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Research

Season rather than habitat affects lynx survival and risk of mortality in the human-dominated landscape of southern Sweden

Henrik Andrén*, Malin Aronsson*, José V. López-Bao, Gustaf Samelius, Guillaume Chapron, Geir Rune Rauset, Heather Hemmingmoore and Jens Persson

H. Andrén (https://orcid.org/0000-0002-5616-2426) ✉ (henrik.andren@slu.se), M. Aronsson (https://orcid.org/0000-0002-9026-3765), J. V. López-Bao (http://orcid.org/0000-0001-9213-998X), G. Samelius (http://orcid.org/0000-0002-1067-9796), G. Chapron (http://orcid.org/0000-0002-6727-1070), G. R. Rauset (http://orcid.org/0000-0002-6345-3029), H. Hemmingmoore (http://orcid.org/0000-0002-3550-8475) and J. Persson (http://orcid.org/0000-0003-1405-7561), Grimsö Wildlife Research Station, Dept of Ecology, Swedish Univ. of Agricultural Sciences, Riddarhyttan, Sweden. JVL-B also at: Research Unit of Biodiversity (UO/CSIC/PA), Oviedo Univ., Mieres, Spain. GS also at: Snow Leopard Trust, Seattle, WA, USA. GRR also at: Norwegian Inst. for Nature Research (NINA), Torgarden, Trondheim, Norway.

Landscapes are mosaics of habitat associated with different risks and resources, including human activities, which can affect individual survival in wildlife. Different relationships between habitat characteristics and human-caused and natural mortality can result in attractive sinks. We used individual-based data from 97 Eurasian lynx *Lynx lynx* monitored for 160 exposure-years to link adult survival and the risk of mortality to home range habitat characteristics in the human-dominated landscape of southern Sweden. Human-caused mortality (i.e. legal hunting, poaching and vehicle accidents) dominated mortality causes (24 out of 37 deaths). We did not detect any strong effects of habitat characterises explaining the variation in mortality risk in lynx. Although the density of roe deer affects several aspects of lynx ecology, we could not detect any effects of roe deer density on lynx survival, probably because roe deer density was sufficiently high in our study area. Instead, seasonal variation was the main factor influencing mortality in lynx. Mortality was highest during the hunting season for lynx (16 February–31 March), as well as during autumn and winter, probably because lynx poaching occurs opportunistically during the hunting season for moose and roe deer. We did not find any indication that human activity created attractive sinks for lynx, since there were no contrasting patterns between human-caused and natural mortality in terms of habitat characteristics. One explanation for the limited influence of the home range characteristics may be that lynx in our study died from multiple causes. Therefore, it is less likely that one or a few habitat characteristics could explain the risk of mortality at the home range scale. There is strong evidence that lynx can coexist with humans in multi-use and human-dominated landscapes, even without large protected areas, if the management regimes are favourable.

Keywords: attractive sink, hunting, lynx, mortality, poaching, roe deer

Introduction

Variation in individual fitness is a key factor affecting the abundance and distribution of organisms (Fretwell and Lucas 1969, Morris 2003). Landscapes consist of a mosaic of habitats associated with different risks and resources. These differences in habitat qualities influence the fitness of animals, and thus impact population dynamics, i.e. a demographic surplus in good quality habitats whereas poor quality habitats tend to yield a demographic deficit (Wiens 1976, Pulliam 1988). Understanding the link between habitats and variation in survival across the landscape is important (Gaillard et al. 2010), because human activities and environmental change affect the majority of ecosystems worldwide (Walther et al. 2002).

Individuals face a trade-off between mortality risks and resource availability in areas where abundant resources are combined with high mortality, which may create attractive sink (Gaona et al. 1998, Delibes et al. 2001, Basille et al. 2009). Many wildlife species face two contrasting types of mortality factors, human-caused and natural, that can be associated to different landscapes of risk (Lone et al. 2014). If these two major mortality factors have contrasting relationships between habitats (i.e. habitats with high human-caused mortality are also habitats with low natural mortality), and if human-caused mortality causes a negative growth rate, then human activities create an attractive sink (Delibes et al. 2001). Furthermore, hunting efforts are often higher in areas that are more accessible to humans and management actions (e.g. lethal control) can be higher in conflict areas, which can enhance the variation in human-caused mortality across the landscape (Sunde et al. 1998, Novaro et al. 2000, 2005, Johnson et al. 2004, Smith et al. 2010, Ciuti et al. 2012).

In the human-dominated landscape of Europe, Eurasian lynx *Lynx lynx* and other large carnivores are recovering (Linnell et al. 2001, Chapron et al. 2014). In these multi-use landscapes, the main causes of lynx mortality are anthropogenic, including legal hunting, poaching and vehicle accidents (Breitenmoser et al. 1993, Jedrzejewski et al. 1996, Andrén et al. 2006), and lynx hunting mortality often increases with increasing road density, and is often higher than would otherwise be expected close to small forest roads (Sunde et al. 1998, Bunnefeld et al. 2006, Basille et al. 2013).

In order to understand the mechanisms explaining the abundance and distribution of Eurasian lynx, we investigated lynx survival and the risk of mortality in relation to home range habitat characteristics in the multi-use landscape of southern Sweden. To do this, we used a long-term individual-based telemetry study (1996–2016), linking the survival of 97 adult lynx monitored for a total of 160 exposure years to both structural (e.g. cover type) and functional habitat (e.g. prey density and human activity) variables (Gaillard et al. 2010). We assessed survival at the home range scale, corresponding to the level of second-order habitat selection (Johnson 1980), as hierarchical habitat selection predicts that the most limiting factor should drive the selection at coarser spatial scales, i.e. there should be stronger selection regarding where to locate the home range than the selection within the home range (Rettie and Messier 2000).

Based on the hypothesis that landscapes consist of a mosaic of habitats with different resources and risks, we predicted that human-caused mortality should increase with road density (increased human access; Sunde et al. 1998), but decrease with proportion forest and ruggedness (proxies for escape cover; Rauset et al. 2016). We also predicted that natural mortality should decrease with roe deer *Capreolus capreolus* density (the main prey for lynx in southern Sweden; Nilsen et al. 2009), forest/agricultural edge (proxy for roe deer density, Bunnefeld et al. 2006, Basille et al. 2009), but that it should increase with lynx density at a given roe deer density, i.e. resources per capita should affect mortality (Vucetich and Peterson 2004).

Furthermore, we specifically investigated factors influencing the risk of human-caused versus natural mortality, to assess the formation of attractive sinks in the landscape. To test if different factors influence the risk of human-caused versus natural mortality, we included the interaction between hunting season and other variables, as human-caused mortality varies over the year and dominates during the hunting season, whereas natural mortality is more common during the rest of the year (Andrén et al. 2006). For example, if roe deer density decreases the mortality risk during the non-hunting season, whereas it increases the mortality risk during hunting season, then hunting and human caused mortality may cause an attractive sink.

Methods

Study area

This study was done in southern Sweden (56°N–61°N, 12°E–18°E, Fig. 1, 140 000 km²). The northern part of the study area is within the boreal zone and the southern part is within the hemiboreal zone (Esseen et al. 1997). The study area is dominated by forests, covering 68%, and is intensively managed for pulp and timber (mainly Norway spruce *Picea abies*, scots pine *Pinus sylvestris* and birch *Betula* spp.), creating a mosaic of even-aged forest stands of various successional stages. Agricultural land covers 22% of the study area. The mean primary road density is 0.41 km km⁻², secondary road density is 1.34 km km⁻² and mean human density is 62 km⁻². Primary productivity, proportion of agricultural land, and densities of humans and roads increase towards the south in the study area. Roe deer is the main prey for lynx in the study area (Andrén and Liberg 2015) and roe deer density increases towards the south. Other prey species in the study area are fallow deer *Dama dama* that occur locally at high densities, red deer *Cervus elaphus*, wild boar *Sus scrofa*, mountain hare *Lepus timidus* and European hare *Lepus europaeus*. For detailed information on lynx habitat selection in the area, see Hemmingmoore et al. (2020).
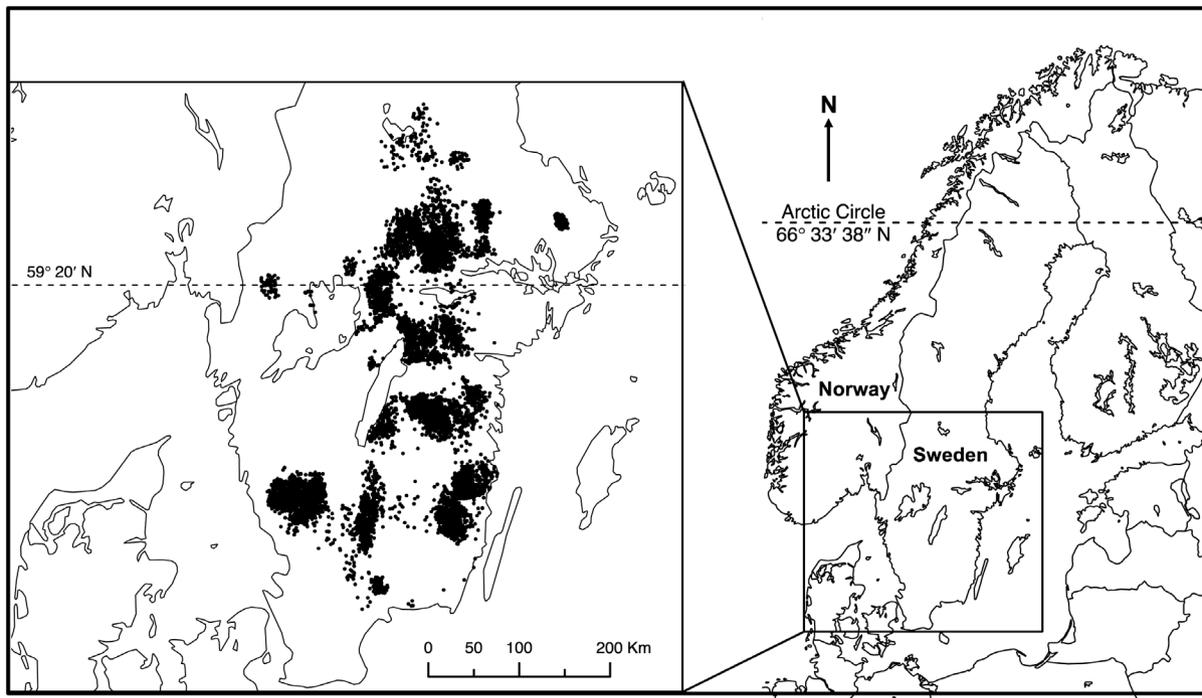
Figure 1. Map over the study area in southern Sweden with telemetry locations from 97 adult (≥ 2 years old) lynx monitored between 1996 and 2016, with an inserted map showing the location of the study area in Scandinavia.

Lynx capture and monitoring

We used demographic and location data from 97 radio-collared adult (≥ 2 years old) lynx (42 females and 55 males) monitored for a total of 160 exposure years (77 female and 83 male exposure years) between 1996 and 2016. Lynx were captured and immobilized using strict handling protocols (Andrén et al. 2006, Arnemo and Evans 2017) approved by the Swedish Animal Ethics Committee (permits C275/95 and C16/0). Lynx were fitted with VHF radio-collars in 1996–2010 (Telonics MOD335 or MOD400NH, Telonics Inc., Mesa, AZ, USA) and GPS-collars in 2008–2016 (GPS plus mini, Vectronic Aerospace, GmbH, Berlin Germany). Relocations of VHF-collared animals ranged from several times per day to 1–2 times per month whereas GPS-collared animals were programmed to take at least one position per day.

Radio-collars were equipped with mortality sensors, which allowed us to detect and investigate mortality events in the field. In addition, all dead animals were sent to the Swedish National Veterinary Institute for necropsy. Poaching is generally very difficult to determine and quantify (Andrén et al. 2006, 2020, Persson et al. 2009, 2015, Liberg et al. 2012). Poaching could be confirmed when a lynx carcass was found with a gunshot wound or when the radio-transmitter was found cut off. However, to separate between suspected poaching and unknown disappearance (such as rapid long-distance dispersal or transmitter failure) we used the criteria defined by Andrén et al. (2006). Consequently, we defined suspected poaching as when the lost animal was a resident adult equipped with a transmitter with at least half of the expected battery life remaining, the transmitter showed no

signs of previous technical problems, and the study area was searched repeatedly for the transmitter from the air. In other cases, the disappearance was classified as unknown fate and was right-censored in the survival analyses.

Space use and habitat characteristics

We estimated lynx home ranges using fixed-kernels (Worton 1989) with the 'adehabitatHR' package (Calenge 2006) in R (<www.r-project.org>) using the 90% isopleth and 0.8 × reference bandwidth (following Aronsson et al. 2016). During the study period, the number of locations acquired per individual varied extensively as radio-tracking technology developed. To reduce biases due to different sampling frequencies between animals and years (Börger et al. 2006), we randomly sampled 1 location/day/individual. Home range estimates were generated on an annual scale (i.e. from 1st June in year t to 31st May in year t + 1, as lynx generally give birth from late May to early June; Mattisson et al. 2020) and only for animals with ≥ 25 annual locations. Above this threshold, home range size was not greatly influenced by the number of locations, based on simulations using individuals with more than 100 locations (Aronsson et al. 2016). For animals with < 25 locations per year (39 exposure years or 32% of the total monitoring time) we estimated 'areas of use' by adding sex-specific buffers around each location. The buffer radius used was half the average distance moved per day based on the movement pattern of all individuals in the dataset (1265 m for females and 3032 m for males). Furthermore, we defined animals as moving (i.e. shifted home range) if they ventured into an area that they had not used previously and remained

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in this new area without returning back for > 3 months (6 males moved during the study period). For these individuals, we split the annual home ranges into separate areas (i.e. representing the area used before and after they moved).

We obtained land cover from a 25 × 25 m digital land cover map (Swedish Land Cover [SMD], National Land Survey of Sweden). We focused on two land cover classes: *agricultural land* (SMD codes 17–20, 31–32 and 51) and *forest* (SMD codes 40–50, 53–55 and 59). We pooled all forest types, as lynx selected positively for coniferous, deciduous, mixed and young forest (Hemmingmoore et al. 2020). The proportion of agricultural land and proportion of forest within a lynx home range (or area of use) were highly correlated (r = −0.80). We therefore did not include both these variables in the same model. We focused on the proportion of forest in our analyses because previous studies have shown that lynx occurrence is positively related to forest cover (Sunde et al. 1998, Basille et al. 2009, Hemmingmoore et al. 2020), but we also included the proportion of agricultural land in another set of models. The edge length between forest and agricultural land was also estimated from the same digital land cover map, as edge length can be used as a proxy for roe deer density (Bunnefeld et al. 2006, Basille et al. 2009). We calculated the *density of edge* (km km⁻²) by dividing the length of forest/agricultural edge in the home range or area of use by the area of the home range or area of use. Additionally, we used *roe deer harvest* (yearly number of roe deer shot per km²) at the hunting district level in Sweden (Swedish Association for Hunting and Wildlife Management, available at: <www.viltdata.se>) as an alternative proxy for roe deer density. Roe deer hunting bag statistics is a good functional proxy for roe deer density on lynx home range scale, as it is related to several other measurements of roe deer density (Aronsson et al. 2016). We calculated the roe deer harvest within each annual lynx home range or area of use as the area-weighted average roe deer harvest across overlapping hunting districts. For *lynx density*, we used lynx monitoring results where density of lynx family groups (i.e. female with kittens) was estimated at a regional scale based on snow tracking in January and February each year (Linnell et al. 2007). We used *density of secondary roads* (unpaved forest roads) as proxies for human activity and hunters' access to the landscape (Sunde et al. 1998, Bunnefeld et al. 2006, Basille et al. 2013). Length of secondary roads within each lynx home range and area of use was obtained from the Swedish Transport Administration database (<www.trafikverket.se>) and we calculated the density of secondary roads (km km⁻²) by dividing

the length of roads in the home range by the area of the home range and area of use. We estimated terrain *ruggedness* using vector ruggedness measure following Sappington et al. (2007), and this measure (VRM-index) ranges between 0 and 1, but usually with small values. We used elevation data from the National Land Survey of Sweden as input data with a spatial resolution of 50 × 50 m. The VRM values were very small in this study indicating a very flat landscape with low variation in slope and aspect between the core cell and its eight neighbours. Ruggedness was used as a proxy for safety for lynx (White et al. 2015, Rauset et al. 2016). Mean, standard deviation (SD) and range of all explanatory variables used are given in Table 1, and the correlations among explanatory variables are given in the Supporting information.

Survival analyses

We estimated lynx survival by using Kaplan–Meier staggered entry (Pollock et al. 1989) and the Andersen–Gill formulation of the Cox proportional hazards model (Andersen and Gill 1982) to examine how mortality of lynx varied in relation to sex, season, habitat characteristics (Table 1) and year (to account for broad scale temporal differences in survival). We stratified the data for cause of mortality as described in Heisey and Patterson (2006) to take competing risks into account. The Cox proportional hazards models allow for left truncation (individuals enter into the study at different time) and right censoring (individuals leave the study before they died) of data, categorical and continuous variables and discontinuous intervals of risk (Johnson et al. 2004). When we did not have information that determined the date of mortality, we assumed that mortality occurred 40% from the date the animal was lastly relocated to the date when mortality was detected (Johnson 1979). We used a seasonally recurrent timescale with the origin defined as 1 June in the Cox proportional hazards models (Fieberg and DelGiudice 2009), and we included individual ID as a random effect using Cluster(ID) as most lynx were monitored over several years and therefore reoccurred several times in the models. We built all hazard models and tested the assumption of proportional hazards using the '*survival*' package in R (Therneau 2015).

Thirty-seven lynx (38%) died during the study period and 60 lynx (62%) were right-censored (i.e. either alive at the end of the study [6 lynx] or when the collar stopped functioning due to end of battery or malfunctions [54 lynx]). In addition to the habitat characteristic described above we also included

Table 1. Mean (± SD), coefficient of variation (CV) and range for the explanatory variables used in the survival analyses. The explanatory variables were measured at the spatial scale of an annual lynx home range.

Variable	Mean ± SD	CV (%)	Range
Agricultural land (proportion)	0.11 ± 0.069	66	0.0–0.44
Forest (proportion)	0.76 ± 0.071	9	0.45–0.99
Secondary roads (km km⁻²)	1.44 ± 0.33	23	0.20–2.65
Roe deer harvest (n km⁻²)	0.65 ± 0.33	50	0.12–2.37
Lynx density (family groups/1000 km²)	1.81 ± 1.31	73	0.0–4.14
Forest/agricultural edge length (km km⁻²)	1.10 ± 0.54	49	0.0–2.91
Ruggedness (VRM-index)	0.00070 ± 0.00050	78	0.0–0.0034

year, *sex* and *season* as explanatory variables in the analysis. The year was divided into four different seasons; *Hunting season* (16 February–31 March), *Spring* (1 April–31 May), *Summer* (that includes reproduction, 1 June–30 September; mean birth date 30 May, Mattisson et al. 2020), and *Winter* (1 October–15 February). The winter season includes the moose *Alces alces* hunting season in southern Sweden.

In the first stage of the analysis, we conducted several sets of survival analysis; using all mortality causes, only human-caused mortality and only natural mortality. When we analysed lynx survival for human-caused mortality, lynx dying from natural causes were right censored and vice versa. Furthermore, we tested the sensitivity of possible misclassification of suspected poaching by reanalysing the data with four cases of suspected poaching being classed as right censored. We limited the number of explanatory variables in our models to two variables (all possible combination but no interaction), due to the small sample size (97 individuals). Season alone resulted in three coefficients (i.e. four-level factor with one level as reference category) and the addition of a second variable thus resulted in a total of four coefficients estimated from a sample size of 97 (i.e. an interaction with season would have result in the estimation of seven coefficients).

In the second stage of the analysis, we tested for the possibility of human-caused mortality creating an attractive sink in the landscape and we needed to include interactions between 'hunting season' and the habitat variables. Therefore, we reduced to two seasons; '*Hunting*' versus '*Non-hunting season*' (i.e. spring, summer and winter seasons pooled). Models including the interactions results in the estimation of three coefficients. This stage of the analysis was done using all mortality causes (i.e. not separating between human-caused and natural mortality).

We based all model selection on Akaike information criterion corrected for small sample sizes (AICc) where sample size was number of individuals (n = 97). We used Moran's I index to test for spatial autocorrelation using the '*ape*' package in R (Paradis and Schliep 2018). Means are presented with standard errors unless otherwise stated.

Results

Adult lynx had an average yearly survival of 0.788 ± 0.031 (Fig. 2), and there was no significant difference in yearly survival between females (0.783 ± 0.043) and males (0.794 ± 0.042; p = 0.94). Legal harvest (27%), poaching and suspected poaching (22%) and disease (22%) were the main causes of mortality (Table 2). Lynx mortality was highest during February and March (Fig. 2), which corresponded to the hunting season for lynx in Sweden.
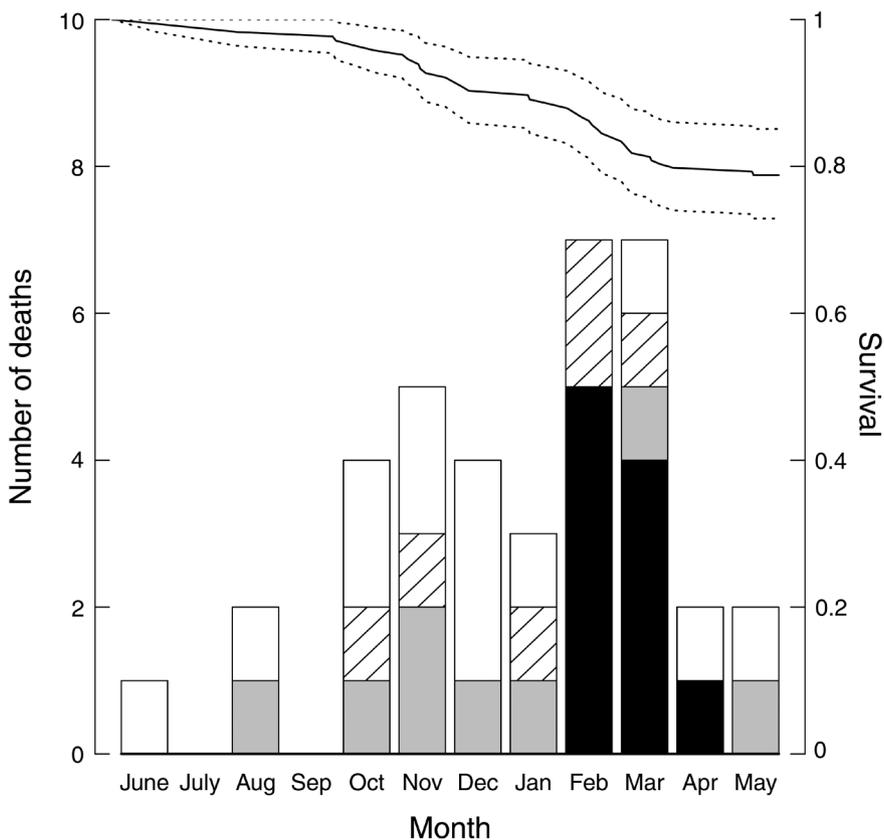
Figure 2. Survival estimates with 95% confidence limits (dotted lines) and cause of lynx mortality in relation to month (June–May). Black bars show mortality caused by legal hunting, grey bars poaching, hatched bars vehicle accidents and white bars disease and unknown cause of mortality.

In the first stage of the analysis (using four seasons and limiting to two explanatory variables), the most parsimonious model explaining the variation in lynx survival for all causes of mortality and only human caused mortality included only season (i.e. hunting season and spring, summer and winter), with the lowest survival during the hunting season and the highest survival during summer (Fig. 3, Table 3a, c, Supporting information). Excluding four lynx that were classified as suspected poaching did not influence the model selection results (Table 3b). For natural mortality (i.e. disease, killed by another lynx and unknown mortality causes), the null model was the most parsimonious model describing the variation in lynx survival (Table 3d). For models other than the most parsimonious models, the coefficients for the additional variables largely overlapped zero. Therefore, there were limited support for relationships between lynx survival and these additional variables (Supporting information). Including proportion of agricultural land instead of proportion of forest did not change the model ranking. Models including proportion of agricultural land had ΔAICc > 2.33 compared to the most parsimonious models. The assumption of time-independent proportional hazard was fulfilled (p > 0.54; Supporting information). We could not detect any spatial autocorrelation in the residuals for the most parsimonious models for different causes of mortality (p > 0.21 in all cases, Supporting information).

In the second stage of the analysis (using the two-level hunting and non-hunting season and allowing for interactions between season and habitat characteristic), the most parsimonious model included the season and lynx density interaction. However, the second-best model only included hunting versus non-hunting season and had similar support (ΔAICc = 0.35). Thus, there was some support for lynx density affecting lynx survival differently during the hunting and non-hunting season; lynx mortality increased with lynx density during the hunting season, whereas there was no effect of lynx density on lynx mortality during the non-hunting season (Table 4, Supporting information). The assumption of time-independent proportional hazard was fulfilled also for this set of models (p > 0.25; Supporting information). The other models including interactions between hunting versus non-hunting season and other variables had very weak support; secondary roads (ΔAICc = 3.50), proportion of forest (ΔAICc = 4.10), forest/agricultural edge (ΔAICc = 4.12), roe deer harvest (ΔAICc = 4.73) and ruggedness (ΔAICc = 4.79).

Table 2. Causes of mortality for 37 radio-collared adult lynx (2 years and older) in southern Sweden, 1996–2016.

Mortality	Male	Female	Total
Vehicle accidents	3	3	6 (16%)
Legal hunting	7	3	10 (27%)
Poaching	1	3	4 (11%)
Suspected poaching	3	1	4 (11%)
Disease[a]	2	6	8 (22%)
Killed by another lynx	1	0	1 (2%)
Unknown cause of mortality	2	2	4 (11%)

[a] 1 male and 6 females dying from sarcoptic mange.
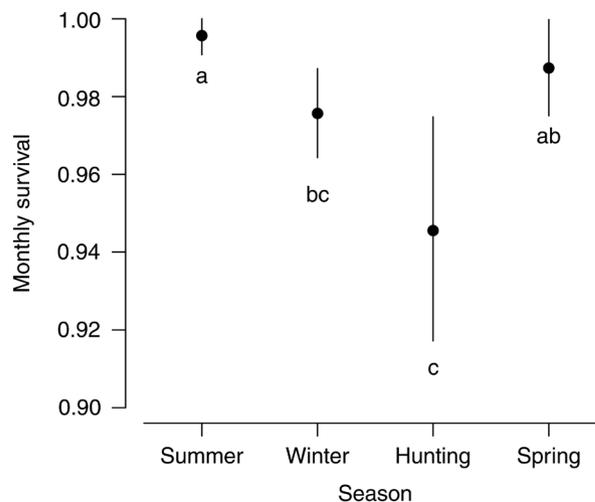
Figure 3. Monthly survival estimates during the different seasons (summer [1 June–30 September], winter [1 October–15 February], hunting season [16 February–31 March], spring [1 April–31 May]). Significant differences between groups are indicated by the different letters.

Discussion

Contrary to our predictions, we did not find any strong effects of structural or functional habitat characteristics explaining the variation in mortality risk in lynx in southern Sweden. Furthermore, we could not detect any contrasting patterns between human-caused and natural mortality for lynx, as there was no support of models including the interaction between hunting season and habitat characteristics, which could be an indication of an attractive sink. Instead, seasonal variation was the main factor influencing both the overall and human-caused mortality in lynx, while for the subset of natural mortality, the null model had the highest support and we could not detect any support for seasonal variation in survival (Table 3). This study also showed that human-caused mortality dominated (65% of the deaths, Table 2) and lynx mortality was highest during the lynx hunting season (16 February–31 March) and lowest during spring and summer (Fig. 2, 3). The decreased survival in the autumn and winter was likely also due to human activity, as season had limited effect on explaining natural mortality in lynx (Table 3d). The lower survival during October to January could probably be explained by higher poaching during this period (5 out of 8 cases of poaching and probable poaching occurred during this period) than during the rest of the year (Fig. 2, Andrén et al. 2006). This was probably because poaching occurred opportunistically during the hunting season for moose (second week in October–28 February) and roe deer (male roe deer from 15 August and all roe deer from 1 October to 31 January) in southern Sweden (Andrén et al. 2006). O'Neil et al. (2017) also found higher mortality in wolves *Canis lupus* during early winter. They gave two plausible explanations; that the wolf kill rate on white-tailed deer was lower during early winter than late winter (Vucetich et al. 2012) which can influence survival or, alternatively, that wolves were more vulnerable

Table 3. Highest-ranked candidate models evaluating the risk of (a) all causes of mortality, (b) all causes of mortality except four lynx where we suspected poaching, (c) human-caused mortality (i.e. vehicle accidents, legal hunting, poaching and suspected poaching) and (d) natural mortality (i.e. disease, killed by another lynx and unknown mortality) in southern Sweden (1996–2016). For each model we show AIC corrected for small sample size (AIC_c), difference in AIC_c relative to the highest-ranked model (ΔAIC_c). For simplicity, only models with ΔAIC_c < 2 and the null models are shown. We also show the coefficients ± SE for the parameter estimates for the variables added to the model. The nine explanatory variables are abbreviated as follows; season (S, 4-levels; summer, winter, hunting and spring, where hunting was the reference category), proportion of forest (F), edge length between forest and agricultural land (E), roe deer harvest (Ro), lynx density (L) ruggedness (Ru), year (Y), secondary roads (2-R) and Sex (2-levels where female was the reference category). Supporting information show the lynx mortality risk (hazard) as a function of the variables included in these highest-ranked candidate models.

Model	AIC_c	ΔAIC_c	Parameter	Coefficient ± SE
(a) All mortality causes (number of deaths = 37)				
S	443.41	0	Spring	−1.64 ± 0.58[a]
			Summer	−2.66 ± 0.70[a]
			Winter	−0.89 ± 0.49[a]
S + F	445.25	1.84	Forest	1.99 ± 3.02
S + E	445.35	1.94	Edge length	−0.25 ± 0.30
Null	460.21	16.80		
(b) Alternative all mortality causes (excluding suspected poaching, number of deaths = 33)				
S	390.66	0	Spring	−1.94 ± 0.69[a]
			Summer	−3.14 ± 0.86[a]
			Winter	−1.09 ± 0.50[a]
Null	410.43	19.77		
(c) Human-caused mortality (number of deaths = 24)				
S	284.65	0	Spring	−2.14 ± 0.75[a]
			Summer	−3.52 ± 1.01[a]
			Winter	−1.34 ± 0.65[a]
S + L	285.90	1.25	Lynx density	0.20 ± 0.16
S + E	286.08	1.43	Edge length	−0.49 ± 0.41
S + Y	286.43	1.78	Year	−0.040 ± 0.037
Null	300.75	16.10		
(d) Natural mortality (number of deaths = 13)				
Null	159.49	0	–	–
Y	160.73	1.24	Year	0.052 ± 0.038
Sex	160.95	1.46	Sex	−0.53 ± 0.57[b]
Ru	161.11	1.62	Ruggedness	−0.053 ± 0.053
L	161.42	1.93	Lynx density	−0.14 ± 0.19

[a] In relation to 'hunting season' which was the reference.
[b] Males in relation to females (females coded as 0; males coded as 1).

to poaching during winter. We suggest that decreased lynx survival during winter in our study was driven by human caused mortality rather than seasonal variation in kill rate, because Andrén and Liberg (2015) found no differences in

Table 4. Parameter estimates for the models including the hunting/non-hunting season × lynx density interaction for the model that included all mortality. The hunting season was 16 February–31 March and the non-hunting season was 1 April–15 February (i.e. spring, summer and winter seasons pooled). Supporting information shows the lynx mortality risk (hazard) as a function of lynx density during the hunting and non-hunting seasons.

Variable	Coefficient ± SE
Hunting season (reference season)[a]	0 (baseline hazard)
Non-hunting season[a]	−1.44 ± 1.29
Lynx density (hunting season)[a]	0.47 ± 0.27
Hunting season × lynx density[a]	−0.58 ± 0.32
Lynx density (non-hunting season)[b]	−0.11 ± 0.14

[a] Hunting season as reference and coded as 0; non-hunting season coded as 1.
[b] Effect of lynx density during the non-hunting season (−0.11 = 0.47 + [−0.58]).

kill rate by lynx on roe deer between summer and winter in the same part of Sweden that our study was conducted. These results were not sensitive to whether the four lynx, suspected to be poached, were included as dead or right censored in the analysis (Table 3a–b).

We found different effects of lynx density during the hunting and non-hunting seasons; lynx density increased the mortality risk during the hunting season, while during the non-hunting season (e.g. spring, summer and winter seasons pooled) there was no detectable influence of lynx density on lynx mortality risk (Table 4; Supporting information). That mortality risk increased with lynx density during the hunting season was probably an effect of the quota setting strategy. In northern Sweden the lynx hunting quota system has been evaluated and can be described as a threshold harvest with increasing proportion, i.e. below a certain threshold there was no lynx harvest, but above the threshold the proportion of lynx harvested increased (Andrén et al. 2020). In southern Sweden the lynx hunting quota is set in a similar way, the number of lynx has to be above the minimum goal for a given county before hunting is allowed (SEPA 2016).

As the density of their main prey (roe deer) affects many aspects of lynx ecology such as home range size (Herfindal et al. 2005, Aronsson et al. 2016), reproduction (Nilsen et al. 2010, 2012, but see López-Bao et al. 2019) and body size (Yom-Tov et al. 2010), it was surprising that there was no evidence that roe deer density affected lynx survival. The lack of support for roe deer density explaining variation in lynx mortality was probably due to the ability of lynx to maintain a high kill rate even at low roe deer densities (Nilsen et al. 2009), thereby limiting the impact of roe deer density on survival by lynx. Furthermore, 85% of all roe deer harvest measurements in the dataset used here correspond to a higher roe deer density than the inclination point of two roe deer per km^2 in the type II functional response (Nilsen et al. 2009) and therefore would not be expected to influence lynx mortality at this density. Furthermore, roe deer density did not influence lynx reproductive output within the same area (López-Bao et al. 2019). Thus, from a lynx survival perspective, roe deer density is presumably sufficiently high in our study area and throughout the study period.

We did not identify any home range characteristics that affected the risk of human-caused mortality in lynx (Table 3b), and thus there was an even risk of human-caused mortality throughout the landscape. Human activity may cause attractive sinks if human-caused and natural mortality have contrasting relationships in different habitats (i.e. habitats with high human caused mortality are also habitats with low natural mortality), and if human-caused mortality causes a negative growth rate. However, we found no support for models including the interaction between hunting season and habitat characteristics. Thus, there seems to be no strong contrasting effects of habitat variables on mortality risk during the hunting season and non-hunting season. Furthermore, within the same study area, López-Bao et al. (2019) found no evidence that human activities or roe deer density were key factors influencing the probability of reproduction, litter size or juvenile survival in lynx. Therefore, our results and those by López-Bao et al. (2019) suggest that human activities have not created attractive sinks for lynx in southern Sweden.

In Norway, the neighbouring country sharing the same lynx population, Basille et al. (2013) showed that lynx hunting mortality increased with road density within lynx home ranges (at finer scale; 1 × 1 km pixels), whereas environmental variables did not influence the risk of poaching. Furthermore, Sunde et al. (1998) and Bunnefeld et al. (2006) found that lynx were shot closer to roads than expected at random. The differences in factors affecting survival of lynx between the two countries could be explained by southern Sweden having a higher density of forest roads (mean 1.44 km km^{-2}; Table 1) than Norway (mean 0.89 km km^{-2}; Basille et al. 2013) or that the studies were conducted at somewhat different scales (home range scale in our study and 1 × 1 km pixels within home ranges in Basille et al. 2013), although the overall mean of a landscape variable is not influenced by the spatial extent of the pixels (Turner and Gardner 1991). The higher road density in southern Sweden makes the entire landscape more accessible to hunters and could, in part,

explain the difference in the effect of road density between Sweden and Norway. Furthermore, we did not find any contrasting patterns in human caused and natural mortality for lynx in southern Sweden as was partly demonstrated by Bunnefeld et al. (2006) in Norway. However, lynx are also subjected to different management strategies in Sweden and Norway. During our study period, the population goals for lynx were considerably lower in Norway compared to Sweden (Ministry of the Environment 2003, SEPA 2016) resulting in higher hunting pressure as a means to limit the population in Norway (Andrén et al. 2006, Linnell et al. 2010). In our study, legal hunting caused 27% of lynx mortality, compared to 51% in Norway (Basille et al. 2013). Thus, the impact of different mortality causes differs between the two countries.

The lack of a significant relationship between home range characteristics and survival by lynx could be an effect of small sample size. In this study we followed 97 lynx during 160 exposure years, of which 37 lynx died during the study period. This sample size is within the range of comparable studies of survival in relation to habitat characteristics in carnivores (Supporting information). Therefore, we suggest that it was not lower statistical power that caused habitat characteristics to have limited influence on the risk of mortality in lynx in our study. Instead, we suggest that one or a few habitat characteristics at the home range scale could not explain the risk of mortality associated with several very different mortality causes in the diverse and human-dominated landscape of southern Sweden.

Several studies have found lower survival and higher human-caused mortality of carnivores outside compared to inside protected areas (Gaona et al. 1998, Johnson et al. 2004, Schwartz et al. 2006, Smith et al. 2010, Ruth et al. 2011, Newby et al. 2013, Pereira and Novaro 2014). However, Rauset et al. (2016) found that poaching was higher inside the large and remote national parks in northern Sweden when compared to the surrounding unprotected areas outside these parks and therefore cautioned that national parks may not always provide the protection that they often are assumed to provide. The importance of protected areas for carnivores may thus vary among areas and different regions of the world. In large parts of Europe, for example, carnivores coexist with people in multiuse landscapes outside protected areas (Chapron et al. 2014). Moreover, contrasting management regimes within the same population can affect demographic and spatial dynamics, as has been shown for wolverine management where higher hunting pressure in Norway creates a source-sink dynamic between Sweden and Norway (Gervasi et al. 2015).

We have shown seasonal variation rather than home range characteristics was the main factor affecting the risk of mortality for lynx in the human-dominated landscape of southern Sweden. We have also shown that the main causes of lynx mortality were anthropogenic and highest during the lynx hunting season, and the harvest rate seemed to be adjusted according to lynx density. Lynx recolonized the southernmost part of Sweden (the southern half of our study area; Hemmingmoore et al. 2020) during this study and the population has increased by about 17% per year during the last 16 years ($\lambda = 1.17 \pm 0.03$ SD, Andrén 2019). There is thus ample

evidence that lynx can coexist with humans in multi-use and human-dominated landscapes, even without large protected areas, if the management regimes are favourable.

Author contributions

HA and MA are both co-first authors. HA, GS and JP conceived the idea and designed the study. MA, JVLB, GS and HH prepared the database. MA, JVLB and GS did the spatial analyses. HA and MA did the statistical analyses. HA and MA led the writing of the manuscript. All authors contributed to writing of the manuscript and approved the final version for publication.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ksn02v75c> (Andrén et al. 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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