Effects of hunting with hounds on a non-target species living on the edge of a protected area

Stefano Grignolio a,*, Enrico Merli b, Paolo Bongi a, Simone Ciuti a,1, Marco Apollonio a

aDepartment of Zoology and Evolutionary Genetics, University of Sassari, Via Muroni 25, I-07100 Sassari, Italy
bWildlife Service, Province of Piacenza, C.so Garibaldi 50, I-29100 Piacenza, Italy

Abstract

The impact of hunting on wildlife is a complex phenomenon which varies in space and across time, and yet limited knowledge is available on it. This is especially the case of the indirect effects of hunting on the behaviour of target as well as non-target species. Here we analyze how hunting affected the spatial behaviour of 62 radiocollared roe deer (Capreolus capreolus) in a protected area adjacent to areas where hunting with hounds (target species: wild boar and hares) and stalking with rifles from high seats without dogs (target species: roe deer) were permitted during the hunting season. Our results showed that hunting caused a significant increase in the home range size of monitored deer, as well as a “reserve effect”, whereby roe deer used the protected area as a refuge from hunters. These behavioural responses were significant only at times when hunting with hounds was conducted, even though roe deer was not the target species of this technique. Reactions to the perceived risk of predation varied among age and sex classes, with yearling being more sensitive and using the protected area more than adults. As shown in our study, hunting harassment provoked by drives with hounds significantly affects the behaviour of non-target species. Therefore, the use of long-legged hounds represents a variable that should be carefully evaluated by wildlife managers in their management plans and conservation policies, especially when endangered or vulnerable species are present.

Keywords: Roe deer, Hunting techniques, Protected area, Hunting with hounds, Conservation policies, Reserve effect

1. Introduction

Hunting has been recognized as a crucial factor in the biological and cultural evolution of man (Klein, 1989), whereas limited information is currently available on its ecological effects on prey populations, and, more generally, on biodiversity. The role played by humans in the extinction or reduction of the distribution range of many large vertebrate species is commonly acknowledged.

Several protected areas have been established across the world during the last few decades in order to address the dangers posed by human beings. Undoubtedly, protected areas have contributed to the conservation of several species, and, more generally, of biodiversity (e.g., Caro, 1999). In this regard, it is important to assess how human activities along the borders of protected areas can affect the distribution of species outside as well as inside the reserves. For instance, information is scarce on how certain human activities, including a range of hunting techniques, can result in abnormal concentrations of wildlife in protected areas and related negative effects (e.g., increase in browsing pressure, decrease in soil quality, modification of micro- and macro-invertebrate communities). The impact of human activities on wildlife, and of hunting in particular, is often complex and varies in space and across time, although its actual effects are still poorly understood (Blumstein et al., 2005; Jayakody et al., 2008; Stankovich, 2008). In particular, ungulate population dynamics are greatly influenced by harvesting (e.g., Toïgo et al., 2008), whereas only recently interest increased regarding the effects of hunting on the genetic structure of populations as well as on the distribution of key phenotypes (Allendorf et al., 2008; Coltman et al., 2003).

In this general framework, very little is known about the indirect effects of human harassment (particularly of hunting) on prey behaviour, population dynamics and life history (Milner-Gulland et al., 2004; Proaktor et al., 2007). Several authors argued that hunting is able to shape the fright behaviour of birds (Madsen, 1985; Madsen and Fox, 1995) and mammals (Jeppesen, 1987a,b; Shultz and Bailey, 1978) in response to humans, even though such a response was tested empirically only in recent years and produced heterogeneous findings. Colman et al. (2001) tested the flight distance in reindeer (Rangifer tarandus) as a response to human presence and did not find any evidence of it, while, Reimers et al. (2009) showed that reindeer flight-initiation distance increased following the introduction of hunting. A study conducted on roe deer (Capreolus capreolus) found that individuals living in...
hunting areas seemed to respond more sensitively to man than individuals living in areas where hunting was banned (de Boer et al., 2004). A correct assessment of different forms of wildlife harassment should take into account not only the flight distance (Enggist-Düblin and Ingold, 2003), but also other behavioural responses such as modifications to home range and feeding behaviour (e.g.: Ciuti and Apollonio, 2008; St Clair and Forrest, 2009; Tolon et al., 2009).

There is empirical evidence that hunting with high numbers of men and dogs may have a strong impact on cull intensity as well as on animal disturbance (Sforzi and Lovari, 2000). As some of the traditional hunting techniques employed in central and southern Europe do entail the use of hounds, several authors analysed the influence of hunting with hounds on prey behaviour. In a study on red deer (Cervus elaphus), Jeppesen (1987b) recorded and distinguished two behavioural modifications in response to hunting with hounds: the immediate escape, occurring at the beginning of the disturbance, and the late escape, occurring at the end of it. The late escape was shown by animals that were pursued by hounds, but also by animals that were not chased. Also Sund et al. (2009) showed that hunting disturbance induced prolonged behavioural modification, with red deer hinds showing migration as a general response-type to hunting harassment. As regards ungulates in particular, hunting harassment also modified the habitat selection (individuals spent more time in densely vegetated areas) and encouraged crepuscular and nocturnal rather than diurnal activity (Kamler et al., 2007; Kilgo et al., 1998; Kufeld et al., 1988).

Our study tested the influence of hunting on the spatial behaviour of the most common European ungulate, the roe deer, and considered a protected area (hunting forbidden throughout the year) surrounded by districts where hunting with hounds (target species: wild boar Sus scrofa and hare Lepus europaeus) alternated with stalking from fixed high seats (target species: roe deer) and no hunting of any kind was permitted for 5 months each year. We adopted two approaches to study how roe deer modified spatial behaviour as a response to these hunting techniques. First, we assessed home range size variation as a response to a set of explanatory variables on a broad scale; second, we computed the probability of a roe deer being outside or inside the protected area, roe deer living outside and on the edge of it were expected to increase mobility and home range size, as well as to find refuge in it.

2. Methods

2.1. Data collection

The study was conducted in a mountainous area located on the Tuscan slope of the Apennines in the province of Arezzo, Italy (43°48’N, 11°49’E). The borders of the study site (8612 ha) were determined through the Minimum Convex Polygon by computing all roe deer locations collected from 2001 to 2005. A protected area (Oasi Alpe di Catenaia, OAC, 2795 ha) was located within the study site, with non-fenced borders delimited by vertical road signs. The elevation of the area ranges between 300 and 1514 m a.s.l. (Fig. 1), with peaks located within OAC, where snow usually falls from October to April. During this research, the density of roe deer estimated by means of drive censuses performed in forested areas was 21.2 head/km² (min = 17.5; max = 25.2) inside OAC, and 44.5 head/km² (min = 36.6; max = 51.2) outside OAC.

The habitat composition inside and outside OAC differed (Fig. 1). Outside OAC, deciduous coppice forests (mainly oak, Quercus spp, and chestnut, Castanea sativa) were prevalent with a harvest frequency of 20 years. These forests were characterised by a high density of young trees, and, as a consequence, by a rich undergrowth vegetation. High deciduous forests (mainly beech Fagus sylvatica) and conifer forests (Pinus nigra, Abies alba, Pseudotsuga menziesii) characterised by a scarce undergrowth vegetation prevailed inside OAC, where harvest frequency was around

![Fig. 1. Habitat composition of the study site, within (A) and outside (B) the protected area “Oasi dell’Alpe di Catenaia” (OAC), and its altitudinal range (C).](image-url)
50–70 years. As shown by Bongi et al. (2008), habitats with rich undergrowth vegetation and scarce visibility outside OAC were selected by female roe deer as suitable birth places during the fawning season. In general, low elevation areas outside OAC (Fig. 1) were more suitable habitats for roe deer than those inside OAC, as confirmed by the higher deer density recorded outside OAC. The natural roe deer predators in the study area were red fox (Vulpes vulpes) and wolf (Canis lupus).

Hunting was forbidden inside OAC and regulated outside OAC. We distinguished three hunting seasons (Table 1): (i) no hunting; (ii) roe deer stalking with rifles and without hounds (hunting from high seats within areas assigned to individual hunters; hunting was permitted all days excluding Tuesdays and Fridays); (iii) hunting with hounds (target species being wild boar and brown hare). In particular, hunting of wild boar began on the third Sunday of September and ended on January 31st (Table 1). Wild boar hunting was permitted on Wednesdays, Saturdays and Sundays, and included battues (i.e. dog drives) with 30–50 hunters (no less than 25 hunters by law) and many hounds. The hunting of hare occurred between the third Sunday of September and the second Sunday of December, and was permitted all days except Tuesdays and Fridays. The hunting of hare included one or more hunters, and no more than two or three hounds for each hunter. In both hunting techniques hunters usually kept hounds on a leash during the preliminary phase of hunting. When hounds found traces of prey, the hunters loosed the dogs and followed them. Hounds pursued roe deer in some cases: this behaviour was mainly due to inadequate training of the hounds, especially of young dogs. Hunters used different hound breeds, but in most cases they used Maremman hounds (shoulder height: 48–54 cm; weight: 13–23 kg).

Roe deer were captured by means of vertical drop nets, hand caught, blindfolded, fitted with Televilt radiocollars (Televilt, Sweden) and released. We monitored 62 radio-collared individuals (age and sex class at capture: 11 adult males, 12 adult females, 39 yearlings) by discontinuous radio-tracking from March 2001 to April 2005. We used Televilt receivers and 4-element Yagi antennas to triangulate the position of deer 8–12 times per month. We distributed locations uniformly over the day within at least 48 h of one another to avoid temporal and spatial correlation biases. We chose this long time interval in order to let the deer move across their home ranges, inside and outside the OAC (Börger et al., 2006). Before beginning this research, the accuracy of fixes was determined in the field using test transmitters placed in various habitats, which enabled us to use an error polygon of 1 ha. To reduce bias, animals were located from a distance of 100–300 m (see Bongi et al., 2008 for details).

### 2.2. Data analysis

#### 2.2.1. Spatial analysis

Home ranges were estimated by the 90% Kernel method (Börger et al., 2006) using the Ranges VI software (Kenward et al., 2003). Seasonal home ranges and 45-day home ranges were computed for deer located at least 12 times during each period (seasonal home ranges: \( n^\text{fix/individual/season} \pm SD 24.2 \pm 6.7; 45\text{-day home ranges: } n^\text{fix/individual/period} 15.0 \pm 2.4\)). According to Börger et al. (2006), the Kernel method gives accurate home range estimates with at least 10 fixes, while large deer samples are necessary to address the high home range inter-individual variation in this cervid. Regarding 45-day home ranges, we computed “stalking home ranges” using locations collected between August 1st and September 15th, and “hounds home ranges” using locations collected from September 16th to October 31st (Table 1). We chose 45-day periods in order to compare home ranges computed over comparable time intervals during which different hunting techniques were employed.

#### 2.2.2. Habitat analyses

In analysing the effects of hunting on deer spatial behaviour we took into account the influence of habitat parameters and types, by addressing resource availability at the individual home range level, as suggested by Thomas and Taylor’s design 3 (Thomas and Taylor, 1990). We used a seasonal scale to examine seasonal variation in habitat use by deer thus following Said et al. (2009) suggestion that habitat use analysis enables a better understanding of behavioural patterns only when carried out on a seasonal scale. Seasons were defined as follows: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February).

First, we grouped seasonal home ranges according to the habitat types (see Fig. 1 for habitat availability) included within individual home ranges. This was accomplished by means of Hierarchical Cluster Analysis, the consistency of which was ascertained using the ClValid R-package (Brock et al., 2008) and by comparing the results of different clustering methods and groups (3, 4, or 5 groups of home ranges). Home range coverage was computed using ArcView 3.2 (ESRI Inc., Redlands, USA). Individual home ranges were then classified into the following three groups, according to the relative abundance of the six habitat types (Appendix A): COPPICES HRS (almost entirely covered by deciduous coppice forest), HETEROGENEOUS HRS (mainly covered by conifer forest, shrubs, and mixed forest), and HIGH-DECIDUOUS HRS (mainly covered by high deciduous forest).

Second, an availability index (AI) was developed for each habitat type within each individual seasonal home range, as follows:

\[
AI = (x_\text{in} - x_\text{out})/x_\text{in} + x_\text{out}
\]

where \(x_\text{in}\) and \(x_\text{out}\) were the proportions of the given habitat type in the individual home range inside and outside OAC, respectively. The index ranged from \(-1\) (i.e., the habitat type within the home range was completely outside OAC) to 1 (i.e., completely inside OAC), with 0 indicating either no use of the habitat type, or equal proportions within the HR of areas located inside and outside OAC. This procedure enabled us to standardize the differences in habitat availability inside and outside OAC among individuals and home ranges.

### Table 1

Hunting practices and times in the province of Arezzo (central Italy).

<table>
<thead>
<tr>
<th>Hunting season</th>
<th>No hunting</th>
<th>Roe deer stalking</th>
<th>Hunting with hounds</th>
</tr>
</thead>
<tbody>
<tr>
<td>2001</td>
<td>1st March–1st August; 14th September–15th September</td>
<td>1st August–13th September</td>
<td>16th September–31st December</td>
</tr>
</tbody>
</table>
Deciduous coppice forest was the most suitable among the available habitat types for roe deer, affecting its presence and distribution (Bongi et al., 2008; Nilsen et al., 2004; Sai’d et al., 2005). To avoid collinearity issues, the Pearson correlation coefficient was calculated to build a correlation matrix among AI values of seasonal home ranges. We excluded habitat types when their AI values were correlated ($|r_p| > 0.15$) to the value recorded for deciduous coppice forest.

2.2.3. Statistical analyses

We analysed the effect of hunting on the spatial behaviour of roe deer by fitting Linear Mixed Effects Models (LMM; nlme R-package, lme procedure) to log-transformed 45-day period home range sizes as response variables. These home ranges were grouped according to their position with respect to OAC as follows: (i) INSIDE HOME RANGES (HRs): at least 90% of the home-range was inside OAC; (ii) OUTSIDE HRs (at least 90% outside OAC); (iii) BORDER HRs (other cases). The following variables were considered fixed effects in the models:

(i) “Hunting factor”, i.e. the hunting technique permitted during the period in which the positions of home ranges were recorded with respect to OAC. Arrangements of this factor were derived from the combination of two hunting techniques (roe deer stalking, hunting with hounds) and three home range positions: INSIDE HRs, OUTSIDE HRs and BORDER HRs.
(ii) “Sex-age”; i.e. yearlings of both sexes (not adult), adult females (age >2 y.o.) and adult males (age >2 y.o.).
(iii) “Season”; considering that 45-day period home ranges were calculated from 1st August to 30th October, this variable could assume only two values, i.e. summer and autumn;
(iv) “Cluster habitat”, i.e. the categorical variable (COPPICES HRs, HETEROGENEOUS HRs, HIGH-DECIDUOUS HRs) obtained by means of Cluster analysis. As shown by several authors (Nicholson et al., 1997; Sai’d et al., 2009; Tufto et al., 1996), only a seasonal scale allows for the understanding of habitat use behavioural patterns. Thus, we used the classification of seasonal home ranges according to the varying proportions of habitat types (Appendix A).

Deer were monitored for as long as possible, i.e. until either they died or the radio collars ceased to transmit. As a consequence, deer contributed to the analysis to different extents which varied according to when each individual was captured and to the different duration of tracking. To avoid pseudoreplication issues, we considered deer identity as a random factor in all our models so as to account for the different contributions of individuals to the population behaviour, as suggested by Hurlbert (1984).

Moreover, yearlings that were entered in the analysis as non-adults during the first year of monitoring, were considered as adults during the following years (shift of age class considered). Eventually, the roe deer ID was a unique value assigned to the same deer, regardless of the monitoring period, and the shift of age class. The year of study was not found to affect the variability of the dependent variable significantly. Thus, it was excluded from our analysis.

A final set of 11 LMMs of increasing complexity were related to the home range size (see Table 2): four models accounted for single fixed factors, while five other models accounted for combinations of fixed factors. We did not consider any model which included both season and hunting factor, since there was a collinearity between hunting techniques and seasons. Finally, two models accounted for three variables simultaneously, again excluding the presence of hunting factor and season in the same model. Once the best model was identified by means of minimum AICc (Burnham and Anderson, 2002) and model ranking and weighing, the effect of each variable was obtained by averaging the regression coefficients of the models (Burnham and Anderson, 2002), as shown below:

$$\hat{B} = \sum_{i=1}^{11} w_i \hat{B}_i$$

where $\hat{B}$ is the averaged regression coefficient, $w_i$ is the Akaike weight of the $i$th model, and $\hat{B}_i$ is the estimated regression coefficient of the variable in the $i$th model.

Generalised Linear Mixed Models with binomial error distribution (GLMM; lme4 R package, glmer procedure) were applied using the location (inside = 0; outside = 1) of each fix as the response

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**Table 2**

<table>
<thead>
<tr>
<th>Model</th>
<th>-2 Log Likelihood</th>
<th>$N$ of parameters</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_j$</th>
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</thead>
<tbody>
<tr>
<td>Cluster habitat + hunting factor</td>
<td>599</td>
<td>10</td>
<td>620.75</td>
<td>0</td>
<td>0.56822</td>
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<tr>
<td>Cluster habitat + hunting factor + sex-age</td>
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<td>12</td>
<td>621.82</td>
<td>1.07</td>
<td>0.33275</td>
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<tr>
<td>Hunting factor</td>
<td>608</td>
<td>8</td>
<td>625.28</td>
<td>4.53</td>
<td>0.055894</td>
</tr>
<tr>
<td>Hunting factor + sex-age</td>
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<td>10</td>
<td>626.24</td>
<td>5.49</td>
<td>0.03651</td>
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<tr>
<td>Cluster habitat</td>
<td>622</td>
<td>5</td>
<td>632.07</td>
<td>11.32</td>
<td>0.00198</td>
</tr>
<tr>
<td>Cluster habitat + sex-age</td>
<td>619</td>
<td>7</td>
<td>633.52</td>
<td>12.77</td>
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<td>6</td>
<td>635.74</td>
<td>14.98</td>
<td>0.00032</td>
</tr>
<tr>
<td>Cluster habitat + season + sex-age</td>
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<td>8</td>
<td>637.23</td>
<td>16.48</td>
<td>0.00015</td>
</tr>
<tr>
<td>Sex-age</td>
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<td>637.72</td>
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<tr>
<td>Season</td>
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<tr>
<td>Season + sex-age</td>
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<td>6</td>
<td>641.31</td>
<td>20.56</td>
<td>0.00002</td>
</tr>
</tbody>
</table>

**Predictors**

<table>
<thead>
<tr>
<th>Predictors</th>
<th>$\Sigma w_j$</th>
<th>$N$ of models</th>
<th>Fixed effects</th>
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<tbody>
<tr>
<td>Hunting factor</td>
<td>0.9964</td>
<td>4</td>
<td>Hunting factor [stalking period]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hunting factor [position INSIDE OAC]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hunting factor [position OUTSIDE OAC]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hunting factor [stalking period – position INSIDE OAC]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hunting factor [stalking period – position OUTSIDE OAC]</td>
</tr>
<tr>
<td>Cluster habitat</td>
<td>0.9044</td>
<td>6</td>
<td>Cluster habitat [HETEROGENEOUS]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cluster habitat [HIGH-DECIDUOUS]</td>
</tr>
<tr>
<td>Sex-age</td>
<td>0.3705</td>
<td>6</td>
<td>Adult male</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Yearling</td>
</tr>
<tr>
<td>Season</td>
<td>0.0005</td>
<td>4</td>
<td>Season [summer]</td>
</tr>
</tbody>
</table>
variable. Only fixes belonging to BORDER HRs were considered, since in that case only roe deer could choose among areas inside or outside OAC. In order to avoid pseudoreplication issues, we considered deer identity as a random factor in all the models using the same approach adopted in the broad scale analyses. The following independent variables were considered in the models:

(i) “Hunting techniques”, i.e. roe deer stalking, hunting with hounds, and hunting not permitted. This is not to be confused with “hunting factor” from the previous set of models.

(ii) “Sex-age”, as defined in the previous set of models.

(iii) “Season”, i.e. spring, summer, autumn, and winter.

(iv) “Habitat”, in this case we considered both the availability index (AI) and the classification carried out in the cluster analysis.

Eight GLMMs of increasing complexity were fitted to the data (Table 3). Model comparison and multimodel averaging were computed as previously described for LMMs. All analyses were run in R 2.8.1 (R Development Core Team, 2007).

3. Results

3.1. LMMs with home range size as response variable (broad scale)

Ninety-five 45-day home ranges were computed when roe deer stalking occurred (mean ± SE; 84 ± 11 ha), while 86 home ranges were computed when hunting with hounds was permitted (86 ± 15 ha). As regards OAC borders, when roe deer stalking or hunting with hounds was permitted, 73 home ranges were located inside OAC (55 ± 8 ha), 25 outside OAC (110 ± 35 ha), and 84 across its borders (105 ± 14 ha). During the same period, 55 home ranges were computed for adult males (95 ± 16 ha), 103 for adult females (92 ± 12 ha), and 23 for yearlings of both sexes (41 ± 7 ha). Finally, we reported 29 COPPICES HRs (48 ± 8 ha), 77 HETEROCIOUS HRs (120 ± 17 ha), and 75 HIGH-DECIDUOUS HRs (64 ± 11 ha).

Comparison among candidate linear mixed models (LMMs) pointed out the importance of hunting factor and cluster habitat in affecting the variability of 45-day home range sizes (Table 2, top panel). However, sex-age classes also contributed to explaining such variability, as shown by the 2nd ranked selected model (ΔAICc < 2; Table 2, top panel). The model averaging (Table 2, bottom panel) clearly showed how roe deer home range sizes were strongly affected by hunting, the hunting factor accounting for the highest value of Akaike weights. Home range sizes inside OAC were smaller than those outside: the difference was minimal when roe deer stalking occurred, and larger when hunting with hounds was permitted. Hunting with hounds increased the gap in roe deer home range sizes between inside and outside OAC: home range sizes recorded outside OAC when roe deer stalking occurred were smaller (74 ± 27 ha) than those recorded outside OAC (256 ± 130 ha) when hunting with hounds was permitted. Such differences were not found for home ranges recorded inside OAC, where hunting was never permitted, when roe deer stalking and hunting with hounds were permitted outside OAC (58 ± 11 ha and 51 ± 13 ha, respectively). Regarding the influence of habitat composition on roe deer home range sizes, HETEROCIOUS HRs were found to be larger than HIGH-DECIDUOUS HRs and COPPICES HRs.

3.2. Selection of availability indexes (AI)

The average AI calculated for each habitat type showed a higher availability of four habitat types inside OAC than outside (High deciduous forest, Conifer forest, Mixed forest and Shrub; Appendix B). Only meadows and pastures and deciduous coppice forests were more available in the portions of the home ranges located outside OAC than inside. AI indexes of Al_conifer forest and Al_meadows and pastures were highly correlated to AI_deciduous coppice forest (Appendix B). As a consequence, only Al_deciduous coppice forest, Al_shrubs and Al_mixed forests were used in subsequent models.

3.3. GLMMs with fixes inside or outside OAC as the binomial response variable (fine scale)

We considered 342 seasonal home ranges (n = 57 roe deer) located across the borders of OAC (i.e., BORDER HRs) accounting for 8261 locations (4682 inside and 3579 outside OAC). We collected 2112 locations during roe deer stalking and 4003 when hunting with hounds was permitted. As regards sex and age
classes, 1251 fixes were collected for yearling roe deer, 2661 for adult males, and 4349 for adult females. Finally, 2345 fixes fell into COPPICE HRs, 3834 into HETEROGENEOUS HRs, and 2082 into HIGH-DECIDUOUS HRs.

A comparison among candidate GLMM models showed high AICc differences (ΔAICc ≥ 2.0) with the exception of the first two models (ΔAICc = 0.01) (Table 3). The two highest ranking models showed that the probability of a roe deer being outside OAC was strongly affected by habitat features, season, hunting technique, and age-sex class differences. As shown via model averaging (Table 3), the probability of a roe deer being outside OAC increased either during roe deer stalking or when hunting with hounds was not permitted. The probability was highest in autumn, when, on the contrary, yearlings (non-adult) showed a higher probability of being inside OAC than outside, the opposite of what we recorded for adult deer. As regards the habitat features, fixes of home ranges falling into COPPICE HRs had a higher probability of being outside OAC than inside, whereas the opposite was found for the other cluster groups. Finally, the higher the coverage of shrubs or mixed forest within the home range portion inside OAC, the lower the probability of a roe deer being outside OAC.

4. Discussion

In recent years, the importance of implementing behavioural studies in conservation biology has been widely acknowledged (Festa-Bianchet and Apollonio, 2003; Sutherland, 1998; Sutherland and Gill, 2001), and there has been an increasing focus on how human exploitation affects wildlife populations in terms of behaviour and population biology. Several studies indicate that exploitation of wildlife alters population densities and dynamics (Caro, 1999; Fischer and Linsenmair, 2001). Since many hunters target (intentionally or unintentionally) males, demography suffers from a female-biased sex ratio (Bunnefeld et al., 2009; Fischer and Linsenmair, 2002), and this may negatively affect wildlife population dynamics (Ginsberg and Milner-Gulland, 1994; Solberg et al., 2002) and/or the individual life history with an unnatural selection (Colman et al., 2003). Whereas the direct impact of hunting on deer population dynamics has been documented (e.g., McCullough, 1979; Nelson and Mech, 1986), little is known about its effects on deer behaviour. Deer may respond to hunting by avoiding areas with human activity (Apollonio et al., 2005; Dorrance et al., 1979; Rost and Bailey, 1979) and by modifying spatial behaviour (Jeppeesen, 1987a; Sund et al., 2009), activity (Kamler et al., 2007; Vogel, 1989), habitat selection (Kilgo et al., 1998; Kufeld et al., 1988; Swenson, 1982), and group size (Jedrzejewski et al., 2006). Our study analyzed the issue of wildlife exploitation and hunting harassment from a novel perspective, i.e., through a focus on spatial behaviour modifications as a response to hunting disturbance even when roe deer is a non-target species.

Our first prediction proved correct in that hunting was found to cause a significant increase in the home range size of monitored deer and also provoked a ‘reserv effect’, with roe deer using the protected area (OAC) as a refuge. These behavioural responses were significant only when hunting with hounds was conducted – thus confirming our second prediction – even though the roe deer was not the target species of this hunting technique. Finally, our third prediction was only partially confirmed, since only yearling deer (but not adult females, as expected) showed a higher use of OAC than adult males. To the best of our knowledge, no previous research investigated the effects of hunting techniques and focused on the effects of hunting with hounds on non-target species. In our case study, drives with long-legged hounds modified roe deer spatial behaviour. In particular, roe deer significantly increased their home range sizes outside OAC and found refuge inside OAC. The presence of numerous hounds outside OAC likely provoked fright, flight, and movement towards the inner areas of OAC. During wild boar and hare hunting (i.e., hunting with hounds), the average size of an outside OAC home range was five times as much as home range size inside OAC. We also recorded a similar trend during roe deer stalking, but with a lower magnitude. As a matter of fact, home range sizes outside OAC were 27% larger than those inside. Hunters culled most animals at the beginning of roe deer hunting season (e.g., late summer and early autumn) when this cervid is a non gregarious species (Hewison et al., 1998). This behavioural characteristic helps to explain why stalking with rifles from high seats likely caused a very localised harassment to isolated deer. After the shot, the hunter would take the kill away, and the harassment in the area would last a few minutes only. On the contrary, hunting drives with hounds could last for a whole day. While ungulates may suffer no substantial fitness costs when disturbance rates are either low or moderate, several empirical studies suggested that high disturbance rates could reduce their reproductive success and possibly impact on population dynamics (Harrington and Veitch, 1992; Phillips and Aldredge, 2002; Yarmoloy et al., 1988). Bateson and Bradshaw (1997) showed that, by virtue of their evolutionary or individual history, red deer are not well-adapted to cope with the level of activity imposed on them when hunted with dogs. Long hunts, with their physiological effects on deer (disruption of muscle tissue, depletion of carbohydrate resources, high levels of β-endorphin and cortisol) can also indirectly modify their survival rates and life history (Bateson and Bradshaw 1997). In our study case, hare and wild boar hunting occurred simultaneously in the same areas. Accordingly, we knew we could not test the differential effect of the two hunting techniques, but their cumulative effect only. As a result, we could only argue (but not demonstrate) that wild boar hunting most likely had a stronger effect on the behaviour of roe deer when compared to hare hunting. Likewise, we could not ascertain whether the use of short legged hounds may disturb roe deer behaviour to a lesser extent, given that in our study site hunters used long-legged hounds only. This predicted differential effect should be investigated in future studies to provide proper knowledge and avoid undesirable effects on prey populations. Furthermore, given that hunting with hounds is perceived by both target and non-target prey species, the consequences of the use of long-legged hounds should be carefully evaluated by wildlife managers, especially when endangered or vulnerable species are also present in the hunting area. It is a fact that some European countries limit the use of long-legged hounds to specific seasons (Apollonio et al., 2010).

It is crucial to note that OAC was located on the main ridge of a mountain, and roe deer were forced by hunting with hounds to use this area as a refuge during the autumn–winter period. Thus, deer were obliged to use elevated areas exactly when the probability of finding snow cover was higher. As a consequence, the presence of hounds forced roe deer to concentrate in the small protected area, where the climatic conditions were more adverse and the habitat types unsuitable. Such a behaviour is obviously contrary to common expectations (Mysterud, 1999). In autumn and winter we would expect roe deer to reach the bottom of valleys, thus avoiding low temperatures and snow cover: this natural behaviour was shown in the roe deer population of the Foreste Casentinesi National Park, i.e. a large and protected natural area 10-km far from OAC where hunting was forbidden throughout the year (Lamberti et al., 2004; Rossi et al., 2003). Uphill movements may have an important energy cost, especially when carried out during an adverse season. Moreover, the use of sub-optimal habitats together with the concentration of deer may strongly affect life histories and population dynamics (Kilgo et al., 1998; Kufeld et al., 1988; Swenson, 1982). We expected roe deer to increase home
range sizes in a sub-optimal area (i.e. inside OAC, Tufto et al., 1996), but our results showed that roe deer home range sizes outside OAC were actually larger. Roe deer adopted a conservative strategy as a consequence of hunting harassment outside the protected area. They selected safe but sub-optimal areas inside OAC and avoided unsafe areas outside OAC. The increase of density inside a protected area as a consequence of hunting activities is well known in diverse species and natural areas (e.g. Caro et al., 1998). Di Bitetti et al. (2008) showed that hunting may affect the abundance and the activity patterns of sympatric game species. The probability for dwarf brocket (Mazama nana) and red brocketts (Mazama americana) being recorded seemed to vary according to the different levels of protection (Di Bitetti et al., 2008). A further important outcome of the prolonged increase in deer density inside OAC is the higher potential impact of browsing on vegetation: this is especially relevant since the density increases at a time of the year when most of the roe deer’s diet consists of browsing twigs and bramble leaves due to scarce ground herbs (Duncan et al., 1998). During the hunting season, intense human harassment may lead to concentration of individuals inside the protected area. Several authors showed that an increase in herbivore density may produce changes in vegetation (Milchunas and Lauernoth, 1993), while the high density of large herbivores may result in several other modifications. Invertebrates are sensitive to small physical habitat modifications. For example, soil compaction due to trampling by ungulates can affect burrowing invertebrate communities (Bromham et al., 1999; Wardle et al., 2001), while the decrease in litter accumulation due to the presence of deer may affect detritivore communities (Andersen et al., 1990; Bromham et al., 1999). The potential impact of large herbivore densities on small mammals (review in Flowerdew and Ellwood, 2001) and on the birds (Fuller, 2001; McShea and Rappole, 1997) is clear and documented in temperate areas.

In a recent paper on moose (Alces alces), Neumann et al. (2009) suggested that some individuals were more sensitive to hunting disturbance than their population. This work suggested that moose may perceive the human predation risk to be similar to other predation risks. Our findings showed that human harassment induced different responses in deer of different age which consequently used protected areas to different extents. Ungulate response to human disturbance has been compared to a response to predation, wherein humans can play the role of predators (Ciuti et al., 2004; Frid, 2003; Grignolio et al., 2007). Indeed, in our case study, we found a significant behavioural difference among age classes: even though adult roe deer are commonly expected to be more alert than younger deer, and to show longer flight distances than fawns because of their many (negative) experiences with humans (Caro, 2005), they were unexpectedly found outside OAC more often than young roe deer. Yearling roe deer showed a higher use of areas inside OAC. It can thus be argued that young deer were more sensitive to dog harassment because free-roaming dogs impacted upon ungulate dynamics mostly by preying on young individuals (Gaillard et al., 1998; Manor and Saltz, 2003). An alternative explanation could be that adult roe deer have learned the position of “safe places” to be used during the hunts, thus being more likely to remain outside OAC during hunting sessions.

The duration and overlapping of different hunting techniques should be evaluated in relation to the deer population status, the presence of protected areas, the geographical and morphological features of such areas, and the existence of corridors which connect them. Particularly, like any other kind of human harassment, hunting with hounds should only last for a brief period in order to reduce the indirect negative effects on both target and non-target species. Accordingly, we believe that managers should consider all the effects of hunting with hounds pointed out by our findings, including those on non-target prey species, especially when vulnerable species are present. Protected areas should be established, properly distributed, and managed by local governments in order to prevent consistent movements by deer populations with consequent undesirable side-effects on population dynamics and damage to biodiversity. Special attention should be paid to the hunting techniques employed along the borders of protected areas in view of the impact they can have on mammal populations living across hunted and protected grounds. Conflicting interests between hunting associations and conservationists, for example, have been numerous in the past and are still frequent in many countries (e.g. Sinclair, 1997). A detailed analysis of our findings suggests that any conservation plan should include a comprehensive examination of landscape connectivity (e.g., protected areas, ecological corridors) and an integrated hunting plan for several species which considers all the different hunting techniques and their effects: this would increase abundance, diversity, and distribution of animals, thus reducing conflicts and environmental damages.

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Appendix A

Seasonal roe deer home ranges (namely HIGH-DECIDUOUS HOME RANGES, HETEROGENEOUS HOME RANGES, and COPPICE HOME RANGES) grouped by means of Hierarchical Cluster analysis according to predominant habitat types included within home ranges (see text for details). Average (SE) percentages of habitat types included within home ranges are reported.

<table>
<thead>
<tr>
<th></th>
<th>Deciduous copice forest (%)</th>
<th>High deciduous forest (%)</th>
<th>Conifer forest (%)</th>
<th>Mixed forest (%)</th>
<th>Shrubs (%)</th>
<th>Meadows and pastures (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>HIGH-DECIDUOUS HOME RANGES (n = 231)</td>
<td>27.6 (0.98)</td>
<td>54.6 (0.75)</td>
<td>11.3 (0.64)</td>
<td>1.0 (0.19)</td>
<td>3.7 (0.46)</td>
<td>1.7 (0.46)</td>
</tr>
<tr>
<td>HETEROGENEOUS HOME RANGES (n = 252)</td>
<td>41.7 (1.33)</td>
<td>24.0 (0.71)</td>
<td>16.0 (0.89)</td>
<td>4.5 (0.55)</td>
<td>7.5 (0.77)</td>
<td>6.2 (1.03)</td>
</tr>
<tr>
<td>COPPICE HOME RANGES (n = 151)</td>
<td>80.0 (0.72)</td>
<td>9.3 (0.62)</td>
<td>2.6 (0.25)</td>
<td>0.5 (0.14)</td>
<td>1.4 (0.22)</td>
<td>6.2 (0.49)</td>
</tr>
</tbody>
</table>
Correlations (Pearson correlation coefficients, $r_p$) recorded between the average seasonal home range Availability Index (AI) of each habitat type and that of deciduous coppice forest ($n = 342$ seasonal home-ranges). AIs of habitat types that had a correlation of $|r_p| > 0.15$ with $A_{\text{deciduous coppice forest}}$ were excluded from the following steps of analysis (see text for details).

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>AI (ES)</th>
<th>$r_p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous coppice forest</td>
<td>–0.2 (0.03)</td>
<td>–</td>
</tr>
<tr>
<td>High deciduous forest</td>
<td>0.8 (0.02)</td>
<td>–0.17</td>
</tr>
<tr>
<td>Conifer forest</td>
<td>0.3 (0.04)</td>
<td>0.51</td>
</tr>
<tr>
<td>Mixed forest</td>
<td>0.1 (0.03)</td>
<td>0.05</td>
</tr>
<tr>
<td>Shrubs</td>
<td>0.1 (0.03)</td>
<td>–0.04</td>
</tr>
<tr>
<td>Meadows and pastures</td>
<td>–0.4 (0.03)</td>
<td>0.68</td>
</tr>
</tbody>
</table>

References


Ciuti, S., Davini, S., Luccarini, S., Apollonio, M., 2004. Could the predation risk between the average seasonal home range Availability Index (AI) of deciduous coppice forest were excluded from the fol-


