



Anthropogenic environmental traps: Where do wolves kill their prey in a commercial forest?



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ABSTRACT

Selection of kill sites is an important part of predation. In human-modified habitats, anthropogenic landscape features may increase or decrease hunting efficiency of predators. We investigated which habitat attributes increase predation success in wolf *Canis lupus* hunting for ungulates in an intensively managed forest of western Poland. We used GPS telemetry and snow-tracking to locate kill sites. Habitat characteristics of 66 kill sites differed from those of 66 non-kill sites. Proximity of habitat edges, waterbodies or watercourses, and forestry fences increased the probability of a successful kill. Kill-site characteristics differed between the two main prey species. Red deer *Cervus elaphus* were killed mostly near habitat edges and water (81% and 36% of kill sites, respectively), and in younger forest stands. Roe deer *Capreolus capreolus* were killed primarily near forestry fences (43% of kill sites). We conclude that forestry management may influence prey vulnerability and prey selection by wolves. Management practices create environmental traps (e.g. fences, habitat edges) that help wolves to kill their prey. This knowledge can be applied in forest management to facilitate ungulate-damage prevention, for instance by small instead of large-scale clear-cuts. Our results also suggest that keeping some natural habitat elements such as swamps, ponds or fallen trees may positively correlate with wolf hunting efficiency and possibly add to the ungulate control in commercial forests. Therefore, the presence of wolves in commercial forests may be a situation with benefits for forestry and wolf conservation.

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1. Introduction

Hunting efficiency influences predator fitness, and as such, is under strong natural selection (Krebs, 1978; Barbosa and Castellanos, 2004). Predators may optimise their feeding by selecting habitats that offer the best hunting opportunities in terms of net energy gain (Stephens and Krebs, 1986). Different landscape and habitat attributes may be important at different stages of predation (Hebblewhite et al., 2005; Hopcraft et al., 2005; Davidson et al., 2012; McPhee et al., 2012). This creates heterogeneity in predation risk across the landscape (Lima and Dill, 1990; Hebblewhite et al., 2005). Where predators choose to hunt is affected by prey density, detectability and predictability (Travis and Palmer, 2005; Nachman, 2006), but kills occur in areas where the prey is easy to capture, which may not necessarily coincide with areas of high

prey density (Bergman et al., 2006; Theuerkauf and Rouys, 2008; McPhee et al., 2012). This phenomenon has been reported in both ambush predators (Hopcraft et al., 2005; Podgórski et al., 2008) and coursing predators (Gula, 2004; Rhodes and Rhodes, 2004; Kauffman et al., 2007). Several habitat features may provide stalking cover for a predator or impede the escape of prey (Hopcraft et al., 2005; Balme et al., 2007; Halofsky and Ripple, 2008).

The selection of hunting areas and characteristics of kill sites also depend on which prey is the target (Barbosa and Castellanos, 2004). Body size, vigilance, social behaviour, active defence and speed of escape affect relative prey catchability and energetic value, and thus contribute to optimal prey choice in generalist predators (Barbosa and Castellanos, 2004; Benhaiem et al., 2008). Finally, various prey species differ in habitat use, which may in turn influence space use by predators during hunting (Barbosa and Castellanos, 2004; Schartel and Schaubert, 2016). Therefore, the association between hunting success and habitat characteristics strongly depends on the target species (Fuller et al., 2007; Schartel and Schaubert, 2016).

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Human-mediated changes in the landscape can affect predator-prey relationships (Wittmer et al., 2007; Kuijper et al., 2016). Such changes include landscape transformations caused by agricultural practices (Sweitzer et al., 1997) and habitat fragmentation (Crooks and Soulé, 1999). Forest management practices can also alter habitat and modify the rates and spatial patterns of predation (Kunkel and Pletscher, 2000). Intensive forest management is considered to negatively affect some predators, especially large carnivores that often suffer from logging-related disturbance and associated road development (Nielsen et al., 2008). Intensive forestry practices simplify forest stands, which may deteriorate foraging conditions for carnivore species that need stalking cover and habitat complexity to kill their prey (Podgórski et al., 2008). On the other hand, forest management may help to improve predation success of carnivores. For instance, logging often leads to increased fragmentation, which exposes animals to predation, as reported in birds (reviewed in Stephens et al., 2004) and woodland caribou *Rangifer tarandus* (Bergerud and Ballard, 1988). However, the effects of man-made habitat alterations on predator-prey systems remain largely unknown. Understanding these effects is crucial for effective conservation of large carnivores, especially nowadays, while they are returning to their former, meanwhile usually modified, habitats (Chapron et al., 2014).

Several studies showed that wolves *Canis lupus* select frozen water bodies, streams, deep snow, slopes, or habitat edges to kill their prey (Gula, 2004; Hebblewhite et al., 2005; Bergman et al., 2006; Ripple and Beschta, 2006; Kauffman et al., 2007; McPhee et al., 2012; Gervasi et al., 2013). The habitat characteristics of kill sites vary among study areas, prey species, and prey age (Gervasi et al., 2013; Montgomery et al., 2014). The spatial patterns of predation risk caused by wolves may vary even among sympatric prey species, due to their different distribution and antipredator behaviour (Gervasi et al., 2013; Mech et al., 2015). However, most of the above-mentioned studies were conducted in protected areas of North America, which offer heterogeneous and relatively unchanged habitats (but see Gervasi et al., 2013). In contrast, wolves recolonising forests of Central and Western Europe must cope with heavily modified, human-dominated landscapes (Chapron et al., 2014). In western Poland, wolves became rare after a state-sanctioned eradication programme in the 1960s and 1970s (Okarma, 1993). After increased recovery and population growth since 2000, wolves have now settled in most of the large forested areas of western Poland, preying mostly on red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, and wild boar *Sus scrofa* (Nowak et al., 2011; Nowak and Mysłajek, 2016). These three ungulate species differ considerably in body size, food habits, habitat use, maximal running speed and anti-predator responses (Garland, 1983; Matrai and Kabai, 1989; Borkowski, 2004; Heard-Booth and Kirk, 2012; Kuijper et al., 2014). For example, the roe deer is a small ungulate feeding mainly on forbs, whereas the larger red deer prefers grasses and sedges (Latham et al., 1999). Unlike roe deer, adult red deer sometimes stand their ground and fight the wolves when attacked, or they escape to water (Mech et al., 2015). Moreover, due to dissimilarities in their body size, habitat structure may hamper the escape of these two species differently. Therefore, differences in habitat use, body size and anti-predator behaviour should lead to inter-specific variation in habitat characteristics of kill sites.

In this study, we investigated wolf kill-site characteristics in an intensively managed commercial forest of western Poland. We compared fine-scale landscape features of kill sites with other wolf locations. We hypothesised that:

- (1) Kill sites will be more common near structures that impede prey escape (e.g. fences, dense young plantations, fallen trees), and thus increase the probability of successful killing.

- (2) Habitat characteristics will affect the occurrence of kill sites of red deer and roe deer differently due to their different body size and anti-predator behaviour.

2. Materials and methods

2.1. Study area

Our study area was the western part of the Lower Silesia Forest, southwestern Poland (ca. 260 km², Fig. 1), encompassing four forest districts: Ruszów, Wymiarki, Pieńsk and Węgliniec. The area is flat and mean altitude ranges from 120 to 160 m a.s.l. Average annual temperature during the study period was 9.7 °C, with mean daily values ranging from −16.3 to 29.5 °C (Institute of Meteorology and Water Management, Poland). Snow cover during the study persisted for 7–71 (average 24) days each winter, with snow cover depth up to 10 cm (Institute of Meteorology and Water Management, Poland). Woodlands occupy 83% of the area (Fig. 1) and consist mostly of Scots pine *Pinus sylvestris* stands with admixtures of Norway spruce *Picea abies*, birch *Betula* spp. and oak *Quercus* spp. The study area has been harvested for timber since the Middle Ages, but sustainable forestry involving reforestation began in the 19th century (Bena, 2012). Currently, the forest management involves intensive logging, reforestation and fencing of young stands to prevent browsing by ungulates. The chain-link forestry fences are 2 m high, and their density is ca. 0.9 km/km². Fenced stands occupy 2.5% of the forest and an average area of a fenced plantation is about 0.02 km² (data of State Forestry Districts Ruszów and Wymiarki). Wetlands used to be common in this region, but permanent drainage resulted in strongly transformed vegetation and an extensive system of drainage ditches (Bazarnik et al., 1998). Planting trees in wetland habitats is associated with ploughing. These areas, characterized by deep (up to 0.5 m) parallel grooves in soil, represent the only sites with considerable terrain ruggedness. The forest is divided into rectangular compartments of about 750 × 370 m, each accessible via a dense network of forest roads (ca. 6 km/km²). There is one large river (the Lusatian Neisse) and several small streams crossing the study area, and a few artificial water reservoirs built for fishing, fire management and water retention purposes. Ungulate species occurring in the study area include red deer (2.9 individuals/km²), roe deer (3.5 individuals/km²) and wild boar (9 individuals/km²), and in very low densities fallow deer *Dama dama* and elk *Alces alces* (data of Ruszów State Forestry District). The wolf is currently the only large carnivore species here. The human population density is ca. 25 inhabitants/km² (Central Statistical Office of Poland, 2014). The density of public roads is about 0.11 km/km² and of railway lines about 0.12 km/km².

2.2. Surveys of kill sites

From December 2012 to May 2016, we identified wolf kill sites by three methods: (1) GPS telemetry of radio-collared wolves (37 kill sites), (2) snow-tracking (18 kill sites) and (3) information from foresters and other collaborators (11 kill sites). We used trained dogs to facilitate searching for carcasses. We found kill sites of 30 roe deer, 34 red deer, and two wild boars (Fig. 1).

We inspected GPS locations of three wolves belonging to two packs, equipped with GPS collars (LOTEK Wireless Inc., Canada): a young female (December 2012 – January 2013), a breeding female (January 2015 – May 2016) and a young male from the same pack (January – May 2016). The home ranges of the two packs partially overlapped because they originated from one pack that split its territory. The GPS collars were scheduled to obtain a location every 1–2 h. We visited the telemetry locations as soon as possible, usually within 3 days of the GPS fix. To ensure that wolves were the cause

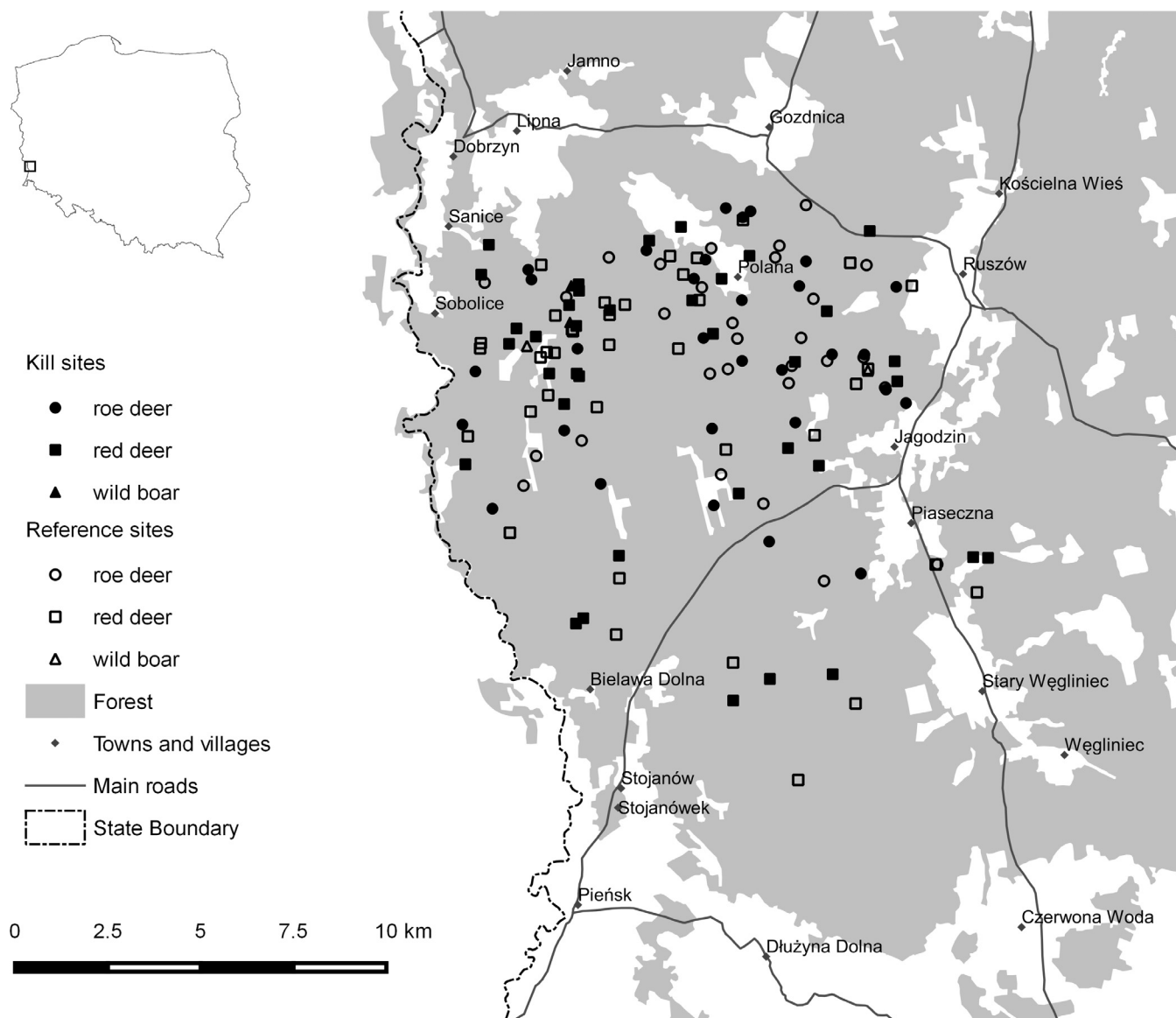


Fig. 1. Study area with locations of sites where wolves killed roe deer, red deer and wild boar (kill sites), and reference wolf locations (reference sites), in the Lower Silesia Forest, Poland, in 2012–2016.

of death of the ungulate, we only included fresh kills, for which the estimated time of death coincided with the time of GPS fix of the wolves.

We snow-tracked ca. 600 km of wolf trails during the winter seasons of 2011/12–2015/16. We conducted snow-tracking within the home ranges of the packs monitored by telemetry. We also obtained information about fresh wolf kills from forestry personnel and other people working in the forest. We only used fresh kill sites found within the known wolf home ranges.

To compare the characteristics of kill sites with non-kill sites, we generated 66 random reference locations. For kill sites found during field inspections of telemetry locations, we selected another GPS location of the same wolf, about 1 km from the kill site and acquired within the same 24-h period. For kill sites found during snow-tracking, we selected a point located on the same snow-track at a straight-line distance of 1 km from the kill site. For kill sites reported by local collaborators, we chose a wolf telemetry location in approximately the same time period and within the distance of about 1 km.

We identified the exact location where the animal was killed based primarily on the amount of blood and the remains of the stomach content. Within a 30-m radius of each kill and reference site, we assessed the following elements of forest structure that correlate with visibility and the easiness for prey to run through the forest: tree circumference, tree density, and undergrowth cover; and other structures affecting the prey's ability to escape:

1. Distances to the 10 nearest trees (higher than 4 m), as a measure of tree cover and density.
2. Circumferences at breast height of the 10 nearest trees, as a measure of forest age.
3. Undergrowth cover (proportion of area covered by bushes and trees of 1–4 m height).
4. Presence/absence of habitat edge (i.e., distinct change in habitat type, usually a borderline between forest stands of markedly different age or tree density or between open and forested areas).
5. Presence/absence of habitat structures that could potentially impede the prey's escape:

- water (drainage ditch, river, reservoir, swampy or flooded area)
- rough terrain (usually a result of ploughing for reforestation)
- fallen trees (windfall or after logging)
- fence.

2.3. Statistical analysis

We used a generalised linear mixed model (GLMM) with binomial error variance and logit-link function to test which environmental variables are the most important predictors of wolf kill-site occurrence. We used the lme4 package (Bates et al., 2015) in R 3.2.3 (R Development Core Team, 2016). We built models predicting occurrence of kill sites for all prey species pooled (red deer, roe deer and wild boar). We additionally built models predicting occurrence of kill sites of only red deer and only roe deer. In all models, we used the above-mentioned habitat features as fixed explanatory variables (Table 1). We excluded habitat edges from the analyses if a fence was also present. Variance inflation factors were below 2 for all variables. In models explaining the occurrence of kill sites of all prey species, we included the following categorical random factors: identity of a paired kill and reference site, prey species, season, and wolf pack identity. We used the same random variables, with the exception for the prey species, in models predicting kill-site occurrence for red deer and roe deer.

We used Akaike information criterion (AICc) for model selection. We did not consider models of $\Delta\text{AICc} < 2$ as different from the highest-ranking model (Burnham and Anderson, 2002). We estimated function slopes through model averaging, including models with ΔAICc below 4 (Burnham and Anderson, 2002). We performed model selection and averaging using the MuMIn R package (Bartoń, 2015). We used square root (undergrowth cover) or natural logarithm (average distance to nearest trees) transformations to meet the assumption of homoscedasticity (Quinn and Keough, 2002). In all regression models, we standardised continuous variables (mean = 0 and standard deviation = 1) for direct comparison of slopes. We calculated R^2 in GLMMs according to Nakagawa and Schielzeth (2013) and presented the marginal R^2_m associated with the variance explained by fixed factors.

In addition to multivariate GLMMs, we determined the independent contribution of the explanatory variables on the occurrence of kill sites by hierarchical partitioning. We performed hierarchical partitioning using the hier.part package version 1.0-3 (Walsh and Mac Nally, 2005). We used binomial distribution and log-likelihood as goodness-of-fit measures. Hierarchical partitioning computes the increased fit for all models containing a given variable, compared to an equivalent model without that variable. Then, we computed the average improvement in fit across all models containing that predictor. This process results in the estimation of the independent contribution of each explanatory variable (I), and the joint contribution (J) resulting from correlation with other variables (Mac Nally, 2002), which allows the

determination of relative independent contribution of each predictor (% I). We considered a predictor with the percentage of I exceeding $100/K$ (where K is the number of predictors) as to have high explanatory power (Mac Nally, 2002). We used randomisation tests (with 200 replicates) that yield z-scores to determine statistical significance of the relative independent contribution of each predictor based on the upper limit of its 95% confidence interval (Mac Nally, 2002).

3. Results

Ten models best predicted occurrence of wolf kill sites of all prey species (Table S1). Wolves mostly killed their prey near habitat edges, water or forestry fences (Table 1, Fig. 2). The presence of these three habitat attributes were the most important determinants of kill-site distribution (Fig. 3a). The best models also contained effects of undergrowth cover, mean tree circumference, mean distance to ten nearest trees, fallen trees and rough terrain (Table S1), however the confidence interval of these estimates in the GLMMs overlapped with zero (Table 2). Hierarchical partitioning yielded similar results: habitat edge, water and forestry fence had the highest and most significant independent contribution to predicting kill-site occurrence (Fig. 3). Moreover, this analysis suggested that the tree circumference and undergrowth cover reduced the deviance in kill-site occurrence (Fig. 3b).

Seven models best predicted occurrence of wolf kill sites of red deer (Table S1). Wolves killed red deer mainly near habitat edges (81% of red deer kill sites were located near habitat edge) and water (36%), in young forest stands (Table 2, Fig. 2). Model averaging also indicated that habitat edge, water and tree circumference had the highest values of importance (Fig. 3a). Best models also included effects of undergrowth cover, distance to the nearest tree, fallen trees and rough terrain (Table S1), however the confidence interval of these estimates in the GLMM overlapped with zero (Table 2). Hierarchical partitioning confirmed the results from model averaging (Fig. 3). No other variable contributed significantly and independently to the reduction in deviance (Fig. 3).

Eleven models best predicted occurrence of wolf kill sites of roe deer (Table S1). Wolves primarily killed roe deer near forestry fences: 43% of kill sites were located inside or next to the forest enclosures (Table 2, Fig. 2). Best models also included effects of undergrowth cover, tree circumference, habitat edge and rough terrain (Table S1), however their estimates in GLMMs overlapped with zero (Table 2). Hierarchical partitioning confirmed that presence of a fence was the only variable that had a significant independent contribution to predicting kill-site occurrence (Fig. 3).

4. Discussion

Our results showed that fine-scale habitat features helped wolves to kill their prey. These features primarily comprised structures that impede the prey's escape, indicating that catchability is important in shaping spatial variation in predation risk in this predator-prey system. This corroborates the results of other authors, who found that habitat attributes affected vulnerability of red deer, roe deer and elk to wolf predation more than prey density (Kunkel and Pletscher, 2000; Gula, 2004; Hebblewhite et al., 2005; Kauffman et al., 2007; Gervasi et al., 2013). In contrast to these studies, however, we demonstrate that habitat features that help wolves to capture their prey are often man-made products of forest management. Therefore, the combination of forest management and wolf behaviour in intensively managed forest areas may affect populations of large herbivores and therefore contributes to ecological processes triggered by forestry practices (Ripple et al., 2001; Fortin et al., 2005; Gardner et al., 2009).

Table 1

Characteristics (mean with 95% confidence intervals, or frequency of occurrence with Bonferroni intervals (Byers et al., 1984)) of the investigated variables for 66 wolf kill sites and 66 reference sites in the Lower Silesia Forest, western Poland, in 2012–2016.

Variable	Kill sites	Reference sites
Mean distance to the nearest tree (m)	8.1 ± 1.5	5.8 ± 1.0
Mean tree circumference (cm)	63 ± 6	70 ± 7
Undergrowth cover (%)	33 ± 7	21 ± 5
Presence of habitat edge (%)	73 ± 12	50 ± 14
Presence of water (%)	27 ± 12	11 ± 8
Presence of rough terrain (%)	41 ± 13	35 ± 13
Presence of fallen trees (%)	44 ± 13	35 ± 13
Presence of fence (%)	21 ± 11	6 ± 6

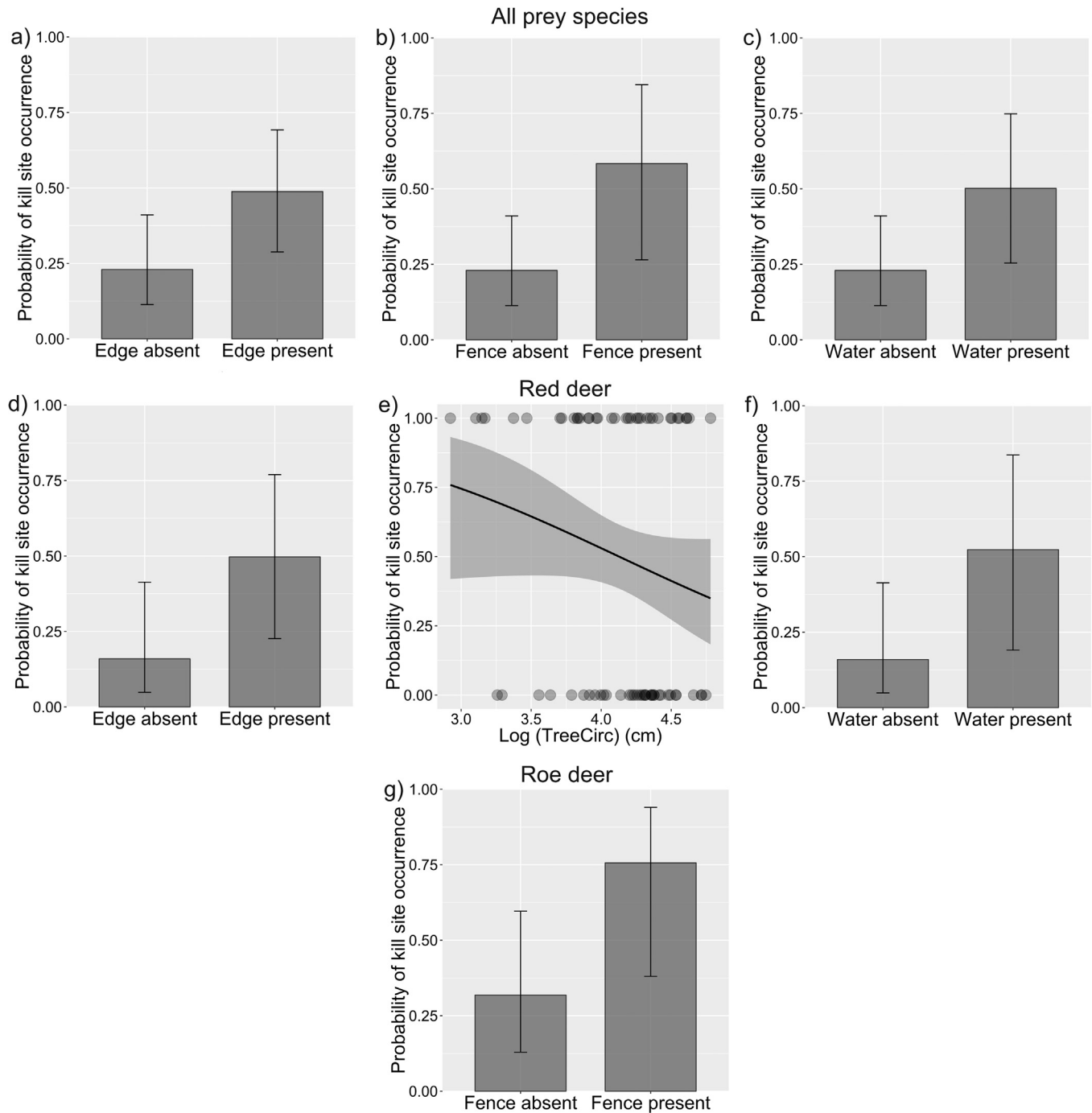


Fig. 2. Variables affecting the probability (GLMM) of occurrence with 95% confidence intervals (whiskers) of 66 wolf kill sites in the Lower Silesia Forest, western Poland, 2012–2016. Upper panel: the effect of presence of (a) habitat edge, (b) forestry fence and (c) water on the occurrence of kill sites of all prey species; middle panel: the effect of (d) presence of habitat edge, (e) mean tree circumference and (f) presence of water on the occurrence of kill sites of red deer; bottom: the effect of (g) presence of a fence on the occurrence of kill sites of roe deer.

Proximity of forestry fences, habitat edges, waterbodies and watercourses were the most important factors affecting prey vulnerability to wolves in our study. Fencing appeared to considerably affect hunting behaviour of wolves. The use of fences by predators to facilitate hunting has been reported in a few other carnivores, but not in wolves. For instance, wild dogs *Lycaon pictus* killed up to 40% of their prey near fences in South Africa (Rhodes and Rhodes, 2004; Davies-Mostert et al., 2013). Fences affected both prey selection and hunting efficiency in wild dogs, because fence-imposed kills comprised larger prey species (Rhodes and

Rhodes, 2004; Davies-Mostert et al., 2013). Wildlife exclusion fences have also been shown to modify predation patterns of lions *Panthera leo* (Dupuis-Desormaux et al., 2015, 2016). There are no published records of predator-prey encounters involving forestry enclosures in the wild (but see Kossak, 1989 for captive roe deer killed by wild Eurasian lynx *Lynx lynx*). In our study, wolves frequently used forestry fences to seize their prey, especially roe deer. Forestry fences are often partially damaged by ungulates trying to get into the fenced area to forage on young trees, which allows also wolves to enter the enclosure. Most kills occurred in the corners of

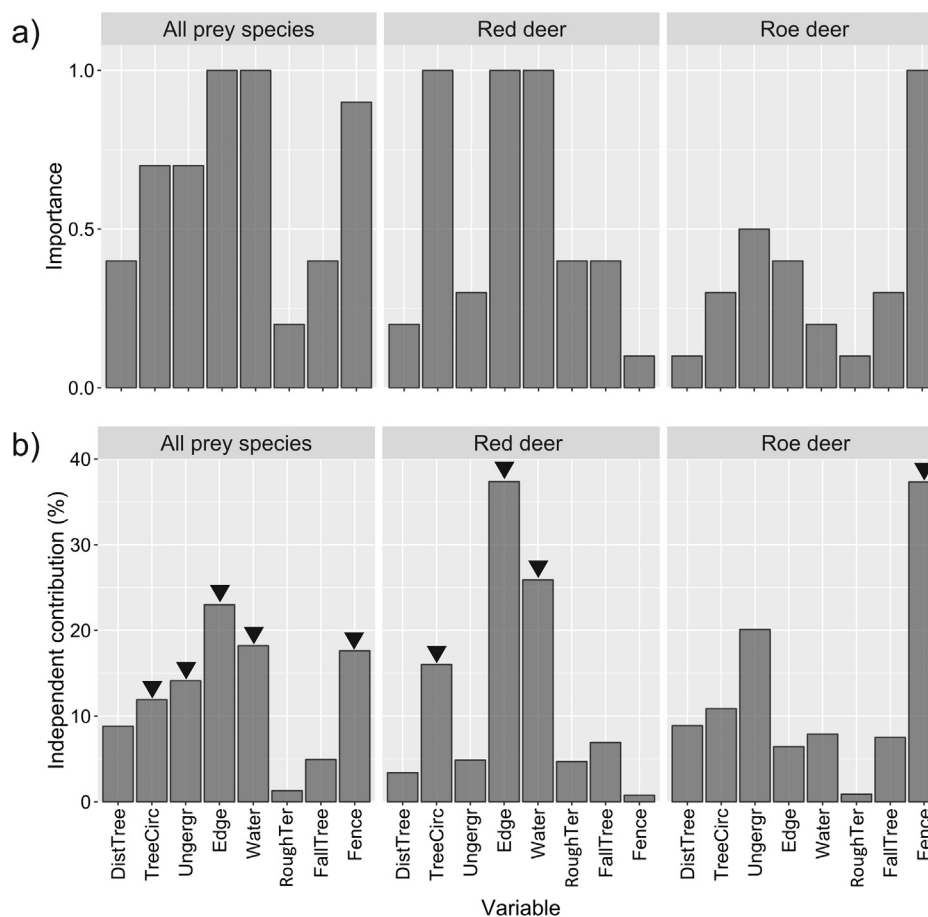


Fig. 3. Factors affecting the probability of wolf kill-site occurrence in the Lower Silesia Forest, western Poland, 2012–2016. (a) Importance of variables used to explain occurrence of wolf kill sites of all prey species (left panel), red deer (central panel) and roe deer (right panel). (b) Decomposition of the total reduction in deviance associated with environmental variables into independent components using the hierarchical partitioning method. Variables that had the strongest and statistically significant ($P < 0.05$) impact on reduction of deviance in wolf kill-site occurrence are marked with triangles. Variables include: mean distance to the nearest tree (DistTree), mean tree circumference (TreeCirc), undergrowth cover (Undergr), and presence of the following habitat features: habitat edge (Edge), waterbodies or watercourses (Water), rough terrain (RoughTer), fallen trees (FallTree) and forestry fence (Fence).

fenced areas, suggesting that wolves usually chased their prey into a corner of the enclosure and killed it there. Thus, our results and supporting observations confirm the hypothesis that fences can act as prey-traps (Ford and Clevenger, 2010). Presence of fences may interact with prey selection, enabling wolves to kill individuals of a different age, sex and condition than what they would kill otherwise (Okarma, 1991; Van Dyk and Slotow, 2003).

Besides fences, most habitat features used by wolves to improve their hunting success were also a result of forest management. Most of habitat edges consisted of borderlines between forest subdivisions created by forestry practices. Moreover, two thirds of kill sites that occurred near water were located at drainage ditches. This implies that forest management practices, i.e. fencing, drainage and logging, have an important role in shaping the spatial patterns in predation risk, predation rate and prey selection in our study area.

Habitat edges have been suggested to facilitate wolf hunting on elk and red deer in North America (Kunkel and Pletscher, 2000; Bergman et al., 2006). Although ungulates often seek cover in dense habitats, Bergman et al. (2006) reported that wolves frequently killed red deer after crossing a habitat edge. Thus, a borderline between two habitats may introduce a structural change that slows down the prey's escape. Moreover, many species avoid crossing habitat edges (Ries et al., 2004), therefore a kill has a greater chance to happen close to the edge if an escaping prey runs along a habitat edge rather than crossing it.

Wild ungulates chased by wolves often try to escape into water, as found in white-tailed deer *Odocoileus virginianus*, caribou, elk and red deer (Mech et al., 2015). However, water only constitutes a refuge if it is deep enough to force the shorter-legged wolves to swim or if there is a strong current (Mech et al., 2015). In our study, most of the water kills took place in shallow (less than 0.5 m) ditches and streams, corroborating earlier studies on white-tailed deer in Minnesota (Mech et al., 1971) and red deer in the Bieszczady Mountains (Gula, 2004).

Our results indicate that other variables are also worth considering when investigating wolf hunting behaviour. Tree density, undergrowth cover, presence of fallen trees and rough terrain were found in some of the best models, indicating a potential role of those habitat features in facilitating wolf hunting. However, they lacked significance in analyses of kill sites distribution, possibly due to limited sample size.

The inter-specific variation in factors increasing vulnerability to predation found in this study can be partially explained by behavioural and morphological differences of prey. Red deer may escape to water more often than smaller species, because they are sufficiently large to force wolves to swim while they can still walk. Furthermore, red deer were more frequently killed close to habitat edges than roe deer probably because their size handicaps them more in dense habitats. Likewise, red deer may be hampered more than smaller species in younger and denser forest stands. Thus, escaping to water, crossing habitat edges and running into

Table 2

Averaged estimates with 95% confidence intervals (CIs) of the function slopes of variables present in the most parsimonious GLMMs describing the occurrence of 66 wolf kill sites of all prey species and the occurrence of kill sites of the most common prey species: red deer ($n = 36$) and roe deer ($n = 30$) in the Lower Silesia Forest, western Poland, in 2012–2016. Variables with CIs that do not include zero are in bold.

Source of variation	Estimate \pm CI
<i>All species</i>	
Intercept	-1.21 ± 0.85
Mean distance to the nearest tree	0.36 ± 0.54
Mean tree circumference	-0.45 ± 0.47
Undergrowth cover	0.39 ± 0.42
Presence of habitat edge	1.16 ± 0.86
Presence of water	1.22 ± 1.08
Presence of rough terrain	0.31 ± 0.82
Presence of fallen trees	0.52 ± 0.82
Presence of fence	1.55 ± 1.36
<i>Red deer</i>	
Intercept	-1.66 ± 1.31
Mean distance to the nearest tree	0.29 ± 0.68
Mean tree circumference	-0.64 ± 0.64
Undergrowth cover	0.31 ± 0.58
Presence of habitat edge	1.65 ± 1.22
Presence of water	1.76 ± 1.54
Presence of rough terrain	0.79 ± 1.23
Presence of fallen trees	0.85 ± 1.22
Presence of fence	-0.17 ± 3.03
<i>Roe deer</i>	
Intercept	-0.76 ± 1.15
Mean distance to the nearest tree	0.20 ± 0.79
Mean tree circumference	-0.39 ± 0.64
Undergrowth cover	0.54 ± 0.65
Presence of habitat edge	0.96 ± 1.38
Presence of water	0.80 ± 2.11
Presence of rough terrain	-0.15 ± 1.23
Presence of fallen trees	0.82 ± 1.35
Presence of fence	1.89 ± 1.62

dense forest stands may be viewed as a symptom of limited behavioural plasticity, a phenomenon linked to behavioural syndromes (Sih et al., 2004).

The high occurrence of roe deer kills inside forest enclosures may be explained in two ways. Small body size makes it easier for roe deer to enter the enclosures through holes in the fence than for red deer. Secondly, when chased inside an enclosure by humans or predators, roe deer display a more chaotic behaviour, which can lead to self-injuries when hitting the fence and thus make them easy to capture (Tomasz Pietrzykowski, Wymiarki Forestry District pers. comm.). Conversely, red deer are more capable of finding their way out, and when chased into the fence, they are able to jump over or knock it down (Andrzej Drgas and Łukasz Żarkowski, Ruzsów Forestry District pers. comm.). The high rate of roe deer killing inside fenced areas raises the question why this species does not avoid the proximity to fences. This may reflect the lack of continuity in predator presence in the study area; wolves were repeatedly extirpated during the last two centuries (Okarma, 1993). Because the combined presence of fences and wolves is a relatively new phenomenon in the roe deer history of this area, it may cause an effect analogous to prey's naivety (Berger et al., 2001). However, it is also possible that predation risk near the fences is not high enough to exceed the potential energetic gain from feeding in fenced plantations (Stephens and Krebs, 1986). In this case, we would not expect a change in behaviour of prey in the future.

Man-made changes in the landscape play a central role in predator-prey behavioural relationships, which in turn can impact ecosystem structure and function. Specifically, human-induced alterations may interact with the natural selection imposed by predators, and their potential to affect prey behaviour, numbers

and distribution. While many studies have explored predation patterns in protected areas (Fortin et al., 2005; Hebblewhite et al., 2005; Kauffman et al., 2007), several fundamental questions to predator-prey relationships have yet to be fully tested in ecosystems shaped by human activity (Kuijper et al., 2016). Wolves in our study area face a scarcity of deep snow cover, creeks, deep river valleys and swamps, which are features that facilitate hunting in other areas (Gula, 2004; Kauffman et al., 2007; McPhee et al., 2012). Instead, it seems that wolves have incorporated man-made habitat features into their hunting strategy to increase efficiency. This supports previous findings on the great behavioural plasticity of this species (Packard, 2003; Theuerkauf, 2009). Consequently, the vicinity of fences, habitat edges and water become areas of elevated predation risk for roe deer and red deer, analogically to river valleys in Yellowstone and areas with high density of tree logs in the Białowieża Forest (Laundré et al., 2001; Kuijper et al., 2015). Thus, ungulates can potentially learn to avoid approaching these habitat elements and increase their vigilance level when feeding in their vicinity, especially in areas where wolves are often present (Forester et al., 2007; Kuijper et al., 2015). This should be especially true inside fenced areas, because usually both start of the hunt and the subsequent kill take place there. The other habitat elements should be avoided by deer during the actual chase, but not necessary during normal activities, because wolves usually pursue their prey over long distances before seizing it (Mech et al., 2015). This means also that the risk to be chased and the risk to be killed by wolves is not equal over space, which might cause that prey will not avoid areas with high risk to be killed. However, in areas where people hunt wildlife, effects of human disturbance on ungulates' behaviour may exceed those of natural predators (Ciuti et al., 2012).

Our results provide evidence that large carnivores benefit from certain forest management practices. This relationship is potentially reciprocal: by increasing wolf hunting success on the two main species causing damages to forest stands (red deer and roe deer), forest management enhances the ability of wolves to reduce numbers of these prey species and affect their behaviour. For example, smaller forest subdivisions create a higher density of habitat edges, which wolves use for hunting. This suggests that small clear-cuts, rather than large ones, may limit ungulate-caused damages to forest stands in areas where wolves are present, by providing favourable conditions for wolf hunting. Interestingly, wolves may help to make fencing more effective in preventing ungulate damage by eliminating individuals that are inside the enclosures and by modifying deer behaviour (preventing them from entering forestry enclosures). Thus, presence of wolves may be beneficial for forestry and the outcome of this study is an example of possibility for a reconciliation of forestry and conservation of this carnivore. Moreover, our results suggest that maintaining some natural habitat elements such as waterbodies, swamps, natural understorey or fallen trees may positively correlate with wolf hunting efficiency and possibly add to the ungulate control in commercial forests.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.04.013>.

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