

Safety first: seasonal and diel habitat selection patterns by red deer in a contrasted landscape

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Abstract

Spatially heterogeneous landscapes provide solutions to the forage-safety trade-off when animals can access risky but energetically rewarding patches, or safer but resource-poor patches. It can be advantageous for an animal to secure access to habitat heterogeneity at a broader scale in order to be able to dynamically adjust finer scale habitat use through time. We tested the hypothesis of a forage-safety trade-off optimization tactic in a hunted red deer (*Cervus elaphus*) population following a large accidental forest fire. We used telemetry data and fitted resource selection functions at the second- and third-order scales. We then integrated the order-specific probabilities into single, all-in-one multi-level layers that synthetically captured the habitat selection patterns across scales by informing landscape-scale annual habitat selectivity with finer within-home-range seasonal and diel processes. At the landscape scale, red deer anchored their home-range at the interface of the disturbed and undisturbed patches, thereby securing habitat heterogeneity. This consequently enabled them to modulate within-home-range habitat selection depending on the season and the time of the day. In both seasons, red deer consistently used the burnt area for cover more during the day, and foraged in the unburnt forest and open fields at night. Interestingly there were no major seasonal differences in this diel habitat selection patterns. Increased mortality risk during the hunting season did not substantially change their spatial behaviour. We conclude that year-round avoidance of non-lethal human disturbance is the main driver of red deer habitat use in this system.

Introduction

Animal space-use patterns result from the need to balance access to limiting resources with avoidance of competition (Vanak *et al.*, 2013), predation risk (Thaker *et al.*, 2011; Wirsing & Ripple, 2011; Lone *et al.*, 2014; Moll *et al.*, 2017), or human disturbance (Ciuti *et al.*, 2012; Kuijper *et al.*, 2016; Stabach *et al.*, 2016; Bötsch, Tablado & Jenni, 2017; Müller *et al.*, 2017; Smith *et al.*, 2017). Spatially heterogeneous landscapes provide solutions to the forage-safety trade-off when animals can access risky but energetically rewarding patches, or safer patches with lower resources abundance or quality (landscape of fear) (Bjørneraas *et al.*, 2011; Basille *et al.*, 2015; Padié *et al.*, 2015; Filla *et al.*, 2017). Resource availability and risk also vary over time (Hebblewhite, Merrill & McDermid, 2008; Latombe, Fortin & Parrott, 2014). Thus, habitat selection – the disproportional use of habitats to their availability in the landscape (Johnson, 1980; Manly *et al.*,

2002) – can differ among seasons (Morelle & Lejeune, 2015; Bonnot *et al.*, 2016; Lone *et al.*, 2017), around the diel cycle (Lone *et al.*, 2017; Filla *et al.*, 2017; Kohl *et al.*, 2018; Martin *et al.*, 2018), among behavioural states or activity levels (Lesmerises, Johnson & St-Laurent, 2017; Blecha, Boone & Alldredge, 2018).

Habitat selection is therefore a spatiotemporal scale-dependent hierarchical process, classically conceptualized as a suite of nested orders (Johnson, 1980; Meyer & Thuiller, 2006). Selection operated at broader scales constrains habitat availability, and thus selection, at finer scales. Conversely, large-scale patterns can result from individual behavioural processes at finer scales (Avgar *et al.*, 2016; Paton & Matthiopoulos, 2016; Van Moorter *et al.*, 2016). It has been argued that animals should avoid factors most limiting to their fitness at broader spatial scales, that is mortality risk, while selecting for forage quality at finer scale (Rettie & Messier, 2000; Chapman *et al.*, 2011). Alternatively, to optimize the forage-safety trade-off, it

can be advantageous for an animal to secure access to habitat heterogeneity at a broader scale in order to be able to adjust habitat use at finer scale dynamically over time (Herfindal *et al.*, 2009; van Beest *et al.*, 2010). Use of habitats relative to their availability is context-dependent (Laforge *et al.*, 2016; Gaudry *et al.*, 2018), however, how the forage-safety trade-off is optimized in relatively homogenous landscapes remains poorly understood (Schmidt & Kuijper, 2015).

Large-scale environmental disturbances such as storms or forest fires can impact the distribution, quality and quantity of available resources (Widmer *et al.*, 2004; Gigliotti *et al.*, 2017; Yeldell *et al.*, 2017) by creating patches of contrasted levels of resource availability in the landscape (Vanbianchi, Murphy & Hodges, 2017; Spitz *et al.*, 2018). Structural changes in the vegetation following disturbance can also create zones more or less favourable to predation and thereby modify the landscape of fear (Atuo & O'Connell, 2017). Beside predators, hunting and other human activities create disturbance and risk that affect animals' habitat use in a fashion analogue to the fear of predation (Tolon *et al.*, 2009; Ciuti *et al.*, 2012; Cromsigt *et al.*, 2013; Lone *et al.*, 2015, 2017; Norum *et al.*, 2015; Little *et al.*, 2016; Bötsch *et al.*, 2017). In such landscapes, animals are therefore expected to place their home-ranges at the interface of patches of contrasting forage quality and risk levels to be able to solve the forage-safety trade-off (Yeldell *et al.*, 2017).

Large-scale disturbance events are rare in Europe, a relatively recent example being the Lothar winter storm in December 1999 (Widmer *et al.*, 2004). Herein, we took the opportunity of a large accidental forest fire to test this hypothesis of post-disturbance forage-safety trade-off optimization tactic in a hunted red deer (*Cervus elaphus*) population. Specifically, we modelled habitat selection by red deer during the pre-thicket and thicket successional stages 13–14 years after the fire at the annual, seasonal and diel temporal scales. In these pre-thicket and thicket stages following the fire the post-disturbance areas provided ample cover, but were less abundant in food resources than undisturbed forests (Borkowski, 2004; Borkowski *et al.*, 2016). We predicted that at the second order of selection (Johnson, 1980; Meyer & Thuiller, 2006) red deer should place their annual home-ranges at the fire edge interface (prediction 1). Such home-range placement tactic would enable access to both the burnt (poor forage, good cover) and the unburnt (good forage, poorer cover) areas. This would enable red deer to modulate within-home-range habitat use at the third order of selection: (1) seasonally with regard to the increased risk during the hunting season when they are expected to use more the safer burnt area (prediction 2); and (2) daily with regard to the decreased disturbance and risk at night when they are expected to use more energetically rewarding habitats in unburnt forest and open fields (prediction 3).

To test these predictions, we used resource selection functions (RSF; Manly *et al.*, 2002) to model (1) selectivity of annual home-range placement at the second order of selection, and to model within-home-range third-order selection specific to (2) seasonal hunting levels, and (3) time of the day. For each of the temporal combinations, we then (4) integrated models across both orders of selection to account for scale dependencies (DeCesare *et al.*, 2012; Fattebert *et al.*, 2018). We discuss the

implications of the outcome of the different models for our understanding of multi-scale optimization tactics of the forage-safety trade-off in red deer in human-dominated landscapes with seasonal hunting.

Materials and methods

Study area

We studied red deer in the Rudy Raciborskie Forest District (50.19°N, 18.45°E; 215 km²; Fig. 1), south-western Poland in 2006–2007. The region is characterized by mild winters, with an average of 45 days with snow cover between December and February. Snow depth rarely exceeding 5 cm. The area is flat and elevation ranges between 180 and 307 m.a.s.l.

In 1992, an accidental fire burnt c. 42 km² of forest in the district (c. 90 km² in total). After the fire, the area was regenerated during 1993–1997. About 16 km² were planted with Scots pine (*Pinus silvestris*), 5 km² with common birch (*Betula pendula*) plantations and another 5 km² with other species, mostly larch (*Larix decidua*). Planted stands were interspersed with 17 km² of naturally regenerated stands in which pine and birch each covered half of the area. Fourteen years after the fire, the disturbed patches were dominated by pre-thicket and thicket stages, providing abundant cover (Borkowski, 2004; Borkowski *et al.*, 2016). Also, lowered post-fire soil quality favoured wood-small reed (*Calamagrostis epigejos*) expansion (Łukaszewicz, 1998). Wood-small reed is usually avoided by red deer, unless it is young (Dzięciołowski, 1969), and therefore the understory did not provide favourable food conditions.

This forest complex is interspersed with open areas mainly used for agriculture, with fields surrounding villages (Fig. 1). No villages or agricultural fields were at the interface between

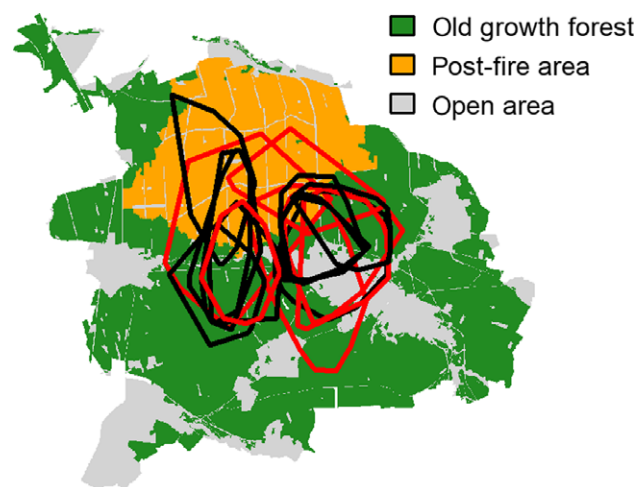


Figure 1 Minimum Convex Polygon (MCP) home-ranges of 16 red deer (black: males; red: females) in the pre-thicket and thicket phase following a forest fire in the Rudy Raciborskie Forest District, south-western Poland, 2005–2006. The orange area delineates the perimeter of the burnt area.

the disturbed and the undisturbed areas, and the density of public roads was low. Recreational use of the area included hiking, and harvesting of forest berries and mushrooms. There was no permanent presence of large carnivore predators in the study area. Hunting in the post-disturbance area was more difficult due to short visibility in the thicket vegetation, and shooting would only be possible along the forest roads and a few open areas. A previous pellet-count study found that habitat use by red deer and roe deer (*Capreolus capreolus*) was similar, and interspecific competition is not considered to be an important factor in this study area (Borkowski & Ukalska, 2008). Population densities were estimated between 4–6 and 6–10 individuals*km⁻² of forest area for red deer and roe deer respectively. Fallow deer (*Dama dama*) are uncommon, whereas wild boar (*Sus scrofa*) are relatively common, but density estimates were not available.

Seasons

In order to investigate the effect of hunting on red deer selection pattern, we divided the dataset into two contrasting periods (thereafter ‘seasons’) according to regimes of red deer hunting during the course of the study (Borkowski *et al.*, 2016): *no-hunting* from 1 March to 31 August and *hunting*: red deer males—from 16 September to end of February; females—from 1 October to 15 January, calves from 1 October to end of February. In practice, a great majority of the females, at least 50–60% of the males and a similar proportion of the calves are harvested by mid-December. The total harvest is estimated to be c. 20–25% of the population (J. Borkowski pers. obs.). During the *hunting* season (i.e. 16.09–15.12), roe deer, fallow deer and wild boar are also hunted. Hunters were present in the field daily, mainly at dawn and dusk, and drive hunts were organized during daytime on weekends. Wild boar hunting was also allowed at night.

Capture and tracking

We captured red deer using drop-nets method between December 2004–March 2005 and December 2005–March 2006 at the interface between the post-disturbance and undisturbed areas. We outfitted red deer with VHF radio collars (Biotrack, TW-5 transmitter, Wareham, UK). We relocated each individual using triangulation 1–3 times per 24-h period three times per week, with at least 1 day break between consecutive tracking sessions. We estimated locational error at <50 m (Borkowski *et al.*, 2016).

Habitat selection analyses

Use-available design

We analysed red deer habitat selection at two orders using resources selection functions (RSF; Manly *et al.*, 2002). We used data of 16 red deer (10 females, six males) with relocations in each of the two seasons to compute annual minimum convex polygon home-ranges (MCP; Hayne, 1949) (Fig. 1). To sample resource use at the landscape scale home-range

placement second order of selection (S2) (Johnson, 1980; Meyer & Thuiller, 2006), we generated a number of random points equal to the mean number of relocations per individual in each annual home range. To sample landscape availability at S2, we generated a set of random pseudo-absences in the whole study area to sample landscape availability at a 1:5 used-available ratio, following Fattebert *et al.* (2018). At the within-home-range third order of selection (S3), we defined telemetry relocations as used points. To sample resource availability, we generated random pseudo-absences within each individual’s annual home-range at a 1:5 ratio. We stratified the S3 presences and pseudo-absences according to season (hunting; no hunting) and time of the day (day; night).

Landscape variables

We reclassified local forest map in 10 vegetation categories based on the predominant (>50%) tree species in combination with the age class of the stand. We defined two dominant vegetation types: Scots pine (*Pinus sylvestris*) and other than pine, mostly silver birch (*Betula pendula*). We classified the stands into five age-classes: young plantations (0–5 years), pre-thickets (6–15 years), thickets (16–25 years), pole-sized forests (26–50 years) and mature forests (>50 years) (Table 1). We classified non-forested pixels as open areas (including forest edges, meadows and mostly arable fields) or settlements. To turn the landcover data into continuous variables, we extracted the proportion of each landcover type at 50 × 50 m resolution (analytical grain), congruent with our locational accuracy. We also calculated the distance to roads (including forest roads), to human settlements and to the interface between the disturbed and the undisturbed area. We transformed the distance variables with exponential decays (Whittington *et al.*, 2011) of the form

$$1 - e^{-\alpha d} \quad (1)$$

where d is the distance in kilometres and α was set to define different thresholds for declining effects of roads, human settlements, or the interface with the burnt patch at 50, 100, 250, 500, 1000 and 2000 m.

Resource selection functions

We extracted all the values of the landscape variables at each used and available point using the package raster (Hijmans, 2016) in R version 3.4.0 (R Core Team, 2017). At each selection order, we fitted generalized linear models with binomial error distribution (logistic regression) to the used-available data. For each of the distance variables separately, we fitted simple logistic regressions to the linear distance and to each exponential decay. We selected the model with the lowest value of the Akaike’s Information Criterion corrected for small sample size (AICc) to identify the best distance threshold. We then screened for collinearity among all environmental variables using a threshold Spearman’s rho ($|r| > 0.6$). We combined all uncorrelated covariates in a multiple regression and we conducted a manual backward-stepwise model

Table 1 Coefficients and associated standard errors of resource selection functions (RSF) for red deer habitat selection at the second (S2) and third (S3) order scales in the pre-thicket and thicket phase following a forest fire in the Rudy Raciborskie Forest District, south-western Poland, 2005-2006

Variable	Second order (S2)		Third order (S3)							
	Annual		No-hunting night time		No-hunting night time		Hunting day time		Hunting night time	
	β	SE	β	SE	β	SE	β	SE	β	SE
Intercept	-1.050	0.137	-3.587	0.178	-3.164	0.534	-2.771	0.201	-2.730	0.312
% Pine										
Young	-	-	-	-	1.545	0.773	-	-	-	-
Pre-thicket	0.335	0.150	1.241	0.224	1.203	0.549	1.555	0.157	0.603	0.272
Thicket	0.471	0.178	1.843	0.238	1.229	0.623	0.997	0.330	-	-
Pole size	0.507	0.143	1.806	0.190	1.175	0.563	0.742	0.238	-	-
Old growth	0.260	0.126	1.238	0.178	1.572	0.546	-	-	-	-
% Non-pine										
Young	-	-	-	-	-	-	-	-	-	-
Pre-thicket	0.397	0.167	1.550	0.241	2.144	0.548	1.404	0.193	0.887	0.343
Thicket	-	-	1.758	0.480	-	-	-	-	-	-
Pole size	-	-	1.822	0.353	2.388	0.633	-	-	1.029	0.460
Old growth	-	-	-	-	-	-	-	-	1.097	0.415
Dist. to interface (unburnt)	-0.001 ^a	0.00002	-	-	-	-	-	-	0.576	0.262
Dist. to interface (burnt)	-1.403 ^b	0.106	0.761 ^c	0.194	-	-	-	-	-	-
Open	0.730	0.129	-	-	1.716	0.550	-	-	0.489	0.182
Dist. to houses	1.228 ^d	0.133	-	-	-	-	-	-	-	-
Dist. to roads	-0.001 ^e	0.0001	0.620 ^f	0.136	-	-	0.450 ^f	0.227	0.518 ^f	0.228

All coefficients presented were significant in final models following manual stepwise backward reduction.

Optimized effect scales of distance variables were: (a) linear; (b) 50-m exponential decay; (c) 100-m exponential decay; (d) 2-km exponential decay; (e) linear; (f) 500-m exponential decay.

selection procedure. We removed all non-significant variables from the multivariate model until the effects of all remaining variables were significant $P < 0.05$ (Hosmer, Lemeshow & Sturdivant, 2013). We projected S2 and S3 predicted values (w) over the entire study area to generate order-specific resource selection function (RSF) maps, following Manly *et al.* (2002), as

$$w_{\text{RSF}(x)} = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n) \quad (2)$$

where β_i is the coefficient of variable x_i . We rescaled the resulting RSF predicted values between 0 and 1 (DeCesare *et al.*, 2012), as

$$w_{\text{RSF}} = (w_{\text{RSF}(x)} - w_{\text{RSFmin}}) / (w_{\text{RSFmax}} - w_{\text{RSFmin}}) \quad (3)$$

Multi-level integration

In the classic nested hierarchical design, inferences about habitat selection patterns remain order-specific (Boyce, 2006; Mayor *et al.*, 2009). The conditional dependency among orders of resource selection can be explicitly modelled by integrating orders of selection into a single, all-in-one surface that informs large-scale selection patterns with local, fine scale processes (DeCesare *et al.*, 2012; Pitman *et al.*, 2017; Zeller *et al.*, 2017; Fattebert *et al.*, 2018). We integrated S2 with each seasonal and time of the day combination at S3 (four models) by multiplying the relative probabilities across orders following

DeCesare *et al.* (2012), as

$$w_{\text{MRSF}} = P(S_2) \times P(S_3) \quad (4)$$

Results

Home-range placement (S2)

For home-range placement at the second-order scale (S2), red deer selected old-growth pine stands and pole-size stands in the unburnt area (Table 1). They also selected for pine and non-pine pre-thickets and pine thickets in the burnt area. We found no statistically significant selection or avoidance of the other age classes of non-pine stands. Red deer also selected open areas at this scale. Red deer avoided proximity to human settlements up to 2 km and appeared to place their home ranges closer to roads than random. They selected the interface of the burnt and the unburnt areas. Red deer sharply decreased their selection of habitats further than 50 m from the interface into the burnt areas and linearly into the unburnt area, resulting in a higher probability of use along the interface (Fig. 2).

Within-home-range habitat selection (S3)

Within their home-ranges (S3), similar to S2, red deer selected pine stands over non-pine forests, except for pre-thickets (Table 1). S3 selection differed among seasons and time of the

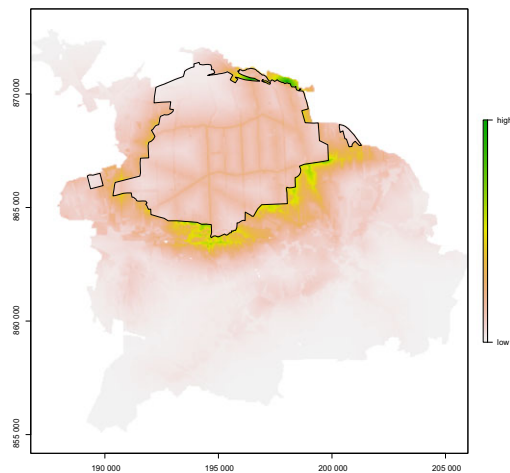


Figure 2 Annual predicted probability of habitat use for red deer derived from a second-order selection function (RSF) in the pre-thicket and thicket phase following a forest fire in the Rudy Raciborskie Forest District, south-western Poland, 2005–2006. The black line delineates the perimeter of the burnt area.

day (Table 1, Fig. 3). Within their home-ranges (S3), red deer avoided roads, contrary to S2 selection, except at night in the no-hunting season when the areas alongside the roads were used proportionally to their availability (Table 1, Fig. 3). There were clear differences in diel habitat use. Red deer selected the burned area during daytime and at night, they selected the unburned forest and the open areas (Fig. 3). In details, during daytime, selection for the burned area was relatively more intense in the hunting season than when red deer were not hunted. Accordingly, nighttime selection for the burned area was stronger in the no-hunting season relative to the hunting season. In the no-hunting season, red deer departed farther from the interface into the burned area during the daytime. Conversely, in the hunting season, red deer tended to move farther into the unburned area at night.

Multi-level habitat selection

Multi-level integration synthetically revealed the main differences in habitat selection by red deer between daytime and nighttime and between seasons across both scales (Figs. 4 and 5). In both seasons, red deer selected the burnt area and avoided open areas during the day. Red deer used open areas at night in both seasons, but remained close to the interface. Diel inter-seasonal habitat selection patterns were comparable. However, during the hunting season red deer appeared to use the unburnt habitats at the interface slightly less during the day and more at night than during the non-hunting season (Fig. 5).

Discussion

We show that red deer employed a tactic of home-range placement that enabled them to contextually modulate within-home-range habitat selection, thereby optimizing the forage-safety trade-off.

Red deer selected for the interface of the burnt (poor forage, good cover) and unburnt (good forage, poorer cover) areas at the second-order scale. This was consistent with our expectation that red deer would secure habitat heterogeneity within their annual home range (prediction 1). This in turn allowed them to shift habitats at the third order, either to access food resources or to avoid disturbance and risk. During the day, red deer displayed strong selection for tickets in the post-burn area that provided higher protective cover than unburnt forest stands. This pattern was in accordance to our expectation that red deer would avoid disturbance and mortality risk in the hunting season, and avoid other non-lethal human disturbance during the non-hunting season (prediction 3). Congruently, red deer selected unburnt and open habitats mostly at night, when disturbance was low or hunting risk was null.

While habitat selection is expected to be affected by avoidance of mortality risk during the hunting season, for example in red deer (Lone *et al.*, 2015), roe deer (Benhaïem *et al.*, 2008; Martin *et al.*, 2018), or wild boar (Tolon *et al.*, 2009; Saïd *et al.*, 2012), we interestingly found no major seasonal difference in the diel habitat selection patterns by red deer in our study area (Figs. 4 and 5). Mortality risk during the hunting season did not appear to change their behaviour, contrary to our expectation that red deer would seek more cover in the hunting season than in the non-hunting season (prediction 2). Non-lethal human disturbance therefore appears to be a strong driver of red deer habitat selection in the no-hunting season in this human-dominated landscape. In general, there is growing evidence that non-lethal human disturbance has significant impact on wildlife behaviour (Stabach *et al.*, 2016; Bötsch *et al.*, 2017; Filla *et al.*, 2017; Lesmerises *et al.*, 2017; Scholten, Moe & Hegland, 2018; Wisdom *et al.*, 2018; Zbyryt *et al.*, 2018). We acknowledge, however, that there was some hunting on other species (roe deer males: from 1 May and wild boar males: all year long) outside the red deer hunting season we defined (see Methods), though much less than in autumn when red deer themselves are hunted. Hunting of other species might have contributed to the effects of non-lethal disturbance on red deer habitat selection. For instance, hunting wild boar with hounds affected space-use of roe deer as a non-target species (Grignolio *et al.*, 2011).

At both spatial scales, red deer selected for pine (mostly in the burnt area), over non-pine forests (mostly in the unburnt area) except for pre-thickets. This result points to a prioritization of cover safety over forage quality and palatability. Herbivores are expected to derive nutritional benefits from burns at the early stages post-disturbance, but use of burnt patches can return to pre-disturbance levels within c. 15 years (Spitz *et al.*, 2018). The way ungulates achieve the forage-safety trade-off across spatiotemporal scales depends of various factors such as diet, seasonal resource distribution and quality (Hebblewhite & Merrill, 2009; Bjørneraas *et al.*, 2011; Bonnot *et al.*, 2016), or the context of predation, for example single- or multi-predator (Thaker *et al.*, 2011; Latombe *et al.*, 2014; Lone *et al.*, 2014, 2017), carnivore or human (Lone *et al.*, 2014, 2017; Norum *et al.*, 2015), or hunting intensity (Padié *et al.*, 2015; Little *et al.*, 2016). Variations in diet and reproductive tactics largely explain differences between different ungulate species. For

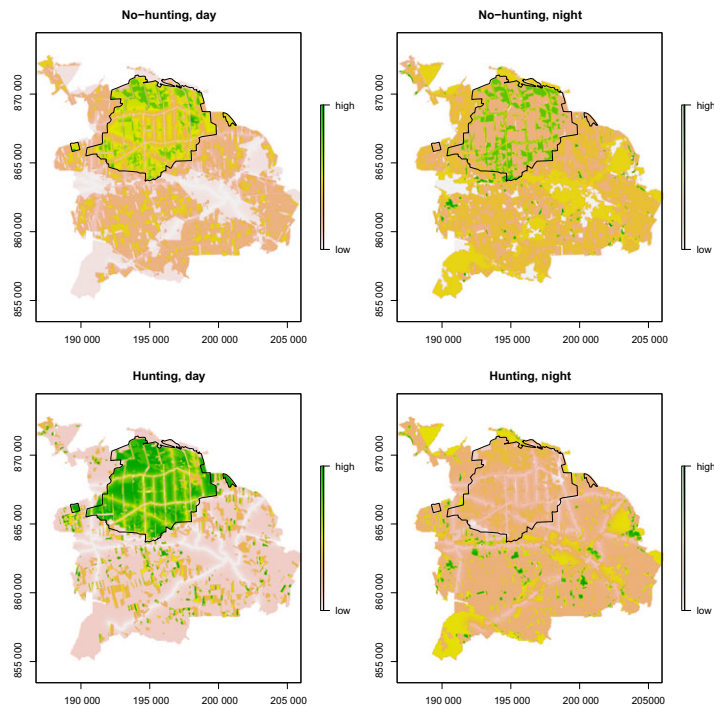


Figure 3 Diel and seasonal predicted probability of habitat use for red deer derived from third-order resource selection functions (RSF) in the pre-thicket and thicket phase following a forest fire in the Rudy Raciborskie Forest District, south-western Poland, 2005–2006. The black line delineates the perimeter of the burnt area.

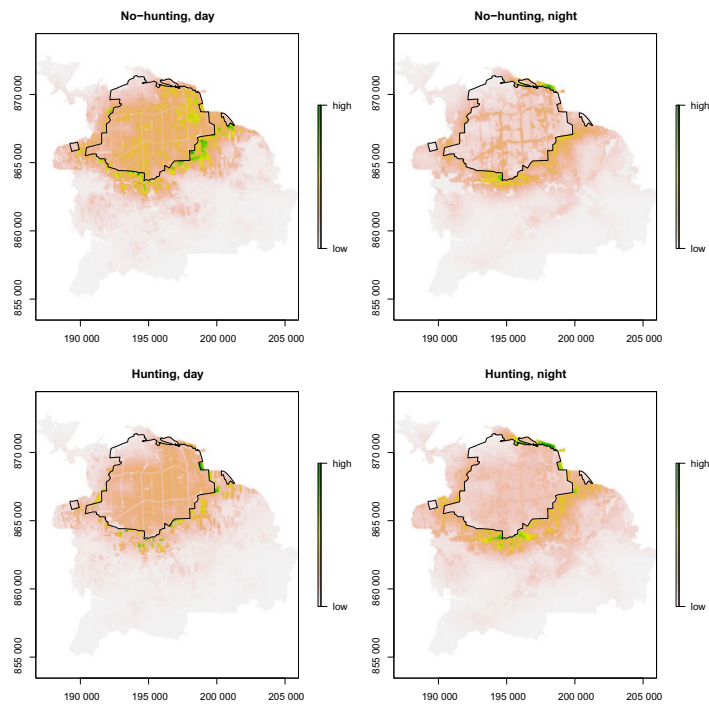


Figure 4 Multi-level diel and seasonal predicted probability of habitat use for red deer derived from the multi-level integration of a second-order with third-order resource selection functions (RSF) in the pre-thicket and thicket phase following a forest fire in the Rudy Raciborskie Forest District, south-western Poland, 2005–2006. The black line delineates the perimeter of the burnt area.

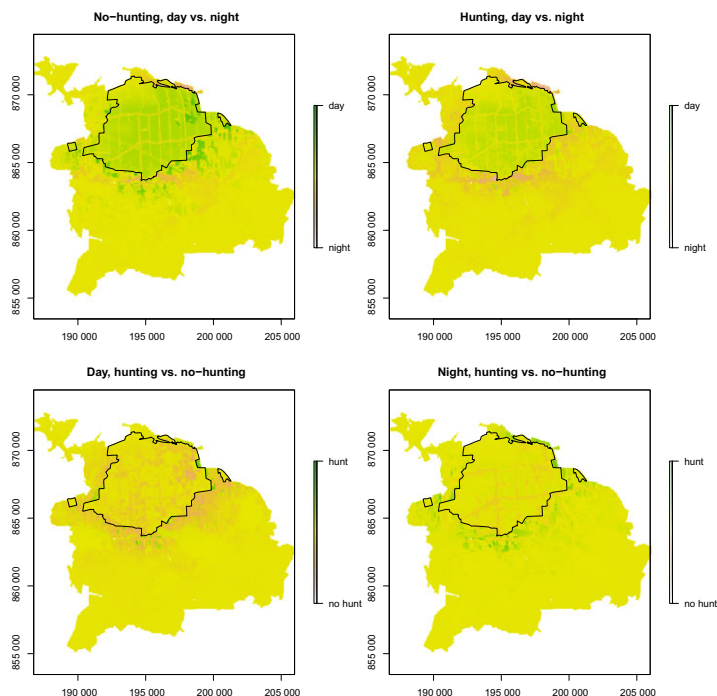


Figure 5 Relative difference in the multi-level diel and seasonal predicted probability of habitat use for red deer in the pre-thicket and thicket phase following a forest fire in the Rudy Raciborskie Forest District, south-western Poland, 2005–2006. The black line delineates the perimeter of the burnt area.

example roe deer, a specialist feeder and an income breeder, needs to precisely track vegetation changes and select habitats accordingly (Borkowski, 2004; Widmer *et al.*, 2004). Roe deer therefore rather select habitats with a high risk of predation at both the second and third order of selection, that is selection for forage is most important (Dupke *et al.*, 2017), and adjust to hunting risk through within-home-range selection rather than at larger spatial scales (Padié *et al.*, 2015). For capital breeders and intermediate mixed-feeders like red deer, on the other hand, selection of habitat based mainly on the availability and quality of resource is of lesser importance. This explains why capital breeders display a stronger selection pattern against predation risk than income breeders do (Hebblewhite & Merrill, 2009).

When accounting for conditional dependencies across scales of selection, multi-level integration clearly highlighted the importance of the interface between the burnt and the unburnt patches for optimizing the forage-safety trade-off. Following home-range placement at the interface, selected habitats in the unburnt area were in fact not used far away from this interface (Fig. 4). The interface therefore acted as an anchor in the landscape, from which red deer did not pull away. Similar anchoring effect has been observed in wild boar living in close proximity to a nature reserve (Tolon *et al.*, 2009). Wild boar responded to spatiotemporal variations in predation risk at the second order, placing their home range at the interface of the hunted managed forest and the reserve, where no hunting occurred. Individuals living in close proximity to the nature reserve shifted to the refuge areas when risk increased, while

animals living further away did not adopt this shifting tactic (Tolon *et al.*, 2009).

Interestingly, avoidance of human settlement was not apparent at the within-home-range third-order scale of selection. This suggests that avoidance of human settlements was mostly achieved at the second order. Home-range placement and second-order selection decisions are deemed to be more important with regard to risk avoidance and have stronger effect on survival and fitness than selection at finer scale (Rettie & Messier, 2000; Chapman *et al.*, 2011). We could not formally test for different tactic of space use and habitat selection in our study area, as we captured red deer at the interface of the burnt and the unburnt areas. It is therefore likely that we did not track individuals present in the study area that did not have access to the interface. Individuals that would not have access to contrasted vegetation patches would likely adopt other within-home-range habitat selection tactics to mitigate disturbance and risk of predation or hunting.

It has been shown that the proportion of forests in the home range, landscape complexity and habitat diversity, can play a major role in predicting hunting mortality (Merli *et al.*, 2017). In this regard, it is noteworthy that all 16 individuals tracked in this study survived the 2006–2007 hunting season. It would be worthwhile gathering data of individuals that actually got shot to understand if they differed in their behaviour and habitat selection patterns (Bonnot *et al.*, 2015), and somewhat failed to optimize the forage-safety trade-off (Lone *et al.*, 2015; Thurfjell, Ciuti & Boyce, 2017). Due to limited sample size, we could not meaningfully test for sexual

differences in habitat selection either. Home-range placement at the disturbance interface seemed similar between sexes (Fig. 1). At the third order though, one could expect males to take more risks than females, especially in the rutting season, which corresponds to the peak of the red deer hunting season. Females should show more risk-adverse behaviour than males to protect offspring (Saïd *et al.*, 2012; Lesmerises *et al.*, 2017).

Conclusion

We integrated order-specific habitat selection models to inform study area-scale annual habitat suitability with finer scale diel and seasonal within-home-range processes in red deer. The resultant multi-level layers synthetically captured habitat selection patterns across scales in single, all-in-one maps. Selection for the fire disturbance interface at the home-range placement level was key in this system. This enabled within-home-range selection for the burnt patch for cover, together with an avoidance of the open field in proximity to human settlement during the day. At night, red deer selected more for the open areas for forage. Daytime avoidance of human disturbance in all seasons appeared to be the main driver of red deer habitat use in this predator-free, human-dominated landscape with contrasted spatial variation in food resource and protective cover following a large-scale accidental forest fire. This highlights the pivotal role of large-scale natural disturbance in creating heterogeneity in the landscape, which enables animals to modulate their space use through time.

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Authors' Contribution

JB, JU, JJ, KM and JF conceived the ideas and designed methodology; JB, JJ and KM collected the data; JF and KM analysed the data; JF, KM and JB led the writing of the paper. All authors contributed critically to the drafts and gave final approval for publication.

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