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A landscape of coexistence for a large predator in a human dominated landscape

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Human related mortality is a major threat for large carnivores all over the world and there is increasing evidence that large predators respond to human related risks in a similar way as prey respond to predation risk. This insight recently led to the conceptual development of a landscape of coexistence that can be used to identify areas which can sustain large predator populations in human dominated landscapes. In this study we applied the landscape of coexistence concept to a large predator in Europe. We investigated to what extent Eurasian lynx *Lynx lynx* habitat selection is affected by human disturbance in a human dominated landscape. More specifically, we were interested in the existence of a tradeoff between the availability of roe deer, one of their main prey and avoidance of human disturbance and how this affects the spatio-temporal space use patterns of lynx. We found that lynx face a tradeoff between high prey availability and avoidance of human disturbance and that they respond to this by using areas of high prey availability (but also high human disturbance) during the night when human activity is low. Furthermore our analysis showed that lynx increase their travelling speed and remain more in cover when they are close to areas of high human disturbance. Despite clear behavioral adjustments in response to human presence, prey availability still proved to be the most important predictor of lynx occurrence at small spatial scale, whereas human disturbance was considerably less important. The results of our study demonstrate how spatio-temporal adaptations in habitat selection enable large carnivores to persist in human dominated landscapes and demonstrate the usefulness of the concept of a landscape of coexistence to develop adaptive management plans for endangered populations of large carnivores.

Human impact has reached almost every corner of our planet, and areas of low human impact are becoming increasingly rare. As a consequence, nearly everywhere animals have to deal with human-altered environments (Sih et al. 2011). Living in areas of high human impact, such as the surroundings of human settlements, often comes with costs, but at the same time may also bring some benefits. One of the costs of living in proximity to humans is an increased mortality risk, for instance due to traffic accidents (Fahrig and Rytwinski 2009), collision with power lines (Rioux et al. 2013), poisoning (Marquez et al. 2013), or legal and illegal hunting (Corlett 2007). On the other hand, human-altered environments also have their benefits (Sih et al. 2011). For example, agricultural land is often highly productive and may offer rich resources, e.g. for herbivores (Marshall and Moonen 2002) or for meso-predators that feed on commensal species (Linnell et al. 2005).

These costs and benefits of living in human-altered environments lead to tradeoffs. This is especially true for large predators (Oriol-Cotteril et al. 2015). Many prey species of large predators occur at higher densities in proximity to humans (Linnell et al. 2005), yet this is also where the predators suffer most from high human-induced mortalities because people are afraid of large predators or compete with them for resources. This tradeoff between risk taking and resource abundance that large predators face can turn human-altered environments into sink habitats (Bunnefeld et al. 2006). Human-caused mortality is a major threat for large terrestrial carnivores in many parts of the world today and mitigating human–carnivore conflicts constitutes an important challenge for the conservation of these species (Chapron et al. 2014, Ripple et al. 2014).

To improve our ability to conserve large carnivores, Oriol-Cotteril et al. (2015) recently introduced the concept of a landscape of coexistence. The landscape of coexistence identifies areas in space and time where the human-caused mortality risk is low enough to enable long-term coexistence of large terrestrial carnivores with humans. The idea is based on the landscape of fear concept, which explains how the risk of predation is shaping space use patterns and habitat selection of prey (Brown et al. 1999). In the landscape of fear, tradeoffs between risk avoidance and selection of resources indirectly affect prey survival and reproduction and there is strong evidence that such indirect effects may outweigh the direct consumptive effects of predation on prey population dynamics in many systems (Werner and Peacor 2003, Preisser et al. 2005, Peckarsky et al. 2008). The landscape of coexistence concept posits that the distribution of human-related risks forms a landscape of fear for large carnivores and may therefore explain large parts of the distribution and behavioral ecology of these species in human-altered environments. Thus, understanding the landscape of coexistence will be important for the conservation of large terrestrial carnivores in areas of high human impact.

The concept of the landscape of coexistence makes predictions that can be used to test whether human-related risks are important in driving predator space use and habitat selection in human dominated landscapes (Table 1 in Oriol-Cotteril et al. 2015). For example, the landscape of coexistence predicts that predator space use is affected more by minimizing contact with humans than by natural factors, such as prey distribution or competition with other carnivores. To be able to use resource rich habitats nevertheless, predators may shift their activity temporally to times of low human activity. Moreover, large predators may prefer remaining in cover when in close proximity to humans, and may minimize the time spent in high-risk areas by increasing travelling speed and showing more directed movement. Avoidance of humans by large predators is also expected to lead to less consumption of livestock than would be expected from their abundance and vulnerability. Finally, like prey large carnivores may exhibit increased vigilance behavior in proximity of humans. These predictions provide a conceptual framework that allows estimating the extent to which human disturbance affects predator behavior and ecology. These insights, in turn, can be used to identify areas of special importance for the landscape of coexistence, thus aiding the management and conservation of large predators.

Table 1. Model output for the lynx SSF model. Positive regression coefficients correspond to preference whereas negative coefficients correspond to avoidance. Coefficients for year- and time -interactions have to be examined in combination and require plotting for interpretation (Fig. 2–4). B = beta coefficients, SE = standard errors; ysin, ycos, ysin2, ycos2: year harmonics; dsin, dcos, dsin2, dcos2: time harmonics.

Variable names	beta	SE	p-value (Wald)
Habitat type	–0.406	0.063	< 0.001
Habitat type:ycos2	–0.153	0.034	< 0.001
Habitat type:dsin	–0.162	0.040	< 0.001
Habitat type:dsin2	0.197	0.056	< 0.001
Habitat type:dcos2	–0.098	0.048	0.041
Altitude	0.325	0.080	< 0.001
Altitude sq	–0.306	0.040	< 0.001
Altitude:ycos	–0.209	0.064	0.001
Altitude:ysin2	–0.289	0.059	< 0.001
Altitude:dcos	–0.062	0.066	0.345
Altitude:dsin2	–0.121	0.028	< 0.001
Step length	–0.090	0.087	0.304
Deer availability	0.732	0.066	< 0.001
Deer availability sq	–0.090	0.014	< 0.001
Deer availability:ysin2	0.068	0.036	0.057
Deer availability:ycos2	0.047	0.028	0.091
Deer availability:dsin	–0.080	0.026	0.002
Deer availability:dcos	0.095	0.048	0.047
Human dist. Index	–0.147	0.034	< 0.001
Hum dist. Index sq	–0.054	0.007	< 0.001
Human dist:ysin	0.095	0.024	< 0.001
Human dist:ycos	0.104	0.025	< 0.001
Human dist:ycos2	–0.030	0.025	0.227
Human dist:dsin	–0.123	0.035	< 0.001
Human dist:dcos	0.122	0.039	0.002
Human dist:Step length	0.062	0.009	< 0.001
Human dist:Habitat type	–0.094	0.033	0.004

In this paper we apply the landscape of coexistence concept to a large European predator to understand how the tradeoffs between risk taking and resource abundance affect habitat selection in strongly human-altered environments. To this end, we studied the Eurasian lynx *Lynx lynx*, the largest felid predator in Europe. An important prey species of Eurasian lynx in many parts of its range is the European roe deer *Capreolus capreolus*, which is found at highest densities close to humans (Danilkin and Hewison 1996, Jobin et al. 2000, Sunde et al. 2000a). Previous studies have shown that lynx are attracted to areas of intermediate human impact at large spatial scales, but avoid proximity to humans at smaller scales (Bunnefeld et al. 2006, Basille et al 2009, Bouyer et al. 2015). Nonetheless, human-related mortalities such as vehicle collisions or hunting are the most important causes of death for lynx in many parts of Europe (Schmidt-Posthaus et al 2002, Andrén et al. 2006, Basille et al. 2013). Due to the presence of this apparent tradeoff between food and safety the lynx constitutes a good study system for testing the landscape of coexistence concept (Bunnefeld et al. 2006, Basille et al. 2009). Hence, in our study we tested the landscape of coexistence concept, focusing on spatio-temporal variation in small-scale habitat selection of lynx. Specifically, we tested the following five predictions:

1) A positive relationship exists between human disturbance and roe deer availability resulting in a tradeoff between food and safety for lynx.
2) Lynx use areas of high deer availability during times of low human activity in order to minimize risky encounters with humans, while still being able to use good foraging grounds.
3) Lynx move faster and remain more in cover when moving through areas of high human disturbance to reduce the time spent vulnerable and the risk of being detected by humans.
4) Human disturbance is more important in driving lynx habitat selection than deer availability.
5) Lynx kill less livestock than would be expected from availability in their habitat because they avoid close human proximity.

Methods

Study area

Our study was conducted in the northwestern Swiss Alps (NWSA). The study area covered roughly 1500 km^2 (center coordinates 46°55′99.05″N, 7°51′30.52″E) and ranged in altitude between 600 m and 3500 m a.s.l. The region is populated by humans (33 inhabitants km^{-2}) with most human settlements situated at the valley bottoms. Valley bottoms and lower slopes have been deforested since the middle ages for agricultural use. Remaining forests (about 30% of the total area) are situated mostly on the higher slopes and are highly fragmented. The treeline lies between 1800 m and 1950 m. Roe deer and chamois are the main wild prey species of lynx in the area (Molinari-Jobin et. al 2002). The abundance of roe deer in the study area is estimated to be roughly 3600 animals, whereas population estimates for chamois lie at roughly 5000 animals (yearly report of the cantonal hunting authorities 2014). In addition, every year roughly 7000 sheep graze on Alpine summer pastures between April and September (Office for agriculture of the Canton of Berne). Roughly 3000 sheep are kept at lower altitudes for the remaining period of the year on fenced pastures close to human settlements. The majority of sheep herds (ca 90%) in the study area are not efficiently protected from lynx attacks (e.g. by livestock guardian dogs or shepards) and hence constitute potentially easy prey for lynx (Moa et al. 2006, Gervasi et al. 2014). The entire region is used intensively for recreational purposes (Pesenti and Zimmermann 2013). Lynx in the study area are not legally hunted, however humans pose an important mortality risk for lynx through vehicular collisions and poaching (ca 30% of total mortality; Schmidt-Posthaus et al. 2002). The lynx population in our study area was well known from previous radio-telemetry studies (Breitenmoser and Haller 1993, Molinari-Jobin et al. 2007) and repeated camera-trapping censuses (Pesenti and Zimmermann 2013). Lynx density in the region was estimated at 2.13 independent lynx 100 km^{-2} from a camera-trapping census in winter 2011/12 (Zimmermann et al. 2012).

GPS data

Lynx location data and kill sites

Between 2011 and 2014 we captured 15 lynx (seven females and eight males). The capture protocol for lynx has been described in detail elsewhere (Vogt et al. 2016). In brief, lynx were captured by one of three methods: at fresh kills using foot snares or a remotely controlled teleinjection system (Ryser et al. 2005), or in large double-door live traps. Captured lynx were immobilized and equipped with GPS-GSM radio collars and released at the site of capture.

GPS fix intervals ranged between one and nine hours, with a majority of intervals at three hours (48%; see section on step selection functions for a description on how we dealt with interval heterogeneity). The GPS error for this study was estimated at 8.8 m (± 1.3 m SE; described in Vogt et al. 2016). Outliers, such as single isolated locations, were removed from the data set (n = 520). Only adult and resident lynx were considered in this study. Data from two lynx were removed from the analysis because they were either ill or subadult individuals during the entire monitoring period. Finally, for one male lynx we excluded two obvious excursions to another part of the Alps before it became resident in the study area. After data processing 19 128 locations from 13 individual lynx remained (six females and seven males, Fig. 1). The number of locations per individual ranged between 415 and 2425 (mean = 1471, SD = 788.6) comprising between 140 and 567 (mean = 322, SD = 178) monitoring days per individual.

Livestock depredation of lynx was assessed from 554 kills located between 2011 and 2015 by either checking GPS clusters of radio collared lynx (503), by snow tracking (36) or by reports from local game wardens (15). Considering only the three ungulate prey species (roe deer, chamois and sheep) and assuming prey selection to occur according to abundance, one would expect $7000/(3600 + 5000) = 0.8$ sheep per wild ungulate kill to occur during the summer months (April–September) and 0.4 sheep per wild ungulate for the rest of the year.

Roe deer location data

Between November 2011 and April 2013 we captured roe deer (n = 65) using drive nets or box traps and equipped them with GPS collars recording locations every 30 minutes (n = 1 351 368 locations; detailed description in Gehr 2016, Fig. 1). Because mean GPS error (27 m) was large with respect to the mean step length of 54 m (Visscher 2006) we rarefied the data to 2 h fix intervals resulting in a mean step length of 123 m for a total of n = 302 633 deer locations.

Environmental variables

GIS-layers for assigning habitat attributes to GPS locations were provided by the federal office of topography (Swisstopo). Vector layers included habitat type, roads and buildings ($SwissTLM^{3D}$ 2013). We summarized habitat type into two categories: Forests, open forests, scrubland, and hedges were categorized as cover habitat. Everything else, i.e. agricultural land, alpine meadows, settlement area or rocky habitat was categorized as open habitat. As one could expect rocky habitat to provide more concealment than other open habitats, we performed a preliminary univariate SSF for habitat type with 3 categories, namely rocky habitat (reference category), open habitat and cover, which revealed that lynx did not select differently for rocky habitat than for other open habitats ($\beta_{open} = 0.059$, $p = 0.333$). Thus, for further analysis we used cover as the reference category (dummy encoding 0) and modelled selection of open habitat (dummy encoding 1). We calculated building density using a negative exponential smoothing kernel that decreased rapidly with distance from the building (kernel density of a single building dropped below 50% within 20 m and disappeared beyond 100 m; R-code by Björn Reineking, adapted from R-package EBImage – Pau et al. 2010). As a consequence, the distribution of the variable ‘building density’ was strongly right skewed and we applied a power transformation of the tenth root to achieve a less skewed distribution of this variable (Quinn and Keough 2002). Finally we used a digital elevation model ($SwissALTI^{3D}$ 2013, DEM, 10 × 10 m resolution) to calculate altitude, slope and exposition (southern exposition versus all other cardinal directions).

Statistical analyses

Our main interest was in how temporal variation in human activity and deer availability shape the landscape of coexistence for the Eurasian lynx in the Alps. Thus, we first constructed human disturbance and deer availability indices as described below and then modelled the response in habitat selection of lynx for these two predictors as a function of time and season using step selection functions.

Time dependence of habitat variables

An important aspect of the landscape of coexistence is the temporal dynamics of habitat selection and human avoidance. To capture these patterns we modelled temporal dynamics on a continuous scale. We considered time of day and day of year as two different temporal scales. To model the diurnal and seasonal patterns of selection of human disturbance and deer availability, we followed the approach used in Forester et al. (2009). We considered interaction terms between model predictors and four harmonics of time of day (TOD; calculated as decimal hours for each step) and day of year (DOY) respectively (TOD: $s_{1TOD} = \sin(2\pi t/24)$, $s_{2TOD} = \sin(4\pi t/24)$, $c_{1TOD} = \cos(2\pi t/24)$, $c_{2TOD} = \cos(4\pi t/24)$ and for DOY: $s_{1DOY} = \sin(2\pi t/365)$, $s_{2DOY} = \sin(4\pi t/365)$, $c_{1DOY} = \cos(2\pi t/365)$, $c_{2DOY} = \cos(4\pi t/365)$). To reduce the number of interaction terms in the final lynx model we assessed the functional relationships between each of the four main predictor variables with TOD and DOY using a full model including all eight time harmonics. For the final model we then removed all time interactions with p-values smaller than 0.1 and refitted this reduced model (see Supplementary materials Appendix 1 for a discussion of this approach). We standardized time of day to coordinated universal time (UTC). Difference to local time was one hour in winter (CET) and two hours in summer (CEST) due to daylight saving time.

Human disturbance

We constructed a human disturbance index which was comprised of building density and distance to the closest road, as these parameters have been shown to correlate with human disturbance and to affect habitat selection of lynx (Zimmermann and Breitenmoser 2002, Basille et al. 2009, 2013) and many other large mammals (Coulon et al. 2008, Northrup et al. 2012, Zimmermann et al. 2014). We calculated the human disturbance index as the difference between the scaled house density and road distance.

Deer availability

Chamois and roe deer are the two main prey species of lynx in the study area (40% and 34% of identified kills respectively). Since chamois are much less associated with humans than roe deer we only considered here the tradeoff between roe deer availability and human disturbance. Nonetheless, the presence of an alternative prey that is less associated with humans may weaken the tradeoff between prey availability and risk avoidance. However, because chamois occurred in the entire study area, we could not test how the presence of chamois affected the landscape of coexistence. We thus built a time specific resource selection function (RSF; Boyce et al. 2003, Forester et al. 2009) for 65 radio collared roe deer to predict the probability of deer occurrence as a function of habitat covariates at the two above mentioned temporal scales TOD and DOY. We used the 100% minimum convex polygons (MCP) to assess habitat availability at the home range scale for deer (Johnson 1980). From these home ranges we then drew random locations to delineate availability in a ratio of 10 random locations per used deer location. The following habitat variables known to be important for roe deer habitat selection were included in the model (Danilkin and Hewison 1996, Mysterud et al. 1999, Coulon et al. 2008): human disturbance index (as described above), habitat type (open versus cover), distance to the closest cover edge (in meters; always positive regardless whether inside cover or in the open), altitude (m a.s.l.), slope (degrees), and southern exposition of slopes (dummy variable for southern exposed slopes = 1 and 0 for all other expositions). For human disturbance, altitude and slope we included a quadratic term to allow for non-linear dependencies between selection and those covariates. Each random location was assigned a random time of day and day of year drawn from the observed deer locations in order to model temporal variation in habitat selection as explained for the lynx model above. Due to the large number of deer locations, model reduction using p-values as for the lynx model was not practical (i.e. almost all coefficients were highly significant despite some very small effect sizes). Therefore we used univariate models (including all time interactions) to determine for which predictor TOD and/or DOY interactions were important (see Supplementary material Appendix 1 for a detailed description; Fig. A1–A2). We then included four time harmonics for all DOY interactions and two time harmonics for all TOD interactions that remained in the final model in order to reduce the number of variables. We modelled DOY interactions for southern exposition and altitude and TOD interactions for habitat type, distance to cover edges and slope (Table 1). For the human disturbance index we included both TOD and DOY interactions. To be consistent with the lynx step selection function, we did not fit temporal main effects (Table 1). Finally we built the RSF using logistic regression (Boyce et al. 2003), where

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)$$

represents the RSF score and the β's are the regression coefficients for the corresponding covariates ($x_1, \ldots, x_n$). All continuous covariates were standardized (mean of 0 and SD of 1). We tested for collinearity between main predictor variables using variance inflation factors. The highest variance inflation factor for continuous covariates was 1.63, which suggests that multicollinearity was not an issue in our model (Zuur et al. 2009). The goodness of fit of the model was assessed using cross validation methods as described below for the lynx model.

Temporal variation in lynx habitat selection – step selection function

To model how lynx overcome the tradeoff between avoidance of human disturbance and selection of high deer availability we used step selection functions (SSF; Fortin et al. 2005, Forester et al. 2009, Thurfjell et al. 2014). SSF are resource selection functions that take individual movement into account by comparing environmental attributes of realized animal locations with alternative random steps in a matched case-control design. Steps were characterized by the step length (the straight-line segment between two successive locations) and the turning angle (the angle between the previous and the current step). Each step was then assigned habitat variables and predation risk found at the end of the step. The SSF took the exponential form (analogous to the deer RSF) and was estimated using conditional logistic regression, which assesses the resource selection of an animal conditionally on a choice set of possible random steps. We used the empirical step length and turning angle distribution of the ensemble of all observed lynx steps to draw the random steps (Forester et al. 2009). To account for differences in step lengths and turning angles for different fix intervals we first regularized the data by excluding all steps with fix intervals greater than six hours ($n = 1226$; see Coulon et al. 2008 for a similar approach) and subsequently divided the remaining lynx steps into three fix interval categories of similar step length distributions (< 70 min, 70–190 min, 190–370 min). Finally we drew 10 random steps and turning angles per used location from these three different empirical distributions. Step lengths and turning angles were drawn in pairs (Thurfjell et al. 2014). In order to restrict the analysis to actively moving animals we excluded all steps shorter than 5 × the gps error (44 m, $n = 5943$; Visscher 2006). In the end we used 13 185 steps of 13 lynx (between 335 and 1916 locations per lynx; mean = 1014, SD = 568.4).

The SSF model for lynx habitat selection is summarized in Table 1. In addition to the human disturbance index and deer availability we also included altitude and habitat type (open versus cover) as main predictors in the SSF model, as these parameters have been shown to be important variables for lynx habitat selection (Gehr 2016). Forester et al. (2009) suggested to use linear splines for step length in order to obtain unbiased estimates of the regression coefficients (Forester et al. 2009, Warton and Aarts 2013). We tested the influence of linear splines on regression coefficients but found only marginal differences between a model including linear splines and one without splines. We therefore refrained from using linear splines to keep the model as simple as possible. Furthermore, we added quadratic terms for human disturbance, deer availability, and altitude since lynx have been shown to select for intermediate values for all three predictors (Basille et al. 2009, Bouyer et al. 2015, Gehr 2016). To test whether lynx adjust their movement speed or habitat selection in areas of higher human disturbance, we included an interaction term between human disturbance at the beginning of a step and step length on one hand (to test whether lynx speed up when in areas of high human disturbance) and human disturbance at the end of a step and habitat type on the other hand (to test whether lynx remain more in cover in areas of high human disturbance). Finally we added the temporal interaction terms for TOD and DOY as discussed above for the four main predictor variables. Conditional logistic regression does not allow to fit main effects for predictors that are constant within choice sets (Allison 1991), which was the case for time of day and day of year. Consequently we fitted temporal predictors only as interaction terms (Table 1). Altitude and human disturbance index were centered and standardized (mean = 0, SD = 1) whereas prey availability was only standardized (SD = 1) for easier interpretation of results. The maximum VIF for the main predictors was 2.25 suggesting that multicollinearity was not an issue.

To account for serial autocorrelation in the data we applied a two-step SSF (Fieberg et al. 2010, Thurfjell et al. 2014). The statistical idea of this approach is to fit separate models for each animal and to average the coefficient estimates over all individuals. This approach is sometimes favored over a generalized linear mixed model because it bypasses computational complexities of likelihood maximization (Craiu et al. 2011), and it solves the issue of complex correlation structures when combining used and available steps in one model, something that is difficult to achieve using standard modelling techniques (Fieberg et al. 2010). The R-package TwoStepCLogit (Craiu et al. 2011) was used to fit the model.

Model assessment – goodness of fit and relative importance

We assessed the goodness of fit of the lynx model as well as the deer model using cross validation methods, repeatedly setting aside three lynx/deer as the test data set and using the remaining animals to build the model (Boyce et al. 2002, Wiens et al. 2008). For the validation, we divided the SSF/RSF values of the random steps/locations into ten equal sized bins and used the SSF/RSF values of the used steps/locations for the corresponding bin ranks. The Spearman rank correlation between the bin rank and the frequency of used steps per bin is a measure of model fit, where large correlations can be interpreted as a good model fit (Wiens et al. 2008). We repeated this step 100 times, each time using a different training and test data set from all possible permutations (choosing three out of all lynx without replacements). In the end we tested the percentage of Spearman rank correlations that were above the critical value of 0.564 (which corresponds to a correlation on the $\alpha = 0.05$ level for $n = 10$ pairs), and reported the mean correlation values over the 100 trials (Wiens et al. 2008).

To investigate the principal drivers of lynx space use we estimated the relative importance of the individual regression terms as described in Ewald et al. 2014 (where the relative importance of all predictors sums to 1, see Supplementary material Appendix 1 for a detailed description) and then summed the relative importance of the four main predictors with their higher order interactions (time harmonics and quadratic terms). We visualized temporal dynamics in habitat selection using pointwise confidence intervals of w(x) for all predictor values (Fox 2003).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.h35fj> (Gehr et al. 2017).

Results

Human disturbance and deer availability

Locations of radio-collared lynx were found in areas of lower human disturbance than locations of radio-collared roe deer ($\text{mean}_{\text{lynx}} = -0.12$, $\text{mean}_{\text{deer}} = 1.54$, $t_{13,574.8} = -124.04$,

$p_{t\text{-test}} < 0.001$). In general, the highest human disturbance was found in the valley bottoms where settlements are situated.

Roe deer habitat selection, as a proxy for deer availability, showed strong temporal and seasonal fluctuations (Supplementary material Appendix 1 Table A1, Fig. A3–A4). Roe deer selected for steeper slopes and stayed more in protective cover or close to cover edges during daytime in comparison to night time (Supplementary material Appendix 1 Fig. A3). At the seasonal scale deer were found at lower altitudes closer to humans in winter and early spring (Supplementary material Appendix 1 Fig. A4). Furthermore deer selected for southern exposed slopes during months when snow covered the ground. On the other hand, there was no strong diurnal pattern of selection for human disturbance (Supplementary material Appendix 1 Fig. A3). K fold cross validation showed that the data fitted the model well ($r_{CV100} = 0.97$, SD = 0.12 with 98% of trials above the critical value of 0.564).

Human disturbance and deer availability followed a non-linear relationship with a general increase in deer availability with increasing human disturbance (Supplementary material Appendix 1 Fig. A5). Thus, a clear tradeoff existed between selecting for high deer availability and avoiding high human disturbance as expected from prediction 1.

Lynx habitat selection

The results of the SSF revealed that lynx habitat selection shows strong temporal and seasonal fluctuations (Table 1). In general lynx avoid open habitat and prefer intermediate altitudes. However, avoidance of open habitat is much weaker during twilight than during night or day hours, and in winter lynx are found at considerably lower altitudes than during the rest of the year (Fig. 2). Furthermore lynx strongly selected for high deer availability, while at the same time avoiding high human disturbance. However, the functional relationship for avoidance of human disturbance was non-linear, as indicated by the clearly negative quadratic term, with avoidance of both high but also very low human disturbance (Table 1). There was also strong evidence for a non-linear influence of deer density, as indicated by the positive quadratic term. Lynx responded to the tradeoff between deer availability and human disturbance by selecting areas of high deer availability during times of low human activity, i.e. during late evening and night, thereby confirming prediction 2 (Fig. 3). Nonetheless, during winter (between November and March) lynx showed much weaker avoidance of human disturbance and stronger selection for deer availability than during the rest of the year (Fig. 4). For deer availability there was however a second peak of selection during summer. Finally, lynx moved faster and selected more for cover when moving in areas of higher human disturbance as predicted by prediction 3 (Table 1). The data fit the model well, as shown by the results of the k-fold cross validation ($r_{CV100} = 0.95$, SD = 0.05 with 100% of trials above the critical value of 0.564).

Inspection of the relative importance of the model predictors indicated that deer availability was by far the most important predictor for lynx space use patterns

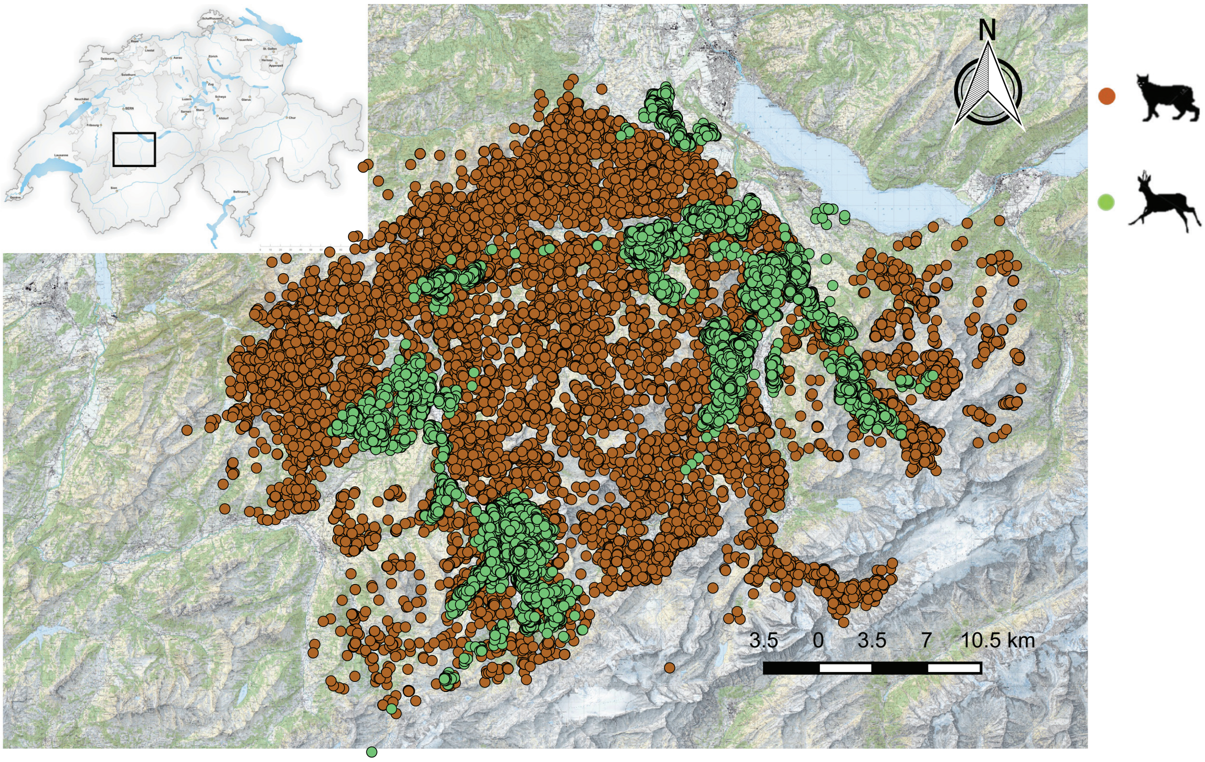

Figure 1. Map of the study area in the northwestern Alps of Switzerland including all GPS locations for lynx (orange) and roe deer (green) respectively.

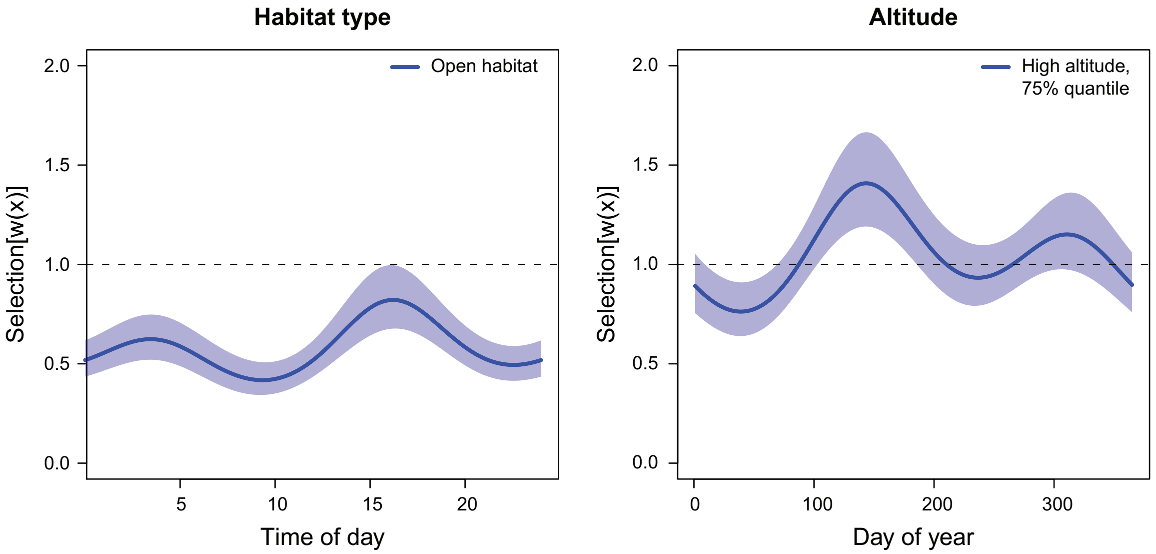

Figure 2. Lynx diurnal and seasonal selection patterns of open habitat and altitude respectively. The two panels show interactions between the two predictor variables and the time harmonics for TOD and DOY respectively in the SSF model for lynx. DOY interactions are fixed at January 1 for the diurnal selection patterns and TOD interactions are fixed at midnight for the seasonal selection patterns (choice of date and time are arbitrary). The blue shading indicates the pointwise 95% confidence intervals for the respective curves. The dotted line for w(x) = 1 represents no selection. Thus values of w(x) greater than 1 indicate selection whereas values of w(x) smaller than 1 indicate avoidance relative to the reference (cover habitat for habitat type and mean altitude for altitude). Because we used coordinated universal time (UTC), time curves for TOD are shifted by one (for central European time; CET) and 2 h (for central European summer time; CEST) respectively with respect to local time. w(x): SSF score, TOD: Time of day, DOY: day of year.

(rel. importance = 0.55) whereas the relative importance of human disturbance was much lower (0.16). This finding contradicts prediction 4. Altitude was the second most important predictor (0.2) whereas habitat type had the lowest relative importance (0.08; Supplementary material Appendix 1 Table A2).

Livestock depredation

Occasional depredation of livestock (mainly domestic sheep) occurred but was rare (0.6% of identified kills during the summer months and 2.2% during the rest of the year). This rate of livestock depredation (0.01 and 0.03 livestock per wild

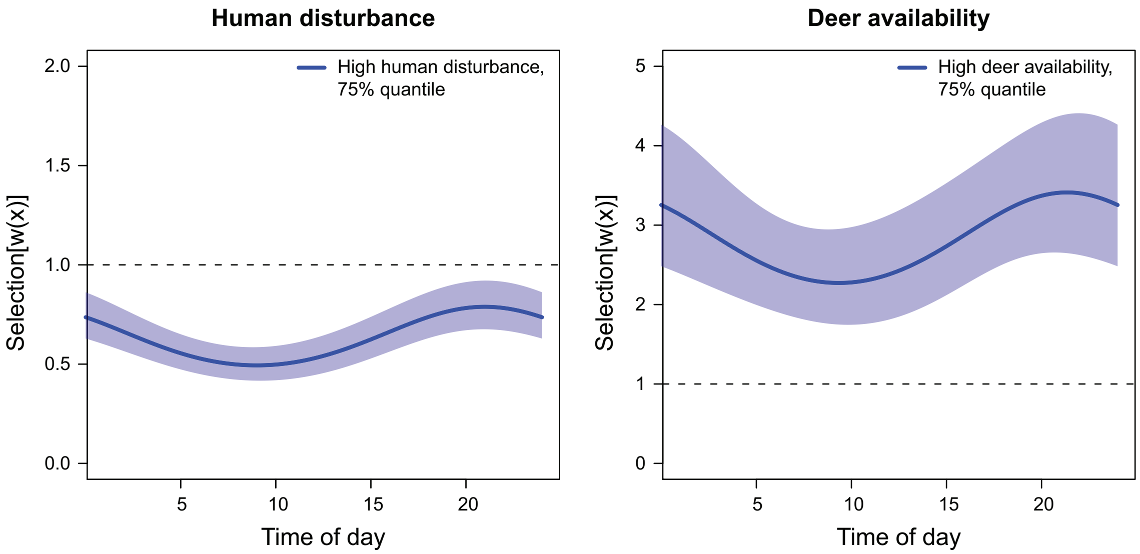

Figure 3. Lynx diurnal selection patterns for deer availability and human disturbance respectively. The two panels show interactions between the two predictor variables and the time harmonics for TOD in the SSF model for lynx. The DOY interactions are fixed at 1 January. The blue shading indicates the pointwise 95% confidence intervals for the respective curve. The dotted line for w(x) = 1 represents no selection. Thus values of w(x) greater than 1 indicate selection whereas values of w(x) smaller than 1 indicate avoidance relative to the reference (zero deer availability and mean human disturbance respectively). Because we used coordinated universal time (UTC), time curves for TOD are shifted by one (for central European time; CET) and 2 h (for central European summer time; CEST) respectively with respect to local time. w(x): SSF score, TOD: Time of day.

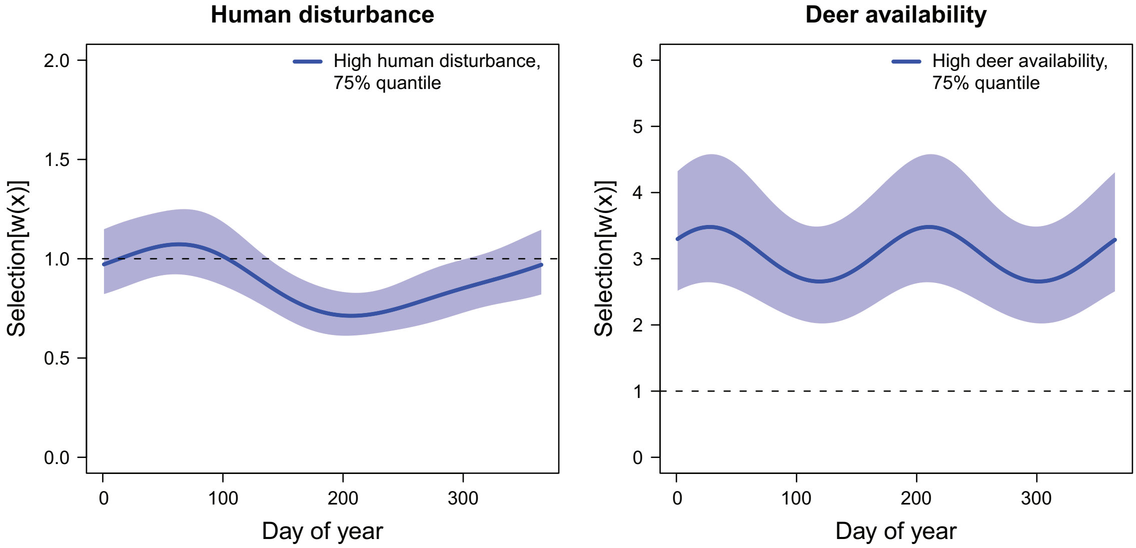

Figure 4. Lynx seasonal selection patterns for human disturbance and deer availability respectively. The two panels show interactions between the two predictor variables and the time harmonics of DOY in the SSF model for lynx. The TOD interactions are fixed at midnight. The blue shading indicates the pointwise 95% confidence intervals for the respective curve. The dotted line for w(x) = 1 represents no selection. Thus values of w(x) greater than 1 indicate selection whereas values of w(x) smaller than 1 indicate avoidance relative to the reference (zero deer availability and mean human disturbance respectively). w(x): SSF score, DOY: Day of year.

ungulate in summer and the rest of the year, respectively) is much lower than what was expected from the abundance of the different ungulate species (0.8) thus indicating strong avoidance of domestic animals by lynx ($p_{prop.test} < 0.0001$) as anticipated by prediction 5.

Discussion

In this study we analyzed the landscape of coexistence for the Eurasian lynx, the largest felid predator in Europe, and showed that in our study site lynx face a tradeoff between high human disturbance and high deer availability (prediction 1) which implied that avoiding the latter is potentially associated with considerable foraging costs for lynx. By testing specific predictions based on the landscape of coexistence concept formulated by Oriol-Cotteril et al. (2015; predictions 2–5), we showed that lynx respond to this tradeoff by spatio-temporally adjusting their habitat selection and movement patterns in order to minimize human disturbance while still utilizing areas of high deer availability.

Lynx reacted to the existing tradeoff between food and safety by using areas of high deer availability, but also high human disturbance during times of low human activity (prediction 2). Avoidance of high human disturbance was lowest during dark hours when lynx are most active (Schmidt 1999, Heurich et al. 2014) and highest during the day. Temporal shifts in space use patterns in response to human activity seem to be a common reaction of large carnivores (e.g. brown bears – Ordiz et al. 2011, 2012, lions – Valeix et al. 2012, Oriol-Cotteril et al. 2015, wolves – Theuerkauf et al. 2003, Theuerkauf 2009, or cougars – Van Dyke et al. 1986). The costs of this avoidance behavior is difficult to assess but may differ among carnivores due to differences in diurnal activity patterns (Oriol-Cotteril et al. 2015). For most felid species the costs may be fairly low under most circumstances given their crepuscular and nocturnal activity peaks whereas costs for predators also active during the day, such as wolves or bears might be higher. Habitat selection of lynx also fluctuated seasonally with less avoidance of human disturbance during the winter months when snow cover is forcing both prey and predators to move to lower altitudes, closer to human settlements and disturbance. However, human activities are also reduced during this time period (agricultural activities are reduced and many roads are inaccessible due to snow cover) and thus the probability of risky encounters may be reduced for lynx, minimizing the costs of this downward shift. These results show that behavioral adjustments at both large and small temporal scale enable lynx to use areas of high human disturbance during temporal refuge windows of low human activity.

Depending on the proximity to humans, lynx further adjusted their movement patterns and habitat choice at a fine spatial scale. We found that lynx increased their travelling speed and remained more in cover (as defined in the method section) when moving in areas of high human disturbance (prediction 3). This finding suggests that lynx perceive human proximity as a threat and try to minimize the probability of encountering humans when moving through high risk areas. We cannot completely rule out that this result is in part due to lynx hunting in areas of high human disturbance, thus moving fast and in forests. However, given that lynx are ambush predators we would expect travelling speed to be low during active hunting behavior. Increased travelling speed through areas of high human disturbance and increased use of cover to reduce human encounters have also been found in other large carnivores (e.g. increased traveling speed in cougars and lions: Dickson et al. 2005, Valeix et al. 2012, Oriol-Cotteril et al. 2015; increased use of dense cover in spotted hyenas and brown bears: Boydston et al. 2003, Preatoni et al. 2005), suggesting that these behavioral adjustments are common among large predators. Taken together, these results show that behavioral adjustments at different spatial and temporal scales enable lynx to persist in areas of high human disturbance but high prey availability. Thus large carnivores do not completely abandon resource rich habitats that are near human settlements, they adjust their behavior to use them in a way and at times that reduce the risk of encountering humans.

The landscape of coexistence concept predicts that the spatio-temporal use of the landscape should be mainly driven by human disturbance in areas with high human-related risks, whereas prey availability and intra- and inter-specific competition should be more important in more natural environments (prediction 4; Oriol-Cotteril et al. 2015, Table 1). In contrast to this prediction, our analyses revealed that deer availability explained substantially more variation in lynx habitat selection and space use patterns than human disturbance. Thus, even though lynx clearly adjust their behavior in response to human disturbance they do not seem to be strongly constrained by human-related risks, despite the fact that humans are an important cause of lynx mortality in the study area. This finding may suggest that a strong association of prey with human disturbance might force lynx to take high risks in order to catch enough prey and emphasizes the importance of mitigating human-related mortality of large carnivores in a landscape of coexistence. Nonetheless, the presence of chamois as important alternative prey species in areas of low human disturbance likely affects the landscape of coexistence for the lynx in our study area. In this context it is surprising that deer availability still accounted for 56% of the variation in lynx habitat selection explained by the model. As highlighted by a recent study on Amur tigers in Siberia, taking the availability of all prey species into account improves the understanding of how prey occurrence shapes habitat selection of a predator (Petrunenko et al. 2016). Thus, including information on the distribution and availability of chamois in a future study will help to better understand the importance of alternative prey for the landscape of coexistence for lynx in the Alps.

In our study area lynx clearly avoided feeding on livestock (mainly sheep) compared to their availability (prediction 5). Given the high availability and naivety of sheep as prey during the summer months this result is surprising and might suggest that lynx avoid killing sheep to avoid human-related risks (see Moa et al. 2006 for a more detailed discussion on lynx in Norway). The high availability of alternative prey in the study area may be an important factor preventing lynx from switching to abundant livestock (see Valeix et al. 2012 for an example with lions). The importance of available alternative prey can be seen in Norway where lynx rely heavily on the abundant livestock prey (Sunde et al. 2000b, Gervasi et al. 2014). However, the lower productivity of the habitat in this region seems to support much lower densities of roe deer and other small prey than in our study area, forcing lynx to utilize the highly abundant livestock (mainly reindeer and sheep). Other studies on prey selection of large carnivores have also found avoidance of livestock when alternative wild prey was abundant (e.g. lions: Tumenta et al. 2013, wild dogs: Woodroffe et al. 2007, or snow leopards: Ghoddousi et al. 2016). Our results thus add to the body of literature showing that large carnivores avoid killing livestock if wild prey is abundant most likely in order to avoid human-related risks.

The results of this study show that the landscape of coexistence for lynx in the Alps includes areas of high human density and disturbance. Lynx are able to persist in human dominated landscapes by utilizing temporal refuge windows of low human activity to access areas of high deer availability close to humans. When moving through these areas lynx further adjust their fine scale habitat selection and movement patterns to minimize the risk of human encounters. Depredation on livestock often poses major challenges for the landscape of coexistence of large carnivores in many parts of the world as it affects the willingness of the local human population to live side by side with these animals (Linnell et al. 1999, Hemson et al. 2009). The strong tendency of lynx to kill livestock much less than expected based on livestock abundance mitigates the potential for human–carnivore conflict and emphasizes the importance of healthy wild prey populations to sustain large carnivores in human dominated landscapes (Khorozyan et al. 2015). In summary, as long as there is enough wild prey and sufficient cover available, human dominated landscapes in Europe should be able to sustain healthy lynx populations in a wide variety of circumstances. The major challenge for lynx and large carnivore conservation in general will be to mitigate human-related mortality in human-dominated landscapes. This study has shown that the concept of a landscape of coexistence can be useful for developing adaptive management plans for endangered populations of large carnivores and help in focusing conservation efforts.

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Supplementary material (available online as Appendix oik-04182 at <www.oikosjournal.org/appendix/oik-04182>). Appendix 1.