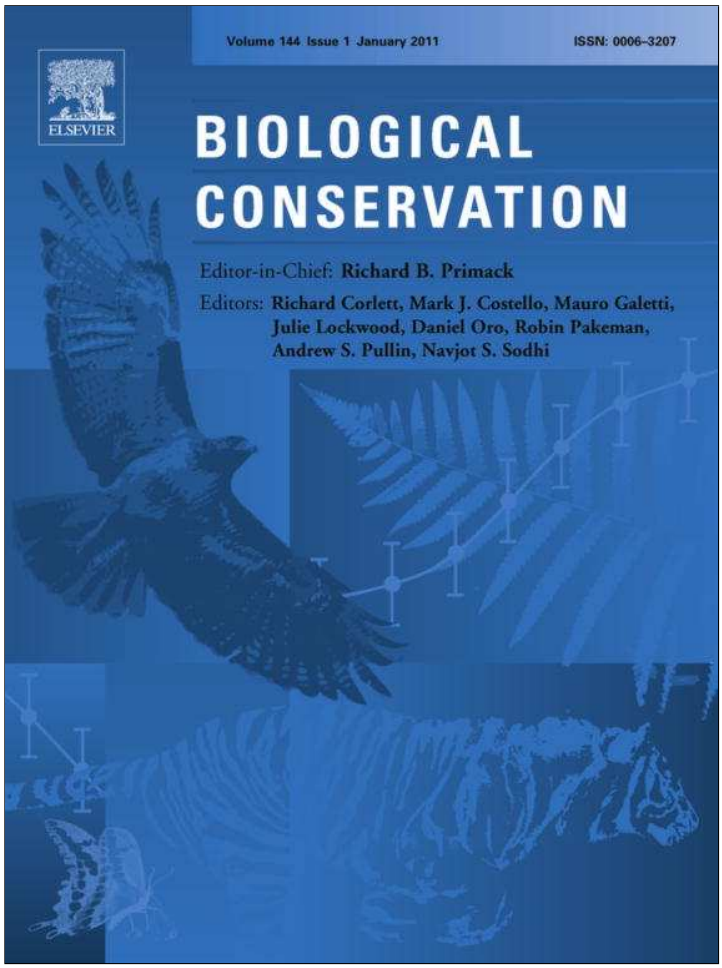
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Biological Conservation 144 (2011) 641–649

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

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]

[a] Department of Zoology and Evolutionary Genetics, University of Sassari, Via Muroni 25, I-07100 Sassari, Italy
[b] Wildlife Service, Province of Piacenza, C.so Garibaldi 50, I-29100 Piacenza, Italy

ARTICLE INFO

Article history:
Received 22 March 2010
Received in revised form 25 October 2010
Accepted 31 October 2010
Available online 15 December 2010

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

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.

© 2010 Elsevier Ltd. All rights reserved.

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; Stankowich, 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

* Corresponding author. Tel.: +39 079228667; fax: +39 079228665.
E-mail address: sgrigno@uniss.it (S. Grignolio).
[1] Present address: Biological Sciences, University of Alberta, Edmonton, Canada T6G 2E9.

0006-3207/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2010.10.022

Author's personal copy

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 Sunde 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 hares *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 according to explanatory variables on a finer scale. Thus, our predictions were as follows:

(1) Due to the hunting harassment occurring outside 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) Hunting with hounds was predicted to significantly affect roe deer spatial behaviour, despite this not being the target species.
(3) Given the differential response to predation risk commonly recorded among sex and age classes in ungulates (Grignolio et al., 2007; Main et al., 1996; Ruckstuhl and Neuhaus, 2005), more sensitive individuals such as females and yearlings were predicted to be more likely than adult males to seek refuge in the protected area, thus taking advantage of the "reserve effect".

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/km^2 (min = 17.5; max = 25.2) inside OAC, and 44.5 head/km^2 (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

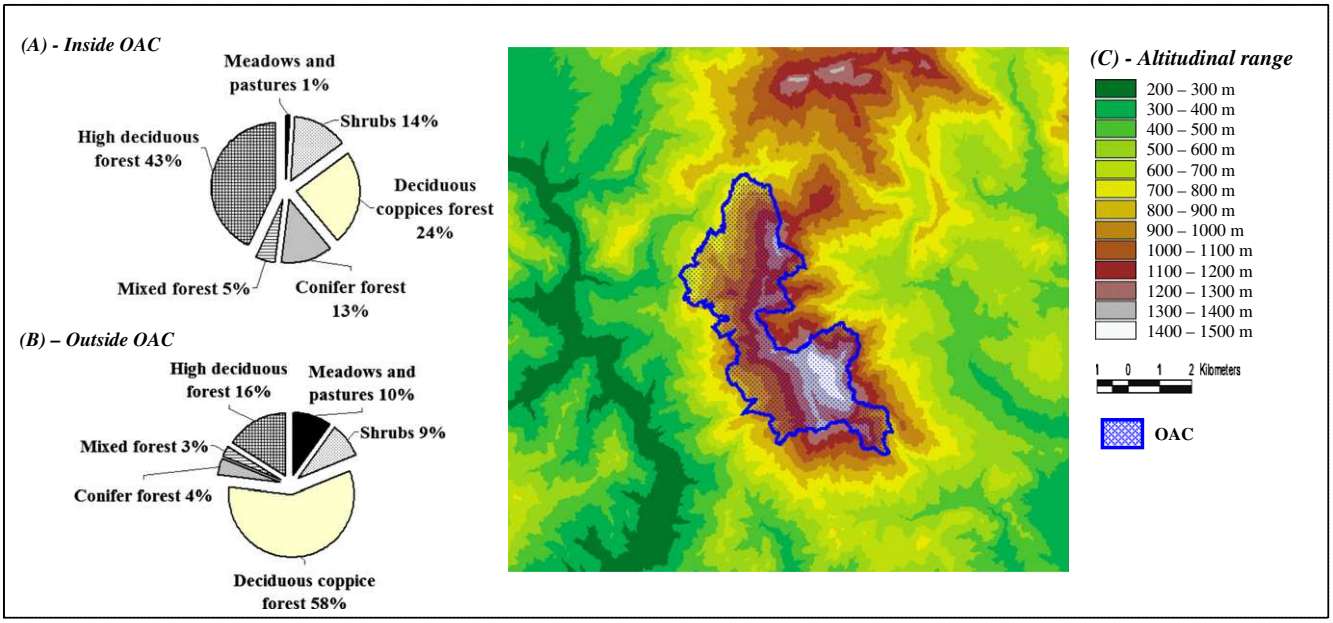


Fig. 1. Habitat composition of the study site, within (A) and outside (B) the protected area "Oasi dell'Alpe di Catenaia" (OAC), and its altitudinal range (C).

Author's personal copy

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 Maremmani 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).

Table 1
Hunting practices and times in the province of Arezzo (central Italy).

Hunting season	No hunting	Roe deer stalking	Hunting with hounds
2001	1st March–1st August; 14th September–15th September	1st August–13th September	16th September–31st December
2002	1st February–1st August; 12th September–21st September	2nd August–11th September	1st January–31st January; 22th September–31st December
2003	1st February–10th February; 1st March–31st July; 13th September–20th September	1st February–28th February 1st August–12th September	1st January–31st January; 21st September–31st December
2004	1st February–11th February; 1st March–31st July; 16th September–18th September	12th February–29th February; 1st August–15th September	1st January–31st January; 19th September–31st December
2005	1st February–11th February; 1st March–30th April	12th February–28th February	1st January–31st January

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° fix/individual/season: mean ± SD 24.2 ± 6.7; 45-days home ranges: n° fix/individual/period: 15.0 ± 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 Saïd 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:

$$AI = (x_{in} - x_{out})/x_{in} + x_{out})$$

where x_{in} and x_{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.

Author's personal copy

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; Saïd 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; Saïd 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 AIC_c (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:

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

where $\widehat{\widehat{B}}$ is the averaged regression coefficient, w_i is the Akaike weight of the *ith* model, and B_i is the estimated regression coefficient of the variable in the *ith* 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

Table 2
Top panel: model inference and ranking of candidate LMMs according to the Akaike Information Criterion (AIC_c) and the Akaike weights (w_j). The log-transformed home range size was used as the response variable (see text for details). *Bottom panel*: multi-model inference, relative importance of predictor variables (Σw_j) and effect estimates $\widehat{\widehat{\beta}}$ (SE) via model averaging.

Model	−2 Log Likelihood	N° of parameters	AIC_c	ΔAIC_c	w_j
Cluster habitat + hunting factor	599	10	620.75	0	0.56822
Cluster habitat + hunting factor + sex-age	596	12	621.82	1.07	0.33275
Hunting factor	608	8	625.28	4.53	0.05894
Hunting factor + sex-age	605	10	626.24	5.49	0.03651
Cluster habitat	622	5	632.07	11.32	0.00198
Cluster habitat + sex-age	619	7	633.52	12.77	0.00096
Cluster habitat + season	623	6	635.74	14.98	0.00032
Cluster habitat + season + sex-age	620	8	637.23	16.48	0.00015
Sex-age	627	5	637.72	16.97	0.00012
Season	632	4	639.81	19.05	0.00004
Season + sex-age	629	6	641.31	20.56	0.00002

Predictors	Σw_j	N° of models	Fixed effects	$\widehat{\widehat{\beta}}$ (SE)
Hunting factor	0.9964	4	Hunting factor [stalking period]	0.53 (0.297)
			Hunting factor [position INSIDE OAC]	−0.66 (0.281)
			Hunting factor [position OUTSIDE OAC]	1.18 (0.431)
			Hunting factor [stalking period – position INSIDE OAC]	−0.47 (0.384)
			Hunting factor [stalking period – position OUTSIDE OAC]	−2.28 (0.663)
Cluster habitat	0.9044	6	Cluster habitat [HETEROGENEOUS]	0.92 (0.300)
			Cluster habitat [HIGH-DECIDUOUS]	0.44 (0.341)
Sex-age	0.3705	6	Adult male	0.28 (0.377)
			Yearling	−0.54 (0.632)
Season	0.0005	4	Season [summer]	0.01 (0.186)

Author's personal copy

Table 3

Top panel: Probability of a roe deer being outside the OAC. Candidate binomial GLMMs, model inference and ranking on the basis of AIC_c and Akaike weights (w_j) are reported for each model. *Bottom panel:* multi-model inference, relative importance of predictor variables and effect estimates $\widehat{\beta}$ (SE) via model averaging (see text for details).

Model	−2 Log Likelihood	N° of parameters	AIC_c	ΔAIC_c	w_j
Habitat + season + hunting technique	9170	12	9194.04	0	0.5014
Habitat + season + sex-age + hunting technique	9166	14	9194.05	0.01	0.4981
Habitat + sex-age + hunting technique	9186	11	9208.03	13.99	0.0005
Habitat + season	9256	10	9276.03	81.99	0.0000
Habitat + hunting technique	9252	12	9276.04	82.00	0.0000
Habitat + season + sex-age	9252	12	9276.04	82.00	0.0000
Habitat	9306	7	9319.01	124.98	0.0000
Habitat + sex-age	9302	9	9321.02	126.98	0.0000

Predictors	Σw_j	N° of models	Fixed effects	$\widehat{\beta}$ (SE)
Habitat	1.0000	8	$AI_{deciduous\ coppice\ forest}$	0.01 (0.131)
			AI_{shrubs}	−0.35 (0.058)
			$AI_{mixed\ forest}$	−0.22 (0.067)
			Habitat [HETEROGENEOUS HOME RANGES]	−1.05 (0.078)
			Habitat [HIGH-DECIDUOUS HOME RANGES]	−1.64 (0.116)
Hunting technique	1.0000	4	Hunting technique [no hunting]	0.67 (0.103)
			Hunting technique [roe deer stalking]	0.84 (0.091)
Season	0.9995	4	Season [spring]	−0.39 (0.116)
			Season [summer]	−0.22 (0.105)
			Season [winter]	−0.31 (0.078)
Sex-age	0.4986	4	Adult male	0.01 (0.182)
			Yearling	−0.22 (0.126)

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 83 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 (90 ± 13 ha), and 23 for yearlings of both sexes (41 ± 7 ha). Finally, we reported 29 COPPICES HRs (48 ± 8 ha), 77 HETEROGENEOUS 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 ($\Delta AIC_c < 2$; 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, HETEROGENEOUS 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 Shrubs; 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 $AI_{conifer\ forest}$ and $AI_{meadows\ and\ pastures}$ were highly correlated to $AI_{deciduous\ coppice\ forest}$ (Appendix B). As a consequence, only $AI_{deciduous\ coppice\ forest}$, AI_{shrubs} and $AI_{mixed\ forests}$ 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

Author's personal copy

classes, 1251 fixes were collected for yearling roe deer, 2661 for adult males, and 4349 for adult females. Finally, 2345 fixes fell into COPPICES HRs, 3834 into HETEROGENEOUS HRs, and 2082 into HIGH-DECIDUOUS HRs.

A comparison among candidate GLMM models showed high AIC_c differences ($\Delta AIC_c \gg 2.0$) with the exception of the first two models ($\Delta AIC_c = 0.01$) (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 (Coltman 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., 1975; Rost and Bailey, 1979) and by modifying spatial behaviour (Jeppesen, 1987b; Sunde 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 'reserve 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 cull 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 Alldredge, 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

Author's personal copy

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 brockets (*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 Lauenroth, 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.

Acknowledgments

This study was funded by Regione Toscana, Provincia di Arezzo, MIPAF, and Italian Ministry for the University and Research (PRIN 2005). We are indebted to Dr. P. Banti, Dr. G. Chianucci, Dr. P. Pedone and Dr. L. Mattioli. We also thank G. Meacci and the hunters of the association URCA. We declare that we have not any direct financial benefits that could result from the publication of this ms. The English version was reviewed and edited by Andrea Binelli and Brian Thomson. We thank two anonymous reviewers for their comments.

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.

	Deciduous coppice forest (%)	High deciduous forest (%)	Conifer forest (%)	Mixed forest (%)	Shrubs (%)	Meadows and pastures (%)
HIGH-DECIDUOUS HOME RANGES (n = 231)	27.6 (0.98)	54.6 (0.75)	11.3 (0.64)	1.0 (0.19)	3.7 (0.46)	1.7 (0.46)
HETEROGENEOUS HOME RANGES (n = 252)	41.7 (1.33)	24.0 (0.71)	16.0 (0.89)	4.5 (0.55)	7.5 (0.77)	6.2 (1.03)
COPPICE HOME RANGES (n = 151)	80.0 (0.72)	9.3 (0.62)	2.6 (0.25)	0.5 (0.14)	1.4 (0.22)	6.2 (0.49)

Author's personal copy

Appendix B

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 $AI_{\text{deciduous coppice forest}}$ were excluded from the following steps of analysis (see text for details).

Habitat type	AI (ES)	r_p
Deciduous coppice forest	−0.2 (0.03)	–
High deciduous forest	0.8 (0.02)	−0.17
Conifer forest	0.3 (0.04)	0.51
Mixed forest	0.1 (0.03)	0.05
Shrubs	0.1 (0.03)	−0.04
Meadows and pastures	−0.4 (0.03)	0.68

References

Allendorf, F.W., England, P.R., Luikart, G., Ritchie, P.A., Ryman, N., 2008. Genetic effects of harvest on wild animal populations. Trends in Ecology & Evolution 23, 327–337.

Andersen, H., Bakker, J.P., Brongers, M., Heydemann, B., Irmler, U., 1990. Long-term changes of salt marsh communities by cattle grazing. Vegetatio 89, 137–148.

Apollonio, M., Ciuti, S., Luccarini, S., 2005. Long term influence of human presence on spatial sexual segregation in fallow deer (*Dama dama*). Journal of Mammalogy 86, 937–946.

Apollonio, M., Anderson, R., Putman, R., 2010. Ungulate Management in Europe in the XXI Century. Cambridge University Press, Cambridge.

Bateson, P., Bradshaw, E.L., 1997. Physiological effects of hunting red deer (*Cervus elaphus*). Proceedings of the Royal Society of London Series B 264, 1707–1714.

Blumstein, D.T., Fernandez-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. Journal of Applied Ecology 42, 943–953.

Bongi, P., Ciuti, S., Grignolio, S., Del Frate, M., Simi, S., Gandelli, D., Apollonio, M., 2008. Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of Zoology 276, 242–251.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., Coulson, T., 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75, 1393–1405.

Brock, G., Pihur, V., Datta, S., Datta, S., 2008. ClValid: an R package for cluster validation. Journal of Statistical Software 25, 1–22.

Bromham, L., Cardillo, M., Bennett, A.F., Elgar, M.A., 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Australian Journal of Ecology 24, 1999–2007.

Bunnefeld, N., Baines, D., Newborn, D., Milner-Gulland, E.J., 2009. Factors affecting unintentional harvesting selectivity in a monomorphic species. Journal of Animal Ecology 78, 485–492.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference. A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Caro, T.M., 1999. Densities of mammals in partially protected areas: the Katavi ecosystem of western Tanzania. Journal of Applied Ecology 36, 205–217.

Caro, T.M., 2005. Antipredator Defenses in Birds and Mammals. The University Chicago Press, Chicago.

Caro, T.M., Pelkey, N., Borner, M., Severre, E.L.M., Campbell, K.L.I., Huish, S.A., Ole Kuwai, J., Farm, B.P., Woodworth, B.L., 1998. The impact of tourist hunting on large mammals in Tanzania: an initial assessment. African Journal of Ecology 36, 321–346.

Ciuti, S., Apollonio, M., 2008. Ecological sexual segregation in fallow deer (*Dama dama*): a multispatial and multitemporal approach. Behavioral Ecology and Sociobiology 62, 1747–1759.

Ciuti, S., Davini, S., Luccarini, S., Apollonio, M., 2004. Could the predation risk hypothesis explain large-scale spatial sexual segregation in fallow deer (*Dama dama*)? Behavioral Ecology and Sociobiology 56, 552–564.

Colman, J.E., Jacobsen, B.W., Reimers, E., 2001. Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocation by humans on foot. Wildlife Biology 7, 275–283.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C., Festa-Bianchet, M., 2003. Undesirable evolutionary consequence of trophy hunting. Nature 426, 655–658.

de Boer, H.Y., van Breukelen, L., Hootsmans, M.J.M., van Wieren, S.E., 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildlife Biology 10, 35–41.

R Development Core Team, 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (Austria).

Di Bitetti, M.S., Paviolo, A., Ferrari, C.A., De Angelo, C., Di Blanco, Y., 2008. Differential responses to hunting in two sympatric species of Brocket Deer (*Mazama americana* and *M Nana*). Biotropica 40, 636–645.

Dorrance, M.J., Savage, P.J., Huff, D.E., 1975. Effects of snow-mobiles on white tailed deer. Journal of Wildlife Management 39, 563–569.

Duncan, P., Tixier, H., Hoffmann, R.R., Lechner-Doll, M., 1998. Feeding strategies and the physiology of digestion in roe deer. In: Andersen, R. (Ed.), The European Roe Deer: The Biology of Success. Scandinavian University Press, Oslo. pp. 91–118.

Enggist-Düblin, P., Ingold, P., 2003. Modelling the impact of different forms of wildlife harassment, exemplified by a quantitative comparison of the effects of hikers and paragliders on feeding and space use of chamois *Rupicapra rupicapra*. Wildlife Biology 9, 37–45.

Festa-Bianchet, M., Apollonio, M., 2003. Animal Behaviour and Wildlife Conservation. Island Press, Washington, DC.

Fischer, F., Linsenmair, K.E., 2001. Spatial and temporal habitat use of kob antelopes (*Kobus kob kob*, Erxleben 1777) in the Comoé National Park, Ivory Coast as revealed by radio tracking. African Journal of Ecology 39, 249–256.

Fischer, F., Linsenmair, K.E., 2002. Demography of a West-African kob antelope (*Kobus kob kob*) population. African Journal of Ecology 40, 130–137.

Flowerdew, J.R., Ellwood, S.A., 2001. Impacts of woodland deer on small mammal ecology. Forestry 74, 277–287.

Frid, A., 2003. Dall's sheep responses to overflights by helicopter and fixed-wing aircraft. Biological Conservation 110, 387–399.

Fuller, R.J., 2001. Responses of woodland birds to increasing number of deer: a review of evidence and mechanism. Forestry 74, 289–298.

Gaillard, J.M., Andersen, R., Delorme, D., Linnell, J.D.C., 1998. Family effects on growth and survival of juvenile roe deer. Ecology 79, 2878–2889.

Ginsberg, J.R., Milner-Gulland, E.J., 1994. Sex-biased harvesting and population dynamics in ungulate: implications for conservation and sustainable use. Conservation Biology 8, 157–166.

Grignolio, S., Rossi, I., Bassano, B., Apollonio, M., 2007. Predation risk as a factor affecting sexual segregation in Alpine ibex. Journal of Mammalogy 88, 1488–1497.

Harrington, F.H., Veitch, A.M., 1992. Calving success of woodland caribou exposed to low-level jet fighter overflights. Arctic 45, 213–218.

Hewison, A.J.M., Vincent, J.-P., Reby, D., 1998. Social organisation of European roe deer. In: Andersen, R., Duncan, P., Linnell, J.D.C. (Eds.), The European Roe Deer: The Biology of Success. Scandinavian University Press, Oslo. pp. 189–219.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54, 187–211.

Jayakody, S., Sibbald, A.M., Gordon, I.J., Lambin, X., 2008. Red deer *Cervus elaphus* vigilance behaviour differs with habitat type and human disturbance. Wildlife Biology 14, 81–91.

Jedrzejewski, W., Spaedtke, H., Kamler, J.f., Jedrzejewska, B., Stenkewitz, U., 2006. Group size dynamics of red deer in Bialowieza primeval forest, Poland. Journal of Wildlife Management 70, 1054–1059.

Jeppesen, J.L., 1987a. The disturbing effects of orienteering and hunting on roe deer (*Capreolus capreolus*). Danish Review of Game Biology 13, 2–25.

Jeppesen, J.L., 1987b. Impact of human disturbance on home range, movements and activity of red deer (*Cervus elaphus*) in a Danish environmental. Danish Review of Game Biology 13, 1–38.

Kamler, J.F., Jedrzejewska, B., Jedrzejewski, W., 2007. Activity patterns of red deer in Bialowieza National Park, Poland. Journal of Mammalogy 88, 508–514.

Kenward, R.E., South, A.B., Walls, S.S., 2003. Ranges & vl.2: for the analysis of tracking and location data. Anatrack Ltd., Wharehem (UK).

Kilgo, J.C., Labisky, R.F., Fritzen, D.E., 1998. Influences of hunting on the behaviour of white-tailed deer: implications for conservation of the Florida panther. Conservation Biology 12, 1359–1364.

Klein, R.G., 1989. The Human Career. Human Biological and Cultural Origins. University of Chicago Press, Chicago.

Kufeld, R.C., Bowden, D.C., Schrupp, D.L., 1988. Influence of hunting on movements of female mule deer. Journal of Range Management 41, 70–72.

Lamberti, P., Mauri, L., Apollonio, M., 2004. Two distinct patterns of spatial behaviour of female roe deer (*Capreolus capreolus*) in a mountain habitat. Ethology Ecology & Evolution 16, 41–53.

Madsen, J., 1985. Impact of disturbance on field utilization of Pink-footed Geese in West Jutland, Denmark. Biological Conservation 33, 53–63.

Madsen, J., Fox, A.D., 1995. Impacts of hunting disturbance on waterbirds – a review. Wildlife Biology 1, 193–207.

Main, M.B., Weckerly, F.W., Bleich, V., 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77, 449–461.

Manor, R., Saltz, D., 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecological Applications 13, 1830–1834.

McCullough, D.R., 1979. The George Reserve Deer Herd: Population Ecology of a K-Selected Species. University of Michigan Press, Ann Arbour.

McShea, W.J., Rappole, J.H., 1997. Herbivores and the ecology of forest understory birds. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The Science of Overabundance. Deer Ecology and Population Management. Smithsonian Institution Press, Washington. pp. 289–309.

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soil over a global range of environments. Ecological Monographs 63, 327–366.

Milner-Gulland, E.J., Coulson, T., Clutton-Brock, T.H., 2004. Sex differences and data quality as determinants of income from hunting red deer *Cervus elaphus*. Wildlife Biology 10, 187–201.

Mysterud, A., 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology, London 247, 479–486.

Author's personal copy

Nelson, M.E., Mech, L.D., 1986. Mortality of white-tailed deer in northeastern Minnesota. Journal of Wildlife Management 55, 172–176.
Neumann, W., Ericsson, G., Dettlki, H., 2009. The non-impact of hunting on moose *Alces alces* movement, diurnal activity, and activity range. European Journal of Wildlife Research 55, 255–265.
Nicholson, M.C., Bowyer, R.T., Kie, J.G., 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78, 483–504.
Nilsen, E.B., Linnell, J.D.C., Andersen, R., 2004. Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. Journal of Animal Ecology 73, 44–50.
Phillips, G.E., Alldredge, A.W., 2002. Reproductive success of elk following disturbance by humans during calving season. Journal of Wildlife Management 64, 521–530.
Proaktor, G., Coulson, T., Milner-Gulland, E.J., 2007. Evolutionary responses to harvesting in ungulates. Journal of Animal Ecology 76, 669–678.
Reimers, E., Loe, L.E., Eftestol, S., Colman, J.E., Dahle, B., 2009. Effects of hunting on response behaviors of wild reindeer. Journal of Wildlife Management 73, 844–851.
Rossi, I., Lamberti, P., Mauri, L., Apollonio, M., 2003. Home range dynamics of male roe deer *Capreolus capreolus* in a mountainous habitat. Acta Theriologica 48, 425–432.
Rost, G.R., Bailey, J.A., 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43, 634–641.
Ruckstuhl, K.E., Neuhaus, P., 2005. Sexual Segregation in Vertebrates – Ecology of the Two Sexes. Cambridge University Press, New York.
Saïd, S., Gaillard, J.-M., Duncan, P., Guillon, N., Guillon, N., Servanty, S., Pellerin, M., Lefeuvre, K., Martin, C., van Laere, G., 2005. Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. Journal of Zoology 267, 301–308.
Saïd, S., Gaillard, J.-M., Widmer, O., Débias, F., Bourgoin, G., Delorme, D., Roux, C., 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos 118, 1299–1306.
Sforzi, A., Lovari, S., 2000. Some effects of hunting in wild mammalian populations. Ibex Journal of Mountain Ecology 5, 165–171.
Shultz, R.D., Bailey, J.A., 1978. Responses of National Park elk to human activity. Journal of Wildlife Management 42, 91–100.
Sinclair, A.R.E., 1997. Carrying capacity and the overabundance of deer. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The Science of Overabundance. Deer Ecology and Population Management. Smithsonian Institute Press, Washington, DC, pp. 380–394.
Solberg, E.J., Loison, A., Ringsby, T.H., Saether, B.E., Heim, M.H., 2002. Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*. Wildlife Biology 8, 117–128.
St Clair, C.C.S., Forrest, A., 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, *Cervus elaphus*. Behaviour 146, 393–413.
Stankowich, T., 2008. Ungulate flight responses to human disturbance. A review and meta-analysis. Biological Conservation 141, 2159–2173.
Sunde, P., Olesen, C.R., Madesen, T.L., Haugaard, L., 2009. Behavioural response of GPS-collared female red deer *Cervus elaphus* to driven hunts. Wildlife Biology 15, 454–460.
Sutherland, W.J., 1998. The effect of local change in habitat quality on populations of migratory species. Journal of Applied Ecology 35, 418–421.
Sutherland, W.J., Gill, J.A., 2001. The role of behaviour in studying sustainable exploitation. In: Reynolds, J.D., Mace, G.M., Redford, K.H., Robinson, J.G. (Eds.), Conservation of Exploited Species. Cambridge University Press, UK, pp. 259–280.
Swenson, J.E., 1982. Effects of hunting on habitat use by mule deer on mixed-grass prairie in Montana. Wildlife Society Bulletin 10, 115–120.
Thomas, D.L., Taylor, E.J., 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54, 322–330.
Toïgo, C., Servanty, S., Gaillard, J.-M., Brandt, S., Baubet, E., 2008. Disentangling natural from hunting mortality in an intensively hunted wild boar population. Journal of Wildlife Management 72, 1532–1539.
Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C., Baubet, E., 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear Canadian. Journal of Zoology 87, 1129–1137.
Tufto, J., Andersen, R., Linnel, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65, 715–724.
Vogel, W.O., 1989. Response of deer to density and distribution of housing in Montana. Wildlife Society Bulletin 17, 406–413.
Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I., Ghani, A., 2001. Plant removals on perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. Ecological Monographs 69, 179–188.
Yarmoloy, C., Bayer, M., Geist, V., 1988. Behavior responses and reproduction of mule deer, *Odocoileus hemionus*, does following experimental harassment with an all-terrain vehicle. Canadian Field-Naturalist 102, 425–429.