1998). There is empirical evidence that hunting with high numbers of men and dogs have a stronger impact on the harvest as well as on the animal disturbance (Sforzi and Lovari 2000). The European legislation allows hunting different preys in different periods of the year and, as a consequence, hunting harassment could last for long periods in the same area.

Researchers have generally focused on the hunting effects on specific target preys. Moreover, analyses considering different hunting practices on a single prey species have been rarely carried out. Therefore, there is a lack of information about the influence of hunting on non target prey species and, more generally, about the actually diverse influence of different hunting practices on both target and non target prey species. Therefore, the aims of this work are to test if:

i) roe deer modify their spatial behavior and increase the use of protected areas during the stalking season as a consequence of a direct hunting pressure

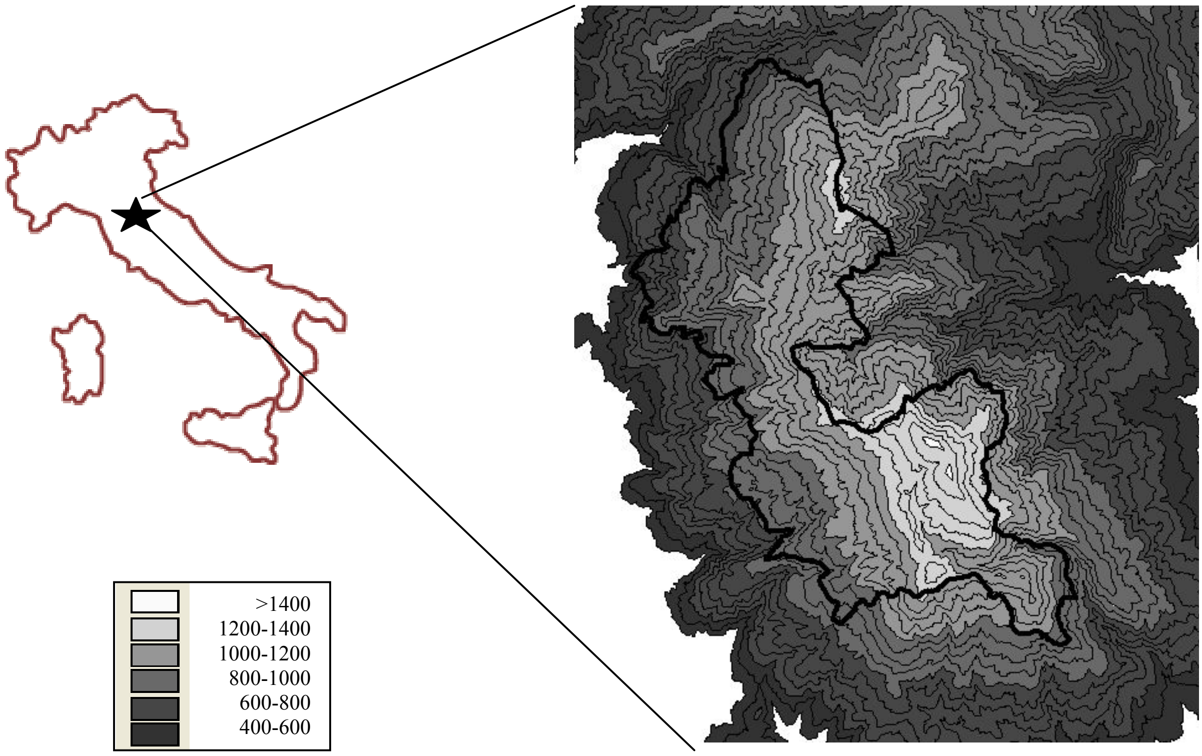
ii) hunting with dogs induces roe deer to find refuge in protected areas, even though they are not the target prey species of this hunting practice

iii) different sex and age classes are affected to a similar degree by the hunting harassment as a consequence of similar body sizes

Study Area

The study was performed in a mountainous habitat located on the Tuscan slope of the Apennine Mountains, in the province of Arezzo, Italy (43°48'N, 11°49'E). We captured roe deer and collected data in an intensive area of about 30.000 ha, within which a strictly protected 3000 ha-wide area (Oasi Alpe di Catenaia, OAC) was located. The climate was temperate and characterized by a high humidity rate, with hot and dry summers and cold and rainy winters. Inside the protected area snow usually fell from October to April, with mean duration of snow cover above 1000 m a.s.l. of 90 days. Highest altitude territories are located within OAC (Fig. 1). Range altitude in the whole area varied from 300 to 1514 m a.s.l..

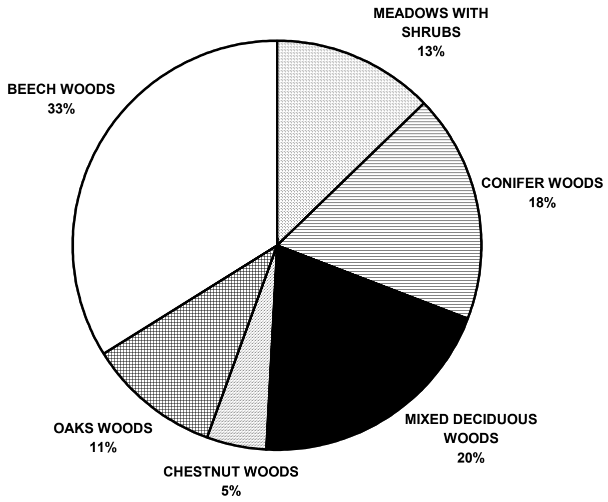
Figure 1. Altitudinal range composition of the roe deer study area (period of study: 2001-2005) in a mountainous area in Central Italy. Bold line represents the boundaries of the protected area of “Oasi Alpe di Catenaia”. Altitudinal range buffers showed in the figure are expressed in meters.



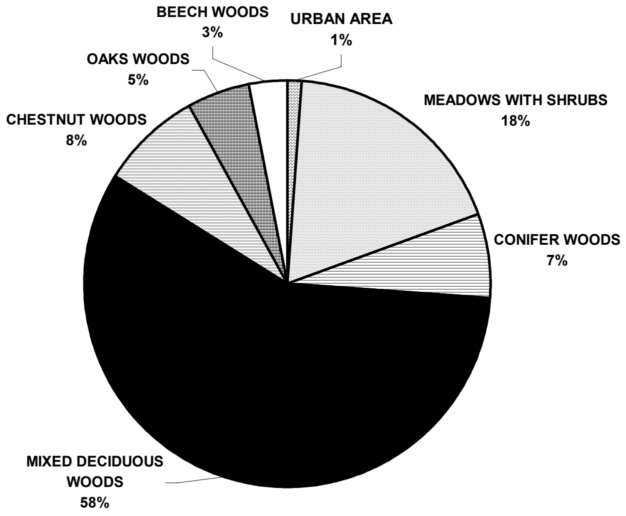
Two different forestry management policies had been adopted, inside and outside OAC respectively. The outcome of such a differentiation was the formation of two distinct habitat arrangements inside and outside OAC. Specifically (Fig.2), the forest with undergrowth vegetation was well represented outside OAC (mixed deciduous woods and oaks woods, both dominated by *Quercus spp* and chestnut woods *Castanea sativa*), while beech woods (*Fagus sylvatica*) and conifer woods (*Pinus nigra, Abies alba, Pseudotsuga menziesii*), i.e. habitats with a small component of undergrowth vegetation, were prevalent inside OAC. In conclusion, differences in roe deer habitat availability between the protected and the unprotected areas were significant, and the area outside OAC could be recognized as a more suitable habitat for this cervid on account of the thicker undergrowth vegetation.

Figure 2. Habitat composition of roe deer study area (2001-2005) inside (a) and outside (b) the boundaries of “Oasi Alpe di Catenaia” protected area (Central Italy).

A) INSIDE AOC



B) OUTSIDE AOC



Hunting inside OAC was strictly forbidden. On the contrary, outside of the protected area different hunting practices were regulated and allowed according to the different periods of the year. More specifically, pursuant to local hunting laws, we distinguished three different hunting seasons, as reported below (Tab. 1):

i) No hunting at all (NH) – Hunting was strictly forbidden also outside OAC.

ii) Roe deer hunting (RDH) – Roe stalking with rifles and without dogs was permitted outside OAC. Provincial rules allowed only roe deer hunting from high fixed seats within areas which were assigned to individual hunters.

iii) hunting with dogs (HWD), i.e. the hunting of wild boar (*Sus scrofa*) and small game (mainly *Lepus europaeus, Phasianus colchicus*) outside OAC. Unlike roe deer hunting, hunting of wild boar included battues with 30-50 hunters (there must be no less then 25 hunters by law) and many dogs, while small game hunting included one or more hunters along with no more than two or three dogs each.

Table 1. Hunting seasons in the province of Arezzo, Italy, from 2002 to 2005.

Year	**No hunting**	**Roe deer hunting**	**Hunting with dogs**
2002	1st January – 31st July 1st– 14th September	1st August – 31st August	15thSeptember 31st December
2003	3rd March –1st August 12th– 20th September	1st February – 2nd March 2nd August – 11th September	1st January – 31st January 21stSeptember – 31 December
2004	1st– 10th February 1st March –31st July 13th– 17th September	11th– 29th February 1st August – 12th September	1st January – 31st January 18thSeptember – 31 December
2005	1st February – 11th February 1st March –31st July 16th – 17th September	12th– 28th February 1st August – 15th September	1st January – 31st January 18thSeptember – 31 December

The only natural predators in the study area were red fox (*Vulpes vulpes*), that usually preyed only upon fawns and wolf (*Canis lupus*). In the Arezzo area wolves are present at high densities (Apollonio et al. 2004, Capitani et al. 2006). Mean pack size is 4.0 ± 0.6. The wolf pack has an high reproductive success and in our study area we had a resident pack that showed a high use of roe deer (Mattioli et al. 2004). The only other ungulate in the study area was wild boar. Free-ranging livestocks were totally absent in the whole territory.

Methods

We conducted the study from March 2001 to April 2005, when we radio-located a total of 57 roe deer (24 males and 33 females) by discontinuous radio-tracking (Swihart and Slade 1985, Harris et al. 1990), for a total of 12,869 fixes. We performed capture sessions by means of a vertical drop net in late winter-early spring, almost every year. Roe deer were hand caught, blindfolded, fitted with Televilt radiocollars (Televilt, Sweden, 150-151 MHz wavebands) and then released. The handling procedure took less than 5 minutes. We used Televilt RX-8910HE receivers and a four-element hand-held Yagi antenna. We determined locations of radio-collared animals by triangulation of the bearings obtained from three different reference points (Springer 1979, Kenward 1987, White and Garrott 1990) using the "loudest signal" method (Springer 1979). At least eight radio-locations per animal were obtained each month. We uniformly distributed locations over the day (discontinuous telemetry) (Swihart and Slade 1985) and took them within at least twelve hours of each other. Then we plotted all the locations on a digital 1:10 000 scale map of the study area (Springer 1979, Kenward 1987). We estimated the accuracy of fixes by taking fixes also on test transmitters which we placed in various habitats within the area (Harris et al. 1990). Accuracy of bearings was less than ± 100 m for fair signals within the central telemetry area (Cederlund 1983). We confirm that the procedures we used in this work conform to all relevant Italian wildlife and animal welfare legislation.

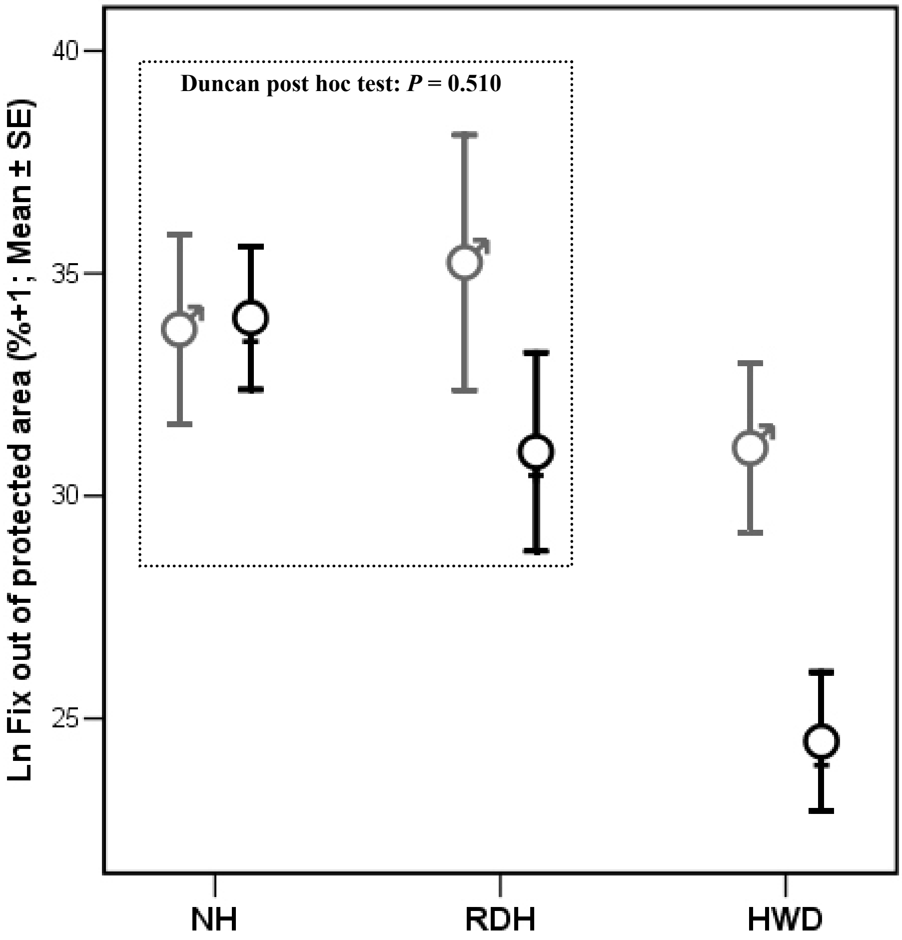
In order to understand the modifications in spatial behavior, we calculated the percentage of fixes outside OAC for each animal in each hunting season. We did not calculate the fixes of the animals that throughout the study period showed more than 95% of the total number of localizations outside or inside OAC. In so doing, we focused on the roe deer that were found to use both areas. Then we transformed the data relating to the percentage of fixes outside OAC into a natural logarithm (LN x+1) for the purpose of statistical analysis to meet assumption of normality. We tested the diverse influence of sex, age class, and hunting practice using a General Linear Model (GLM). We used Duncan test as a *post hoc* test (Sokal and Rohlf 1995) in order to show the statistical differences in the percentage of fixes recorded outside OAC, among age classes and in correlation to different hunting practices. We used the t test for Independent Sample to test the differences between sexes within different hunting practices and between sexes within different age classes. We used SPSS 13.0 program (SPSS Inc., Chicago, Illinois) for statistical analysis and in all tests we set significance at $P \leq 0.05$ (Sokal and Rohlf 1995).

Results

Hunting practices affected roe deer spatial behavior in different ways. Indeed, roe deer percentage of fixes collected outside the protected area (OAC) varied according to the hunting season (*GLM*: $F_{2,349}$ = 5.449, *P* = 0.005). Surprisingly, roe deer stalking did not seem to affect the spatial behavior of this species. In fact, during RDH roe deer did not show a different percentage of fixes outside OAC when compared to the same percentage recorded during NH (*Duncan post hoc test: P* = 0.510, Fig 3). On the contrary, hunting with dogs seemed to cause roe deer to alter their spatial behavior significantly. *Duncan post hoc* test identified the data collected during HWD as a significantly different set of data thus forming a separate sub-group ($P<0.05$) (Fig 3).

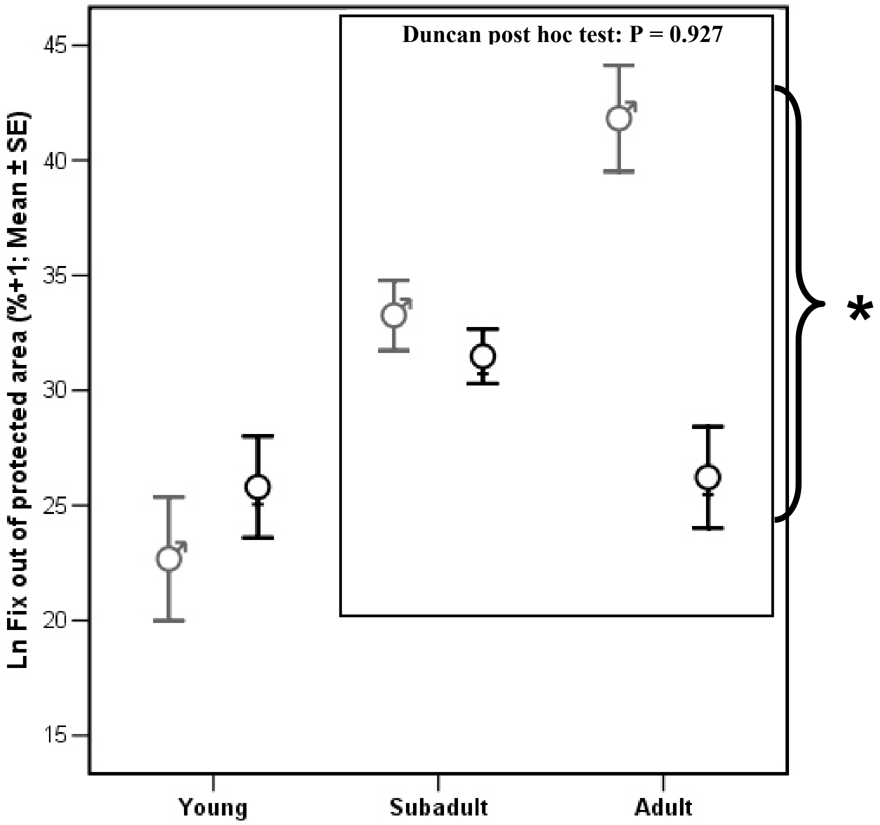
Males and females used areas outside OAC to different degrees (*GLM*: $F_{1,349}$ = 5.601, *P* = 0.019). In order to show in which hunting season males and females exhibited clearly different spatial behaviors, we compared the data collected during all three hunting seasons. Indeed, we found a significant difference between sexes only during HWD (*t test Independent Sample*: *t* = 2.620, *df* = 161, *P* = 0.010), with males (mean ± SE = 11.60% ± 1.40) being outside OAC more frequently than females (8.19% ± 0.97; Fig.3). On the contrary, we did not find any difference between sexes during RDH (*t* = 1.169, *df* = 86, *P* = 0.246) or NH (*t* = -0.096, *df* = 97, *P* = 0.923).

Figure 3. Percentage of fixes collected during a roe deer study (2001-2005) outside of the protected area of Oasi Alpe di Catenaia (Central Italy). Black bar with ♀ symbol represents female data while grey bar with ♂ symbol represents male data. *X* axis represents different hunting practices (NH = no hunting, RDH = roe deer hunting, HWD = hunting with dogs; see study area section for further details). Duncan post hoc test subdivided the data into two sub sample groups (broken line with statistic results).



We also found that roe deer spatial behavior was affected by hunting pressure to different degrees which varied according to age classes. In fact, we found a significant age-class related difference in the percentage of fixes recorded outside OAC (*GLM*: $F_{2,349}$ = 6.528, *P* = 0.002). Young roe deer (one year old) showed the lowest percentage of fixes outside OAC, while sub-adult (2-3 years old) and adult deer (more than 3 years old) had a similarly (*Duncan post hoc test: P* = 0.927) higher (*P* < 0.05) percentage of fixes outside OAC (Fig 4). Accordingly, of all age classes, young roe deer were those who showed more extreme avoidance behaviors once they were under hunting pressure. (Fig. 4).

Figure 4. Percentage of fixes collected during a roe deer study (2001-2005) outside of the protected area of Oasi Alpe di Catenaia (Central Italy). Black bar with ♀ symbol represents female data while grey bar with ♂ symbol represents male data. *X* axis represents different age classes (young = 1 year old; sub-adult = 2-3 years old; adult = more than 3 years old). Duncan post hoc test subdivided the data into two sub sample groups (broken line with statistic results). Braces with asterisk reported differences between sexes within the same age class (t test for Independent Samples: $t = 4.889$, $df = 84.44$, $P < 0.001$).



Provided that the interaction of age class and sexes were found to affect roe deer spatial behavior to a significant degree (*GLM*: $F_{2,349} = 4.887$, $P = 0.008$), we decided to compare the differences between sexes within each age class. Actually we detected a significant difference only between sexes within the adult class (*t test Independent Sample*: young $t = -0.906$, $df = 65$, $P = 0.368$; sub-adult $t = 9.20$, $df = 304$, $P = 0.358$; adult $t = 4.889$, $df = 84.44$, $P < 0.001$; Fig 4).

Discussion

Hunting practices significantly affected roe deer spatial behavior in our study site. Surprisingly, roe deer stalking did not affect the spatial behavior of roe deer, while wild boar and small game hunting caused roe deer to alter their behavior significantly. This result showed an aspect which is usually neglected in the analyses of the effects of hunting on wildlife behavioral modifications. According to our analyses, certain hunting practices, in particular those with the presence of dogs, seemed to be most critical. In the study area, three different hunting practices could be recognized: roe deer stalking without dogs, wild boar and small game hunting with dogs. Differences in the level of harassment caused by these hunting practices were confirmed by roe deer adjustment in terms of spatial behavior. Our results showed that roe deer did not use OAC protected area more intensively during roe deer stalking than during periods when hunting was strictly forbidden everywhere. On the contrary, at times when hunting with dogs (wild boar and small game hunting) was allowed outside the protected area, roe deer moved more frequently into it. Therefore it seems clear that drives performed with dogs were able to modify roe deer spatial behavior in our study site, no matter that during this hunting practice the roe deer was not the target prey. Clearly the high presence of dogs outside OAC encouraged the use of this protected area as a refuge, probably causing fright, flight and movements into OAC. In contrast, considering that roe deer is a non gregarious species (Hewison et al. 1998), stalking with rifles from high seats caused a very localized harassment to isolated roe deer individuals. Moreover, after the shot the hunter would take the killed animal away and the harassment in the area would be limited to a few minutes. On the contrary, large hunting drives with dogs by wild boar hunters might have last for a whole day. Moreover, during large drives it was likely for hunters to lose some dogs, thus prolonging the harassment in the wood for several days.

Researchers seldom analyzed the effects of a species-specific hunting on other species, except for those cases when they assessed how hunting on a prey species could influence the predator dynamics (Fitzgibbon et al. 1995, Kilgo et al. 1998). While the direct impact of hunting on deer population dynamics is quite documented (McCullough 1979, Nelson and Mech 1986), less is known about its effects on deer behavior. Deer may respond to hunting by avoiding human activity areas (Dorrance et al. 1975, Rost and Bailey 1979, Apollonio et al. 2005) and modifying movement (Jeppesen 1987b), activity (Vogel 1989), habitat selection (Swenson 1982, Kufeld et al. 1988, Kilgo et al. 1998) and group size (Jedrzejewski et al. 2006). While different studies had already shown modifications of spatial behavior or habitat selection in roe deer, our findings made clear also that roe deer changed their behavior and used protected areas in response to hunting on other species. An important point emerging as a consequence of roe deer behavioral modifications caused by hunting with dogs is that roe deer showed a higher use of OAC during autumn-winter, i.e. they used areas at highest altitudes even when it was more likely to have snow cover on the ground. Moreover, in autumn and in winter they selected habitats that were definitely less suitable than the outside areas. In fact, within OAC roe deer mainly found beech woods with little undergrowth vegetation and more adverse climatic conditions. OAC was located on the main ridge of a mountain and consequently, in order to reach the protected area animals had to leave the habitats located at the bottom of the valley and to go up slope. Such a behavior is obviously contrary to common expectations. In autumn and winter we would expect roe deer to climb down in order to avoid low temperatures and snow cover, as it was shown in previous studies dealing with roe deer spatial behavior in the Foreste Casentinesi National Park, i.e. a natural territory which was very close to OAC and where hunting was strictly forbidden. Here, roe deer showed two distinct patterns of spatial behavior: stationary and roaming (Rossi et al. 2003, Lamberti et al. 2004). In autumn-winter, roaming individuals showed long winter altitudinal migrations towards lower altitude areas which were located outside the summer home range. Besides that, it was observed that stationary roe deer in the Apennines as well as both stationary and migratory red deer in the Alps (Luccarini et al. 2006) usually moved to lower areas in winter. Accordingly, in our study case hunting pressure seemed to affect roe deer spatial behavior strongly. Moreover, in mixed deciduous woods which were prevalent outside OAC, undergrowth vegetation was more abundant, thus providing more food and hiding places. Accordingly, upward movements may have had an important energetic cost, caused by both the sudden movement, the stress and the use of a sub-optimal habitat just before winter. Use of sub-optimal habitats could affect life histories and population dynamics (Swenson 1982, Kufeld et al. 1988, Kilgo et al. 1998). While ungulates may suffer no substantial fitness costs when disturbance rates are low to moderate, certain empirical studies suggested that high disturbance rates could reduce reproductive success and possibly impact population dynamics (Yarmoloy et al. 1988, Harrington and Veitch 1992, Phillips and Alldredge 2002). These empirical data, though often limited by sample sizes and/or being biased by the correlation to other factors, are consistent with the theoretical models predicting that energy costs affect body condition and reduce the reproductive success of large mammals under high disturbance rates (Bradshaw et al. 1997, White et al. 1999).

Therefore, we also suggest that the altered behavioral patterns of roe deer during HWD may have important implications for the conservation of wolf. The tendency of deer to move into and gather within OAC may stimulate a similar tendency in wolves which are supposed to follow preys as well as avoid hunters and dogs. Increased human disturbance and consequent shift of distribution of wolves could enhance the likelihood of events such as wolf-vehicle collisions and human sightings, which could initiate indiscriminate killings of wolves. Kilgo et al. (1998) argued that hunting on white-tailed deer had positive implications for the conservation of the Florida panther, because during the hunting season deer avoided roads and increased nocturnal activity. These changes reduced the human related risks for panthers and favored predation on deer. Quite the opposite, we hypothesized that in our study area hunting practices increased the risk for wolves because roads were uniformly distributed.

Males and females showed a similar behavior but with different magnitudes. By assessing the percentages of fixes collected outside OAC, we found that during HWD females showed a higher use of the protected area than males. Accordingly, hunting with dogs seemed to cause a spatial sexual segregation on a large time scale. Such a finding differs from former findings on roe deer. According to those findings roe deer was slightly sexually dimorphic and did not exhibit sexual segregation (Andersen et al. 1998, Hewison et al. 1998, Liberg et al. 1998). However, the differential response showed by roe deer according to the sex is definitely consistent with the reproductive strategy-predation risk hypothesis (Mooring et al. 2003), one of the several hypotheses which have been formulated to explain sexual segregation in ungulates (Main et al. 1996, Ruckstuhl and Neuhaus 2000).

According to the *reproductive strategy-predation risk hypothesis* females and males respond to predation risk in different ways because of their different sizes and the presence of newborns with females. As regards other species, human disturbance has been compared to predation, given that humans could play the role of predator (Szemkus et al. 1998, Enggist-Düblin and Ingold 2003, Frid 2003, Ciuti et al. 2004). In our study area females used protected areas more frequently, possibly in order to avoid disturbance and the risks associated to humans. It has been shown that also sex affects cervid behavior to a great extent. Females exhibit more fear of humans than males (Schoener 1971, Jeppesen 1987b, Bullock et al. 1993). Both predation risk and human harassment may evoke different behavioral responses between and within sexes

(Langbein and Putman 1992, Recarte et al. 1998, Manor and Saltz 2003). In fallow deer females have been found to avoid areas characterized by human disturbance, while males tend to use them because of their better forage (Ciuti et al. 2004, Apollonio et al. 2005). No other study on roe deer ever showed a different response to human harassment according to the sex. And above all, we did not find any evidence of the fact that hunting, or other human activities, could cause sexual segregation in a ungulate species whose sexes usually do not segregate.

Males may also use fewer areas within OAC than females, probably because they seem to be more linked to their home range. Moreover, males generally had to respond to other social pressures, in particular during the territorial phase (Liberg et al. 1998). We actually found a significant behavioral difference between age classes too: sub-adult (2-3 yr.) and adult (more than 3 yr.) roe deer had a larger percentage of fixes outside OAC when compared to young roe deer (1 yr.). Adult deer are commonly expected to be more alert than younger deer, and as a result they should show longer flight distances than calves, in virtue of their many (negative) experiences with humans (Andersen et al. 1996). Nevertheless, this was not quite the case in our study. Young roe deer showed a higher use of areas inside OAC, and mothers were probably responsible for this behavior. Moreover, it could be argued that juveniles were more receptive to dog harassment because free-roaming dogs impacted upon ungulate dynamics mostly by preying on young individuals (Gaillard et al. 1998, Manor and Saltz 2004).

In conclusion, hunting practices seemed to modify roe deer spatial behavior since they affected their population structure (i.e. sexual and intra-sexual segregation). Moreover, these changes could affect the population dynamics and life histories, in that they may cause animals to use sub-optimal habitats before a hard season such as winter.

Management Implications

Managers should take into account these new results while planning hunting management. Particularly, they should be concerned about the diverse effects of hunting practices on both target prey and non target prey species. The use of dogs during hunting sessions should be carefully evaluated especially when non hunted and still vulnerable species are present. Prolonged hunting may influence life history of deer and their population dynamics to a significant degree. Duration and overlapping of different hunting practices must be evaluated in relation to deer population status and presence of protected areas. Managers should be concerned with sexual segregation during certain periods of the year, given that the segregation could be evoked by human activities. They should pay attention to sexual segregation, in particular when they develop census schemes and they plan shooting quotas. Protected areas should be founded, well distributed and preserved by local governments in order to prevent consistent movements by deer populations with consequent undesired effects upon the population dynamics.

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Chapter 3

BROWSING PRESSURE AND USE OF COPPICE AREAS BY ROE DEER (*Capreolus capreolus* L.) IN A MOUNTAINOUS HABITAT

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(*Submitted*)

Abstract

In the last decades Italy experienced wood expansion process, increase in the total surface of protected forested areas, and decline in wood exploitation, all of which improved productivity and structural complexity of the forests on one hand, and reinforced expansion and density increase among populations of free-living ungulates on the other hand (Apollonio 2004a). From this reason the need for adjusted management of both, forest and ungulate communities, has arisen; in particular to avoid conflicts between fauna and forest, as damages due to ungulate browsing have been reported more commonly. Taking into account high spatial and temporal variability of vegetation and ungulate communities (Gordon et al. 2004), we studied a particular case to evaluate roe deer influence on tree regeneration in clear-cut areas of turkey oak and chestnut, in the Apennines, Central Italy. In those coppice stands six experimental areas were chosen and after the clear-cut has been applied, fenced (ungulate access excluded) and non-fenced(ungulate access allowed) plots were established. From 2002 to 2005 each plot was surveyed twice a year and the number of sprouts, their biomass, the collar diameter and total height of sprouts were measured. Moreover, at the same time we radio-tracked 76 radio-collared roe deer, and the utilisation index of the clear-cut areas was defined for three periods; i.e. before, during and after the clear-cut harvesting was applied.

The roe deer had different impact on restoration of different tree species in coppice broadleaved forest stands. In the case of chestnut during the first year after the cutting only 30% of stools were browsed, and after 4 years the chestnut plots were without browsing damage. On the contrary, in the turkey oak coppice each stool was damaged by roe deer browsing one year after the harvesting and after 4 years more than 30% of stools were still suffering the damage. After 1st year of clearings the browsing by roe deer did not have a significant effect on height increase or biomass of sprouts in chestnut coppice, but in Turkey oak coppice biomass and height of sprouts in fenced areas differed significantly from those in not fenced areas. Monitoring of radio-collared roe deer confirmed more intense use of Turkey oak clear-cut areas by those individuals during and after the harvesting of wood than before harvesting.

The reasons for utilisation of clear-cut areas by collared roe deer were several.

Firstly, during the wood harvesting high quantity of biomass, e.g. crown foliage, immediately became available for roe deer consumption. Then after the harvesting

intense re-growth produced higher availability of hiding and resting opportunities. Denser understorey provided an optimal environment for hiding for fawns, as well as safe resting places for adults.
Management implications of deer browsing in Apennine forest are discussed in the light of or results.

Introduction

In the last few decades the relationships between wild ungulates and forest ecosystems were deeply investigated, using different methodology to help understanding better these interactions in details. The main goal of the studies was to investigate the complexity of interactions between forest fauna and forest vegetation (Jorritsma et al. 1999, Reimoser et al. 1999, Sipe & Bazzaz 2001, Partl et al. 2002, Horsley et al. 2003).
As a consequence of dramatic social changes in rural and mountainous areas, Italy, as well as other parts of Europe, after the 1960's witnessed forest expansion due to progressive abandonment of former crop lands, fallows and hayfields (Bätzing et al. 1996, Hötch et al. 2005). At the same time, silvicultural systems that conserve the natural processes and functions within the forest ecosystem and tend towards sustainable forest management, became more and more common. On the other hand, since 1980's the total surface of protected forested areas in Italy increased noticeably. Consequently, the areas of middle-aged forest increased and the management of these areas changed, as well. Moreover, the decline in wood exploitation in these areas resulted in higher complexity of forest environment. Both processes improved productivity and structural complexity of forest ecosystems. As a consequence, favourable conditions for reintroduction or expansion of deer species were established. In Italy, the status of deer populations increased significantly (Apollonio 2004a): roe deer (*Capreolus capreolus* L.) and fallow deer (*Dama dama* L.) increased by 300%, while red deer (*Cervus elaphus* L.) population increased by 600% since 1980 (Apollonio 2004b).
Latham (1999) pointed out frequent cases of high ungulate density also in the other parts of Europe. For this reason the damages due to ungulate browsing has been recorded more frequently and forestry is claiming the negative impacts of ungulates on forest vegetation.

During the past years the need for adjusted forest and hunting management has arisen, also in order to take into consideration changed status and structure of populations of herbivores. Moreover, according to Gordon et al. (2004) several studies already proved, that herbivore distribution and influence on natural resources on local and also landscape scale is determined by key resources, such as vegetation, water, shelter, and social aspects of herbivore aggregations. Nevertheless, caution with concluding the issues should be taken due to spatial and temporal variability of the densities of herbivores and vegetation (Gordon et al. 2004) and their population dynamics. In fact, difficulties in generalising the conclusions among different communities or ecosystems should be considered, so separate research for certain areas should be evaluated, as well.
In the Apennines both, coniferous and deciduous forest stands, are present, even though the latter are prevalent. Namely, pure and mixed deciduous forests of beech (*Fagus sylvatica* L.), chestnut (*Castanea sativa* L.), Turkey oak (*Quercus cerris* L.) and downy oak (*Quercus pubescens* Wild.) are present in high percentage. As regard to forest management, coppice system is mostly under private ownership, which controls two thirds of total forest area of Apennines. The coppice areas are mainly concentrated in the sub-mountainous vegetation belt. Oaks and chestnut represent the most common tree species of these areas. On the contrary, high forest system prevails in public ownership, which is largely present in the upper mountainous belt, dominated by beech forests. Both environments are of high importance for ungulates (Jedrzejewska & Jedrzejewsky 1998) and represent one of the most suitable habitats for roe deer and wild boar, which are the more common ungulate species (Apollonio 2004b). The periodic availability of sprouts and fruits of turkey oak, chestnut, and beech trees are important factors influencing ungulate diet. Consequently, we can assume that in case of unbalanced forest and ungulate management, strong conflicts between fauna and forest, can become a critical issue, especially in the case of palatable tree species like oak and chestnut.

In mountainous area of Tuscan Apennine roe deer spatial behaviour may be characterized by alternative strategies leading to spatial stability or shifts among season (Lamberti et al. 2001; Lamberti et al. 2004). In our study area roe deer exibit smaller home range compared to the close Foreste Casentinesi National Pak (Lamberti et al. 2001) or other forested European areas (Mysterud 1999; Danilkin and Hewison 1996. In the study area Alpe di Catenaia the average annual home range size is generally smaller than 200 ha while it may be comprised between 200 and 500 ha in the above mentioned context (Bongi, unpubl. data). Considering food availability there is an obvious consequence of this namely, browsing pressure tend to be higher in the case of small home range than in larger ones; the same browsing pressure is distributed over a small surface.

The second peculiarity of this study area are seasonal movements of deer inside and outside the protected area. Due to the hunting pressure in fact deer used protected area as a refugee during dog hunting. During the hunting season roe deer spent more time in the protected area, so the relative density of animals increased (Bongi et al. submitted). This may result in the increase of browsing pressure on the vegetation during the autumn.

It has been shown, that browsing by roe deer has little effect on individual tree survival, especially after the first 5 years of growth (Black et al. 1979). However, it still represents a problem from the economic point of view, as considerable damages on tree recruitment due to roe deer browsing have been reported. For instance, yew (*Taxus baccata*) showed retarded recruitment under a heavy roe deer browsing pressure (Mysterud and Ostbye 2004). Browsing impacts vary to a substantial degree in regard to different deer densities (Gill 1992; Reimoser 1986), different environmental factors, such as climate, and also cultural factors, like selvicultural techniques, which design the spatial and temporal distribution of resources (Hannan & Whelan 1989; Morellet & Guibert 1999; Mysterud & Ostbye 1999; Putman 1996; Motta 1996; Reimoser & Ellenberg 1999). In fact, high degree of variability in browsing intensity was reported also among separate subsampling areas, which reflects high temporal (seasonality) and spatial (microclimate, vegetation communities etc.) variability of biotic and biotic factors on local scale (Motta 1996; Bergquist 2003, 1999; Jarni et al. 2004). Jarni et al. (2004) pointed out, that also the height class of the saplings plays a decisive role in modifying browsing pressure on regeneration stand. Moreover, this selective browsing behaviour in Dinaric mountains (Slovenia) decreases diversity of saplings in higher height classes, and so influences the future tree composition of forest stands (Jarni et al. 2004). To sum up, it is advisable to define the reasons for browsing pressure/damages for each habitat or management practice separately, to be able to predict changes in browsing pressure due to changes in demography of the ungulate species and/or changes in management practices (Motta 1996).

Even though the issue on habitat suitability of certain types of European habitats for ungulates was already deeply investigated (Ratcliffe 1992, Key 1993, Tabor 1993, Putman 1994), the knowledge about this topic in Italy is still scarce. The aim of this study is to evaluate the effects of roe deer population on tree restoration in clear-cut areas and the impact of browsing on different tree species. In particular, we analysed the impact of roe deer browsing on agamic restoration of turkey oak (*Quercus cerris* L.) and chestnut (*Castanea sativa* Mill.). The conclusions of this study represent a contribution to the development of integrated forest management in Apennine forest ecosystem.

Methods

Study site

The study was carried out in a mountainous area in Arezzo Province (Italy, Tuscany, 43°48'N, 11°49'E). The site was a protected area, called Oasi Alpe di Catenaia (OAC). Altitude in the area ranged from 330 to 1514 m a.s.l. The climate was temperate and characterised by high humidity rate, with hot and dry summers, and cold and rainy winters. 84% of OAC area was covered in forests, mainly in mixed deciduous woods. The main tree species were chestnut (*Castanea sativa*), Turkey oak (*Quercus cerris*) and beech (*Fagus sylvatica*). Coniferous woods were also present, consisting mainly of silver fir (*Abies alba*) and douglas fir (*Pseudotsuga menziesii*). Douglas fir was planted in the area after the 50's according to silvicultural plan for this area.

All the study area was divided into vegetation parcels, which included separate vegetation communities. Each parcel was subject to structural alteration according to a forest management plan. Regional Forest Service ("Comunità Montana del Casentino") organized and performed the forest management plans, which could be applied in two different ways: as clear-cuts or thinning-out cuts. The second strategy was used in both types of woods, broadleaved and coniferous, while the first one only in deciduous broadleaved woods. From economic point of view forest management is economically important trees are sold, both as firewood (Turkey oak, beech) and as timber wood (chestnut, coniferous). Moreover, opened areas, like clear-cuts, were important for newly induced and faster forest restoration.

The ungulate community in the study area consisted of roe deer and wild boar. Densities of both ungulate populations were estimated every year in April or June (Table 1). Hunting in the area is strictly forbidden. However, outside the OAC the hunting activities are intense and comprise deer stalking and wild boar hunting with dogs. The deer predators in the area are wolf and red fox.

Data collection

Six experimental areas, of one hectare, chosen as representative stands of all OAC coppice forests, were established. All studied coppice stands were at the end of their rotation period and were dominated by Turkey oak or chestnut. At first, preliminary dendrometric survey was done, in order to define the representativeness of the stands and their characteristics before treatment. Then, in March 2002, all six experimental coppice stands underwent clear-cutting with the release of 50-60 standards per hectare only, in accordance with the traditional approach in simple coppice system application in Italy. Immediately after, in each experimental area two permanent plots, each cca. 200 m² of size, one fenced and one available to deer browsing, were established. In each plot all the stools were permanently numbered and surveyed. From 2002 to 2005, for each stool number of sprouts, collar diameter (d), total height (h) of sprouts and damages due to deer browsing were recorded at the beginning and at the end of each growing season. At the same time, each stool was classified and ranked according to a synthetic estimate of percentage of browsed sprouts:

Damage class	number of damaged sprouts	damage rank
no damage	0	0
slight damage	<30%	1
medium damage	31-60%	2
heavy damage	>60%	3

In this way we established an easy and little time-consuming approach to evaluate and analyse the dynamics of deer browsing in connection to different treatment (fenced and non-fenced) and different tree species (Turkey oak or chestnut). In fact, we compared the percentage of stools in each damage class and calculated a “browsing index” as average of damage ranks, recorded in each sampling plot.

Moreover, also specific allometric equations were elaborated, in order to evaluate the impact of deer browsing on the biomass of sprouts more accurately. Representative samples of 100 chestnut and Turkey oak sprouts were gathered outside, but close to the experimental plots. In laboratory collar diameter and total height of each sprout was measured and afterwards, the average parameters for all the stools were calculated. Later, sprouts were dried at 85°C in forced air stove until constant weight was reached.

Data obtained were used to elaborate specific allometric relations for woody biomass (dependent variable), based on two (d^2h) independent variables, according to a simple linear model $y = a + bx$. Each survey and allometric equation allowed us to estimate the biomass of each sprout and consequently, of each stool. The impact of deer browsing was evaluated comparing the data from the Turkey oak or chestnut stools from fenced and non-fenced plots by means of one-way ANOVA (Statistica, Statsoft Inc.).

On the other hand, from March 2002 to March 2005 we captured 76 adult roe deer individuals using vertical drop-nets. The animals were equipped with Televilt VHF radio-collars. All individuals were subsequently located by means of discontinuous radio-tracking using Televilt RX-8910 HE and TRX 1000-S Wildlife Materials receivers, and four-element hand-held Yagi antennas. 12 or more locations per animal per month were obtained by triangulation method, where bearings from three reference points are taken. We distributed the bearings uniformly over the day and separated consecutive fixes by an interval of $\geq$ 12 hours to avoid autocorrelation. Accuracy of fixes was determined in the field by using test transmitters placed in various habitats (Harris et al., 1990), which enabled us to use an error polygon of 1 hectare. Average fix error polygon at this size was still smaller enough than the average patch size of separate vegetation communities in our study area, which is relatively large (mean $\pm$ SE: 216.3 ± 92.7 ha). From this reason it was possible to determine habitat use of roe deer in this area.

For the purpose of this study we considered only those fixes, that were determined inside the clear-cut areas. The time frame for grouping the fixes was set into three periods: before, during and after the forest work weighting data with fix recording time. All data for habitat use analysis were processed with ArcView GIS 3.2 software.

We calculated the utilization index for the clear-cut areas, where differences in use of each working area by roe deer was evaluated using the formula below (Fig. 1). In each time period (before, during, and after the forest work) the average number of fix per animal in the area was calculated, and weighted by the duration of each period (number of months). The chi-square test was used for statistical analysis: the observed value represented the utilization index in each period and the expected value represented the utilization index evaluated in total period.

$$\frac{\sum_{i=1}^{n} \text{fix}_{i} \Big/ \sum_{i=1}^{n} \text{roe deer}_{i}}{\sum_{x,j,z=1}^{n} \text{month}_{x,j,z}}$$

Figure 1: Formula for calculating weighted utilisation index for clear-cut areas by collared roe deer in Oasi Alpe di Catenaia.

Table 1: Population densities of both ungulate species in Alpe di Catenaia from 2000 to 2007.

Parameters (no. individuals/ km2)	Years (late winter to late winter)							
	2000-01	2001-02	2002-03	2003-04	2004-05	2005-06	2006-07	Mean ± SE
	Wild boar (*Sus scrofa*)							
Juveniles born in spring	12.47	6.30	7.55	16.16	3.72	7.16	8.12	8.78 ± 1.58
Density in summer	25.32	12.79	15.32	32.80	7.54	14.54	16.49	17.83 ± 3.20
	Roe deer (*Capreolus capreolus*)							
Juveniles born in spring	8.35	7.47	6.94	7.37	5.91	6.26	6.59	6.99 ± 0.31
Density in summer	32.57	29.15	27.08	28.75	23.06	24.41	25.68	27.24 ± 1.22

Results

The roe deer had different impact on agamic restoration of different tree species in coppice broadleaved forest stands. Moreover, there was a difference in browsing effects in relation to time duration, which has passed from the harvest on, and in relation to the tree species. In fact, during the first year after cutting only 30% of chestnut stumps were browsed. Instead, in a Turkey oak coppice every stool was severely browsed by roe deer (Fig. 2).

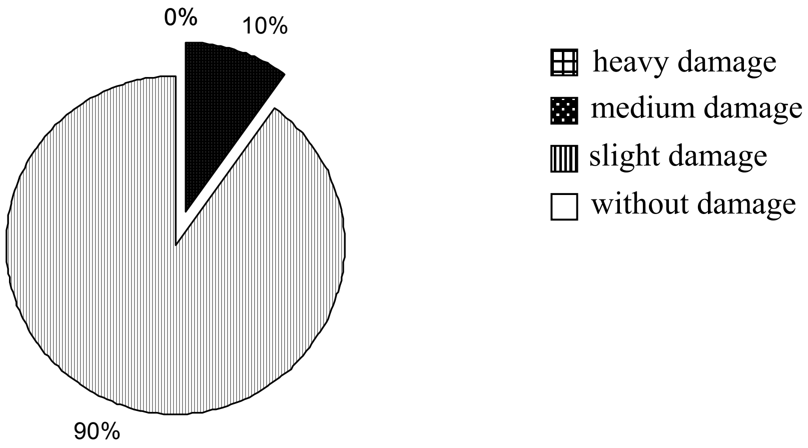


***Figure 2.* Incidence of roe deer browsing on turkey oak stools after 1year**

During the second year after the clearing the same percentage of damage in the chestnut coppice was observed (Fig. 3), but the severity of the browsing was lower. In Turkey oak coppice the damage due to roe deer browsing in the second year, was still above 50% (Fig 4). In the 3rd year, 39% of Turkey oak coppice heavily suffered of roe deer browsing (Fig. 6); instead, the chestnut coppice was almost untouched (Fig. 5).

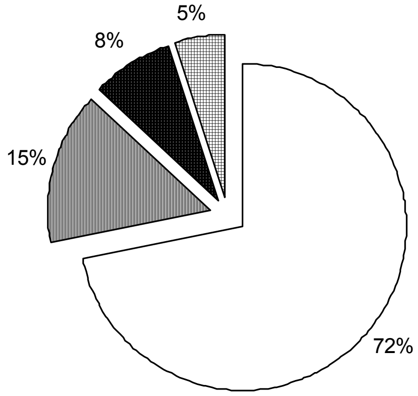


***Figure 3.* Incidence of roe deer browsing on chestnut stools after 2 year**

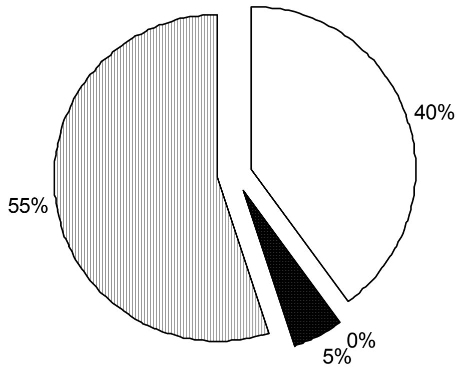
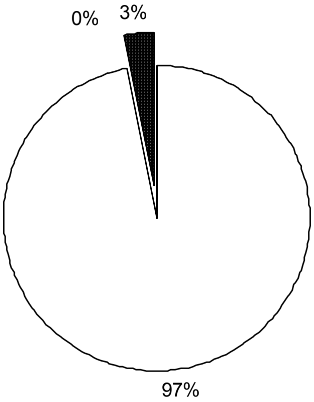


***Figure 4.* Incidence of roe deer browsing on turkey oak stools after 2 year**



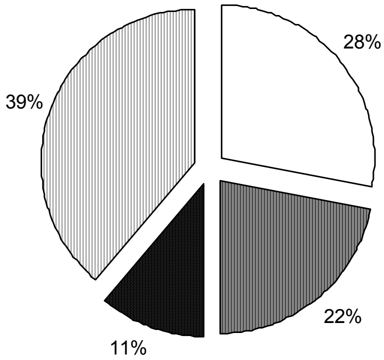
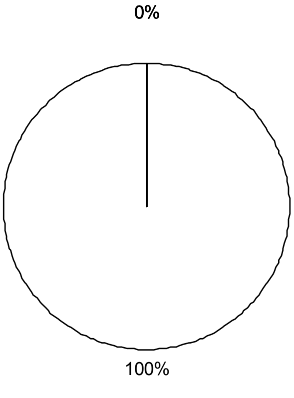


***Figure 5.* Incidence of roe deer browsing on chestnut stools after 3 year**

***Figure 6.* Incidence of roe deer browsing on turkey oak stools after 3 year**

After 4 years the chestnut stands were absolutely without browsing damage (Fig. 7). However, in Turkey oak coppice at the same age more than 30% of stools were still suffering the damage due to browsing (Fig. 8).



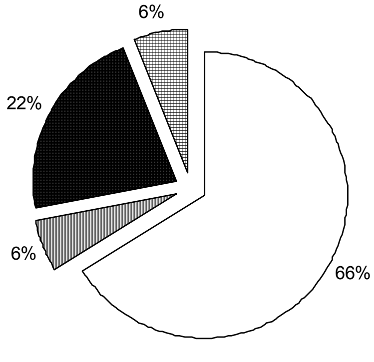


***Figure 7.* Incidence of roe deer browsing on chestnut stools after 3 year**

***Figure 8.* Incidence of roe deer browsing on turkey oak stools after 4 year**

The different level of browsing damage by roe deer was evaluated also in relation to height increase of sprouts. After 1st year of clearings the browsing by roe deer did not have a significant effect on height increase of sprouts in chestnut coppice. Instead, in Turkey oak coppice a statistically significant difference in height of sprouts in fenced areas (no access of roe deer) from compared to unfenced fenced areas (with influence of roe deer) was observed (one-way ANOVA: F = 105,85, p< 0,001) (Fig. 9 and 10). In case of Turkey oak coppice the significantly different sprouts' height between fenced and not fenced areas appeared also in the 4th year after the clearings (one-way ANOVA: F = 13,87, P = 0,0007) (Fig. 10).

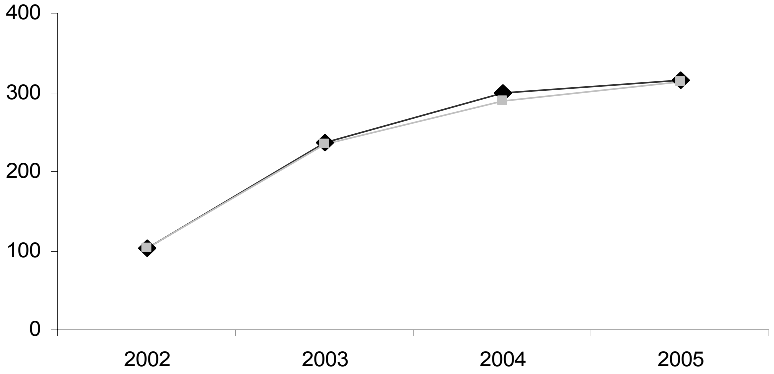


Fig .9 **Height increase in chestnut sprouts**

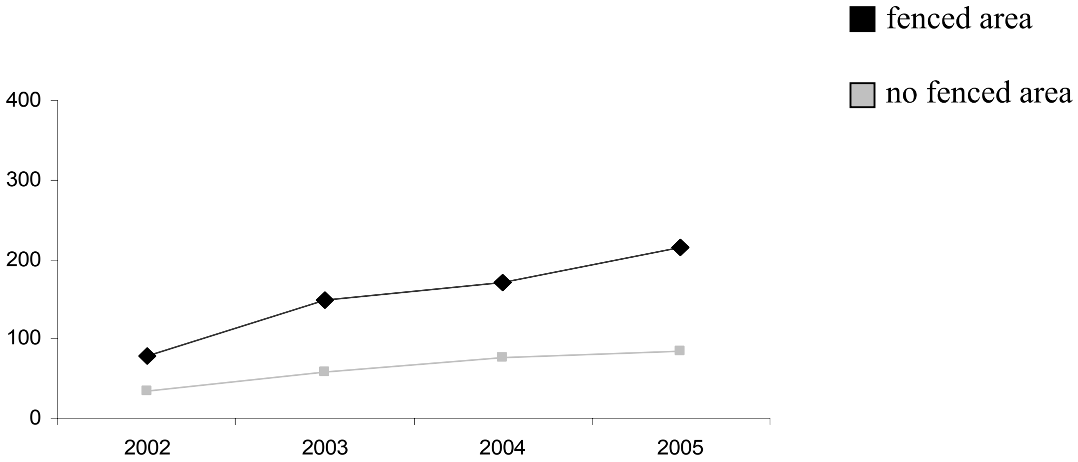


Fig .10 **Height increase in turkey oak sprouts**

Sprout diameter in relation to browsing impact was also evaluated. In the first year after the cut, there was not a significant difference in diameters of sprouts from fenced and non fenced areas in both, chestnut and Turkey oak coppice (Fig. 11 and 12). However, in Turkey oak coppice the mean diameter size of sprouts was significantly smaller in non-fenced areas in comparison to diameters in fenced areas (see Tab. 2 and Fig. 12) from the second year after the clearing on.

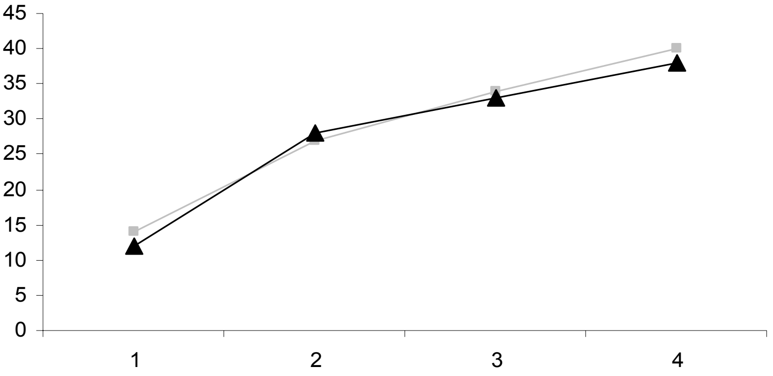


Fig .11 **Diameter increase in chestnut sprouts**

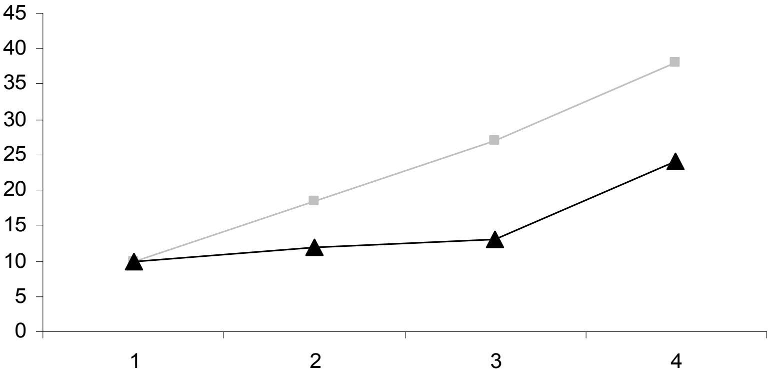


Fig .12 **Diameter increase in turkey oak stools**

Table 2*: Average and variance values for height, diameter and biomass of sprouts and stumps in turkey oak coppice for fenced and not fenced areas in Alpe di Catenaia in 2002 and 2005.*

		height (cm)					
		mean	***n. obs.***	***SD***	***GDL***	***F***	***P***
2002	***Fenced***	77,80	20	21,50	1/38	105,85	0,0000
	No-fenced	24,50	20	8,60			
2005	***Fenced***	228,70	19	73,80	1/33	13,87	0,0007
	No-fenced	145,00	16	55,80			
		diameter (cm)					
		mean	***n. obs.***	***SD***	***GDL***	***F***	***P***
2002	***Fenced***	1,00	20	0,20	1/38	0,0002	0,9880
	No-fenced	1,00	20	0,40			
2005	***Fenced***	3,76	19	0,99	1/33	18,68	0,0001
	No-fenced	2,35	16	0,93			
		biomass (gr)					
		mean	***n. obs.***	***SD***	***GDL***	***F***	***P***
2002	***Fenced***	23,30	20	13,10	1/38	17,16	0,0001
	No-fenced	9,80	20	6,40			
2005	***Fenced***	824,28	19	558,66	1/33	14,53	0,0005
	No-fenced	260,50	16	207,96			

In chestnut coppice there was no difference in average biomass of stools between fenced and not fenced areas (Fig. 13), while in Turkey oak coppice there was a significant difference in biomass of stools between fenced and non-fenced areas (Fig. 14).

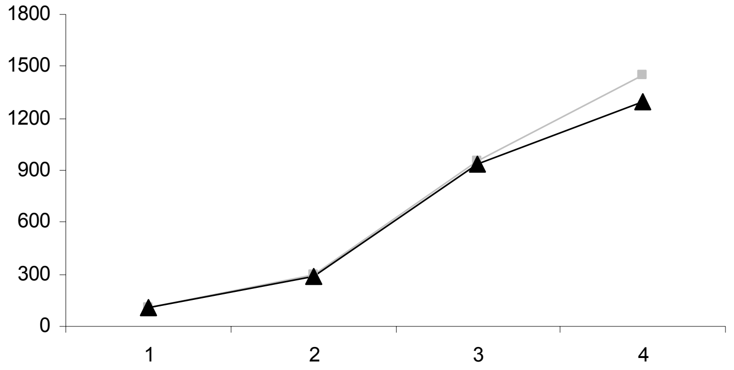


***Fig .13* Biomass increase in chestnut coppice**

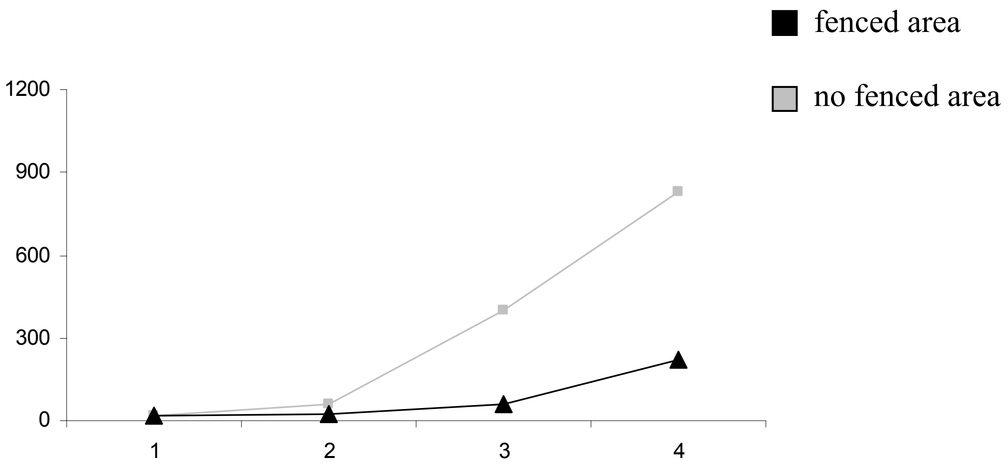


***Fig .14* Biomass increase in turkey oak coppice**

Monitoring of radio-collared roe deer confirmed intense use of clear-cut areas by deer during and after the harvesting of wood. In details, the utilization index for two Turkey oak stands C17-1 and D5-1 showed a significant variation in use in different periods (χ^2= 12,91; df= 2; p<0,01) and (χ^2= 6,56; df= 2; p<0,05) respectively: during and after the harvesting roe deer spent more time inside those areas than before harvesting (Figure 15).

Figure 14. Utilization's index in the different working period in a turkey oak area (C17-1)

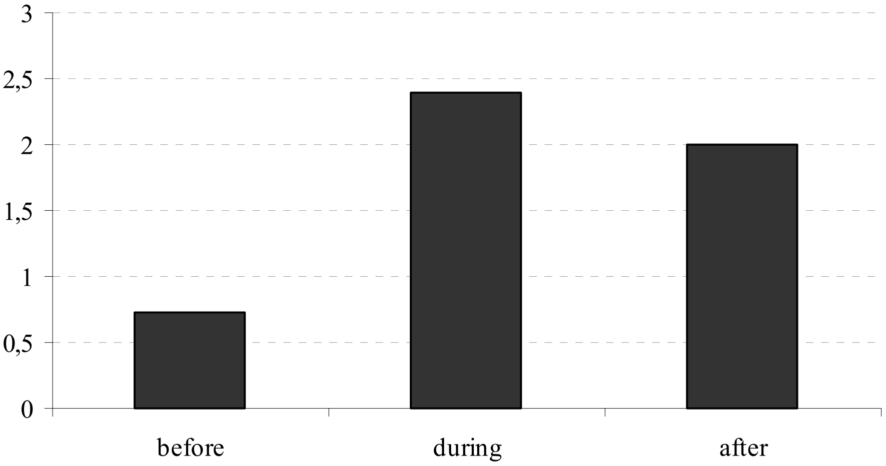
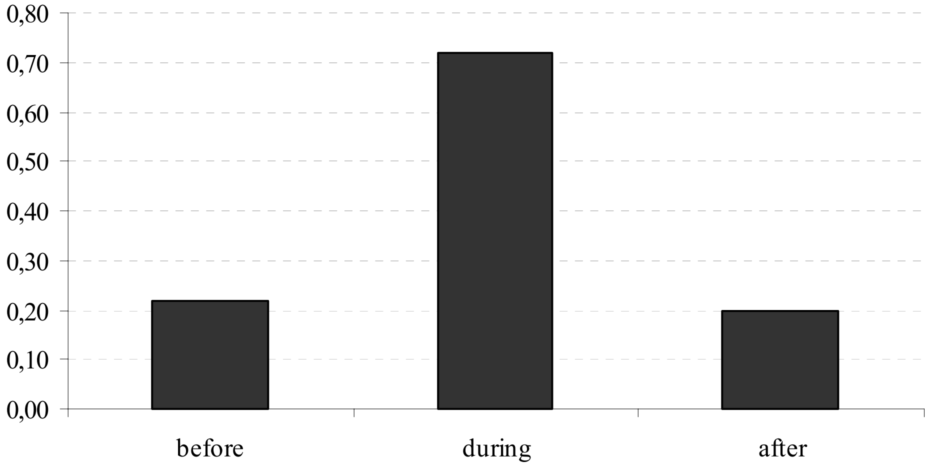


Figure 15. Utilization's index in the different working period in a turkey oak area (D5-1)



Discussion

The overall outcome of the study revealed differences in roe deer browsing impact on different tree species in those tree communities at the clear-cut sites.

Only low level of damage was observed in chestnut coppice, given that in all four years after the clear-cut there was no significant reduction of growth. The browsing effects of roe deer were observed in the first year after the clear-cut only, which then decreased progressively in the following years. However, there was a statistically significant difference between fenced and non fenced areas in oak coppice each year in case of comparison of height and diameter of sprouts, and total biomass. The same findings were found to be true also for the area of Foreste Casentinesi National Park (also Apennine area, north of our study site) (Gualazzi 2004). The reason for smaller level of browsing damage in the chestnut stands is most likely lower preference of chestnut by roe deer than of Turkey oak. In fact, browsing index for the first year after the clear-cut is noticeably lower for the chestnut stands than that for Turkey oak stands. Moreover, due to high growth rate in case of chestnut sprouts (height increase one meter per year) roe deer could browse chestnut saplings until the second year after the clear-cut only.

However, roe deer impact was intense in Turkey oak coppice. In the first year after the clear-cut each Turkey oak sprout was browsed and there was a significant decrease in height of sprouts on non-fenced areas in comparison to the ones in fenced areas. Browsing damage by roe deer continued through the following years, until in the 4th year after the clear-cut 30% of stools were still severely damaged.

For this reason we conclude, that roe deer prefer Turkey oak to a higher degree than chestnut (Casanova & Dell'Omododarme 1990, Gualazzi 2004), and that roe deer selects the foraging sites to a very high degree (Bergmann et al. 2005; Moser et al. 2006; Jarni et al. 2004). We also conclude that the selection of the browsing sites depends also on the food quality (Jarni et al. 2004) and moreover, there should be a difference in palatability between Turkey oak and chestnut tree. Even if it contrast with previously known on roe deer propensity to select species with high tannin contents (Klötzli, 1965, Tixtier et al. 1997). Additionally, the study from a mosaic landscape in Switzerland pointed out, that foraging behaviour of roe deer corresponded to optimal foraging theory in summer and winter, while in the spring the food preference was dictated by other factors than food quality (Moser et al. 2006). Because in our study area wood harvesting was taking place in spring and summer, and the foliage and regrowth were available to roe deer at this time, an even higher level of food selection by roe deer was expected.

In case of plots with Turkey oak coppice there was a significantly different height of sprouts from fenced and non-fenced plots observed. Still, as the declining rate of browsing damages in these stands was recorded, the high stool biomass decrease could be connected to browsing on lateral Turkey oak sprouts. For instance, just some of the Turkey oak sprouts managed to exceed the browsing height, so the browsing damage was related to browsing on the lateral sprouts (Chines et al. 1997).

The radio-tracking data from roe deer were consistent with the findings of vegetation surveys in the turkey oak stands. In fact, the number of localizations of animals inside clear-cut areas increased in both, during and after the forest work. During the wood harvesting high quantity of biomass, e.g. crown foliage, immediately became available for roe deer consumption. Roe deer approached these sites in late afternoons, evenings, and nights, when the foresters were gone, and foraged on the foliage. The utilisation index for these sites was statistically higher in the period of wood harvesting and subsequently, than before harvesting.

Another important aspect is vegetation density, as it is connected to visibility in the stands and utilisation of such sites by roe deer as safe hiding places. On our study site the recruitment of sprouts was high in the first and second year after the establishing of the clear-cuts. That is because, the middle layer of vegetation structure was very dense, which represented an optimal hiding place for fawns, as well as safe resting places for adults (Mysterud and Ims, 1999). Dense coppice stands are especially selected by roe deer females with fawn, as on anti-predator strategy (Bongi et al., 2008).

Our results provided evidence for importance of Turkey oak coppice for roe deer in our study area (feeding place, shelter, time spent in these places). Anyway, importance of certain plant species for the ungulate diet is dictated also by the availability and spatial distribution of these species in particular area (Gordon et al. 2004) and also by species composition of the forest community (Jarni et al. 2004). We suggested, that in our study area, roe deer preferred Turkey oak coppice to chestnut coppice. Moreover, the spatial distribution of coppice areas (e.g. preferred and not preferred stands) influenced spatial behaviour of roe deer, as they concentrated in cut areas.

On the other hand, the results show a relevant impact of roe deer on Turkey oak coppice. Namely, Turkey oak coppice stands were subjected to different regeneration process in fenced and non-fenced plots. It can be concluded, that roe deer can influence the structure of Turkey oak regeneration stands.

This impact can have negative consequences from economical point of view, as Turkey oak coppice regenerated slowly, when roe deer is present. However, it should be considered, that in case of other forest management strategies the browsing influence could be different due to different browsing preferences and different availability of certain plant species (Partl et al. 2002).

From this aspect, it is important to evaluate ungulate densities. Some studies showed that roe density was positively correlated with occurrence and intensity of browsing damages (Gill et al., 1996; Putman, 1996; Welch et al., 1990). Moreover the deer abundance was positively correlated also with the proportion of habitat types providing dense understorey vegetation.

In our study area roe deer density was quite stable during these years, and present management plans aim is to maintain the same population size. So, decline of browsing pressure can not be expected.

Moreover wolf as a roe deer predator dose not seem to be able to regulate roe deer population in this area (Gazzola et al, submit.).

In this context deer-forest relationship should be reconsidered in the light of possible development of serious interference with forest regeneration process.

Management implications

It could be predicted, that forest practice that maintain the deciduous coppice woods did not have a negative impact on roe deer population. In fact, it provided a habitat that is in favour of roe deer individuals in that particular space. However, from economical point of view, roe deer may negatively influence the regeneration process in Turkey oak coppice. Periodical clear-cutting provides additional resources for roe deer in comparison to a high-forest. Taking into consideration present forest management plans and hunting management plans, some negative outcomes of forest flora and fauna interactions are expected. In such case, agreement on adjusted management plans would be necessary, in order to approach differently the problem of roe deer browsing in coppice areas. Both, forest and hunting management plans should include an integrate approach to manage ungulate and tree populations on the basis of coordinated temporal and spatial scale. In details, management plans should include an intercept of periods in population dynamics and life-cycle of both, ungulate and tree species, and adjust the spatial scale of managed forest parcels to the scale of roe deer home range size.

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Third Part

HOW ECOLOGICAL FACTORS MAY AFFTEC ROE DEER SPATIAL BEHAVIOUR AND, CONSEQUENTLY, CENSUS METHODS

Chapter 4

WOLF (C*anis lupus*) IMPACT AND HUNTER IMPACT ON WILD BOAR (*Sus scrofa*) AND ROE DEER (C*apreolus capreolus*).

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Summary

1. Many studies showed as herbivore populations are limited by predation (top-down control). On the other hand, forest productivity seems to have a strong effect on ungulates densities (bottom-up control). The relationships between forest productivity, prey densities and the effects of predation is even more complex in European countries where prey densities are strongly influenced by human impact.

2. Wolf–ungulate and hunter-ungulate interactions were studied in a mountainous region of north-eastern Tuscany (Italy) from May 2000 to April 2007. Wild boar and roe deer constituted the wild ungulate community and their average estimated densities were 17.8 and 27.2 km^{-2} respectively. One pack of 3-6 wolves and 342 hunters utilized the study area (120 km^{2}).

3. Wolves annually removed on average 115 wild boar and 102 roe deer per 100km^{2}. These amounts were equivalent to 8% of wild boar and 4% of roe deer summer census. Additionally, hunters annually removed on average 796 wild boar and 298 roe deer per 100km^{2}. Hunting represented an important mortality factor for wild boar but not for roe deer (52% and 11% of summer density respectively).

4. Wolves and hunters showed a different use of ungulate age classes. Juvenile ungulates were preferred by wolves, whereas hunters positively selected only adult wild boar and didn't select any specific class on roe deer.

5. *Synthesis and application*. Wild boar and roe deer abundances were not affected by wolf predation. The role of wolf predation on wild ungulate populations seemed to be compensatory, while hunting pressure constituted a limiting factor. Wood productivity seems the most important factor in produce wild boar population fluctuations. Seed crop of the previous year played the essential role in regulating wild boar density.

Introduction

Whether and how herbivore populations are limited by predation have been among the most highly debated questions in wildlife management during recent decades. At present, several large carnivore species in Europe are expanding their ranges, which raises concerns of their possible detrimental influence on ungulate populations already subject to hunting harvest. On the other hand, facing the problem of ungulate overabundance in many areas, possible positive effects of predation on biodiversity and forest regeneration have recently been recognised (Jedrzejewska & Jedrzejewski 1998; Berger et al. 2001; Ripple & Beschta 2003) and there is rising interest in reintroducing large carnivores in order to regulate wild ungulate densities.

Against this controversial background, research has started to extend beyond studying single species and has begun to explore interactions between multiple trophic levels. However, naturalists studying large mammals still face difficulties reconciling actual food web theories with their field data (Melis et al. submitted). Empirical studies have revealed contradictory results, identifying both plant resources and predation as the main factors shaping ungulate densities.

The “green world hypothesis” (Hairston et al. 1960) and the hypothesis of exploitation ecosystems (Oksanen et al. 1981, Fretwell 1987, Oksanen & Oksanen 2000) both predict a strong limitation of herbivore populations by predators (top-down control). According to these predictions, at a large scale ungulate densities should not change along a habitat productivity gradient. Predation should keep ungulate numbers in check, reduce browsing pressure and, in this way, influencing lower trophic levels (e.g. forest regeneration). Support for these hypotheses was found by Crête (1999), who found that deer biomass in North America increased along a habitat productivity gradient in the absence of predators, while it remained at a similar level in areas with wolf presence. Evidence for influence of predation on lower trophic levels (trophic cascades) was shown after the reintroduction of wolves in Yellowstone National Park (USA) by Ripple & Beschta (2003), who observed regeneration of cottonwood (*Populus* spp.) in areas with high predation risk, while habitats with less predation risk were still heavily browsed.

By contrast, the so called “plant self-defense hypothesis” (Murdoch 1966) predicts that herbivores are limited by the availability of ingestible plant material (bottom-up control). Positive correlations should be observable between herbivore densities and plant productivity. Predation is seen as compensatory and the extinction of predators should not affect the abundance of lower trophic levels. Several studies have underlined the importance of bottom-up control (Okarma 1995; Peterson et al. 1998; Oksanen & Oksanen 2000; Bieber & Ruf 2005). Melis et al. (2006) identified mean January temperature and vegetation productivity index as the most important factors explaining variation in wild boar densities along a bio geographical gradient. Wolf predation only had a weak effect, its role increasing in southern regions. This suggestion is consistent with the reports from southern Europe, where wild boar was reported as the main, and even preferred, prey of wolves (Telleria & Saez-Royuela 1989; Mattioli et al. 1995; Meriggi & Lovari 1996).

Synthesising both views of predator-prey systems, Arditi & Ginzburg (1989) assumed co-limitation of ungulate populations by food resources and predation. According to their predictions, herbivore densities will increase along a habitat productivity gradient. Simultaneously, predation will limit prey densities at an equilibrium below the carrying capacity determined by plant productivity.

Several recent studies support the view of complex ecosystems in which both, top-down and bottom-up control are at work. Long-term data from Bialowieza Primeval Forest suggests that ungulates were affected by both climate-related food availability and predation (Jedrzejewska & Jedrzejewski 2005). Top-down control increased during periods with cooler climate. Correspondingly, a large-scale study analysing variation in roe deer population density from 80 localities in Europe revealed that top-down control by predation was relatively weak in highly productive environments but increased markedly in regions with low productivity (Melis et al. submitted).

While large-scale studies reveal the patterns of top-down and bottom-up processes, small-scale studies can provide insight into the mechanisms of these processes.

Studying the relationships between forest productivity, prey densities and the effects of predation is getting even more complex in European countries where prey densities and behaviour are strongly influenced by human impact. Almost all habitats in western Eurasia are dominated by humans. Due to the strong reduction of large predator populations, modern game management and alteration of habitat by forestry and agriculture, ungulate populations have reached peak densities in many regions of Europe (Apollonio, Andersen, Putman, eds. 2008). Our study area represents one of these altered, highly productive habitats where a large predator coexists with human hunters. Most studies underlining the role of large carnivore predation as a limiting factor largely neglect the influence of hunting on ungulate populations. However, hunting harvest may mask the effects of predation and influence wolf feeding habits (Gazzola et al. submitted).

The goal of this paper is to estimate combined hunting and predator impact on wild boar and roe deer densities and to disentangle the relative influence of these two factors in limiting ungulate populations. We also investigate the different preferences of wolves and hunters for ungulate age classes. These aims would explain if the top-down control is present in our study area. Moreover we investigate the influence of forest productivity on ungulate densities to understand the bottom-up control.

Study Area

The study was performed in a mountainous habitat located in the Apennine Mountains in the northeastern part of Tuscany, in the province of Arezzo, Italy (43°48’ N, 11°49’ E).

Predator-prey relationships were investigated in an area of 120km^2, which encompasses a strictly protected area of 30 km^2 (Oasi Alpe di Catenaia, OAC). The other portion of the study area was hunting zone.

The altitude varied from 300 to 1514 m a.s.l. Vegetation cover consisted mainly of mixed deciduous woods (76% of total area), dominated by oak (*Quercus spp*), chestnut (*Castanea sativa*) and beech (*Fagus sylvatica*). Coniferous forest (7%) and open areas (16%) were also present.

The climate was temperate with hot and dry summers and cold and rainy winters. The snow usually fell from October to April.

The wild ungulate community comprised two species only: roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Roe deer was the more abundant species and its density was relatively stable throughout the study period. By contrast, wild boar showed wide fluctuations in density. The presence of one stable wolf pack (3-6 individuals) was verified throughout the study period (2000-2007).

Outside the protected area (OAC), hunting practices were allowed and regulated according to different periods of the year. Wild boar were harvested from 1st October until early January. Hunting of wild boar included battues (i.e. dog drives) with 30-50 hunters (at least 25 hunters were required by law) and many dogs. Hunting of roe deer (stalking with rifles but without dogs) was permitted in February and August. 132 deer and 210 wild boar hunters hunted in the study area (120 km^2).

Material and Methods

Wild prey surveys and hunting harvest

Abundance of wild ungulates was determined every year (2000–2007) within the study area. Drive censuses were carried out in spring (following Mattioli et al. 2004) (Provincial Administration of Arezzo) to estimate prey abundance. Population structure was evaluated by direct observations on standardised transects for roe deer and from randomly killed individuals for wild boar. Age and body weights of all ungulates killed in the area were collected from hunters bags. Both deer and boars were aged on the basis of tooth eruption and wear.

Summer abundance of ungulate was calculated on the basis of their spring counts, on the percentage of adult females in the population and on female fertility. The latter data were obtained by counts of foetuses found in females shot by hunters (Hunting Plan Provincial Administration of Arezzo; Cappai et al., unpublished data).

Shooting plans are mandatory for roe deer hunting: they must be issued by hunting districts (ATC), must be linked to any small hunting areas and must be approved by the provincial government. Shooting plans prescribe not only the overall number of individuals to be culled but also the breakdown of this number by age and sex class. Individual hunters are assigned an exact number of animals for each sex and age class.

In the case of wild boar there are, if, only overall hunting quotas, without any cull of sex and age class are random. There is no assignment of an exact number of heads either to individual hunting teams or single hunters.

Wolf status

Wolf pack dynamics were monitored throughout the study period by integrating data obtained from snow-tracking, wolf-howling, molecular analysis, and direct observations.

The largest number of wolves in each wolf pack was accepted as the size of the wolf pack in a given year (following Jedrzejewski et al. 2000).

During the winter season, wolves were tracked in fresh snow (24–48 h after snowfall). When a wolf trail was found, it was followed until the number of individuals travelling along it became distinguishable. The largest number of wolves travelling together within study area was used as an estimate of winter pack size.

Wolf-howling surveys were carried out from late June to the end of October to ascertain the presence of wolf packs and their reproductive status (i.e. birth of a litter). The approach described as a 'saturation census' by Harrington and Mech (1982) was adapted to local requirements, dictated especially by the mountainous topography.

The equipment, artificial stimuli, and session protocols have been described elsewhere (Gazzola et al. 2002). The whole study area was monitored simultaneously by different teams for every working night two.

Each response of packs to the wolf-howling stimulus was recorded. Pack size was determined as the maximum number of pups and adults heard in all replies collected during each summer.

Further data on pack composition was carried out by molecular analysis on non invasive samples (for methods see: Scandura 2005; Scandura et al. 2006). Tissue, hairs, scats, whole blood and blood residuals in snow were used as sources of genomic DNA. Fresh (< 1 week) faecal samples were collected in wolf areas, mostly along tracks in snow, and stored in polypropylene tubes filled with absolute ethanol. Shed hairs were stored dry in plastic or paper envelopes. Blood residuals were found along wolf tracks in snow and collected as described elsewhere (Scandura 2005). As far as possible, all samples were kept cold immediately after their collection and then stored at –18 °C until analysis.

Wolf feeding habits and energy requirements

A net of seven standard scat-trails covered homogeneously the whole study area (total length: 73 km). Scat-trails were performed each month by one operator. Wolf food habits were assessed by scat analysis. Scats were washed in a sieve of 0.5 mm and the prey remains (hairs and bones), fruit and grasses found in every scat were dried at 50°C for 24 h. Prey remains were identified on the basis of a reference collection of mammal hairs. Moreover, the age of the ungulates recovered from wolf scats was determined through the analysis of recognizable bone fragments, teeth, and macroscopic comparison of hairs (see Materials and methods in Mattioli et al. 1995).

Two age classes were distinguished for roe deer and wild boar: juveniles (≤ 1 year of age) and adults (>1 year). When a component could not be assigned to a specific taxonomic group, it was considered to be undetermined.

The relative biomass (Bio) of ungulate species and other mammals was calculated using the volume values. We applied the biomass model of Ciucci et al. (2001): $y = 50.274 + 0.011x$, where y represents the biomass (kg) of prey for each collectable scat and x is the live weight of prey.

Frequencies of various prey species taken by predators compared with the shares of these animals in the communities of ungulates revealed wolf' selectivity. Manly' selectivity index (Manly et al. 1972) was used to describe hunting preferences. The index is given by: $\alpha_i = r_i/n_i\,(1/\sum(r_j/n_j))$ where

α_i = Manly's α (preference index) for prey type i

r_i, r_j = proportion of prey type i or j in the diet (i and j = 1, 2, 3, … m)

n_i, n_j = proportion of prey type i or j in the environment

m = number of prey types possible

When selective feeding does not occur, $\alpha_i = 1/m$. If is greater than ($1/m$), then species i is preferred in the diet. Conversely, if α_i is less than ($1/m$), prey species i is avoid in the diet.

Predation impact and its importance for prey populations were investigated. The magnitude of predation is a product of wolf number and their killing rates. Kill rate was estimated by a theoretical approach using the daily food consumption.

Daily food consumption by wolves was calculated through the field metabolic rate (FMR) for all eutherian mammals (Głowaciński & Profus 1997). The equation, derived from Nagy's formula (1987), is closely correlated with body mass: FMR (kJ/d) = 52.58 $W^{0.862}$, where W is body weight in grams. This allows indirect estimates of total daily energy expenditure of a free-living animal. Data from Italy give an average body weight of 32 kg for an adult wolf (> 1 year old). Calculations based on FMR yielded 2.6 kg of meat per day for an adult wolf.

Predation impact and its importance for prey populations

On the basis of the number of wolves monitored in the study area each year, we calculated the biomass of meat required annually by wolves. Furthermore, on the basis of both the relative importance of the staple prey items in wolf diet (wild boar and roe deer) and the average body mass of prey species consumed by wolves, we calculated the number of prey taken by wolves each year. Predation impact was expressed as percentage of prey densities.

Age comparison of wolf and hunter-killed wild ungulate species (wild boar and roe deer) were analysed. We tested for a significant difference in the age classes (young and adult) utilised by wolf and hunters using the Chi-square test.

We compared data on wolf kills and on hunting bags from 2000 to 2006 with ungulates census data using Spearman's correlation and linear regression. We assumed the significant level at the P=0.05.

Moreover to evaluate the top-down control, we investigated the additive effects of hunters and wolves pressure on prey densities.

In the study area National Selvicultural Institute collected data on annual deciduous woods productivity evaluated as seeds density (Mg/ha) of chestnut (*Castanea sativa*), Turkey oak (*Quercus cerris*), beech (*Fagus sylvatica*). We analysed the relationship between total weight of seed crops (chestnuts, acorns and beech-nuts) and prey density in the following year.

Results

WOLF AND UNGULATE ABUNDANCE

During 2000–2007, we monitored one wolf pack. The pack size ranged from 3 to 6 (Fig. 1). In the study area, the wild ungulate community was comprised only two species: roe deer and wild boar. Roe deer was the most common ungulate species and its density ranged from 23.06 (2004-05) to 32.57 (2000-01). The roe deer quotient of increase was 1.41. Wild boar showed much greater variation (Table 1) reaching a density 4.35 times higher in 2003-04 than in 2004-05.

Figure 1. Wolf pack size during the study period (2000-2007).

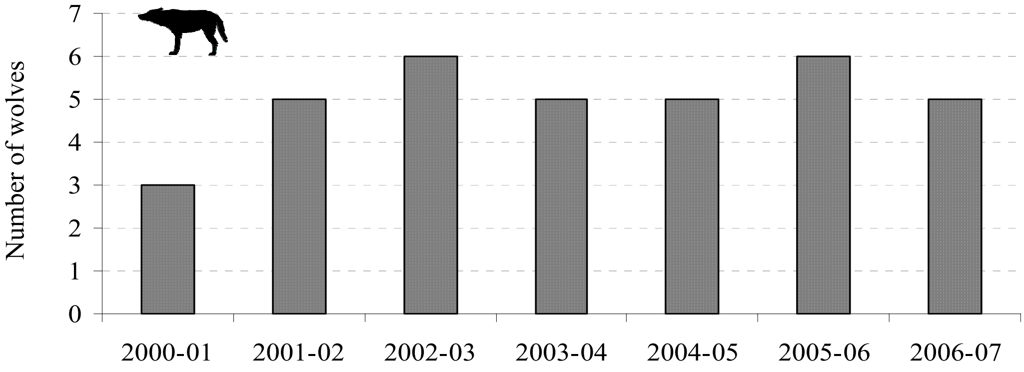


Table 1. Population abundance of staple wolf prey in Alpe di Catenaia (2000-2007).

Parameters (no. individuals/ km^2)	Years (late winter to late winter)							
	2000-01	2001-02	2002-03	2003-04	2004-05	2005-06	2006-07	Mean ± SE
	Wild boar (*Sus scrofa*)							
Density in summer	25.32	12.79	15.32	32.80	7.54	14.54	16.49	17.83 ± 3.20
	Roe deer (*Capreolus capreolus*)							
Density in summer	32.57	29.15	27.08	28.75	23.06	24.41	25.68	27.24 ± 1.22

IMPACT OF WOLF PREDATION AND HUNTING HARVEST ON WILD UNGULATES

Wild ungulates always dominated wolf diet and made up 84.4-98.4% of the biomass consumed by wolves. Wild boar represented the primary prey species (41–71% of total biomass eaten by wolves). Roe deer was the secondary prey and its consumption varied between 24 and 53% during the study period. Livestock, hare and rodents were accessory food items (for the annual wolf diet see Gazzola et al., submitted).

On the basis of the field metabolic rate (FMR) an adult wolf (32 kg) needs 2.56 kg of meat per day. As pack size ranged from 3 to 6 wolves during the study period then wolf-pack food expenditure annually ranged from 2847 to 5694 kg of meat. On the basis of the relative importance of the staple prey items in wolf diet (wild boar and roe deer), we estimated the annual quotas of ungulate species consumed by wolf pack. From 2000-01 to 2006-07, wolves take off 217 ± 17.63 ungulates/100 km^2 (mean ± SE) annually (Table 2).

In terms of absolute numbers of animals killed, the level of predation on both species was quite similar (wild boar: 115 ± 9.56; roe deer: 102 ± 15.86 individuals/100km^2).

Wolf predation on wild boar, expressed as the percentage of animals consumed out of the total numbers of individuals counted in summer, constituted 7.7 ± 1.3%.

During the study period, the impact of wolf predation on the wild boar population ranged from 2.8 to 12.2%; while the wolf impact on roe deer was less variable, ranging from 1.9 to 7.4% (mean value: 3.9 ± 0.8%).

In the same period, hunters harvested 522-1250 wild boar/100km^2 annually (796 ± 127 head/100km^2), while the number of roe deer harvested annually was 252-347 individuals/100 km^2 (298 ± 12 head/100 km^2) (Table 3). Hunting harvest accounted for

51.8 ± 5.8% of the summer density of wild boar, a value much higher than that for roe deer (11.1 ± 0.9%).

Hunting pressure appeared to be a more important factor for wild boar mortality than wolf predation. Together they played a relevant role in the annual harvest on wild boar summer density (54–81%), while in roe deer combined wolf and hunting take-off accounted for a smaller part (12-20% of the summer density).

Table 2. Impact of wolf predation and hunting harvest on wild boar and roe deer in relation to population densities of prey.

Year	Food requirement per wolf estimated by FMR formula (Nagy, 1987)		Hunters	
	Annual predation (no. killed/100 km2)	Annual predation on summer density (%)	Annual harvest (no. killed/100 km2)	Annual harvest on summer density (%)
		Wild boar (*Sus scrofa*)		
2000-01	72	2.8	-	-
2001-02	119	9.3	717	56.0
2002-03	142	9.3	750	48.9
2003-04	120	3.7	1250	38.1
2004-05	92	12.2	522	69.2
2005-06	124	8.5	666	45.8
2006-07	139	8.4	871	52.8
Mean ± SE	115 ± 9.56	7.7 ± 1.3	796 ± 127	51.8 ± 5.8
		Roe deer (*Capreolus capreolus*)		
2000-01	61	1.9	254	7.8
2001-02	95	3.3	252	8.6
2002-03	80	3.0	324	12.0
2003-04	71	2.5	308	10.7
2004-05	172	7.4	288	12.5
2005-06	149	6.1	314	12.9
2006-07	82	3.2	347	13.5
Mean ± SE	102 ± 15.86	3.9 ± 0.8	298 ± 12	11.1 ± 0.9

The age structure of wild boar killed by wolves and by hunters was analysed (Fig. 2). Wolves and hunters showed a different use of wild boar age classes (χ2 wolf-hunter= 94.9 p<0.001). Juvenile wild boar were preferred by wolves (χ2 wolf-census= 24.3

$p<0.001$; Manly's selectivity index: α juvenile= 0.79), whereas hunters positively selected adult wild boar ($\chi 2$ hunter-census = 122.5 $p<0.001$; α adult= 0.752).

We also analysed the age structure of roe deer killed by wolves and by hunters (Fig. 3). Juvenile roe deer were preferred by wolves ($\chi 2$ wolf-census= 79.6 $p<0.001$; α juvenile= 0.829); while hunters didn't select any specific class ($\chi 2$ hunter-census= 2.53 ns.).

Figure 2. Comparison of the age structure of wild boar killed by wolves and by hunters.

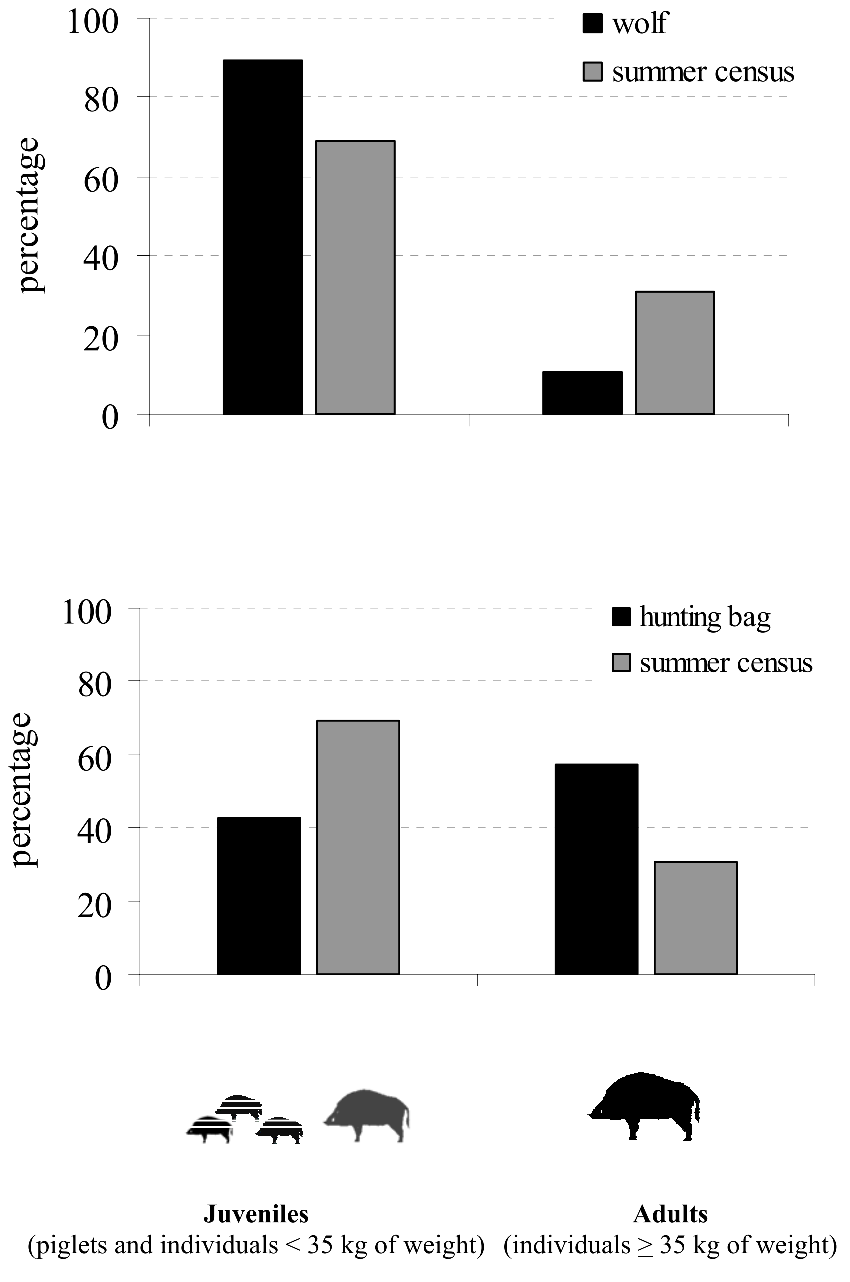
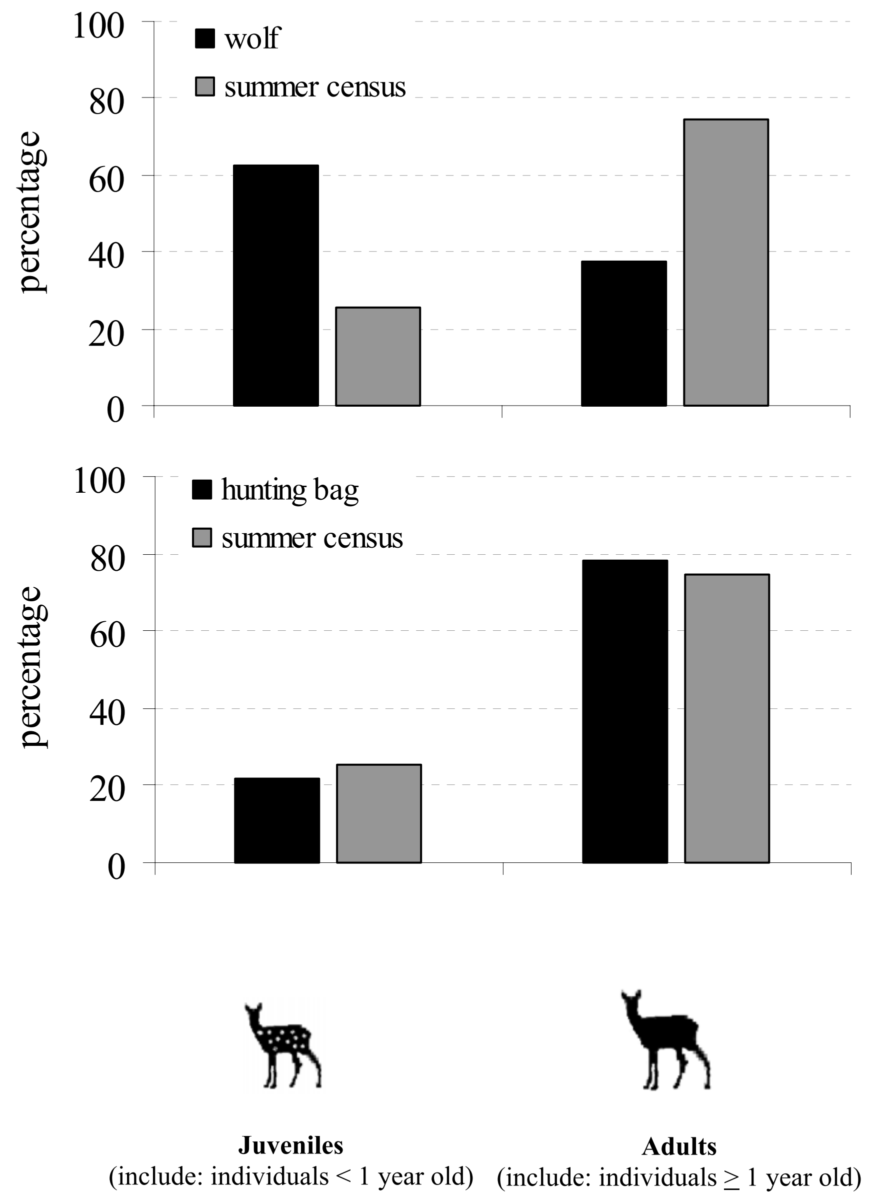


Figure 3. Comparison of age structure of roe deer killed by wolves and by hunters.

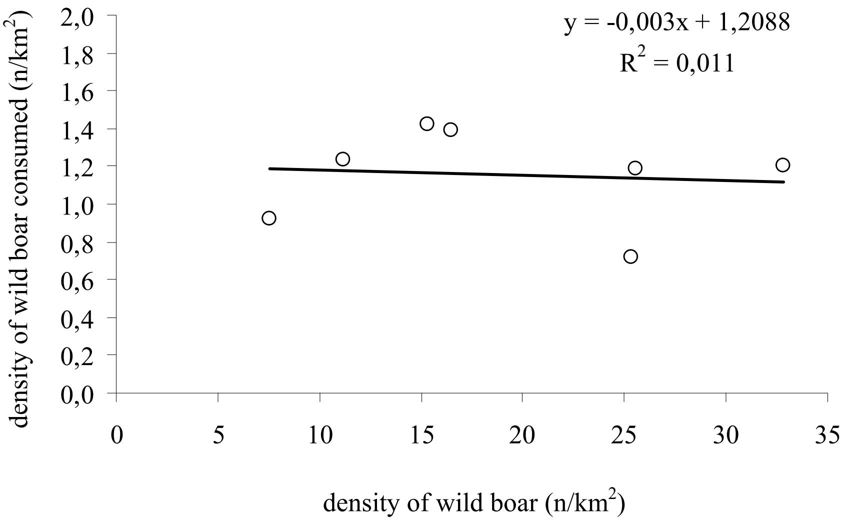


The relationship between prey taken by wolves and by hunters and prey availability was analysed.

Wild boar taken by wolves and wild boar availability didn't show a statistically significant linear relationship (R2= 0.043 F=0.219 P=0.660).

By contrast, the secondary species (roe deer) was taken by wolves in relation to its availability (R2= 0.714 F= 12.48 P=0.017) but appeared to be related to variation in the densities of the primary prey (wild boar) (R2= 0.816 F= 17.74 P=0.014) (Fig. 4). The hunting bag was highly related to wild boar availability (R2= 0.708 F=9.719 P=0.036), but not to roe deer availability (R2= 0.340 F=2.58 P=0.169) (Fig. 5).

Figure 4. Relation between prey availability and number of prey taken by wolves-wild boar and roe deer.



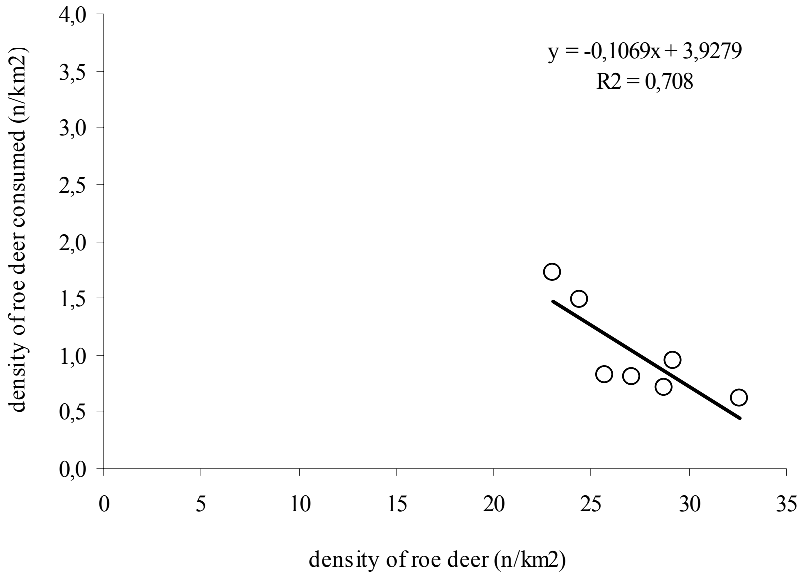
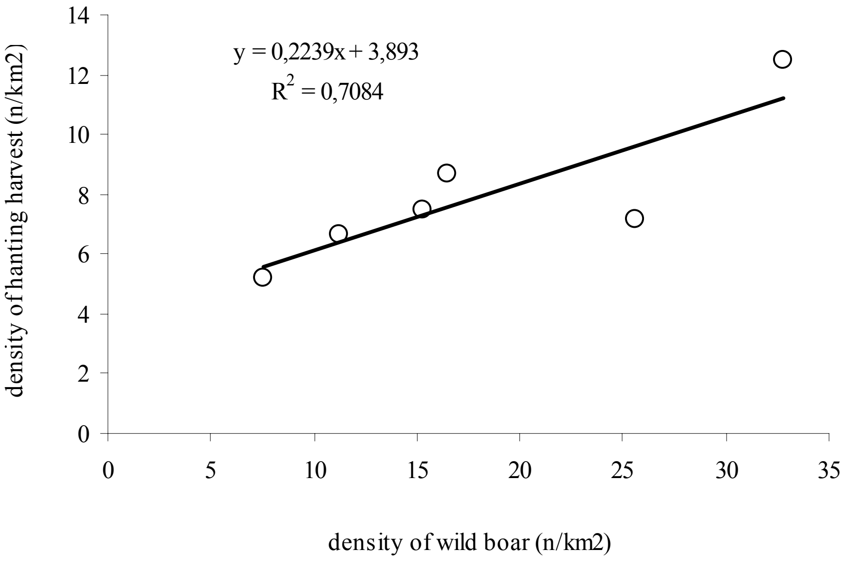
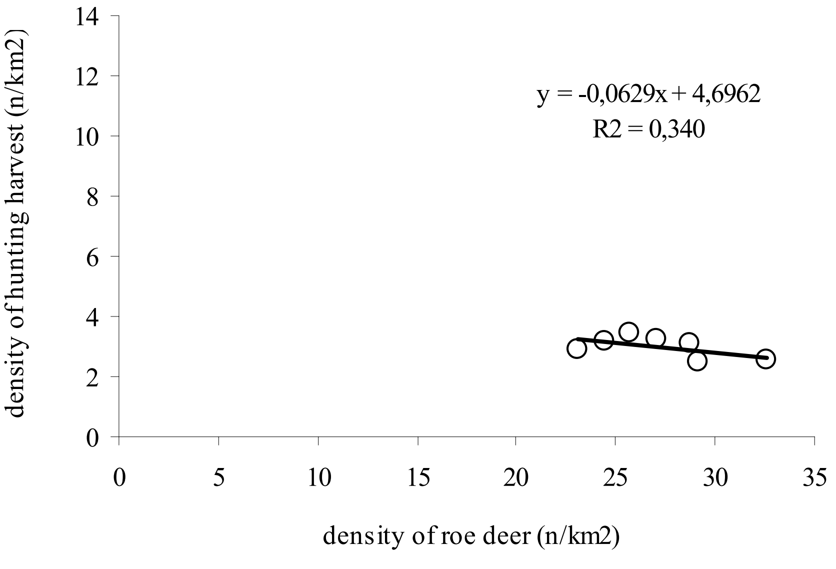


Figure 5. Relation between prey availability and number of prey taken by hunters-wild boar and roe deer.





We related total removal by wolves and hunters in the previous year to the status of the wild boar population in the following year. Annual predation by wolves and hunting harvest combined didn't influence wild boar density in the next year (R2= 0.052 F=0.22 P=0.663) (Fig. 6). Annual predation by wolves and hunting harvest combined didn't influence roe deer density in the next year (R2= 0.394 F= 2.601 P= 0.182).

However, the population density of wild boar was strongly influenced by forest productivity, represented by the quantity of seed crops present in the previous year (R2= 0.706 F=12.004 P=0.018) (Fig. 7). Conversely we didn't observe this relationship for roe deer (R2= 0.333 F= 2.498 P=0.175).

Figure 6. Relation between density of wolf and hunting harvest and wild boar status.

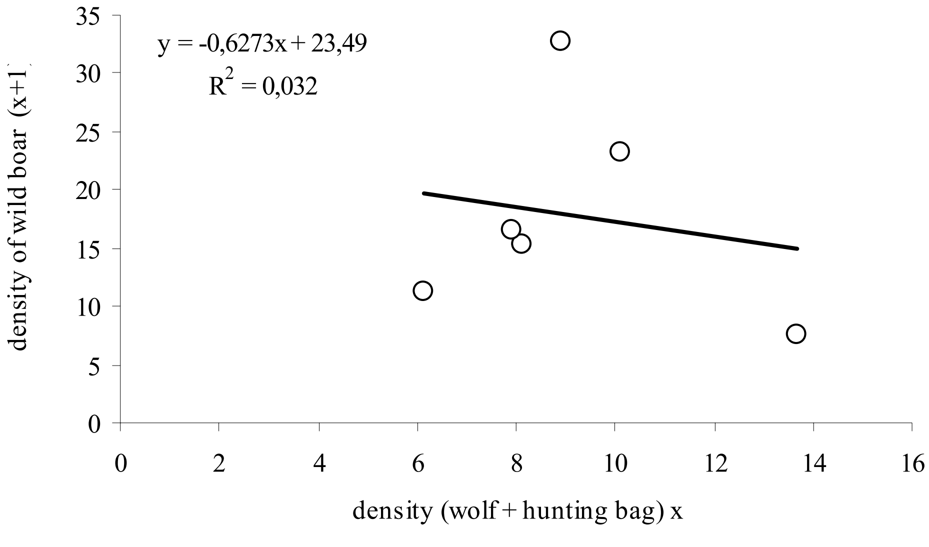
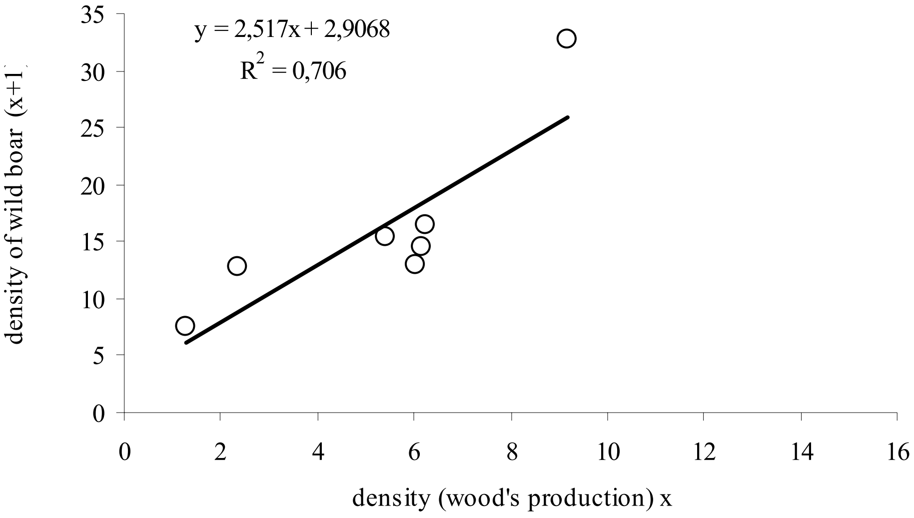


Figure 7. Relation between acorn crops and wild boar status



Considering the annual recruitment on the basis foetuses data and the population structure, we evaluated the magnitude of predation impact (hunters and wolves).

The wild boar hunting harvest amount of the 39% of annual recruitment (range $_{2000\text{-}2007}$= 28-51%), while wolves took off 6% (range $_{2000\text{-}2007}$= 3-9%).

The roe deer hunting harvest amount of the 23% of annual recruitment (range $_{2000\text{-}2007}$= 16-28%), while wolves took off 8% (range $_{2000\text{-}2007}$= 4-15%).

Considering the average number of female taken by hunters and wolves, we can estimated the potential losses caused by two predators.

Wolves took off an average of 8 wild boar adult female and 25 adult female of roe deer, that means a loss potential on recruitment of 39 and 48 juveniles in respectively species. Conversely, hunters taken an average of 225 wild boar adult female and 125 adult female of roe deer, that means a potential recruitment as 1125 and 239 juveniles in respectively species.

Discussion

After decades of research, quantifying the relative importance of top-down and bottom-up control in forest ecosystems is still an argument debated. Even in well studied predator-prey systems it is a difficult task to evaluate the role of top-down forces in shaping ungulate densities (Van Ballenberghe & Ballard 1993).

Some studies provide evidence of predation as an important limiting factor (e.g. Bergerud & Eliot 1986; Gasaway et al. 1992; Jędrzejewska & Jędrzejewski 1998; Rettie & Messier 2000; Kojola et al. 2004), while other authors could not demonstrate strong influences of predation on ungulate densities (Mech et al. 1998; Peterson et al. 1998; Melis et al. 2006; Mech & Nelson 2000; Nores et al. 2008). Some of the authors mentioned above also propose coexistence of bottom-up and top-down forces regulating of ungulate populations (Okarma 1995; Jedrzejewska & Jedrzejewski 2005; Melis et al. 2006; Melis et al. submitted).

Yet another group of studies even assumes a variety of environmental, predator- or prey-related factors to be involved in controlling predator- prey systems (Jedrzejewksi et al. 2002; Mech & Peterson 2003; Sand et al. 2006) and suggests that we actually can't explain half of what we see: Vucetich & Peterson (2004) analysed the relationships between wolves, moose and balsam fir (*Abies balsamea*) in Isle Royale National Park, Lake Superior, USA. More variation in moose population growth rate was explained by bottom-up than top-down processes. Still, the most parsimonious of their models only explained little more than half the variation in population growth rate.

Considering this variety of ambiguous results, it becomes clear that the observed patterns vary greatly among habitats and species involved. Many North American studies exploring bottom-up and top-down control have been carried out in largely undisturbed habitats, where human influence on predator-prey relationships is low (e.g. Mech 1966, Huggard 1993, Forbes & Theberge 1996, Peterson et al. 1998; Smith et al. 2000; Vucetich & Peterson 2004).

In Europe, however, it is more difficult to study the impact of predation, since most forest ecosystems have been drastically altered by humans. Agriculture and modern forestry practices have created favourable habitat for roe deer and wild boar, two species well adapted to modified habitats (Okarma 1995). Global warming reduces winter severity and further releases ungulate populations from an important mortality factor (Okarma 1995, Melis et al. 2006). Together with game management, this allows wild ungulates to reach densities close to carrying capacity in many areas.

Several studies identified hunting harvest as the major source of ungulate mortality and as a stronger limiting factor than predation, habitat quality, disease, winter severity, or accidents (Okarma 1995; Wright et al. 2006; Gazzola et al. 2007). According to Okarma (1995), human hunting drives the populations of ungulates over most of Europe.

Our data are in agreement with this findings, in our study area, hunting harvest removed a much higher percentage from ungulate populations than wolf predation. Moreover, besides a quantitative there is also a qualitative difference between hunting and wolf predation take off ungulate populations.

We observed that wolves primarily remove young, non reproductive animals from both roe deer and wild boar populations, as has been shown by several other studies (Salvador & Abad 1987; Jedrzejewski et al. 1992; Mattioli et al. 1995; Okarma 1995; Meriggi et al. 1996; Jedrzejewski et al. 2002; Mattioli et al. 2004; Mattioli et al. submitted). This result is consistent with the finding that young ungulates are more vulnerable to predation than adults because they are generally slower, less dangerous, and inexperienced with predators (Mech 1970).

On the contrary, hunters focus more on larger animals from reproductive age classes, especially in the case of wild boar. In the case of the roe deer, however age classes were culled by hunters in accord with their relative frequency in the population, following the hunting plane. Wild boar, however, are hunted during drive hunts with dogs and there are, if any, only overall hunting quotas, without assignment to individual hunters. This makes wild boar hunts less selective and it is up to individual hunters to decide how many animals and from which age classes to cull. The consequences of this difference on population dynamics is the stronger regulating impact of hunters on wild boar.

On the contrary, as wolves remained stable in low number they were unable to significantly increase their consumption with rising densities of their primary prey species. The difference in scale between wild boar and wolf densities is so high, that even when utilized more, wild boar populations remain unaffected by predation.

In the case of roe deer, hunting plans prescribe hunting bags on the basis of roe deer densities. However, the hunting period is quite short (one month) and hunters often did not reach the harvest quotas. Thus, no significant relationship between hunting bag and roe deer densities could be observed.

On the contrary for wolves, we found a strong negative relationship between consumption of roe deer and roe deer density. Guarda relazione inversa density-dipendence of roe deer.

It is known that predators' consumption of secondary prey may be shaped by fluctuations of their primary prey (Angelstam et al. 1984). In Bialowieza Primeval Forest, Poland, the use of other prey species in wolf diet was negatively correlated to red deer densities, their main prey (Jedrzejewska & Jedrzejewski 1998). Also in our study area we observed that wolves removed less of their secondary prey (roe deer) when their primary prey (wild boar) were more numerous.

Wolf predation tends to focus primarily on the youngest and most vulnerable members of prey (Mech 1966; Ballard et al. 1987; Huggard 1993; Mattioli et al. 1995), therefore the wolf´s strongest influence on the demography of ungulate populations should lie in the increase of juvenile mortality (Pimlott 1967; Mech 1970; Kunkel & Mech 1994; Hatter & Janz 1994). If wolf predation and hunting harvest are additive, the combination of hunters removing adult animals with high reproductive values and wolves preying heavily on young-of-the-year may negatively affect recruitment (Wright et al. 2006).

In our study area, however, removal by predators and humans did not exceed annual increase of ungulate populations. Furthermore, not even annual predation and hunting pressure together could explain the high fluctuations observed in wild boar numbers. This implies that in our study area the two factors combined may limit but do not regulate ungulate densities.

In fact, it was food availability, i.e. seed crop, which proved to be the most important factor influencing wild boar population dynamics, as was shown also by several other studies (Vos & Sassani 1977; Groot Bruinderink et al. 1994; Okarma 1995; Jedrzejewska et al. 1997; Jedrzejewska & Jedrzejewski 1998; Kruger 1998). The mechanism for this may lie in food competition causing stronger density-dependence in birth and death rates (Melis et al. 2006).

Roe deer populations did not fluctuate much but remained at high densities throughout the study period. Since hunting and predation were compensatory and only removed a small fraction of annual recruitment, roe deer have probably reached the maximum densities determined by food availability. Studies on roe deer life history traits may provide further evidence for this assumption.

In southern Europe the climate is mild and permanent snow cover in winter rarely occurs. Therefore, ungulate and especially wild boar populations are released from an important factor of mortality (Okarma et al. 1995; Volokh 2002, Melis et al. 2006).

Highly productive deciduous forests, consisting to a high percentage of oak and other seed producing tree species like beech and chestnut, are dominant in our study area.

Even in years following oak mast, the forest productivity remains quite high. This means that the peak wild boar densities following oak mast years do not experience such pronounced breakdowns as reported for example from Bialowieza Primeval Forest, where many wild boar died in the winters following mast years (Jedrzejewska & Jedrzejewski 1998).

The results of our study have shown that under these conditions predation and hunting harvest fail to keep ungulate numbers low.

This supports the observations of Jedrzejewska & Jedrzejewski (2005), who showed that the relative impact of predation gets smaller with rising temperatures. Also Melis et al. (submitted) observed that roe deer suffered less from predation in more productive environments.

They proposed both inverse density-dependence of predation impact and a better ability of ungulates to compensate for predation losses by higher reproduction as an explanation for the observed decreasing importance of top-down control in more productive habitats.

In our study area, mean litter size of wild boar was 4.78 (Cappai et al. 2008), a value similar to other European Countries (Náhlik & Sándor 2003). Furthermore, a wide temporal distribution of births was observed in our study area (Cappai et al. 2008).

In European regions where wolves have formerly been extinct, stake holders may raise concerns about the detrimental influence of wolf recolonisation on wild ungulate abundance. Our results show that these concerns are needless in highly productive, human dominated areas like the Apennines, where hunting harvest is not influenced by wolf presence. Nonetheless, more studies need to be carried out examining how wolf predation interacts with other factors of mortality. This knowledge may be especially important for less productive habitats, which do not support high ungulate densities, or when concerning rare and endangered prey species like the case o forest reindeer (*Rangifer tarandus fennicus*) in Finnish Carelia (Kojola et al. 2004).

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Chapter 4

ANTIPREDATOR BEHAVIOUR, SPACE USE AND HABITAT SELECTION IN FEMALE ROE DEERDURING THE FAWNING SEASON IN A WOLF AREA

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Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area

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Keywords
roe deer; *Capreolus capreolus*; home range; habitat selection; predation.

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Abstract

This study investigated the anti-predator strategies adopted by 19 radio-collared female roe deer during the fawning season by monitoring their spatial behaviour and habitat selection by means of radio-tracking. The study was carried out in a forest area of the Apennine Mountains (central Italy), where wolves are natural predators of roe deer and in summer fawns are more frequently predated than adult roe deer. The presence of fawns was monitored by means of direct observations. Roe deer fawns are known to adopt the hiding strategy during the lactation period, when they lie concealed for long periods waiting for their mothers' milk. As a consequence of this, the home-range sizes of mothers were significantly smaller than those of non-mothers during the summer lactation only. In contrast, no significant difference was found in spring, when fawns were absent, or autumn, when they were already weaned. In order to increase the success of the hiding strategy adopted by their fawns against wolf predation, mothers selected denser habitats (deciduous coppice forests) that provided denser undergrowth vegetation and limited visibility. In doing so, mothers traded open areas for forests throughout the fawning season. Indeed, mothers made significant habitat selection throughout the monitored period, and this was marked after the birth of fawns. In contrast, non-mothers generally used habitat types according to their availability. During lactation, the correlation between habitat use by mothers and habitat visibility (assessed using the form of a standard-sized roe deer) was inversely significant. These results taken together highlight the importance of anti-predator strategies adopted by roe deer mothers during the critical phase for fawn survival.

Introduction

During pregnancy, parturition and lactation mammalian females exhibit complex behavioural patterns that are all directed towards the survival of their young (Svare, 1981). According to life-history theory, animals are likely to show levels of parental investment such that the energy expenditure for current offspring is balanced against the effects on the parents' chances of survival and future reproduction (Roff, 1992; Stearns, 1992). In particular, substantial changes in the social behaviour of mammalian females may occur during the final stage of pregnancy and following parturition (Svare, 1981). The presence of offspring may influence the social organization of lactating females (Schwede, Hendrichs & McShea, 1993; Bertrand *et al.*, 1996; Tufto, Andersen & Linnell, 1996), and evoke different activity budget and foraging behaviours (Kohlmann, Muller & Alkon, 1996; Langbein, Scheibe & Eichhorn, 1998; Ruckstuhl & Festa-Bianchet, 1998) as well as space-use modifications (Berger, 1991; Green, 1992; Tufto *et al.*, 1996; Boschi & Nievergelt, 2003; Ciuti *et al.*, 2006; Grignolio *et al.*, 2007*b*). As regards females' space use, researchers reported that during birth and lactation they are likely to enlarge their home range (*Capra pyrenaica* Escos & Alados, 1992; *Capreolus capreolus* Tufto *et al.*, 1996; *Rupicapra rupicapra* Boschi & Nievergelt, 2003) or to reduce it (*Odocoileus virginianus* Schwede *et al.*, 1993; *Dama dama* Ciuti *et al.*, 2006; *Capra ibex* Grignolio *et al.*, 2007*b*).

Among other changes, the presence of young may evoke a modification in mothers' anti-predator strategies (Clutton-Brock, Guinness & Albon, 1982; San José & Braza, 1992; Villaret, Bon & Rivet, 1997; Barten, Bowyer & Jenkins, 2001; Ciuti *et al.*, 2006; Grignolio *et al.*, 2007*a*) to such an extent that it may even induce their isolation from other individuals of the same species (Clutton-Brock & Guinness, 1975; Schwede *et al.*, 1993). The isolation of ungulate mothers and their young is considered essential for the proper formation of the mother–infant bond and serves as additional protection against predators (Lent, 1974; Ozoga, Verme & Bienz, 1982). In response to this need for isolation, does with fawns may reduce their home-range size (Ozoga *et al.*, 1982; Scanlon & Vaughan, 1985; Nixon *et al.*, 1992). Although the degree and duration of isolation before parturition vary among ungulates, it appears to be a general rule among most cervids (Dasmann & Taber, 1956; Altmann, 1963; Clutton-Brock & Guinness, 1975).

Juvenile recruitment is the major factor shaping wild herbivores' population dynamics (Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard *et al.*, 2000) and, where predators are present, it is the most common cause of neonatal mortality in large ungulates (Linnell, Aanes & Andersen, 1995). In response to the high risk of predation to neonates and the associated substantial loss in lifetime productivity (Bergerud, 1971; Garrot, Bartmann & White, 1985; Smith, 1986), ungulates have evolved an array of characteristic maternal-neonate strategies represented by the 'hiding-to-following' spectrum (Rudge, 1970; Geist, 1971; Lent, 1974; Leuthold, 1977). The species of this group are basically classified as either 'hiders' or 'followers', depending on whether the newborns lie concealed for their first few days or actively follow their mothers (Lent, 1974; Ralls, Kranz & Lundrigan, 1986). While 'following' has been viewed as a strategy for avoiding predators in open habitats, 'hiding' is thought to reduce the predation risk in closed habitats (Lent, 1974; Estes & Estes, 1979). As regards this aspect, roe deer is considered to be one of the most markedly hiding species, given that fawns of this cervid lie concealed for prolonged periods during lactation, while waiting for their mothers' milk (Linnell, Wahlström & Gaillard, 1998).

However, the anti-predator strategies adopted by roe deer against wolf *Canis lupus* predation are poorly known, particularly when compared with those adopted against lynx *Lynx lynx* and fox *Vulpes vulpes* predation (e.g. Linnell *et al.*, 1998; Jarnemo, 2004; Panzacchi, 2007). In our study area, the Tuscan slope of the Apennines in the Arezzo province, the role of roe deer in the wolf diet was substantial (Mattioli *et al.*, 2004), with roe deer the second most selected item after wild boar *Sus scrofa*. The use of roe deer increased especially in summer, when fawns were highly selected by wolves (Mattioli *et al.*, 2004). Mattioli *et al.* (2004) also showed that the use of roe deer by wolves was negatively correlated with the percentage of forest cover in five study areas that are close to ours. This result showed the crucial role of habitat characteristics in the ultimate success of the anti-predator strategies adopted by this prey species. Accordingly, we assume that where wolves are present roe deer anti-predator strategies drive patterns of specific habitat selection.

As regards this issue, we made the following two predictions:

Prediction 1 – as a consequence of the hiding strategy adopted by fawns during their first weeks of life, we expected the home-range sizes of mothers to be smaller than those of females without fawns only during early and late lactation (i.e. summer), but not during gestation (spring), nor after lactation (autumn), when fawns are weaned.

Prediction 2 – roe deer mothers seldom move far away (50–150 m) from their young during the first weeks after parturition, when fawns adopt the hiding anti-predator strategy (Linnell *et al.*, 1998). As a consequence of this and the anti-predator strategies adopted by mothers to reduce wolf predation upon their fawns, mothers were expected to select denser habitats where the hiding strategy would be facilitated by the limited visibility.

Material and methods

Study area

The study was carried out in the Catenaia, which is a 4579 ha protected area (its borders are better defined below) located on the Tuscan slope of the Apennines (Arezzo province, Italy, 43°48′N, 11°49′E). The altitude in the area ranges from 330 to 1514 m a.s.l. The climate is temperate and characterized by a high humidity rate, with hot and dry summers, and cold and rainy winters. The study area is forested with 15 habitat types (Fig. 1).

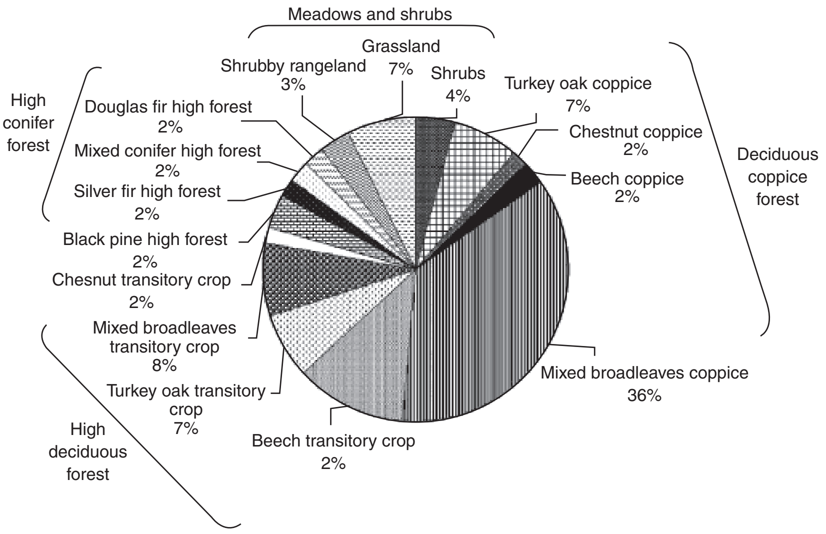

Figure 1 Habitat type composition of the study area (Catenaia protected area, central Italy).

At the time of the study, the only natural predators in the area were wolf and red fox. Wolves were present in the Arezzo Province at high densities, that is three wolves per 100 km^2 (Apollonio *et al.*, 2004), and their mean pack size was 4.0 ± 0.6 (Capitani *et al.*, 2004). Red foxes were present in the study site, even though their presence was recorded to be much lower than that in the low land, where wolves were absent (A. Gazzola, unpubl. data). The only other ungulate in the study area was the wild boar, while free-ranging livestock were totally absent.

Data collection

We captured 19 adult female roe deer using vertical drop nets and fitted the animals with VHF Televilt radiocollars (Lindesberg, Sweden). We subsequently located females by means of discontinuous radio-tracking using Televilt RX-8910 HE receivers and four-element hand-held Yagi antennas. From March to November 2004, we obtained ≥ 12 monthly locations per animal by triangulation of bearings from three reference points. We distributed the bearings uniformly over the day and separated consecutive fixes by an interval of ≥ 12 h. The accuracy of fixes was determined in the field using test transmitters placed in various habitats (Harris *et al.*, 1990), which enabled us to use an error polygon of 1 ha. Despite the large habitat patch size (mean - SE: 216.3 ± 92.7 ha) in our study site, which was larger than the average fix error polygon, an effort was made to obtain accurate fixes so as to determine habitat use in the area; animals were thus located from a distance of 100–300 m. We assessed the presence of fawns with monitored females by means of predictive radio-tracking (MacDonald, Ball & Hough, 1980), also called homing-in (White & Garrott, 1990): from April to November 2004, we performed ≥ 4 monthly observations per each monitored female. Accordingly, the monitored sample was split into females with fawns ($n = 13$) and females without fawns ($n = 6$). Fawns were born during late May. Mothers were always seen in the same habitat patch as their fawns and, more precisely, within 100 m from them. Each lactating female gave birth to one fawn (while only three females gave birth to two fawns each), which survived throughout the study. Radio-collars will be removed at the end of the research.

Data analyses

We assessed seasonal home-range sizes using Ranges VI software (Kenward, South & Walls, 2003) by means of the Kernel method (Worton, 1989). Following Borger *et al.* (2006), we defined home-range sizes using 90 and 50% of the available locations. Seasons were defined as follows: spring (March, April, May), summer (June, July, August) and autumn (September, October, November). We tested for differences between the home-range sizes of females with and without fawns using the *t*-test for independent samples. These analyses were performed using the SPSS 13.0 program. Home-range data were natural log-transformed and subsequently checked for normality using the Kolmogorov–Smirnov test. We assessed the habitat selection using compositional analysis in order to solve the unit-sum constraint typical of compositional data (Aebischer & Robertson, 1992; Aebischer, Robertson & Kenward, 1993). We compared used and available habitats at two levels. We first analysed the home-range selection within the study area by comparing the proportion of habitats in the Kernel 90% home range with the proportion of habitats in the study area (therefore on a broad scale). The study site was defined as the area including all the locations collected during this research and calculated using the Minimum Convex Polygon Method 100% (Kenward *et al.*, 2003). Secondly, we examined the habitat use within the home range by comparing the proportion of fixes in each habitat with the proportion of the habitat in the Kernel 90% contour line (therefore on a fine scale). All data necessary for compositional analysis were obtained with the use of Arc View GIS 3.2. Assuming that habitat use differed from random use, we ranked the habitats according to their relative use at both levels and tested for significant differences among them. Compositional analysis and statistics were computed with an Excel macro (Smith, 2003), which also carried out the randomization procedure recommended by Aebischer *et al.* (1993). This procedure was made necessary because of the potential non-normality of our data (Aebischer *et al.*, 1993). For each compositional analysis of lactating and non-lactating females, habitat use, Wilks's λ and randomized P values were reported as P values of each significant difference between ranks (univariate *t*-test).

Given the high number of habitat types (15), we reduced the number of variables for compositional analysis by pooling the habitat types that had been used by monitored females at least once into the following categories: deciduous coppice forests (DCF: 2295.7 ha, 50.1%), high deciduous forests (HDF: 938.1 ha, 20.5%), high conifer forests (HCF: 549.5 ha, 12.0%), meadows and shrubs (MS: 650.3 ha, 14.2%). Habitat types were associated according to wood structure and visibility information, which were obtained as explained further below. As suggested by Aebischer *et al.* (1993), we reduced the number of habitat types at the second level of compositional analysis by pooling those that were characterized by a similar vegetational structure, that is high forests (HF = HCF + HDF). On the basis of this classification, all the habitats in our database were recorded as being used by monitored females. Misclassified resource selection was thus avoided, as strongly recommended by Bingham, Brennan & Ballard (2007). After the analysis of the habitat selection by females with and without fawns, we finally tested for differences in the habitat use of the two groups by adding this parameter as an independent variable in Wilk's log-ratio matrices and by analysing these matrices by a MANOVA test (Aebischer *et al.*, 1993).

Finally, we sampled the visibility of the 15 habitat types of the study site at the time of roe deer lactation. Eighty-five sampling points were randomly selected within the study area with ArcView 3.2. We determined one sampling point every 50 ha approximately, and the number of sampling points within each habitat type varied according to its relative presence in the study area. For each sampling point, accurately located by means of GPS, we assessed the visibility of a roe deer shape. Specifically, we placed the shape of a standard-sized roe deer in the sampling point and determined its visibility in terms of the percentage of squares observed out of the total squares constituting the shape. The visibility was assessed by observations from the four cardinal points, taken at the height of the wolf's eyes (80 cm), and from the following distances: 10, 30 and 50 m. Therefore, for each habitat type we obtained a mean value of visibility from three sampling distances. Correlations between the visibility in each habitat type and its relative use by monitored females (i.e. the percentage of fixes included in each habitat type for each roe deer female) were tested using the Pearson correlation coefficient after normalization of data by means of natural log-transformation. In all tests significance was set at $P \leq 0.05$.

Results

Space use

Seasonal home-range sizes (Fig. 2) of calving ($n = 13$) and non-calving ($n = 6$) females did not differ statistically in spring (calving females: Kernel 50%: mean ± SE, 59.4 ± 25.9 ha, Kernel 90%: 171.2 ± 85.1 ha; non-calving females: Kernel 50%: 35.1 ± 8.2 ha, Kernel 90%: 103.1 ± 28.5 ha), using both Kernel 90% (t-test for independent samples: d.f. = 17, $t = 0.112$, $P = 0.912$) and Kernel 50% (d.f. = 17, $t = -0.103$, $P = 0.919$). In contrast, summer home-range sizes of calving females (Kernel 50%: 14.6 ± 2.0 ha; Kernel 90%: 36.7 ± 5.4 ha) were significantly smaller than those of non-calving females (Kernel 50%: 25.2 ± 4.1 ha; Kernel 90%: 68.9 ± 13.2 ha) (d.f. = 17, $t = -2.342$ and $P = 0.032$, using Kernel 90%; d.f. = 17, $t = -2.400$ and $P = 0.028$, using Kernel 50%). Finally, autumn home-range sizes of calving (Kernel 50%: 20.8 ± 3.2 ha; Kernel 90%: 53.4 ± 9.2 ha) and non-calving females (Kernel 50%: 22.5 ± 5.6 ha; Kernel 90%: 60.1 ± 18.9 ha) did not differ statistically (d.f. = 17, $t = 0.146$ and $P = 0.886$, using Kernel 90%; d.f. = 17, $t = 0.131$ and $P = 0.899$, using Kernel 50%).

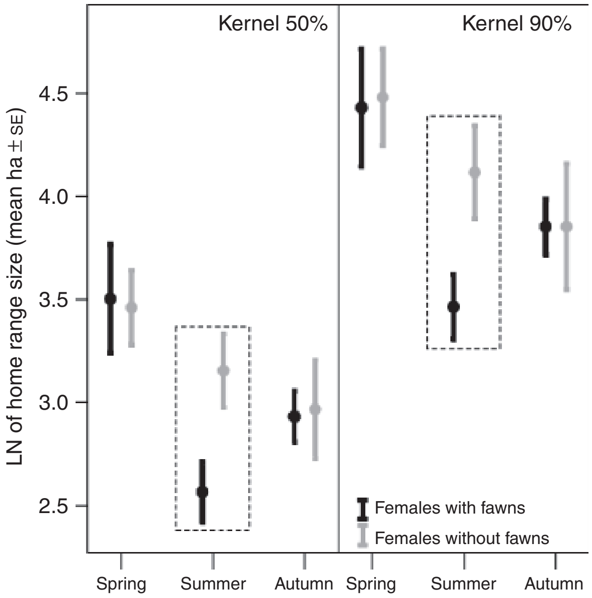

Figure 2 Seasonal home-range sizes recorded for female roe deer with and without fawns in the Catenaia protected area (central Italy) assessed using both Kernel 50% and 90% methods. Broken boxes show significant differences ($P<0.05$) between the two female categories (t-test for independent samples; see text for details).

Compositional analysis of habitat

The compositional analysis of the home ranges within the study area (first level) revealed a significant departure from random use during spring, summer and autumn, only for calving females (Table 1). Indeed, females with and without fawns selected habitat types to different degrees in all seasons and showed contrasting choices for deciduous coppice forests and high deciduous forests (Table 1). These differences in habitat use between females with and without fawns were confirmed by MANOVA (first level: $\lambda = 0.818$, $F = 3.253$, $P = 0.030$).

We report the results of univariate t-tests at the first level of analysis for mothers and non-mothers in Table 2. During late gestation (spring) as well as after weaning (autumn), deciduous coppice forests were selected by mothers over the remaining habitats, and this was markedly significant when the selection of deciduous coppice forests over meadows and shrubs was assessed (Table 2). During lactation (summer) such differences were marked in mothers that significantly selected denser forests (deciduous coppice forests) over both high conifer forests and open areas (meadows and shrubs) (Table 2). As reported in Table 2, mothers significantly avoided open areas (meadows and shrubs), while non-mothers generally selected high deciduous forests over both deciduous coppice forests and high conifer forests (Table 2).

At the second level of compositional analysis, when the proportion of fixes in each habitat was compared with the proportion of the habitat in the Kernel 90% contour line, both calving and non-calving females showed a significant departure from random use in spring (Table 1). The analysis also ranked the habitats used by calving and non-calving females in the same order, even though with different magnitudes, given that only mothers selected both kinds of forests (deciduous coppice and high forests) over open areas (meadows and shrubs) (Tables 1 and 3). On the contrary, after the birth of fawns, that is during summer and autumn, only females with fawns showed a significant departure from random use (Table 1), and females with and without fawns selected habitat types to a different magnitude in both seasons. Specifically (univariate t-tests of compositional analysis; Table 3), females with fawns used meadows significantly less than forests, while this was not true for females without fawns. Differences in habitat use between calving and non-calving females were confirmed by

Table 1 Habitat selection by lactating and non-lactating female roe deer as determined by compositional analysis in the Catenaia protected area, central Italy

		Females with fawns ($n=13$)			Females without fawns ($n=6$)		
Level of analysis	Season	Wilk's λ	P_r	Ranked habitat types	Wilk's λ	P_r	Ranked habitat types
First	Spring	0.4001	**0.0190**	DCF > HDF > HCF > MS	0.3210	0.1950	HDF > DCF > HCF > MS
	Summer	0.1792	**0.0080**	DCF > HDF > HCF > MS	0.1162	0.0970	HDF > DCF > MS > HCF
	Autumn	0.2461	**0.0030**	DCF > HDF > HCF ⋙ MS	0.1996	0.1570	HDF ⋙ DCF > HCF > MS
Second	Spring	0.2901	**0.0090**	DCF > HF ⋙ MS	0.0474	**0.0350**	DCF > HF > MS
	Summer	0.1741	**0.0040**	DCF > HF ⋙ MS	0.9675	0.8710	HF > DCF > MS
	Autumn	0.1935	**0.0030**	HF > DCF ⋙ MS	0.7295	0.5200	DCF > HF > MS

On each line habitat classes to the left of the symbol > are selected over those to the right (⋙ when the difference between two consecutive habitat classes is $P<0.05$). Significant departures from random use are indicated by λ and randomized bold P values (1000 interactions).

In the second level of analysis high forests (HF) were obtained by pooling high deciduous forests (HDF) with high conifer forests (HCF).

DCF, deciduous coppice forests; HCF, high conifer forests; MS, meadows and shrubs.

MANOVA and proved to be pronounced at this second level of analysis (MANOVA second level $\lambda=0.570$, $F=16.630$, $P<0.001$).

Analysis of habitat visibility and relative use during summer

At least 25% of the roe deer shape was visible in all habitat types from a distance of 10 m, while almost opposite results were recorded when the distance was 50 m. From 50 m the roe deer shape was visible only in the last two habitat types (Fig. 3). We recorded a higher variability when we measured the visibility of the shape from 30 m (Fig. 3). Accordingly, during summer, females with fawns used habitat types where visibility was lower, and this inverse correlation was significant when visibility was measured from 30 and 50 m (Pearson's correlation coefficient; 10 m: $R_p=-0.105$, $P=0.167$; 30 m: $R_p=-0.263$, $P<0.001$; 50 m: $R_p=-0.163$, $P=0.030$). On the contrary, the correlation between the specific use of habitat types by females without fawns and the habitat's visibility was never significant (Pearson's correlation coefficient; 10 m: $R_p=-0.002$, $P=0.981$; 30 m: $R_p=-0.139$, $P=0.177$; 50 m: $R_p=-0.030$, $P=0.774$).

Discussion

Seasonal home-range size analysis showed a marked difference in the spatial behaviours of calving and non-calving

Table 2 Results of univariate *t*-tests of compositional analysis of habitat (first level) for roe deer females with fawns (left panel) and without fawns (right panel) in the Catenaia protected area

	Females with fawns			Females without fawns		
First level of analysis	High deciduous forest	High conifer forest	Meadows and shrubs	High deciduous forest	High conifer forest	Meadows and shrubs
Spring						
Deciduous coppice forest	+	+	$+^{(**)}$	−	+	+
High deciduous forest		+	$+^{(**)}$		+	+
High conifer forest			+			+
Summer						
Deciduous coppice forest	+	$+^{(*)}$	$+^{(**)}$	−	+	+
High deciduous forest		+	+		$+^{(*)}$	+
High conifer forest			+			-
Autumn						
Deciduous coppice forest	+	+	$+^{(**)}$	$-^{(*)}$	+	+
High deciduous forest		+	+		$+^{(*)}$	$+^{(*)}$
High conifer forest			$+^{(**)}$			+

Asterisks inside parentheses indicate significant comparisons.

$^{(*)}0.05 \leq P<0.01$.

$^{(**)}0.01 \leq P<0.001$.

Randomized P values (1000 interactions).

Table 3 Results of univariate *t*-tests of compositional analysis of habitat (second level) for roe deer females with fawns (left panel) and without fawns (right panel) in the Catenaia protected area

	Females with fawns		Females without fawns	
Second level of analysis	High forest	Meadows and shrubs	High forest	Meadows and shrubs
Spring				
Deciduous coppice forest	+	$+^{(**)}$	+	$+^{(*)}$
High forest		$+^{(**)}$		+
Summer				
Deciduous coppice forest	+	$+^{(***)}$	–	+
High forest		$+^{(**)}$		+
Autumn				
Deciduous coppice forest	–	$+^{(**)}$	+	+
High forest		$+^{(**)}$		+

Asterisks inside parenthesis indicate significant comparisons.

$^{(*)}0.05 \leq P<0.01$.

$^{(**)}0.01 \leq P<0.001$.

$^{(***)}P \leq 0.001$.

Randomized *P* values (1000 interactions).

female roe deer only when fawns were present. In spring, mothers to be and non-mothers did not use significantly different home-range sizes. In contrast, from June to August, the presence of fawns significantly reduced the home-range sizes of lactating females. This was presumably due to the fact that mothers seldom move far away from their young in the first weeks following parturition, when fawns adopt the hiding anti-predator strategy (Linnell *et al.*, 1998). Reductions in the home-range size for about 6 weeks or even longer following parturition have been documented in female white-tailed deer (Hawkins & Klimstra, 1970; Ozoga *et al.*, 1982; Gavin *et al.*, 1984; McCullough, Hirth & New-House, 1989; Schwede *et al.*, 1993; Bertrand *et al.*, 1996), Alpine ibex (Grignolio *et al.*, 2007*b*) and by several other studies on cervids (Nelson & Mech, 1981; Vincent *et al.*, 1983; Maublanc, 1986; Jeppesen, 1990; Chapman *et al.*, 1993; San José & Lovari, 1998; Ciuti *et al.*, 2006). However, our data did not support the findings of Tufto *et al.* (1996), who asserted that roe deer females without fawns had smaller home ranges, possibly because they only needed to sustain their own energetic requirements.

Indeed, in our study site, where wolves have a high predation impact upon fawns (Mattioli *et al.*, 2004), the hiding behaviour adopted by offspring seemed to be the main factor leading to the limited mobility and the subsequently smaller home-range size of mothers, and this confirmed our first prediction. Panzacchi (2007) showed that the predation risk for fawns increased with an increase in the distance between fawns and mothers and this might be argued to account for the reduction of mothers' home range. Like in other ungulate species, roe deer mothers have to balance two contrasting spatial behaviours: they must not be too close to the fawns so as not to give cues of their bed site (Byers & Byers, 1983; Fitzgibbon, 1993; Jarnemo, 2004) and at the same time they also must not be too far away so as to be able to save them from possible attacks (Lent, 1974; Litvaitis & Bartush, 1980; Fitzgibbon, 1993; Schwede, Hendrichs & Wemmer, 1994), and this is more likely to

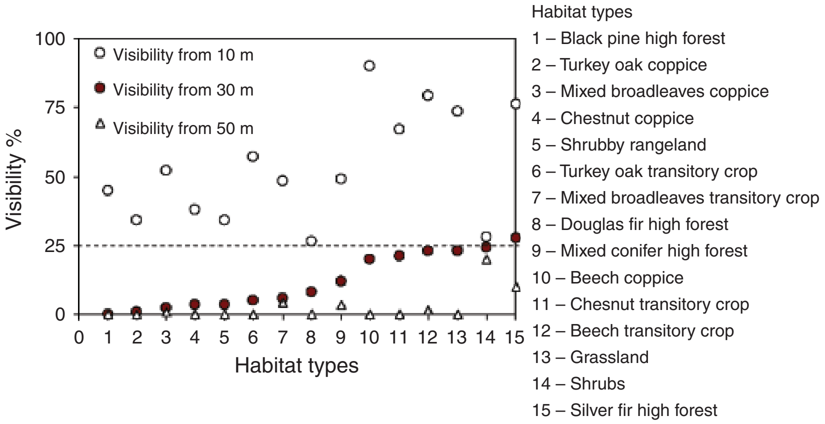

Figure 3 Visibility of different habitat types assessed by means of observations of a roe deer shape from different distances (10, 30 and 50 m) in the Catenaia protected area, central Italy.

occur where red fox is present. As a matter of fact, roe deer females have been observed while successfully saving fawns in their bed sites from attacks by foxes (Jarnemo, 2004). In our study area, the importance of roe deer in the wolf diet was substantial (Mattioli *et al.*, 2004), with roe deer the second most selected item after wild boar. However, both red fox and wild boar were also present and may have affected the behaviour of roe deer mothers. As a consequence, it is difficult to separate the anti-predator responses of roe deer against wolf, red fox and wild boar, respectively, at least as long as data on fox and wild boar predation on roe deer fawns will not be properly collected and analysed in detail. Therefore, our results can only be interpreted in relation to the general anti-predator behaviour of roe deer females, despite referring to an area where the wolf is likely to be the main predator (Mattioli *et al.*, 2004).

The presence of fawns seems to modify mothers' spatial behaviour in other ways too. For instance, mothers also seem to have to trade off between the presence of fawns and environmental conditions. In this respect, Jarnemo *et al.* (2004) showed that roe deer females' reproductive success decreased along with the increase of the amount of open habitats in their home range, but this occurred only in those years when fox abundance was recorded. In contrast, when shortage of foxes was recorded, roe deer females in open habitats had a higher reproductive success than forest-dwelling individuals, and this suggested a habitat trade-off between high-quality forage and neo-natal predation risk (Jarnemo *et al.*, 2004).

In our study site, when fawns were already weaned and did not limit their mothers' movements (autumn), the latter did not show significantly different home-range sizes from those of females without fawns. In conclusion, the main anti-predator strategy adopted by this species seems to be shown by fawns, who lie concealed for long periods during early and late lactation, thus strongly limiting their mothers' movement.

How can mothers increase the success of the hiding strategy adopted by their fawns against predation? It might be argued that roe deer mothers select denser habitats where their fawns can conceal themselves completely while the former move away for feeding activities. The high behavioural plasticity in the habitat selection of ungulate mothers during the fawning period was already shown for fallow deer (e.g. San José & Braza, 1992; Ciuti *et al.*, 2006). In fact, the hiding strategy is usually displayed by species that calve on scrublands or woodlands where the vegetation provides good concealment (Altmann, 1963; Hawkins & Klimstra, 1970; Clutton-Brock & Guinness, 1975; Chapman & Chapman, 1997). As shown by San José & Braza (1992) in a study conducted in Doñana (Spain), and by Ciuti *et al.* (2006) in a study conducted in San Rossore (Italy), fallow deer mothers adapted a hiding strategy in open habitats and selected marshes as the habitat that offers the greatest cover, thus confirming the high plasticity of ungulate mothers' behavioural choices.

Accordingly, our results on roe deer behaviour should be evaluated in relation to the following context. In the forest environment of the Catenaia protected area, mothers showed a behavioural plasticity in that they selected denser habitats, while non-mothers did not, and this difference can be best noticed on a fine scale. Indeed, mothers and non-mothers differed in their habitat selection and habitat use, and differences became evident by analysing the data both on a broad (first level of compositional analysis) and on a fine scale (second level of compositional analysis and correlations between habitat visibility and female use). This result proved that mothers' anti-predator strategy aimed to increase their reproductive success. However, mothers' behavioural modifications were not easily detectable in a homogeneous forest environment. Bed-site selection by 19 radio-collared roe deer fawns was studied in south-eastern Norway (Linnell *et al.*, 1999). In this study, Linnell *et al.* (1999) showed that within the forest, fawns selected bed sites that offered greater concealment, higher vegetation and more canopy cover than random sites. In a Scandinavian area characterized by fox predation on roe deer fawn, Panzacchi (2007) showed that predation risk partially increased with the increase of visibility, thus confirming the similar results obtained by Linnell, Nilsen & Andersen (2004). Roe deer fawns that were killed by red foxes on an island off central Norway used open grassland significantly more than surviving fawns, which used woodland to a greater extent (Aanes & Andersen, 1996), and this supports the hypothesis that hiding is a strategy to avoid predation in dense habitats. Hiding in a bed site with low visibility seems to be a very efficient anti-predator strategy when adopted by roe deer fawns; hence, their mothers' ability to select low-visibility habitat affects predation risk to a great extent (Panzacchi, 2007). This behavioural response was recorded in an area where fox predation was significant, but no data are as yet available on roe deer behavioural adaptations in a wolf area.

The analysis of our data on a broad scale (first level of compositional analysis) showed that only mothers actively selected habitats throughout the monitored period. In particular, while non-mothers selected resources according to their availability, mothers preferred deciduous coppice forests, that is the environment providing a denser vegetation undergrowth, particularly when compared with high forests, meadows and shrubs (Fig. 3). In detail, as evaluated through the univariate comparisons among the resources selected by mothers at the first level of analysis, mothers significantly traded both open areas (meadows and shrubs) and high conifer forests for denser deciduous coppice forests only in summer. The impact of terrestrial predators on roe deer has already been recognized to be thwarted by forest habitats (Aanes & Andersen, 1996; Jarnemo *et al.*, 2004). For instance, a study on the foraging of Eurasian lynxes carried out by means of telemetry and snow tracking in central Norway (Sunde *et al.*, 2000) showed the importance of agricultural land as a foraging habitat for this predator.

In our study case, the second level of compositional analysis did not reveal any difference in the habitat selection of mothers to be and non-mothers in spring, that is when fawns were still absent. In contrast, in summer, that is when fawns were present, mothers began to show a habitat selection, while non-mothers did not. Again, open areas were significantly avoided by mothers also on this fine-scale analysis. Anti-predator strategies adopted by mothers during lactation were pointed out by the fine-scale analysis of habitat visibility. During early and late lactation, the correlation between habitat visibility and relative use by mothers was significantly inverse, while this was not true for non-mothers. These results are consistent with the study on wolf predation upon fawns carried out by Mattioli *et al.* (2004) in the same area. The presence of roe deer fawns in wolf scats increased where the forest cover of the sampling area decreased, thus showing that habitat characteristics may strongly affect the survival of roe deer fawns (Mattioli *et al.*, 2004).

In ungulates, the herd size commonly increases in open habitats: groups are usually smaller in forested habitats and larger in grasslands and other open landscapes (Estes, 1974; Jarman, 1974). Indeed, in closed habitats herbivores are less likely to be detected by predators if they are secretive, and live in small groups or alone (Estes, 1974; Jarman, 1974). This probably explains why female roe deer with fawns selected more closed habitats during lactation. Therefore, the use of denser habitats being characterized by lower visibility may entail two crucial benefits for the reproductive success of this species: firstly, mothers are alone and consequently less detectable by predators; secondly, fawns' hiding strategy is much more successful. The rationale behind hiding is that neonates have such a short detection radius that predators find it too costly to search neonates systematically (Byers & Byers, 1983).

In conclusion, roe deer's anti-predator strategies in our forest environment, one which is characterized by a high density of wolves, can be summarized as follows: fawns lie concealed by the vegetation during the lactation period, thus affecting their mothers' spatial behaviour. At the same time, mothers select denser habitats and consequently increase their fawns' survival success.

Scandinavian studies have shown that red fox is a dominant predator on roe deer fawns (Lindström *et al.*, 1994; Aanes & Andersen, 1996; Jarnemo & Liberg, 2005). Whereas roe deer females are able to actively defend their fawns against an attacking fox (Jarnemo, 2004), this should not be the case with an attacking wolf. Both fox and wild boar are likely to predate on fawns only for a few weeks after their birth, while wolves may very well kill fawns during the whole fawning season (Mattioli *et al.*, 2004). Therefore, the presence of three converging predator pressures, and primarily among them the presence of wolves, may account for such marked differences in the use of dense forests by mothers and non-mothers during the whole fawning season in our study site.

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Conclusion

This work confirmed one of the most crucial issues of wildlife management, i.e., how it's difficult to estimate ungulate population density, especially if the target ungulate is the "elusive" roe deer. That's why in the first part of the thesis I checked for different accuracy and applicability of roe deer census methods. More in detail, diverse census methods were considered according to environmental characteristic, i.e., one of the major factors affecting bias in roe deer density estimation. I summarized concerns about some census methods in figure 1.

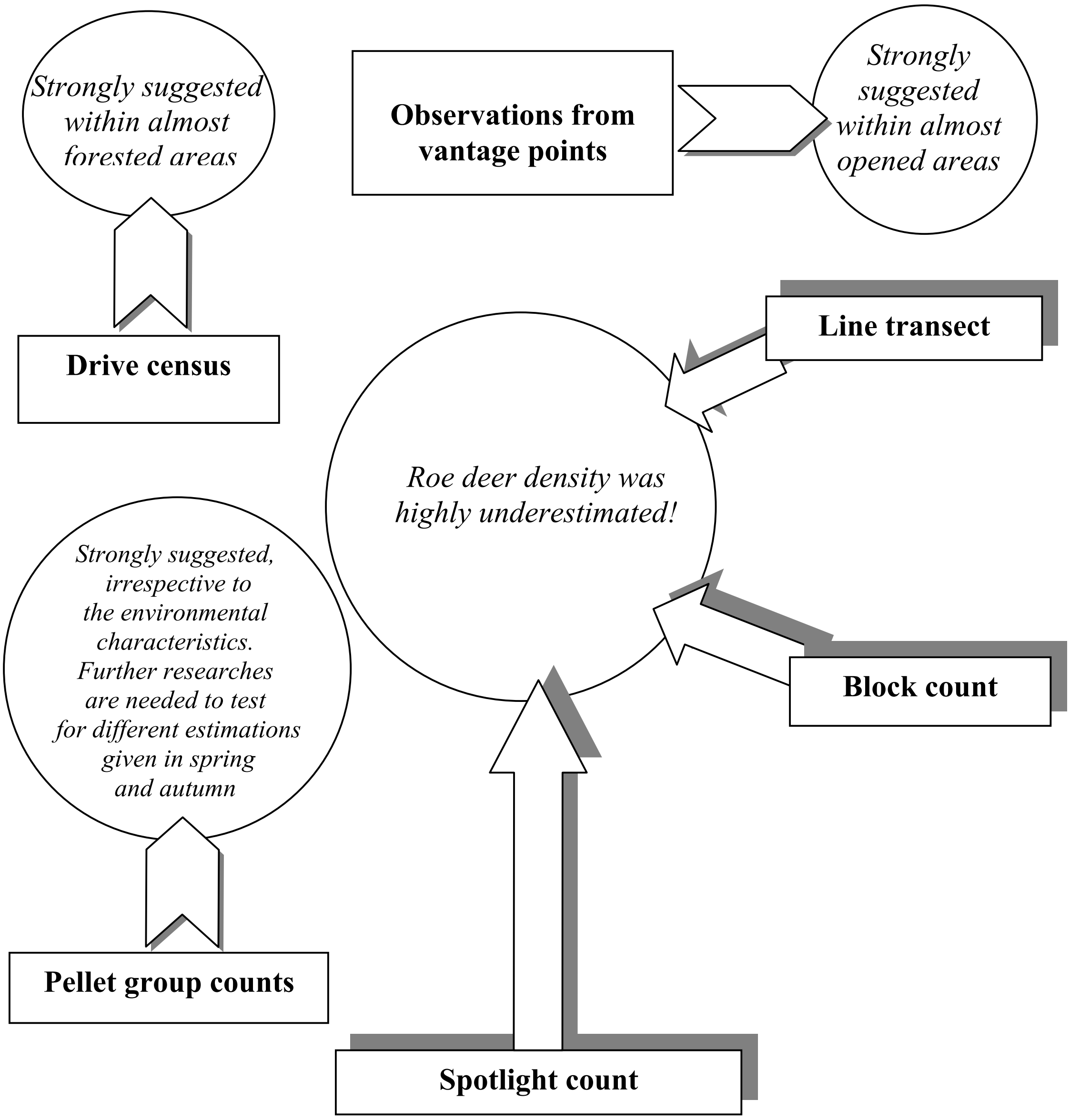

Figure 1. Diverse roe deer estimated density given by different census methods (see *chapter 1* for major details).

As summarized in figure 1, a strong underestimation was given in the use of the line transect, block count, and spotlight count techniques. As a consequence, such methods are strongly not recommended in fragmented areas. Depending on environmental characteristics (open and forest areas), the two best methods are the observation from vantage points and the drive census, while the pellet group count is strongly suggested as a control method. Therefore, the first step to be considered when census have to be planned is to assess the proportion of open and forest areas. In any case, not only the environmental characteristics seem to affect the census methods, and this concern was deeply investigated in the second and third part of this thesis.

In particular, some human (hunting, logging activities) and ecological (prey-predator relationship, behavioural ecology of monitored species) factors should be take into consideration before proceed to plan management activities such censuses, or, in any case, when census data are processed. For example (chapter 2), when hunting practices were allowed, roe deer shifted their center of activity inside protected areas. As a consequence, managers have to contend with roe deer movement as a response to hunting activities, and related deer concentrations inside protected areas during the hunting season. In conclusion, censuses performed inside protected areas may produce biased estimated deer densities. Furthermore, and not less important, logging activities are able to affect deer movement. As a matter of fact, in presence of clear-cutting areas, roe deer were shown to increase the use of this areas during and immediately after forest work (see chapter 3 for major details). Therefore, also in this case it is necessary to know the structure of woodland (and, not less important, the presence of logging activities and the related creation of clear-cutting areas) when census data are processed, given that more roe deer are expected inside or near clear-cutting areas.

As above mentioned, I also considered ecological factors that may affect roe deer spatial behaviour. In a wolf area, for example, females with fawn were shown to use habitat more dense than female without fawn, as a consequence of antipredator strategies adopted by mothers in order to increase the survival of offspring (chapter 5). Therefore, the detectability of roe deer mother with their fawns is lower during the first part of weaning and, consequentely, estimation of the popolation size and population increase may be underestimated during crucial periods of the annual biological cycle of the monitored species. To sum up, managers must be careful when plan censuses or process data on deer density, paying particular effort in considering all factors affecting deer density. Specifically, managers must avoid to be biased by converging factors leading to overestimation of roe deer density: for example, as shown in this thesis, roe deer are concentrated inside protected areas in autumn due to the combined presence of hunting and higher availability of clear-cutting areas (end of logging activities: August).

In conclusion, I summarized both human and ecological factors able to affect census techniques (and census outcomes) in figure 2 and 3, respectively.

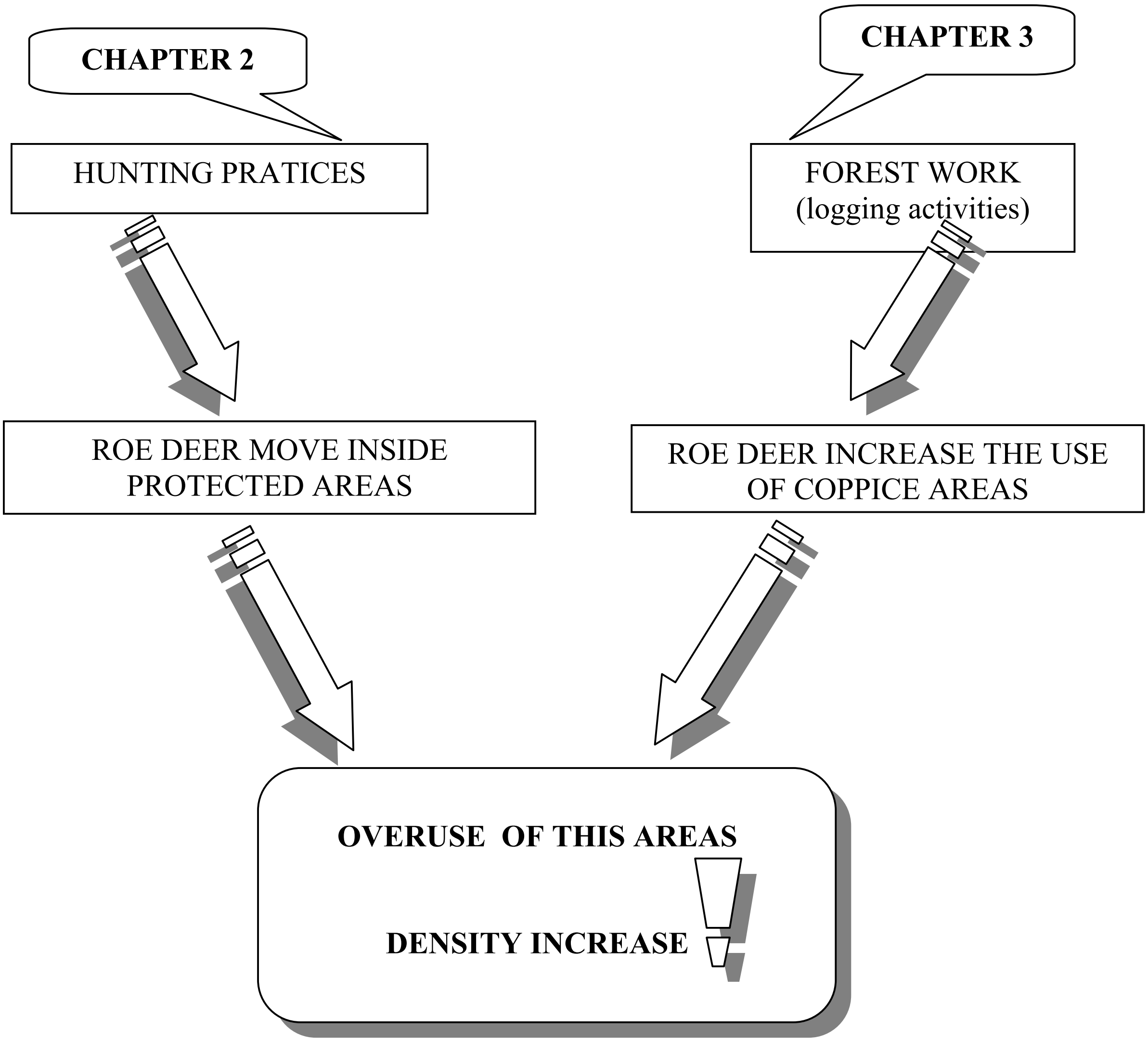

Figure 2. Human factors which may affect roe deer spatial behaviour, and, consequently, density estimation.

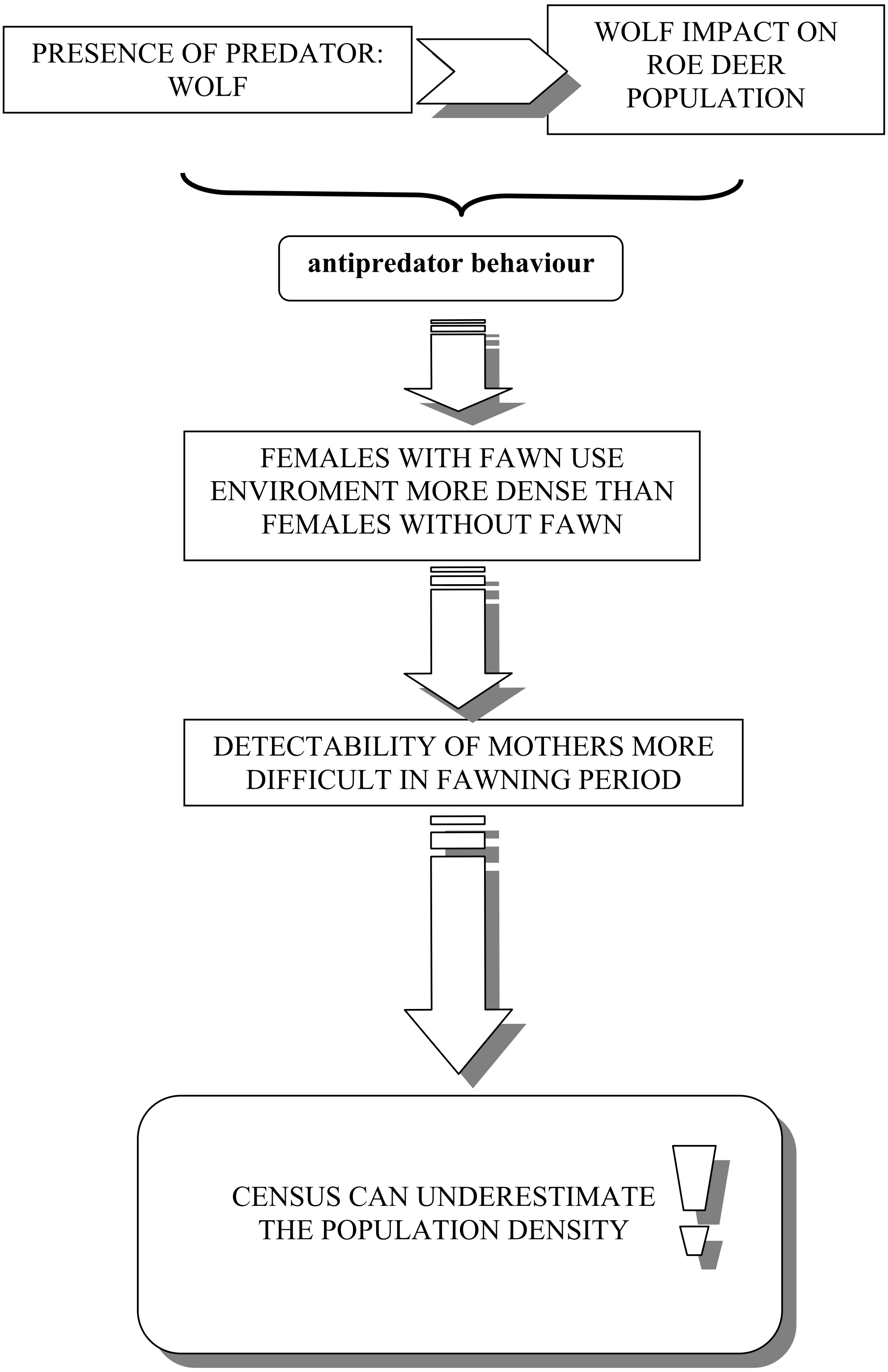
PRESENCE OF PREDATOR: WOLF
WOLF IMPACT ON ROE DEER POPULATION
antipredator behaviour
FEMALES WITH FAWN USE ENVIROMENT MORE DENSE THAN FEMALES WITHOUT FAWN
DETECTABILITY OF MOTHERS MORE DIFFICULT IN FAWNING PERIOD
CENSUS CAN UNDERESTIMATE THE POPULATION DENSITY
!

Figure 3. **Ecological factors which may affect roe deer spatial behaviour, and, consequently, density estimation.**