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Wolf predation on wild ungulates: how slope and habitat cover influence the localization of kill sites

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Abstract

Based on data collected along the Ligurian Apennines and Alps (N-W Italy), we analysed the main environmental and human-related factors influencing the distribution of kill sites of the wolf *Canis lupus*. We mapped and digitized 62 kill sites collected during 2007–2016. Around each kill site, we defined a buffer corresponding to the potential hunting area of wolves. We compared kill site plots and an equal number of random plots. We formulated a model of kill site distribution following an approach presence versus availability by binary logistic regression analysis; we tested the hypothesis that wolf choice of kill sites is influenced by the physiography and the land use of the area. Among the preyed wild ungulates, we identified 23 roe deer *Capreolus capreolus*, 18 fallow deer *Dama dama*, 16 wild boars *Sus scrofa*, and 5 chamois *Rupicapra rupicapra*. Binary logistic regression analysis showed a negative effect of the road density, the urban areas, the mixed forests, and a positive effect of steep slopes and open habitats. Prey are more vulnerable to predators under certain conditions and predators are capable of selecting for these conditions. Wolves achieved this by selecting particular habitats in which to kill their prey: they preferred steep, open habitats far from human presence, where wild ungulates are more easily detectable and chasable.

Key words: *Canis lupus*, hunting habits, kill site distribution modeling, predator–prey interaction, wild ungulates.

Among key factors of predator-prey interactions there is the use of the space, as prey tend to minimize, while predators tend to maximize their spatial overlap (Sih 2005). Usually predators occupy territories encompassing multiple prey species and adapt their spatial and temporal behavior depending on the abundance, distribution, and ecology of prey, in order to increase their encounter rate with them (Jenny and Zuberbühler 2005; Harmsen et al. 2011; Torretta et al. 2016). While hunting, predators need to not only identify space where they can obtain a higher probability of encounter with prey, but also habitats that might increase their predation success. The idea introduced by McPhee et al. (2012) is that predation can be considered a "hierarchical process," whereby predators are constrained to kill prey within the area they select while hunting. Therefore, kill sites are not randomly distributed (Hebblewhite et al. 2005; Kauffman et al. 2007); rather, where kill sites occur is a

function of prey distribution and predictability and environmental factors that influence prey detection, access, or the success of an attack (McPhee et al. 2012).

Environmental factors may affect both anti-predator and hunting strategy of prey and predators. In particular, anti-predator and hunting strategy may vary depending on the type of habitat (Gervasi et al. 2013), and the degree of habitat fragmentation (Zimmermann et al. 2014). The chance of a successful hunt for a predator depends on the habitat type where it detects its prey and on the terrain through which the pursuit takes place (Gorini et al. 2012). For example, certain types of habitat may provide refugia from predation and others may affect the degree of visibility influencing prey group size, vigilance, or activity patterns (Gorini et al. 2012 and references therein). On the other hand, the cover present where prey is detected can affect the distance at which the chase can start (Husseman et al. 2003). The physical structure of

habitats may allow prey to detect predators before these are within the killing distance and thus allowing prey escape (Kunkel and Pletscher 2001).

During the past decades, humans have played, and still play, a keystone role in shaping habitats characteristics. Most of the habitat changes resulted from human activities: habitat loss and deterioration due to human exploitation, habitat fragmentation by transport and power lines, and habitat requalification have all an impact on ecosystems at various trophic levels (Vitousek et al. 1997, Ryall and Fahrig 2006). Many researchers recognized the high variability in the behavioral responses of carnivores to anthropogenic disturbances (Hebblewhite and Merrill 2008) and their potentially important impacts on community structure and on predator–prey interactions (Hebblewhite et al. 2005).

Wolves *Canis lupus* locally adapt their habits depending on those of their prey species, as they showed substantial spatial and temporal overlap with species that constitute the bulk of their diet (Torretta et al. 2016). At the same time, their movements and behaviors are considerably affected by increasing intensity of human presence, which could give less time to search for the prey, to hunt, to access, and consume an item (Musiani et al. 2010). Furthermore, species' habitat selection patterns at a fine scale are influenced by complex interactions between habitat attributes and human disturbances (Lesmerises et al. 2012).

Wolves are generalist apex predators, preying mainly on wild ungulates (Peterson and Ciucci 2003, Mech et al. 2016). Packs roam within their exclusive territory and their members cooperate during the hunt (Mech and Boitani 2003). Wolves are well adapted for cursorial predation with chases ranging from 100 m to >5 km (Mech and Boitani 2004). Many studies found that habitat characteristics mediate predation by influencing the successful identification, the pursuit, and the capture of prey (Kunkel and Pletscher 2000, 2001; Kauffman et al. 2007; McPhee et al. 2012). The aim of this study is to identify the main environmental and human-related factors influencing the distribution of kill sites of the wolf in a Mediterranean region, that is, the Ligurian Apennines and Alps (N-W Italy).

Materials and Methods

Study area

The study was carried out in Liguria (5,343 km² region in N-W Italy; Figure 1); it is characterized by a broad altitude range, from 0 to 2,200 m a.s.l. Climate is temperate continental with the eastern part of the region being more rainy and humid (inland average annual precipitation: 2,000 mm) than the western part (1,000 mm). Forests cover 63.7% of the whole area (broad-leaved woods: 28.7%; coniferous woods: 7.1%; mixed woods: 27.9%). Pastures and scrublands cover 5.3% and 10.3%, respectively. Cultivated lands (12%) are localized along main valleys and permanent crops are dominated by olive trees and vineyards. Urban areas (6.3%) are concentrated near the coasts and along flat and wide valleys.

The wild ungulate community includes the wild boar *Sus scrofa*, widely distributed with high densities (more than 20,000 individuals shot per year), the roe deer *Capreolus capreolus*, abundant in particular in the central part of the region (30.9 individuals per km²), the fallow deer *Dama dama*, present in the provinces of Genoa and Savona (10.7 and 5.8 individuals per km², respectively), and the chamois *Rupicapra rupicapra*, present only in the Alps (14.6 individuals per km²) (Wildlife Services of Ligurian Provinces, unpublished data). Hunters annually harvest these ungulate species. Moreover, the red deer *Cervus elaphus* has a

sporadic presence along the boundaries with Piedmont and Emilia Romagna regions.

Noninvasive genetic sampling estimated a minimum of 5 wolf packs between 2007 and 2013, with an average pack size of 4.2 ± 0.8 individuals (mean $\pm$ SD; Imbert et al. 2016).

Data collection and analysis

We monitored wolf presence using the Tessellation Stratified Sampling (TSS) method (Barabesi and Franceschi 2011), which allows a better distribution of random samples and increases their representativeness (Buckland et al. 2004; Barabesi and Fattorini 2013). Based on the estimated extent of an Apennines wolf pack territory (Ciucci et al. 1997; Caniglia et al. 2014), we subdivided the study region into 60 sample units of 10×10 km grid, as it corresponds to the average space requirements of a pack (Jędrzejewski et al. 2008). In every sample unit, we randomly selected 1 transect among the existing footpaths or secondary roads (total length 288 km; min. = 2.6 km; max. = 10.4 km). From 2007 to 2014, we walked this transect net once a season (Spring: March–May; Summer: June–August; Autumn: September–November; Winter: December–February), so 4 times during each year, to collect wolf signs of presence (scats, prints, carcasses of preyed ungulates, urine), which were located with a GPS recorder and geo-referred using ArcGIS 9.3 (UTM coordinate system, WGS84-32N).

Collected samples corresponding to fresh scats, picking out the external portions, urine, and hair were addressed to genetic analysis. The protocol used for the DNA extraction and analysis was fully explained in Imbert et al. (2016).

We delineated wolf range using the coordinates of genotypes belonging to wolves. We used a fixed kernel estimator (Seaman and Powell 1996) and applied the reference smoothing factor (h_{ref}). We considered 95% isoplethes delineating wolf range (Laver and Kelly 2008).

We considered all the carcasses of wild ungulates preyed by wolves, both those detected during the monitoring and those reported and verified by trained people (e.g., wildlife researchers and volunteers involved in the monitoring) recorded during 2007–2016, reporting the preyed species and possibly some related information (sex, age, proportion of consumption). We ascribed predation events to wolf by observing the carcasses (shape and localization of wounds, consumption, and spacing of canine puncture wounds) and the surroundings of the kill site (wolf signs of presence, e.g., scats, prints, and scratches). Around each kill site we defined a circular buffer corresponding to the potential hunting area of wolves. We used a width of 13 km, corresponding to the average travel distance of wolves during the night to go from dens or resting sites to hunting sites in Italy (Ciucci et al. 1997). We compared the plots where kill sites were recorded and an equal number of random plots within the estimated wolf range. We formulated a model of kill site distribution following an approach presence versus availability by binary logistic regression analysis (BLRA); we tested the hypothesis that wolf choice of kill sites is influenced by the physiography and the land use of the area. In each plot, we measured from the Corine Land Cover III level (scale 1:25,000) and the Digital Elevation Models (DEM; cell size 250 m) the environmental variables used to model the kill site distribution: four slope classes, road and path density, forests, urban and cultivated areas, scrublands, open areas, and bare ground (Table 1). We ran the logistic regression (link function "logit") using the stepwise forward method; we set the Alpha-to-Enter = 0.05 and the Alpha-to-Remove = 0.10. We considered potential multicollinearity among variables using the variance inflation
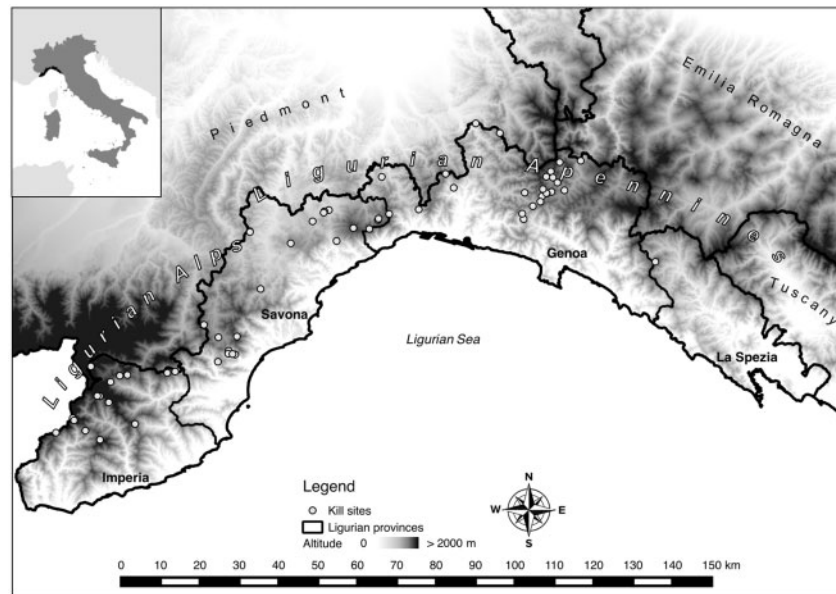
Figure 1. On the top Liguria (in black) within Italy (dark gray); Liguria region with political boundaries (provinces) and wolf kill sites (dots) collected during 2007–2016.

Table 1. Ecogeographical variables measured in the 13-km buffers around the kill sites and used to model kill site distribution

Name	Description	Unit
Slope 0°–19°		%
Slope 20°–39°		%
Slope 40°–59°		%
Slope > 60°		%
Road density	Paved roads	km/km^2
Path density	Paths and gravel roads	km/km^2
Urban areas	Villages, industrial areas, transport units, urban parks	%
Broad-leaved forests		%
Coniferous forests		%
Mixed forests		%
Open areas	Pastures and natural grasslands	%
Cultivated lands	Arable lands and permanent crops	%
Scrublands	Shrub and herbaceous vegetation associations	%
Bare grounds	Rocks and areas with little or no vegetation cover	%

factor (VIF); we retained VIF = 3 as threshold value (Zuur et al. 2010; Dormann et al. 2013). We tested the model performance by the percentage of correct classifications of original cases, Nagelkerke's R^2, the receiver operating characteristic (ROC) curve analysis, and the Hosmer–Lemeshow Goodness of Fit Test (Hosmer and Lemeshow 2000).

Results

On average we surveyed 77.8% of transects per season. We identified 74 distinct wolf genotypes, corresponding to 189 non-invasive DNA samples (98% feces, 1% urine, and 1% hair), collected in the study area from 2007 to 2014; moreover, we identified 12 samples belonging to wolves but without individual identification. Based on

locations of wolf genotypes, pooled across years, we estimated a wolf range with a total extent of 5,068 km^2.

We mapped and digitized 62 kill sites by ArcGis 9.3; 57 cases were collected from 2007 to 2014 during the wolf monitoring project and 5 were collected in 2015–2016 (Figure 1). Among the preyed wild ungulates, we identified 23 roe deer (37.1%), 18 fallow deer (29%), 16 wild boars (25.8%), and 5 chamois (8.1%). We found 1 prey in each kill site, with the exception of a multiple kill of fallow deer ($n = 3$).

More than half of the carcasses were found during the snow cover season (from January to March; $n = 38$). 15 carcasses were found in the altitude range 400–800 m a.s.l.; 29 carcasses in the range 800–1,200 m; 12 carcasses in the range 1,200–1,600m; 6 carcasses in the range 1,600–2,000 m.

BLRA showed a negative effect of the mixed forests, the urban areas, and the road density, the latter without statistical significance, a positive effect of steep slopes (> 60°) and open areas. VIF values of these predictor variables (< 3) indicated the absence of serious multicollinearity (Table 2).

The logistic model explained 45.6% of the variance of the response variable and correctly classified 76.6% of original cases, 82.3% of kill sites, and 71% of control ones. The area under the ROC curve was significantly greater than that of a model that randomly classifies the cases (AUC = 0.828 ± 0.037; $P < 0.001$). Finally, the P-value of the Hosmer–Lemeshow Goodness of Fit Test was > 0.05 indicating a very good model fit (Table 2).

Discussion

The environmental factors influencing the distribution of wolf kill sites detected in this study only partially correspond with those reported from previous studies. Wolf kill sites in Liguria were steep, open habitats (e.g. pastures and grasslands) far from roads and urban areas.

In agreement with Kunkel and Pletscher (2001), we found that hiding-cover levels were lower at kill sites than at random sites.

Table 2. Results of logistic regression analysis between kill sites plots ($n = 62$) and random ones ($n = 62$)

Predictor variables	B	SE	P	e^β (odds ratio)	VIF
Slope $> 60°$	0.749	0.309	0.015	2.116	1.901
Road density	−0.766	0.425	0.071	0.465	1.941
Mixed forests	−1.224	0.420	0.004	0.294	1.551
Open areas	0.685	0.259	0.008	1.984	1.066
Urban areas	−1.210	0.604	0.045	0.298	2.287
Constant	−0.444	0.297	0.135	0.641	
Hosmer–Lemeshow test	$X^2 = 4.360$	$df = 8$	0.823		

Indeed, dense cover can affect the prey capacity to exploit refuges, thus enhance its chances of escaping an attack, and can increase the chance of detection of the predator, because of its noisier approach (Balme et al. 2007). From the prey point of view, open habitats, as pastures and grasslands, usually imply high visibility and high encounter rates with predators but also cause to be more easily alerted, and thus affect the distance at which a hunter may start the chase attempt (Mills et al. 2004). From the predator point of view, in open habitats, prey were easier to locate and catch. Wild ungulates mainly use open habitats during the night as feeding areas, because of the higher quality resources, and more closed habitats during the day, with less forage but a higher degree of shelter (Bonnot et al. 2013 and references therein). Hence, wolves have greater chances of encountering wild ungulates while feeding in open areas. Wild ungulates have to face a constant trade-off between the choice of better food patches and predation risk. This trade-off is mediated by the vigilance behavior, which requires exclusive visual attention to scan the environment, thereby interrupting or slowing down foraging activity (Lima 1995). Wolves usually take advantage of this wavering behavior to start the rush. Moreover, wolves are mainly active from dawn to dusk and this is probably closely related to their hunting pattern, which matches with the activity patterns of wild ungulates (Theuerkauf et al. 2003b, Torretta et al. 2016). If wolves chase prey, open areas might be more suitable to finally kill the prey as they can attack them simultaneously from several sides (Theuerkauf and Rouys 2008).

An interesting, and not of secondary importance, finding of our research was the effect of steep surfaces on kill site location. In our mountainous study area, terrain features appeared to be important in the wolf hunting strategy. In contrast to Kauffman et al. (2007), which found that flat areas were the optimal hunting grounds for wolves, we found a positive effect of steep areas. In Liguria, flat areas usually occur at the valley bottom and close to the shoreline, where human presence is very high. Wolves may find a suitable habitat by selecting steep slopes, in terms of advantage during hunting activities: being on a vantage point possibly with few visual barriers, steep surfaces could enhance the wolf ability to sort through a prey group and scan its members to identify most vulnerable individuals. In addition, Gula (2004) found that wolves killed most of their prey in creeks and deep ravines, where wild ungulates may be easier to intercept, as they have to slow down and change gait.

Similarly to other researches, along the Liguria region, wolves avoid areas with high road and human settlement densities (Theuerkauf et al. 2003a). Roads and urban areas may be barriers to wolf movements and a cause of direct mortality both from vehicle collisions and illegal killing (Kaartinen et al. 2005; Lovari et al. 2007). Moreover, human disturbance associated with roads and urban areas may deter or interfere with wolves when attempting to kill prey, or afterward during carcass consumption. In addition,

Muhly et al. (2011) suggested that high-human activity on roads and trails displaced predators but not prey species, creating spatial refuge from predation during non-hunting seasons. Despite the fact that encounters between wolves and ungulates might be more frequent near linear features, as roads and trails (James and Stuart-Smith 2000; Kunkel and Pletscher 2000; Whittington et al. 2011), the kill sites could be further away after the chase.

In conclusion, although wolves select densely covered habitats to spend most of their time within their territory, they seem to select different habitats, while hunting, to finally kill prey. Forest cover was an important habitat variable influencing wolf distribution and numbers (Jędrzejewski et al. 2004), the localization of dens and *rendez-vous* sites (Capitani et al. 2006), and ensuring abundance of prey species, that is, wild ungulates. Because wolves are socially organized in structured packs hunting within stable and exclusive territories, they know where to find wild prey and where these prey can be most vulnerable to their cursorial predation strategy (Bergman et al. 2006). Hebblewhite et al. (2005) found that topographic features and habitat (i.e., vegetation) determined patterns of wolf–prey encounters and mediated post-encounter outcomes. Pastures and natural grasslands lying along forest edges may correspond to optimal habitats where to find abundant ungulates, particularly during feeding time, and steep slopes guaranteed a vantage position during the stalk, the encounter, the rush, and the chase of prey (Peterson and Ciucci 2003). At the same time, open habitats do not provide refuges to prey and steep terrain may impose a slow escape, increasing the probability of capture.

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