






Research Article


Movement Responses of Roe Deer to Hunting Risk


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ABSTRACT Large herbivores respond to fluctuations in predation and hunting risk. The temporal scale of risk heterogeneity affects behavioral responses and determines the usefulness of metrics to quantify them. We present a conceptual framework to link anti-predator responses to risk fluctuations and appropriate metrics, based on temporal scale. We applied this framework to investigate movement responses of roe deer (*Capreolus capreolus*) to hunting risk, measured using movement rate and home range size. Because movements are also affected by reproductive phases, we considered potential effects of the rut in parallel to hunting risk. We compared movements of male and female roe deer in a protected site versus 2 hunted sites during and outside the hunting season and rut. We detected differences in movement rates in response to different hunting management practices. We did not detect effects for hunting regimes or between sexes during the rut when using home range size as the response variable. During the hunting season, movement rates were lower in the hunted sites than in the protected site, irrespective of sex. We did not observe differences in movement rates among sites outside of the hunting season. Males had higher movement rates than females during the rut in only 1 site. Our findings supported the hypothesis that roe deer decrease movements when exposed to high hunting risk. The effect of the rut on movements was negligible except for 1 study site. We suggest that movement rate is a more useful metric than home range size for assessing movement responses to hunting. © 2018 The Wildlife Society

KEY WORDS anti-predator behavior, *Capreolus capreolus*, home range size, hunting, Italian Alps, large herbivores, movement rate, predator-prey interactions, roe deer.

Predation and hunting can affect prey populations via complex pathways (Schmitz et al. 1997, Lima 1998, Creel and Christianson 2008) by changing abundance, sex ratio, or age composition (Loison et al. 1999, Milner et al. 2007, O’Kane and Macdonald 2016), or by triggering behavioral responses (Kilgo et al. 1998, Creel and Winnie 2005, Fortin et al. 2005). Spatio-temporal variation in predation risk is a necessary condition for behavioral responses to occur (Lima and Dill 1990, Creel et al. 2008, Laundré et al. 2010); particularly, temporal fluctuations of risk play a key role

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in determining the occurrence of responses (Lima and Bednekoff 1999). The risk allocation hypothesis (Lima and Bednekoff 1999) predicts optimal allocation of anti-predator behavior according to the temporal scale of risk; brief, acute pulses of risk should trigger prey responses more than chronic risk. Indeed, some studies have reported that anti-predator responses are less intense during chronic exposure to predation risk than in situations of episodic risk (Gude 2004, Creel et al. 2008; but see Ferrari et al. 2009). Moreover, the temporal scale of risk variation determines the temporal scale at which behavioral responses emerge (Basille et al. 2015). However, the relationship between temporal scales of risk and anti-predator responses has not been well defined.

Anti-predator responses of large herbivores can be thought of as hierarchically organized according to their range of temporal scales (Fig. 1). Flight responses emerge at very fine temporal

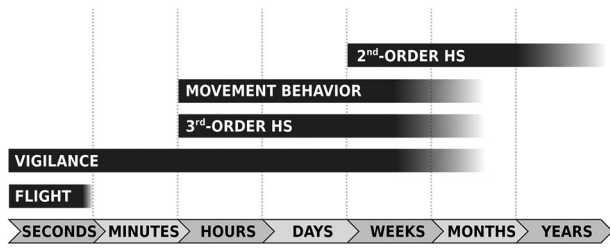


Figure 1. Conceptual representation of a hierarchy of anti-predator responses according to their temporal scale in large herbivores. The black segments depict the range of temporal scales at which responses have been reported in the literature on large herbivores. The faded right limit represents gradual signal decay. HS = habitat selection.

scales (e.g., seconds) as instantaneous reactions to predator detection (Stankowich 2008). Anti-predator responses also include behaviors that can manifest across a broader range of temporal scales. Within this range, the scale at which a response emerges is a function of the scale of risk in the system (see Table S1 for a non-exhaustive review, available online in Supporting Information). Vigilance responses can occur at fine temporal scales in response to short-term increases of perceived risk (Creel et al. 2014) but can persist over broader scales; prey may chronically increase their baseline levels of vigilance in habitats associated to high risk (Hunter and Skinner 1998, Laundré et al. 2001). Movement responses have been detected at the scale of hours or days in elk (*Cervus canadensis*) in response to short-term fluctuations of wolf (*Canis lupus*) predation risk (Proffitt et al. 2009), and at the seasonal scale in response to seasonal variation of hunting risk (Ciuti et al. 2012). Identifying the scale at which responses reflect the temporal scale of risk in a system is necessary for successfully detecting them. At finer scales, responses cannot be detected, as they have not emerged yet, and at broader scales, the signal dissipates (Hebblewhite and Haydon 2010).

Ecologically meaningful temporal scales affect the choice of appropriate metrics. For behaviors that are measurable in real-time, such as vigilance, it is sufficient to integrate measurements over the period of interest (Liley and Creel 2008 at the daily scale, Lung and Childress 2007 at the seasonal scale). However, metrics to quantify behaviors that are not measured in real time present challenges. For example, in large herbivores, movement data are most often acquired through telemetry at the scale of hours or longer. Movement responses have been investigated following 2 different approaches. The first focuses on distance traveled, using metrics such as movement rate (Ciuti et al. 2012). The second focuses on the area covered while moving, using metrics such as home range size (Grignolio et al. 2011). Both approaches quantify movement, but the first uses linear distance, and the second, spatial extent. Home range size is a derived estimate, whose reliability is influenced by the number of locations used to compute it (Swihart and Slade 1985, Seaman et al. 1999, Börger et al. 2006). Movement rate is conceptually and statistically a direct measure of movement because it reflects distance traveled and can be estimated at scales as fine as the resolution of the tracking data (Rhoads et al. 2010,

Owen-Smith et al. 2012). Movement rate is likely a preferable metric to quantify responses to risk because it allows for direct quantification of movement. An increased focus on the range of temporal scales covered by movement rate may lead to novel and relevant findings on anti-predator responses that cannot be captured using coarser metrics. Besides reflecting responses to predation risk, movement behavior may also be influenced by other factors (Frair et al. 2005). These include seasonal patterns such as environmental conditions (e.g., food availability) or reproductive phases (e.g., rut, territoriality, calving).

Roe deer (*Capreolus capreolus*) are the most abundant and widespread large herbivore in Europe and are hunted broadly. Male roe deer are territorial during the breeding season and access to territories is a key determinant of male reproductive success (Hewison et al. 1998). Males establish their territories in early spring and maintain them by intense patrolling until the end of the rut in late August (Hewison et al. 1998, Sempéré et al. 1998). Recent literature has highlighted the ecological effects of humans as predators, reinforcing the role of hunting as a form of predation risk (Frid and Dill 2002, Vermeij 2012, Darimont et al. 2015, Clinchy et al. 2016).

We present a framework to connect anti-predator responses to the pulses of risk that influence them and to metrics useful to quantify them, according to temporal scale. We aimed to isolate the effects of hunting by contrasting roe deer behavior under different management regimes in comparable conditions at the same time of the year. According to the predation risk allocation hypothesis (Lima and Bednekoff 1999), we expected a behavioral response from hunting because it occurred during a well-defined and relatively short time frame. We hypothesized that the temporal scale of variation of risk in our system (months) would affect movements (Fig. 1). We also considered potentially confounding effects of rutting behavior on roe deer movement.

We tested 2 research hypotheses. First, according to the hunting pressure hypothesis, roe deer will reduce their movements in response to hunting pressure. We expected roe deer to decrease their movements in hunted sites to levels lower than those observed in protected sites during the hunting season to reduce encounters with hunters; we expected no differences across study sites outside of the hunting season. Second, we tested the territoriality hypothesis, according to which male roe deer would exhibit more intensive movements than females during the rut (Liberg et al. 1998, Myrsterud et al. 2004). The difference in movement behavior between sexes would then dissipate after the rut, at the end of August. We expected male roe deer in all study sites to exhibit more intense movements during the territorial phase than females, and no difference between males and females after the end of the territorial phase. The hunting pressure hypothesis makes predictions on the relative difference in roe deer movement behavior between study sites in different months (regardless of sex), whereas the territoriality hypothesis makes predictions on the relative difference in movement behavior between sexes in different months (regardless of the study site).

STUDY AREA

We conducted our study in an 800-km² area in the Italian eastern Alps within the Autonomous Province of Trento during 2005–2013. The area had rugged terrain with elevations ranging 400–3,500 m (Cagnacci et al. 2011, Mancinelli et al. 2015, Peters 2015). The climate was continental in the lower valleys to alpine at the highest peaks (Ossi et al. 2015, Peters 2015). Average monthly temperature ranged between -1°C in December and 18°C in July (Ossi et al. 2015). During winter, snow cover was minimal (<20 cm) and discontinuous at the lowest elevations and deeper than 1 m above 1,600 m, where it persisted from December to April (Ramanzin et al. 2007). Agricultural fields dominated the valley bottoms along with deciduous forests, mainly composed by European beech (*Fagus sylvatica*) and European ash (*Fraxinus excelsior*, Peters 2015). At higher elevations, coniferous forests of Norway spruce (*Picea abies*), silver fir (*Abies alba*), and European larch (*Larix decidua*) were dominant (Peters 2015). Alpine grasslands interspersed with mountain pine (*Pinus mugo*) and rhododendron (*Rhododendron* spp.) were present above 1,600 m (Peters 2015). Large herbivore species included roe deer, chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus*), and ibex (*Capra ibex*; Peters 2015). Carnivores included red foxes (*Vulpes vulpes*) and reintroduced brown bears (*Ursus arctos arctos*) at low densities (Peters 2015). We conducted the study in a system of 3 sites (Fig. 2): the protected area on the summit of Mount Bondone, the slopes of Mount Bondone, and the contiguous Rendena Valley. In the first site, hunting was not allowed, whereas in the 2 latter sites hunting was allowed during the prescribed season. Hunting seasons started in the first week of September and were open through November (Provincia Autonoma di Trento, Servizio Foreste e Fauna 2005, 2012). Hunting pressure was concentrated in the first weeks and quotas were usually filled early. Hunting of other species did not temporally or spatially overlap with roe deer hunting.

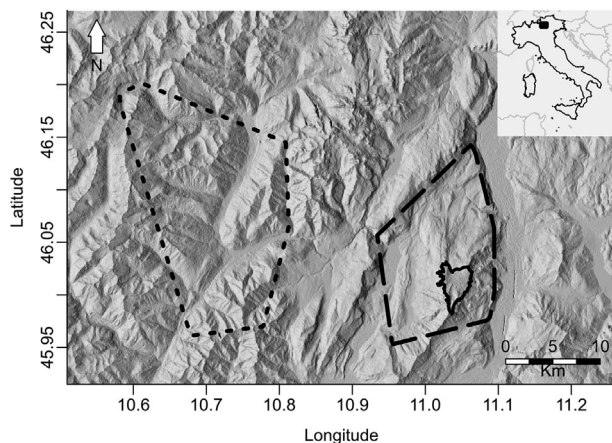


Figure 2. Roe deer study area in the eastern Alps, Autonomous Province of Trento, Italy, 2005–2013. The area is composed of 2 seasonally hunted sites, Rendena Valley hunted (dotted polygon) and Mount Bondone hunted (dashed polygon), and 1 protected site, Mount Bondone protected (solid polygon).

Table 1. Environmental characteristics ($\bar{x} \pm \text{SD}$) of 3 sites composing the study area in the eastern Alps, Autonomous Province of Trento, Italy, 2005–2013. Values for Mount Bondone hunted and protected refer to 2005–2006 and values for Rendena Valley hunted refer to 2012–2013, corresponding to the periods in which we studied roe deer in each site.

Characteristic ^a	Mount Bondone		Rendena Valley
	Protected	Hunted	Hunted
Conservation status	Protected	Hunted	Hunted
<i>n</i> individuals	12	11	9
Males	5	4	4
Females	7	7	5
Roe deer density (deer/km ²)	9.4	3.3	2.0
Elevation (m)	904 ± 284.43		1,047 ± 240.68
Slope (degrees)	22.89 ± 7.65		27.81 ± 6.60
Contingency	0.31 ± 0.05		0.30 ± 0.03
Constancy	0.31 ± 0.08		0.30 ± 0.06
Predictability	0.62 ± 0.07		0.60 ± 0.05
Winter severity (0–1)	0.22 ± 0.15		0.45 ± 0.12
Night lights	24.08 ± 16.38		11.60 ± 13.23
Canopy closure %	43.40 ± 9.69		51.85 ± 11.08
Agriculture %	22.20 ± 21.00		16.67 ± 17.29
Forest %	67.53 ± 20.98		75.83 ± 19.34
Winter temperature (°C)	1.82 ± 1.87		0.93 ± 0.00
Average NDVI	0.84 ± 0.03		0.83 ± 0.02

^a NDVI = normalized difference vegetation index. Contingency = seasonality of NDVI based on 16-day NDVI rasters. Constancy = between-year variability of NDVI based on 16-day NDVI rasters. Predictability = sum of contingency and constancy. Night lights = upwelling radiance from the Operational Linescan System.

Hunting was temporally segregated from the rut, which occurred between May and August (Hewison et al. 1998, Sempéré et al. 1998). The 3 sites were characterized by different densities and sex ratios (Table 1). Roe deer density was high (9 deer/km²; indirect distance sampling; F. Cagnacci, Edmund Mach Foundation, unpublished data) and the sex ratio was balanced in the protected site, as opposed to both hunted sites, where the density was modest (3.5 deer/km², Mount Bondone hunted) to low (2 deer/km², Rendena Valley) and the sex ratio was strongly female-biased (Provincia Autonoma di Trento, Servizio Foreste e Fauna 2016). Environmental conditions (Table 1) and hunting regulations (Provincia Autonoma di Trento, Servizio Foreste e Fauna 2005, 2012) were comparable between study sites at the time of data collection.

METHODS

For the test of the hunting pressure hypothesis, we contrasted roe deer movements in hunted versus protected sites, during and outside of the hunting season. We used the hunted sites in Rendena Valley and Mount Bondone as spatial treatment replicates, whereas we used the protected area on the summit of Mount Bondone as a control site. We used the months of September and October (hunting season) as temporal treatment replicates, and we used the month of August as a control. For the test of the territoriality hypothesis, we used territoriality as a treatment varying across time but not space. We used the month of August (rut) as a treatment in all study sites, and the months of September and October as controls in all study sites. Thus, the temporal arrangement of treatment and controls was opposite between the 2 hypotheses. When testing both hypotheses, we limited the data we used to these 3 months to avoid possible

confounding factors such as migration in early summer and late fall, or response to snow in late fall and winter. In general, environmental conditions and resource availability were homogeneous enough between August and October to allow us to rule out major confounding factors that could contribute to alter roe deer movement behavior. We used movement rate, defined as the distance traveled per hour, as a response variable to quantify a response of roe deer to hunting. We performed the same comparisons using home range size as a response variable.

We captured roe deer during the winters of 2004–2005 and 2005–2006 (Mount Bondone), and 2011–2012 and 2012–2013 (Rendena Valley) using drive nets or box traps at artificial feeding sites. Capture and handling protocols (23.09/2004 for Mount Bondone, 20.09/2011 for Rendena Valley) were approved by the Wildlife Committee of the Autonomous Province of Trento. We equipped adult individuals with global positioning system (GPS) collars (Vectronic Aerospace, Berlin, Germany) programmed to attempt a fix every 4 hours (Mount Bondone) or 3 hours (Rendena Valley). Our analysis used data from individuals for which data were available for the entire period of interest (Aug to Oct) for ≥ 1 season, and for animals in Mount Bondone that were either consistently outside or inside the boundaries of the protected area. This included 9 individuals in Rendena Valley (4 males, 5 females), 11 individuals in Mount Bondone outside of the protected area (4 males, 7 females), and 12 individuals in the protected area of Mount Bondone (5 males, 7 females).

We used GPS locations collected during 3 1-month-long intervals in August, September and October. We visually explored individual trajectories to identify excursions or migrations and, where necessary, we excluded such locations to include only within-home range movements. To compare data from different sampling schedules (3 hr for individuals collared in Rendena Valley and 4 hr for individuals collared in Mount Bondone), we standardized movement rate to the unit hour by dividing the step length (i.e., distance between consecutive GPS locations) by the temporal interval between consecutive GPS locations. We performed a preliminary

analysis to verify that hourly movement rates calculated based on the 2 different sampling schedules were comparable in an ecological context (Figs. S1 and S2, available online in Supporting Information). We estimated weekly home ranges using a 95% kernel utilization distribution (Calenge 2006). We performed all analyses in R 3.3.1 (R Core Team 2016), using the packages *adehabitatLT* for the handling of movement trajectories and *adehabitatHR* for the estimation of home range size (Calenge 2006).

We used information-theoretic model selection to test for the effects of study site, month, sex, and their interactions on movement rate and home range size, while accounting for possible individual differences in behavior. We used generalized linear mixed models (GLMMs) including study site, month, and sex as fixed effects and individual identity as a random effect for both movement rate and home range size as a response variable. For both response variables, we used GLMMs with a normal distribution after log-transformation to meet statistical assumptions. We based model selection on Akaike's Information Criterion corrected for small sample sizes (AIC_c) on a set of 24 models including a null model, 3 single-covariate models, 3 partial additive models (2 covariates), 3 partial interactive models (2 covariates and their interaction), a full additive model (3 covariates), and a full interactive model (3 covariates and their interactions), each with and without random effects. We used $\Delta AIC_c < 2$ as a model selection criterion and handled model uncertainty by computing confidence intervals. We evaluated predictions for the best model at the fixed effects level, and used a bootstrapping procedure to estimate 95% confidence intervals. We compared confidence intervals around estimates among experimental units to assess statistical significance of results. We considered significant differences where the 95% confidence intervals were not overlapping.

RESULTS

Roe deer movement rate was affected by study site, month, and sex (Fig. 3). The best-supported model was the full interactive model with random effect (Table 2), indicating

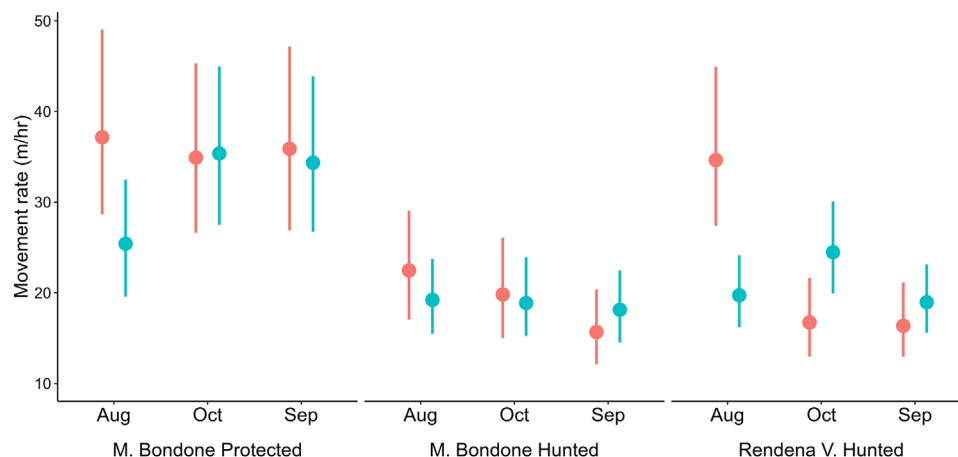


Figure 3. Movement rate of roe deer across site, month, and sex in the eastern Alps, Autonomous Province of Trento, Italy, 2005–2013. We provide maximum likelihood estimates and 95% confidence intervals. Red refers to males, blue to females. M = Mount. V = Valley.

Table 2. Model selection for movement rate of roe deer across site, month, and sex in the eastern Alps, Autonomous Province of Trento, Italy, 2005–2013 ($n = 13,870$ data points).

Model ^a	K	logLik	ΔAIC_c	ω
log(movement) ~ site × month × sex + (1 ID)	20	-21,667.28	0.00	>0.99
log(movement) ~ sex × month + (1 ID)	8	-21,726.49	94.38	<0.01
log(movement) ~ site × month + (1 ID)	11	-21,765.37	178.16	<0.01
log(movement) ~ site + month + (1 ID)	7	-21,786.75	212.89	<0.01
log(movement) ~ site + month + sex + (1 ID)	8	-21,787.92	217.25	<0.01
log(movement) ~ month + (1 ID)	5	-21,794.04	223.48	<0.01
log(movement) ~ sex + month + (1 ID)	6	-21,794.90	227.20	<0.01
log(movement) ~ site + (1 ID)	5	-21,807.97	251.33	<0.01
log(movement) ~ site + sex + (1 ID)	6	-21,809.19	255.76	<0.01
log(movement) ~ site × sex + (1 ID)	8	-21,810.26	261.92	<0.01
log(movement) ~ 1 + (1 ID)	3	-21,815.36	262.11	<0.01
log(movement) ~ sex + (1 ID)	4	-21,816.25	265.89	<0.01
log(movement) ~ site × month × sex	19	-21,868.43	400.31	<0.01
log(movement) ~ site × month	10	-21,993.91	633.23	<0.01
log(movement) ~ site + month + sex	7	-22,012.03	663.45	<0.01
log(movement) ~ site + month	6	-22,021.85	681.09	<0.01
log(movement) ~ site × sex	7	-22,030.98	701.36	<0.01
log(movement) ~ site + sex	5	-22,034.73	704.86	<0.01
log(movement) ~ site	4	-22,044.13	721.66	<0.01
log(movement) ~ month × sex	7	-22,177.00	993.40	<0.01
log(movement) ~ month + sex	5	-22,253.57	1,142.53	<0.01
log(movement) ~ sex	3	-22,274.22	1,179.83	<0.01
log(movement) ~ month	4	-22,273.48	1,180.36	<0.01
log(movement) ~ 1	2	-22,293.03	1,215.45	<0.01

^a Movement = movement rate; 1|ID = individual identity included as a random effect.

that all covariates interactively influenced deer movements, together with individual differences. Predictions for the top model indicated higher movement rates for males compared to females in August in Rendena Valley (mean difference = 14.9 m/hr) but no difference between the sexes in the other study sites (Table 3 and Fig. 3). Movement rate was not different between sexes in September and October in all study sites (Table 3 and Fig. 3). Comparing across sites, there were no differences in movement rate between sexes in August (Table 3 and Fig. 3). In September and October, movement rate was lower in the hunted sites compared to the

Table 3. Results of the best model of movement rate (log(m/hr)) of roe deer across site, month, and sex in the eastern Alps, Autonomous Province of Trento, Italy, 2005–2013. Pseudo- $R^2 = 0.062$. RVH = Rendena Valley hunted, MBH = Mount Bondone hunted.

Variable	β	SE	P
(Intercept)	3.62	0.14	<0.01
RVH	-0.07	0.19	0.71
MBH	-0.50	0.20	0.01
Female	-0.38	0.19	0.05
Sep	-0.03	0.06	0.58
Oct	-0.06	0.06	0.32
RVH × female	-0.18	0.25	0.47
MBH × female	0.22	0.27	0.40
RVH × Sep	-0.71	0.08	<0.01
MBH × Sep	-0.32	0.10	<0.01
RVH × Oct	-0.66	0.09	<0.01
MBH × Oct	-0.06	0.10	0.54
Female × Sep	0.34	0.09	<0.01
Female × Oct	0.39	0.09	<0.01
RVH × female × Sep	0.37	0.11	<0.01
MBH × female × Sep	-0.03	0.14	0.81
RVH × female × Oct	0.55	0.12	<0.01
MBH × female × Oct	-0.29	0.14	0.04

protected site for both sexes (range of mean difference = 15.1–20.2 m/hr). Comparing across months, there were no differences in movement rate within any site and for either sex, except for movement rate of males in Rendena Valley in August, which was higher compared to September and October (Table 3 and Fig. 3).

None of the 3 factors (study site, month, sex) explained the variance in home range size (Fig. 4). The null model with random effect had the lowest AIC_c value in the home range model set, but it was indistinguishable from the model with only study area as a fixed effect and a random effect, and from the interactive model with study area and sex (for both, $\Delta AIC_c < 2$; Table 4).

DISCUSSION

We found evidence that roe deer in the Italian Alps altered their movements in response to hunting risk, whereas activities associated with the rut did not appear to alter movement behavior in our system. Changes in movement rate, but not home range size, supported the hunting pressure hypothesis, suggesting that roe deer movements responded to hunting risk and this was best quantified with a fine-resolution metric. We did not find support for responses in movement rate or home range size under the territoriality hypothesis, except for the pattern observed for movement rate in Rendena Valley. This suggested that movement responses related to the rut may emerge in particular conditions, possibly mediated by density. Our findings highlighted the importance of investigating anti-predator responses using appropriate metrics for each question and system.

We found no differences between movement rate of males and females in any site and month except for Rendena Valley

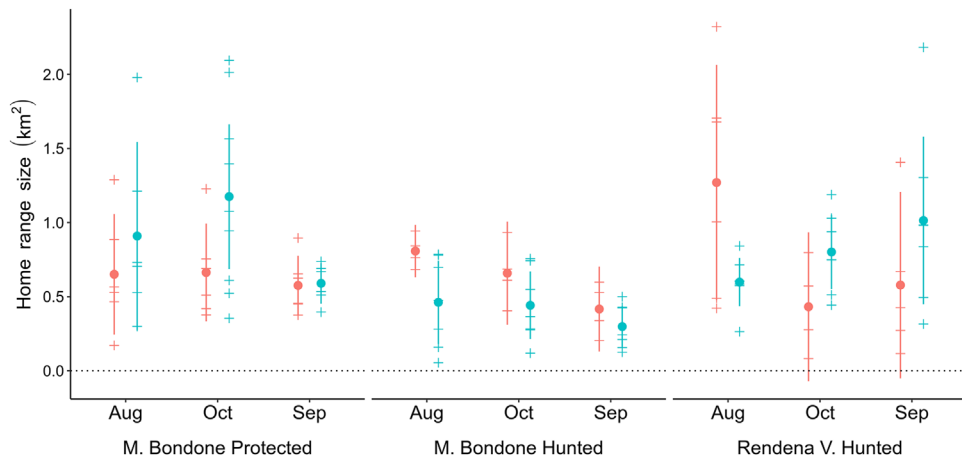


Figure 4. Home range size of roe deer across site, month, and sex in the eastern Alps, Autonomous Province of Trento, Italy, 2005–2013. We provide mean and standard deviation. Individual values are depicted as plus signs. Red refers to males, blue to females. M = Mount. V = Valley.

in August, where males had greater movement rates than females. Although the difference in mean movement rate between sexes was wider in August than in the other months in all sites and qualitatively compatible with the territoriality hypothesis, our results led us to reject this hypothesis. On the other hand, our results supported the hunting pressure hypothesis. We did not find differences across sites outside of the hunting season but found lower movement rates of both sexes in the hunted sites compared to the protected site during the hunting season, except for females in October in the Rendena Valley hunted site. We acknowledge that our study did not allow us to unequivocally isolate the effect of hunting from potential effects resulting from differences in

density and environmental conditions in different sites. Such differences, although minor, could influence the patterns we observed for movement rate. Particularly, roe deer density, winter severity, and proximity to urban areas differed among sites, but we did not formally control for these. The spatio-temporal arrangement of our experimental units, however, led us to conclude that any effects of such confounding factors were minimal. The Mount Bondone sites were contiguous, more similar in deer density, and sampled in the same years, whereas Rendena Valley was farther, had lower deer density, and was sampled in different years than the other sites. Yet, roe deer movement behavior was different during the hunting season between the 2 Mount Bondone

Table 4. Model selection for home range size of roe deer across site, month, and sex in the eastern Alps, Autonomous Province of Trento, Italy, 2005–2013 ($n = 108$ data points).

Model ^a	<i>K</i>	logLik	ΔAIC_c	ω
$\log(\text{home range}) \sim 1 + (1 ID)$	3	-105.38	0.00	0.30
$\log(\text{home range}) \sim \text{site} + (1 ID)$	5	-103.44	0.49	0.24
$\log(\text{home range}) \sim \text{site} \times \text{sex}$	7	-101.31	0.76	0.21
$\log(\text{home range}) \sim \text{sex} + (1 ID)$	4	-106.04	3.49	0.05
$\log(\text{home range}) \sim \text{site} \times \text{sex} + (1 ID)$	8	-101.70	3.87	0.04
$\log(\text{home range}) \sim \text{site} + \text{sex} + (1 ID)$	6	-104.20	4.24	0.04
$\log(\text{home range}) \sim \text{site}$	4	-106.55	4.51	0.03
$\log(\text{home range}) \sim \text{month} + (1 ID)$	5	-105.71	5.03	0.02
$\log(\text{home range}) \sim \text{site} + \text{month} + (1 ID)$	7	-103.80	5.73	0.02
$\log(\text{home range}) \sim \text{site} + \text{month}$	6	-105.01	5.86	0.02
$\log(\text{home range}) \sim \text{site} + \text{sex}$	5	-106.52	6.64	0.01
$\log(\text{home range}) \sim \text{site} + \text{month} + \text{sex}$	7	-104.98	8.09	<0.01
$\log(\text{home range}) \sim \text{month} \times \text{sex} + (1 ID)$	8	-103.91	8.29	<0.01
$\log(\text{home range}) \sim \text{month} + \text{sex} + (1 ID)$	6	-106.38	8.61	<0.01
$\log(\text{home range}) \sim \text{site} + \text{month} + \text{sex} + (1 ID)$	8	-104.55	9.57	<0.01
$\log(\text{home range}) \sim \text{site} \times \text{month} \times \text{sex}$	19	-90.51	10.66	<0.01
$\log(\text{home range}) \sim \text{site} \times \text{month}$	10	-103.08	11.44	<0.01
$\log(\text{home range}) \sim 1$	2	-113.29	13.71	<0.01
$\log(\text{home range}) \sim \text{site} \times \text{month} + (1 ID)$	11	-103.14	14.05	<0.01
$\log(\text{home range}) \sim \text{month}$	4	-111.84	15.09	<0.01
$\log(\text{home range}) \sim \text{sex}$	3	-113.29	15.83	<0.01
$\log(\text{home range}) \sim \text{month} \times \text{sex}$	7	-109.38	16.89	<0.01
$\log(\text{home range}) \sim \text{month} + \text{sex}$	5	-111.84	17.29	<0.01
$\log(\text{home range}) \sim \text{site} \times \text{month} \times \text{sex} + (1 ID)$	20	-92.74	18.16	<0.01

^a 1|ID = individual identity included as a random effect.

sites but consistent between the hunted sites of Mount Bondone and Rendena Valley. Our results are consistent with observations in the literature that large herbivores decrease movements to avoid predators (Frair et al. 2007, Ciuti et al. 2012, Marantz et al. 2016). Decreased movement in response to hunting may result in human-mediated trait-selection (Myserud 2011, Ciuti et al. 2012). If individuals that move more suffer reduced survival probabilities, hunters might exert a selective pressure favoring individuals that are more sedentary when exposed to risk of hunting mortality (Ciuti et al. 2012).

Roe deer respond to predation pressure at different temporal scales by an array of responses. Detection of a threat triggers flight responses modulated by sighting distance and habitat (Bonnot et al. 2017). Roe deer are more vigilant in response to episodic risk (Benhaïem et al. 2008, Eccard et al. 2017). When hunted, roe deer may use refugia (Grignolio et al. 2011) and alter habitat selection between daytime and nighttime (Bonnot et al. 2013). Our findings complement this body of literature, suggesting that roe deer respond to temporally heterogeneous risk conditions by altering their movements. A greater emphasis on the investigation of movement responses using fine-scale metrics may yield novel insight on how predation, hunting, or human disturbance may affect spatial behavior of large herbivores. Movement rate integrates immediate responses, such as flight, and longer-term responses, such as habitat selection, and allows for observing spatial responses at scales as low as hours.

In our study area, hunters were the only predator of adult roe deer at the time of the study. However, in other parts of Europe, roe deer populations are also subject to predation by large carnivores such as lynx (*Lynx lynx*) and wolves (Mattioli et al. 2004, Basille et al. 2009, Wikenros et al. 2009). Based on the risk allocation hypothesis, a chronic presence of predators could lead to attenuated predator responses compared to situations of episodic risk (Lima and Bednekoff 1999). Comparing our findings to roe deer responses to carnivore predation risk, or to combined human and carnivore predation in other parts of their distribution may provide insight on how the behavioral plasticity of roe deer fits in the theoretical framework of the risk allocation hypothesis.

Our results suggested that, in low-density conditions, territorial behavior may lead to more intense movements in male roe deer during the rut to compensate for the lower availability of females. On the other hand, higher density could make females more accessible to males, thus reducing male search effort (Myserud et al. 2004) and limiting movement of males for territory patrolling because of the emergence of social fence mechanisms (i.e., constraints to the spatial extent and arrangement of territories due to the presence of other individuals; Myserud et al. 2011). A better understanding of the role of density in mediating male behavior during the territorial phase would help shed light on a rarely addressed aspect of roe deer behavioral plasticity. Moreover, comparing mortality of male roe deer during and outside the territorial phase in the presence of natural

predators could improve our understanding of the implications of roe deer behavior in the context of a reproduction–safety trade-off.

We found no pattern for home range size between sexes, among study sites, or through time, which may reflect the inappropriateness of home range size as a metric for the response of interest. Home range size may present issues with sampling schedule at our scale of interest, in terms of number of locations and autocorrelation (Seaman et al. 1999, Girard et al. 2002, Börger et al. 2006). Monthly data at 3-hour and 4-hour resolution may not include enough independent locations to allow for robust estimation of roe deer home range size (Fig. S3, available online in Supporting Information). Because it summarizes a series of data points in a single value, home range size may also present problems with sample size that do not arise with other movement metrics (Girard et al. 2002). In this study, we used a minimum of 94 data points per individual when using movement rate as a response variable, versus a single value of home range size summarizing all data points for each individual and month. The number of individuals in our study may not have provided enough power to reach statistical significance when using 1 single compound value per individual, as with home range size. Using home range size to measure movement responses also introduces a conceptual mismatch between behavior and metric. Home range size quantifies the spatial extent of movements over an interval, which is the consequence of movement and not the behavior itself, adding an extra layer of processing between the behavior of interest and the measure.

Previous studies did not detect a movement response using home range size (Vercauteren and Hyngstrom 1998, Kilpatrick and Lima 1999, Jonsson et al. 2000, Lesage et al. 2000). The shortcomings we discussed, alone or in combination, may hinder the detection of responses that do in fact occur when home range size is the metric. Several other studies successfully detected movement responses using home range size (Bongi et al. 2008, Keuling et al. 2008, Grignolio et al. 2011). This discrepancy of results elsewhere suggests that home range size may not be a reliable metric for all systems or species. We stress the importance of selecting a metric that quantifies responses at a meaningful temporal scale given the scale of risk variation in the system. For example, Vercauteren and Hyngstrom (1998) used home range size over 6–8 weeks to quantify movement responses of white-tailed deer (*Odocoileus virginianus*) to a 3-day pulse of hunting risk and found no patterns. We suggest that movement behavior was measured at a temporal scale (6–8 weeks) that was too broad compared to the scale of risk in the system (3 days), potentially leading to detection failure. Unlike home range size, movement rate measures are already ecologically and statistically adequate at temporal scales as low as the resolution of the relocation data and can be integrated to investigate responses at broader scales according to the temporal scale of the driving factors. Echoing previous recommendations (Fieberg and Börger 2012), we advocate for careful selection of metrics to quantify responses at appropriate temporal scales and encourage an

increased use of movement rate as a metric of movement behavior.

MANAGEMENT IMPLICATIONS

When attempting to detect anti-predator responses for conservation or population management, we recommend adopting relatively fine-scale tracking schedules to secure sufficient data availability, ensuring matching between temporal scales of risk and expected responses, and choosing appropriate metrics to quantify the responses of interest. We recommend that these issues are addressed early on before data collection starts, adjusting for system-specific constraints and objectives. In the case of roe deer, we recommend to choose tracking schedules at the scale of hours or finer, and to use movement rate rather than home range size to quantify responses, especially when hunting risk fluctuates at the scale of months or finer.

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LITERATURE CITED

- Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J.-P. Ouellet, and R. Courtois. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology* 96:2622–2631.
- Basille, M., I. Herfindal, H. Santin-Janin, J. D. C. Linnell, J. Odden, R. Andersen, K. Arild Høgda, and J.-M. Gaillard. 2009. What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* 32:683–691.
- Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. J. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour* 76:611–618.
- Bongi, P., S. Ciuti, S. Grignolio, M. D. Frate, S. Simi, D. Gandelli, and M. Apollonio. 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.
- Bonnot, N. C., A. J. M. Hewison, N. Morellet, J.-M. Gaillard, L. Debeffe, O. Couriot, B. Cargnelutti, Y. Chaval, B. Lourtet, P. Kjellander, and C. Vanpé. 2017. Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Animal Behaviour* 124:35–46.
- Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research* 59:185–193.
- Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- Cagnacci, F., S. Focardi, M. Heurich, A. Stache, A. J. M. Hewison, N. Morellet, P. Kjellander, J. D. C. Linnell, A. Mysterud, M. Neteler, L. Delucchi, F. Ossi, and F. Urbano. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos* 120:1790–1802.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012. Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B: Biological Sciences* 279:4407–4416.
- Clinchy, M., L. Y. Zanette, D. Roberts, J. P. Suraci, C. D. Buesching, C. Newman, and D. W. Macdonald. 2016. Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. *Behavioral Ecology* 27:1826–1832.
- Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. *Trends in Ecology & Evolution* 23:194–201.
- Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology* 25:773–784.
- Creel, S., and J. A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69:1181–1189.
- Creel, S., J. A. Winnie, D. Christianson, and S. Liley. 2008. Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour* 76:1139–1146.
- Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. *Science* 349:858–860.
- Eccard, J. A., J. K. Meißner, and M. Heurich. 2017. European roe deer increase vigilance when faced with immediate predation risk by Eurasian lynx. *Ethology* 123:30–40.
- Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. *Animal Behaviour* 78:579–585.
- Fieberg, J., and L. Börger. 2012. Could you please phrase “home range” as a question? *Journal of Mammalogy* 93:890–902.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. *Journal of Wildlife Management* 71:541–554.
- Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20:273–287.
- Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6. <http://www.ecologyandsociety.org/vol6/iss1/art11/>. Accessed 21 Jun 2018.
- Girard, I., J.-P. Ouellet, R. Courtois, C. Dussault, and L. Breton. 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management* 66:1290–1300.
- Grignolio, S., E. Merli, P. Bongi, S. Ciuti, and M. Apollonio. 2011. Effects of hunting with hounds on a non-target species living on the edge of a protected area. *Biological Conservation* 144:641–649.
- Gude, J. A. 2004. Applying risk allocation theory in a large mammal predator-prey system: elk-wolf behavioral interactions. Thesis, Montana State University, Bozeman, USA.
- Hebblewhite, M., and D. T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2303–2312.
- Hewison, A. J. M., J. P. Vincent, and D. Reby. 1998. Social organisation of European roe deer. Pages 189–219 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, Norway.
- Hunter, L. T. B., and J. D. Skinner. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135:195–211.
- Jonsson, P., E. Koskela, and T. Mappes. 2000. Does risk of predation by mammalian predators affect the spacing behaviour of rodents? Two large-scale experiments. *Oecologia* 122:487–492.

- Keuling, O., N. Stier, and M. Roth. 2008. How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? *European Journal of Wildlife Research* 54:729.
- Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology* 12:1359–1364.
- Kilpatrick, H. J., and K. K. Lima. 1999. Effects of archery hunting on movement and activity of female white-tailed deer in an urban landscape. *Wildlife Society Bulletin* 27:433–440.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1–7.
- Lesage, L., M. Crête, J. Huot, A. Dumont, and J.-P. Ouellet. 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. *Canadian Journal of Zoology* 78:1930–1940.
- Liberg, O., A. Johansson, R. Andersen, and J. D. C. Linnell. 1998. Mating system, mating tactics and the function of male territoriality in roe deer. Pages 221–256 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, Norway.
- Liley, S., and S. Creel. 2008. What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology* 19:245–254.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27:215–290.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Loison, A., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and J.-M. Jullien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80:2539–2554.
- Lung, M. A., and M. J. Childress. 2007. The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behavioral Ecology* 18:12–20.
- Mancinelli, S., W. Peters, L. Boitani, M. Hebblewhite, and F. Cagnacci. 2015. Roe deer summer habitat selection at multiple spatio-temporal scales in an Alpine environment. *Hystrix—the Italian Journal of Mammalogy* 26:132–140.
- Marantz, S. A., J. A. Long, S. L. Webb, K. L. Gee, A. R. Little, and S. Demarais. 2016. Impacts of human hunting on spatial behavior of white-tailed deer (*Odocoileus virginianus*). *Canadian Journal of Zoology* 94:853–861.
- Mattioli, L., C. Capitani, E. Avanzinelli, I. Bertelli, A. Gazzola, and M. Apollonio. 2004. Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. *Journal of Zoology* 264:249–258.
- Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology* 21:36–47.
- Mysterud, A. 2011. Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Applied Ecology* 48:827–834.
- Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. *Journal of Zoology* 264:209–215.
- Mysterud, A., L. E. Loe, B. Zimmermann, R. Bischof, V. Veiberg, and E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes—a role for density dependence? *Oikos* 120: 1817–1825.
- O’Kane, C. A. J., and D. W. Macdonald. 2016. An experimental demonstration that predation influences antelope sex ratios and resource-associated mortality. *Basic and Applied Ecology* 17:370–376.
- Ossi, F., J.-M. Gaillard, M. Hebblewhite, and F. Cagnacci. 2015. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. *European Journal of Wildlife Research* 61:111–124.
- Owen-Smith, N., V. Goodall, and P. Fatti. 2012. Applying mixture models to derive activity states of large herbivores from movement rates obtained using GPS telemetry. *Wildlife Research* 39:452–462.
- Peters, W. E. B. 2015. Run to the hills: partial migration in large herbivores. Dissertation, University of Montana, Missoula, USA.
- Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *Journal of Wildlife Management* 73:345–356.
- Provincia Autonoma di Trento, Comitato Faunistico Provinciale. 2005. Prescrizioni tecniche per l’esercizio della caccia in Trentino, 2005–2006. Servizio Foreste e Fauna, Trento, Italy.
- Provincia Autonoma di Trento, Comitato Faunistico Provinciale. 2012. Prescrizioni tecniche per l’esercizio della caccia in Trentino, 2012–2013. Servizio Foreste e Fauna, Trento, Italy.
- Provincia Autonoma di Trento, Ufficio Faunistico. 2016. Analisi delle consistenze e dei prelievi di ungulati, tetraonidi e coturnice, stagione venatoria 2016. Servizio Foreste e Fauna, Trento, Italy.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramanzin, M., E. Sturaro, and D. Zanon. 2007. Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. *Canadian Journal of Zoology* 85:280–289.
- Rhoads, C. L., J. L. Bowman, and B. Eyster. 2010. Home range and movement rates of female exurban white-tailed deer. *Journal of Wildlife Management* 74:987–994.
- Schmitz, O. J., A. P. Beckerman, and K. M. O’Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- Seaman, D. E., J. J. Millsbaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- Sempéré, A. J., R. Maugey, and C. Maugey. 1998. Reproductive physiology of roe deer. Pages 161–188 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, Norway.
- Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation* 141:2159–2173.
- Swihart, R. K., and N. A. Slade. 1985. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management* 49:1019–1025.
- Vercauteren, K. C., and S. E. Hygnstrom. 1998. Effects of agricultural activities and hunting on home ranges of female white-tailed deer. *Journal of Wildlife Management* 62:280–285.
- Vermeij, G. J. 2012. The limits of adaptation: humans and the predator-prey arms race. *Evolution* 66:2007–2014.
- Wikenros, C., H. Sand, P. Wabakken, O. Liberg, and H. C. Pedersen. 2009. Wolf predation on moose and roe deer: chase distances and outcome of encounters. *Acta Theriologica* 54:207–218.

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