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Linear infrastructure and associated wildlife accidents create an ecological trap for an apex predator and scavenger

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HIGHLIGHTS

- Humans are creating ecological traps worldwide and all wildlife is vulnerable to these traps.
- Ecological traps are however difficult to demonstrate and measure.
- We used a unique large multiannual GPS tracking dataset of 74 Golden eagles.
- Results show that the Scandinavian Golden eagle population is in an ecological trap.
- Caused by dependence on carcasses from wildlife traffic accidents along roads and railway lines

GRAPHICAL ABSTRACT

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ABSTRACT

Animals may fall into an 'ecological trap' when they select seemingly attractive habitats at the expense of their fitness. This maladaptive behavior is often the result of rapid, human-induced changes in their natal environment, such as the construction of energy and transportation infrastructure. We tested the ecological trap hypothesis regarding human-created linear infrastructure on a widely distributed apex predator and scavenger—the Golden Eagle (*Aquila chrysaetos*), whose range spans the entire Northern Hemisphere. Roads and railways offer novel and attractive feeding opportunities through traffic-induced mortality of other species, while powerline areas provide perching or nesting sites and scavenging opportunities from electrocuted or collision-killed birds. These conditions may have negative demographic consequences for eagles if these apparent opportunities turn into traps. Using step selection functions, we analyzed habitat selection of 74 GPS-tracked Golden Eagles (37 adults and 37 immatures) during eleven years in Fennoscandia. To assess habitat attractiveness, we used wildlife traffic accident statistics for dominant wild species, and to evaluate demographic consequences, we used mortality data from the GPS-tagged eagles. Our analysis revealed that eagles selected linear features such as roads, railways and powerlines at both the population and individual levels. Both adult and immature eagles consistently selected these features, and the strength of selection for linear features increased with age in immature eagles. The linear features however had 5.5 times higher mortality risk for eagles than other selected habitats indicating the presence of an ecological trap. We discuss the implications of these findings for the conservation and population ecology of apex predators and scavengers, as well as their potential demographic consequences. To mitigate this issue, we urgently recommend the removal of carcasses from roads

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and tracks to prevent ecological traps for raptors and scavenger species worldwide. Additionally, we advocate for the development of methods and strategies to reduce wildlife traffic accidents.

1. Introduction

Animals rely on various cues, such as habitat features, sound, light, and smell, for habitat selection, navigation, foraging, and mate choice. These behaviors aim to increase their survival, reproduction, and ultimately their fitness (Darwin, 1859). However, human alterations to natural ecosystems are rapidly impacting—and sometimes destroying—these critical cues (Sih, 2013). Consequently, animals may select habitats that appear attractive but lead to lower fitness, falling into what is known as an "ecological trap" (Gates and Gysel, 1978; Robertson et al., 2013). Ecological traps have been documented across various animal groups, including insects (Horváth et al., 2010), reptiles (Hawlena et al., 2010), fish (Jeffres and Moyle, 2012), birds (Remeš, 2003), and mammals (Lamb et al., 2017). For example, sea turtle (*Caretta caretta*)) hatchlings, which are naturally guided by reflected moonlight to move towards the ocean, may be drawn to artificial light on a polluted beach, increasing their mortality risk (Witherington, 1997).

For an ecological trap to exist, three criteria must be met: (i) the trap habitat must be either preferred over surrounding habitats (severe trap) or equally selected alongside other habitats (equal preference trap), (ii) individual fitness in the trap habitat must be lower, and (iii) animals must actively move into the trap habitat (Hale et al., 2015; Robertson and Hutto, 2006). Hawlena et al. (2010) demonstrated an equal preference trap where lizards (*Acanthodactylus beershebensis*) selected both natural and human-modified habitats equally, despite higher predator exposure and increased mortality in the latter. Similarly, blackcaps (*Sylvia atricapilla*) selected a human-modified landscape with newly introduced plant species over their natural breeding habitat, resulting in a severe ecological trap with lower breeding success (Remeš, 2003). One major human modification with a high potential to create ecological traps is linear infrastructure, such as roads, railways, and powerlines. These structures often create an attractive, open, and predictable scavenging and hunting ground due to the availability of carrion from traffic accidents or electrocuted animals, while simultaneously posing risks to the apparently benefiting individuals from collisions, barriers, and electrocution (Harris & Scheck, 1991; Seiler, 2001).

Large predators and scavengers, such as eagles and vultures, are particularly vulnerable to these ecological traps. Their ability to move efficiently across landscapes, long lifespan, and strong learning capacity, combined with a lack of natural predators, can result in a failure to recognize novel risks (Ripple et al., 2014). Such species primarily learn through parental care, social interactions, or the predictability of food sources, such as those provided by humans (Cushing, 1944). Additionally, animals often select habitats similar to their natal environment (Davis and Stamps, 2004), and if immature individuals associate a trap habitat with scavenging opportunities or recognize it as a natal habitat, they may continue to use it for years, resulting in long-term negative effects on their survival and reproduction (Fletcher Jr et al., 2015).

One species of particular concern is the Golden Eagle (*Aquila chrysaetos*), a large, long-lived raptor vulnerable to ecological traps. Widely distributed across the Holarctic (Watson, 2010), the Golden Eagle is classified as "near threatened" in Sweden (ArtDatabanken, 2015) and requires special habitat conservation measures under the EU Birds Directive - Annex 1 (European Union, 2009). As apex predators, Golden Eagles are opportunistic and depend on naturally fluctuating prey populations, such as mountain hares (*Lepus timidus*) and grouse species (*Lagopus* spp.), particularly in the boreal forest (Moss et al., 2012; Tjernberg, 1981). In highly seasonal environments with harsh winters, these eagles may rely more on scavenging opportunities when prey is scarce.

A recent study by Eisaguirre et al. (2020) found that Golden Eagles in Alaska selected roads and railways during migration and spent more time in these areas than in other habitats. In Sweden, Golden Eagles display partial migration patterns, primarily influenced by age and winter conditions (Moss et al., 2014). They migrate south between late September and October, returning north in late April to early May (Singh et al., 2017). The Fennoscandian population uses old-growth forests for breeding and clear-cuts or open lands with high prey visibility for hunting, while also taking advantage of scavenging opportunities (Tjernberg, 1981; Watson, 2010; Singh et al., 2017).

In 2019, around 65,000 fatal wildlife accidents were reported on Swedish roads and railways, primarily involving large mammals and eagles. This number has steadily increased from 45,000 in 2010 to around 72,000 (Swedish National Road Administration database, SNRAD - *Nationella Viltolycksrådet*, see Appendix). Between 2010 and 2023, 650 Golden Eagles and White-Tailed Eagles (*Haliaeetus albicilla*) died in traffic collisions (see Figs. 1a, 1b, 1c). According to the Swedish National Museum of Natural History, the main causes of death among recovered Golden Eagles from 2003 to 2011 were collisions with traffic (35.6 %), electrocution and powerline collisions (17.8 %), and starvation or other trauma, including physical injuries (11.9 %) (Ecke et al., 2017).

Given the high mortality of eagles along linear infrastructure, this study aims to determine whether linear infrastructure creates an ecological trap for Golden Eagles. We hypothesize that (i) eagles actively select linear infrastructure (roads, railways, and powerlines) due to scavenging opportunities from wildlife traffic accidents and electrocuted birds, with powerline poles offering advantageous perching sites for hunting. We predict (ii) high mortality rates among eagles in these areas due to collisions and electrocution. Additionally, we may expect (iii) immature eagles to select these habitats more than experienced adults, owing to their lower hunting success. Finally, we hypothesize that (iv) over time, immature eagles will learn to utilize these habitats, with their habitat selection strengthening as they age.

2. Methods and study area

The study uses movement and survival data from 74 GPS-tagged Golden Eagles (37 adults, 37 immatures) from Sweden within a study period of 11 years (2010–2020, Figs. 1a, 1b, 1c). Immatures were classified as birds of <5 years of age, determined based on plumage patterns recommended by the monitoring protocols of the Swedish Environmental Protection Agency, and coordinated by the Swedish Museum of Natural History.

Individual tracking periods ranged from one month to six years with a minimum of 500 relocations (Fig. S1 and S2 Supplementary material). The study individuals ranged over most of Sweden (55–68°N, 12–23°E, Fig. S1 Supplementary material). Adults were captured using remote controlled bownets (Bloom et al., 2007, 2015; Jackman et al., 1994) and tagged with solar-powered, backpack mounted global positioning systems (GPS) representing different transmitter types; in 2010–11, 75 g Microwave Telemetry Inc., USA and 140 g VectronicAerospace GmbH, Germany, and in 2014, 70 g Cellular Tracking Technologies, Inc., USA, with a maximum location error ranging from 10 to 18 m for all transmitters. Immatures were tagged as nestlings approximately two weeks prior to fledgling (Sandgren et al., 2014). All GPS tagging was conducted under Ethical Permits Nos. A57–10, A58–10, A57–10A, A33–13, and A11–2019 from the Swedish Agricultural Board (*Jordbruksverket*) and Research Permit No. NV-07710-19 of The Swedish Environmental Protection Agency (*Naturvårdsverket*).

Forestry is the main land use across the Golden Eagle range in

Sweden. The boreal forest landscape is characterised by cut-over and even-aged forests dominated by Norway Spruce (*Picea abies*) and Scots Pine (*Pinus sylvestris*) (Ecke et al., 2013; Esseen et al., 1997). The remaining landscape is a mixture of forests interspersed with wetlands (lakes, streams and mires) and agricultural land (Helmfried, 1996).

2.1. Habitat data

To characterize the linear features, national distribution of roads, railways and powerlines, and land cover types (10 m cell size) were extracted from the raster layer in a geographic information system (GIS) provided by the Swedish mapping, cadastral and land registration authority (*Lantmäteriet*) and Swedish National Environmental Protection Agency (*Naturvårdsverket, Nationella Marktäckedata,* produced in 2018), respectively. Based on observed high mortality along roads and railways, we refer to linear infrastructure as potential 'trap habitat' further on in the study.

2.2. Wildlife traffic accidents

To characterize habitat attractiveness, we obtained monthly summaries of reported national wildlife traffic accidents along roads and railways for the years 2010–2023 from the SNRAD. White-Tailed Eagle and Golden Eagle are summarized as one species in this database because of difficulties to correctly identify the two eagle species after collision. Locations of these dead eagles were available from 2010 to 2023.

2.3. Golden Eagle survival data

The survival status was compiled for 74 GPS tagged Golden Eagles during the course of the study (2010−2020) with marking date and last known observation date.

2.4. Data analyses

To assess habitat selection of eagles at the population and individual levels, we conducted a step selection analyses (SSF, Avgar et al., 2016, Muff et al., 2020) using the package 'amt' for R (Muff et al., 2020). Locations were converted into linear steps by joining the two consecutive relocations (Fortin et al., 2005; Thurfjell et al., 2014). Step selection function is a statistical tool used to analyze and model the habitat selection and movement patterns of animals or humans. The goal with SSF analysis is to understand the factors that influence the choice of

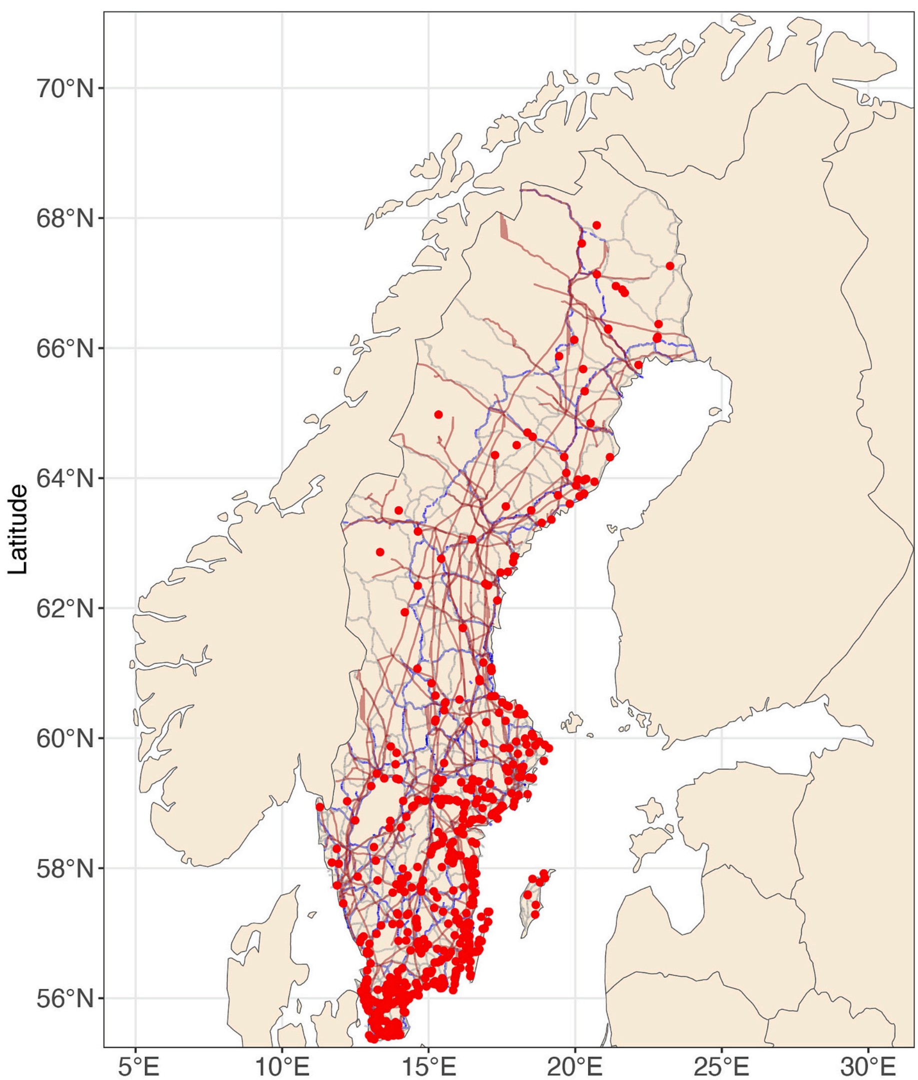

Fig. 1a. Locations of Eagle traffic collisions (red dots) recorded throughout Sweden during 2010–2023 ($n = 650$) by the SNRAD. Primary roads are shown in grey, railway lines in blue and main powerlines in brown.

movement paths. Step selection functions test for habitat selection by conducting a conditional logistic regression as a generalised linear mixed model using glmmTMB package in R, comparing available with used habitat and by including a random factor for individual to incorporate individual level variation (Muff et al., 2020).

Eagle locations were resampled to an interval of h ± 10 min to achieve a regular time interval. For each true eagle step ($n = 1{,}080{,}597$), a set of random steps ($n = 10$) was created as a measure of availability. All step lengths (m) were assumed to follow a gamma distribution and all covariates were extracted at step end (Avgar et al., 2016). The step selection function itself does not directly estimate parameters for a gamma distribution but uses maximum likelihood estimation method. The scale parameter is adjusted based on the covariates.

2.5. Habitat classes

The habitat characterization was adopted from the land cover data, and habitats were classified into six broad categories - 'Open land', 'Wetland', 'Forest', 'Road and Railway', 'Water' and 'Clear cut' with reference to earlier studies on eagle biology (Singh et al., 2017). Open land was a combination of 'Arable land', 'Non-vegetated other open land' and 'Vegetated other open land'.

In addition, distance to linear infrastructure for each step, was estimated as the Euclidean distances (m) to the nearest road, railway and powerline, respectively. These variables were tested in separate models due to a strong correlation between types of infrastructure.

2.6. Age effects and temporal patterns

For testing the effect of age on habitat selection, the models included age - habitat interactions. The results were compared between adults (both sexes) and immatures, with immatures as reference in the model, and individual IDs included as the random effect.

To investigate the learning behavior of immatures, i.e. change in selection strength for linear features over time by immatures ($n = 35$), individual's data was divided into eagle years (e.g. Year - 1, Year - 2 upto Year - 7), where the first year (Year - 1) was defined as the next 365 days after tagging. We then modeled the selection of linear features by immatures over years, by including interaction between the distance to the nearest linear feature (road, railway and powerline) and individual year. Individual years were coded as numeric with a continuous value and individual ID was included as a random effect. All spatial and statistical analyses were performed in R (R version 3.6.1, R Core Team, 2019 and R studio Version 2024.04.2).

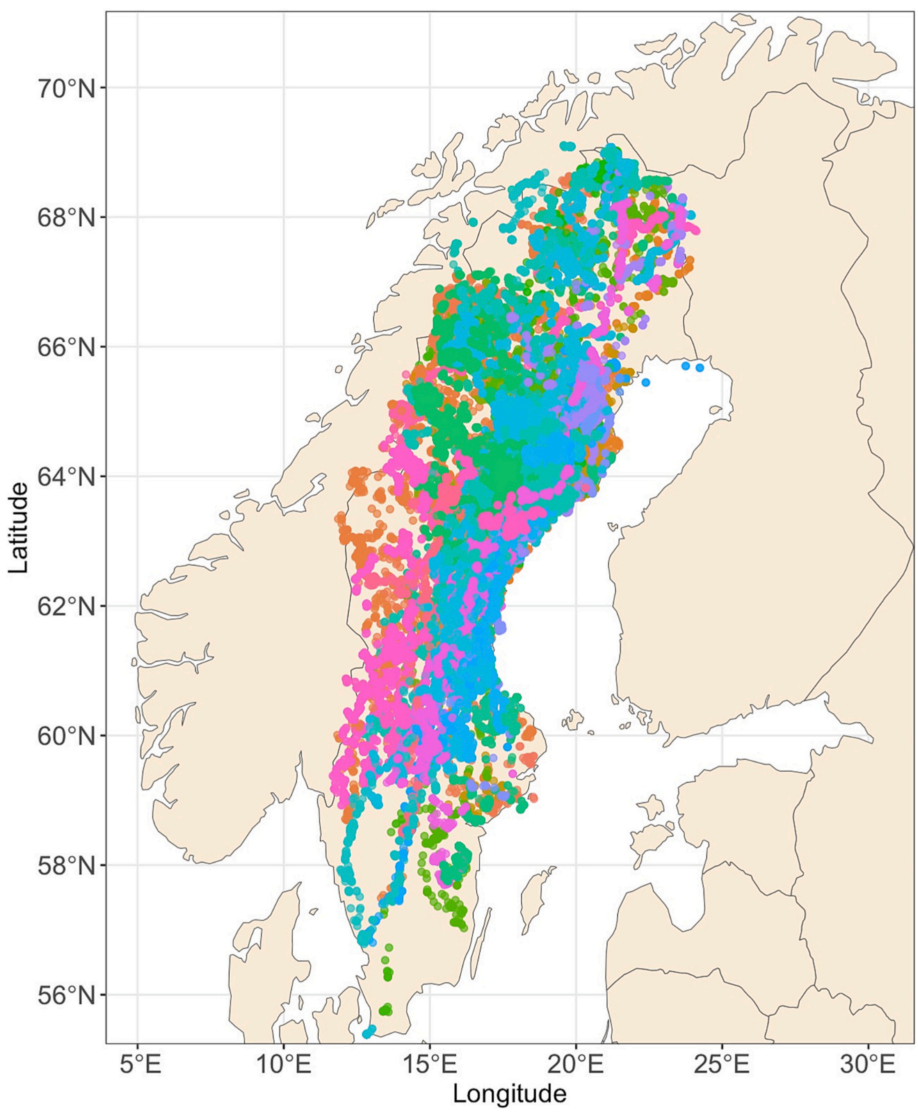

Fig. 1b. Multiannual movement of patterns of 74 studied Golden Eagles within Sweden during 2010–2020 ($n = 1{,}031{,}791$ positions). Individuals are represented by different colored dots and only the positions within Sweden are shown.

2.7. Survival analyses

To assess the fitness consequences of habitat selection, we extracted the survival status for 37 adult and 37 immature GPS marked birds followed in our studies. For the dead individuals, cause of death was either confirmed in the field or we extracted the habitat class for their last known location – forest, clearcut, open land and distance to the nearest linear features (road, railway and powerline). When the individual was dead and the last known location was within 100 m (±20, 30 and 50 m spatial error, for three different transmitter types, CTT Inc., Microwave Telemetry, and Vectronics GmbH) of a linear feature (road/railway/powerline), we attributed the cause of death to that linear feature habitat class. At times powerlines and railways occurred together and distance to both of these features for the last position were identical, we then grouped such observations as trap habitat. We also ascertained this by checking that the last ten positions (at hourly intervals) were within the same vicinity. The three linear features were again combined as trap habitat, as running separately led to problems with model convergence.

We then fitted a Cox proportional hazards model (Cox regression, Cox, 1972), available in the 'survival' package in R, to assess the effect of habitat classes ('open land', 'forest', 'trap habitat', and 'clearcut') and age on survival. There were no last observations recorded in 'wetlands'. Three individuals were removed from the analyses due to a lack of spatial information. Individual status was coded as a binary variable where 1 indicated the event (e.g., death) occurred, and 0 indicated that the event was censored (did not occur during observation time – both survived and unknown). The time variable was calculated as the number of days from the difference between the marking date and the last known date. To ascertain the habitat survival relationship, we also fitted a competing risks model (CRM, Dignam et al., 2012). These models are used to assess the probability of different types of events (risks) and how they relate to habitat. The 'cmprsk' package in R provides the cuminc() function for cumulative incidence function (CIF), which is used in CRM. The event variable is converted into a competing risk framework and cumulative incidence for each risk is estimated. No significant effect of age (adult or immature) was observed on the risk and hence the age variable was not explored further.

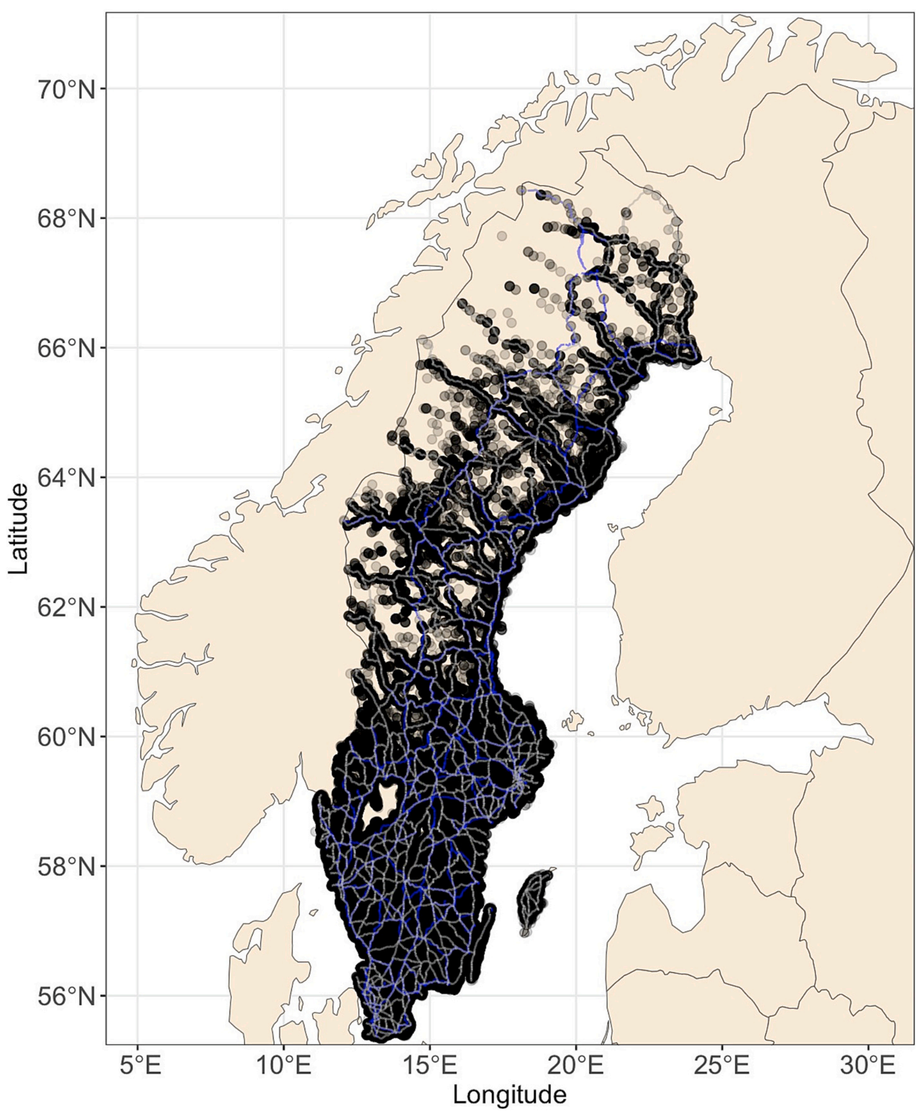

Fig. 1c. Locations of wildlife traffic accidents (n = 657,249) recorded at SNRAD within Sweden during 2010–2023 overlaid on roads and railway lines, reflecting habitat attractiveness. Single observations in light transparent grey resulting in black dots if overlapping. The species included are moose, roe deer, red deer, fallow deer, wild boar, bear, wolf, lynx, wolverine and otter.

3. Results

3.1. Habitat Selection and age effects

A total of 63 (35 Immatures, 28 Adults) individuals with >500 relocations were available for the habitat selection analyses. At the population level, eagles selected for roads and railways, clear cuts, open land and forest indicated by a positive value for the estimate and avoidance of water, compared to wetlands (Table 1, Fig. 2). There was however large individual variation in the selection strength for each habitat type (Table 1), with the largest variance for Open land (variance **σ**=0.7) followed by Clearcut (**σ**=0.23), Wetland (**σ**=0.16), Forest (**σ**=0.15), Road and Railway (**σ**=0.12) and Water (**σ**=0.09) (Table 1).

The selection of habitat types was significantly affected by eagle age, as evidenced by several significant interactions between habitat types and age class (Table 2). Both males and females were more likely to select open land than wetlands, with adult females showing a stronger selection than immatures (Estimate = 1.14, Std.Error = 0.09, Z = 12.66). However, there were no significant differences with respect to selection of roads and railways between the age classes in this model (Table 2). The random intercept for individual eagles (ID) indicated individual variation in habitat selection, and a relatively low variance (**σ**=0.02) suggests that most variation was captured by the fixed effects.

Individually, for each linear feature (road, railway and powerline), all eagles selected areas close to the linear features (indicated by a negative coefficient), and immatures always selected distances significantly closer than the adults (Table 3). As also indicated by the magnitude of the interaction term between linear features and age, the positive estimates (Table 3) suggest that the negative effect of increasing distance from linear features was less pronounced for adults than for immatures. The random variation across individuals was minimal (railways **σ**=0.013, roads **σ**=0.011, powerlines **σ**=0.008).

3.2. Selection of linear features by age and years

The selection of areas closer to linear features changed with age and over time, especially more for immatures (intercept, estimate for road = −2.22, z = −61.9, railway = −2.15, z = −59.2, and powerline = −2.08, z = −65.7), that showed an increasing strength of selection of linear features during the early years of life (distance to roads:year = −0.02, $p < 0.01$, Table 4). Whereas for adults, there was an increasing tendency to select areas away from the linear features over time (Table 4). For adults, a positive and significant estimate for the interaction between distance to road, age and year (Females = 0.04, $p < 0.001$, Males = 0.03, p < 0.01, Table 4), indicates that the negative effect of road distance on selection weakened over time. This implies that females may become more settled at greater distances from roads as time progresses. For railways, adult females and males show increasing tendency for settling away over time, with males being particularly notable for this change (Males = 0.02, p < 0.01, Table 4). Similarly, for powerlines, the shift away over time was stronger overall, but females exhibited a significant shift away over time (Females = 0.03, p < 0.01, Table 4), unlike their response to railway.

Table 1
Summary of Step Selection Functions (SSF) modelling the habitat selection of 63 Golden Eagles in Sweden using GPS tracking data (N = 352,819 locations). Individual eagle ID was the random effect. Positive model coefficients for fixed effects indicate selection and negative indicate avoidance. Wetland habitat is the intercept in the model.

Fixed effects	Term	Estimate	Std. error	Z statistic	p. value
1	(Intercept)	−2.83	0.07	−42.65	0
2	Open land	0.75	0.12	6.2	<0.01
3	Roads and Railways	0.24	0.09	2.61	<0.01
4	Water	−1.97	0.09	−20.87	<0.01
5	Forest	0.82	0.07	12.33	<0.01
6	Clearcut	1.02	0.08	13.19	<0.01

Random effects		Variance	Std.Dev.
1	(Intercept)	0.16	0.4
2	Open land	0.70	0.83
3	Roads and Railways	0.12	0.35
4	Water	0.09	0.31
5	Forest	0.15	0.39
6	Clearcut	0.23	0.48

3.3. Habitat attractiveness

The temporal seasonal trend of wildlife accidents reveals an increasing number of accidents since 2010 (Fig. S2 & S3) and annually towards winter, with two general peaks (Fig. S2 & S3). One peak occurred in May and June and the other occurred during September to December. Overall, the trend serves as an indicator of the attractiveness of roads and railways, based on the number of accidents per month.

3.4. Demographic costs

Data from the national wildlife traffic accidents dataset revealed a consistent spatial pattern of eagle accidents and fatalities across the country (Fig. 1a). Among the 74 GPS-tracked eagles, 22 individuals died (10 adults—5 males and 5 females—and 12 immatures). The remaining 52 eagles (26 adults and 23 immatures) survived (3 were removed from analyses, see methods), though their status remained unknown after the last recorded GPS position, when the transmitters stopped working.

For the 22 dead individuals, cause of death was confirmed in the field for five, and for 17 we extracted the habitat class for their last known position (Fig. 3). Out of 22, 16 died along the linear features denoted as trap habitat, two in clearcuts and four in the forest.

For survival analyses, based on the Cox proportional hazard models, the mortality risk in each habitat category was compared to the 'clearcut', as reference (Table 5). The hazard ratio (HR = 0.73) < 1, suggests a lower hazard compared to the baseline. Forests had a lower hazard risk compared to clearcut (estimate = −0.35), and individuals in forest habitat had 26 % lower risk of mortality (p = 0.72, Fig. 4). The habitat, open land, had a large negative coefficient and very small hazard ratio (estimate = −18.50, HR = 0) indicating a computational problem (due to perfect separation). It suggests that no events (or very few) occurred in the open land habitat, leading to an infinite or near-zero HR. The trap habitat had a substantially higher risk (estimate = 1.70) than in clearcut. The hazard ratio of 5.49 indicates that individuals in the trap habitat have approximately 5.5 times higher risk of experiencing the event compared to the baseline habitat (Table 5). This is statistically significant at the 5 % level ($p < 0.05$), indicating that the effect of the trap habitat is important in predicting Golden Eagle survival. All tests confirm a strong model fit. A high Concordance (= 0.747) measures how well the model discriminates between individuals who died and survived, a likelihood ratio test = 29.2 (p < 0.05), tests the overall model fit. A highly significant p-value ($p < 0.01$) suggests that the model, including the habitat variables, significantly improves the prediction of mortality compared to a null model without any covariates. Finally, the Wald test = 15.65 (p < 0.01), again indicates that the model is a significant predictor of survival.

The CRM results mirror those of survival analyses. The test statistic (Grey's test = 31.95, p-value<0.01) shows that the model, which includes habitat as a covariate, is highly significant in predicting the cumulative incidence of death (Fig. S4). The clearcut and forest habitats had similar cumulative incidences (around 17 % and 15 %, respectively), with relatively stable and precise estimates across the time points. The risk of the mortality in the open land habitat was 0 at all time points, suggesting no events occurred there (or they were censored). In

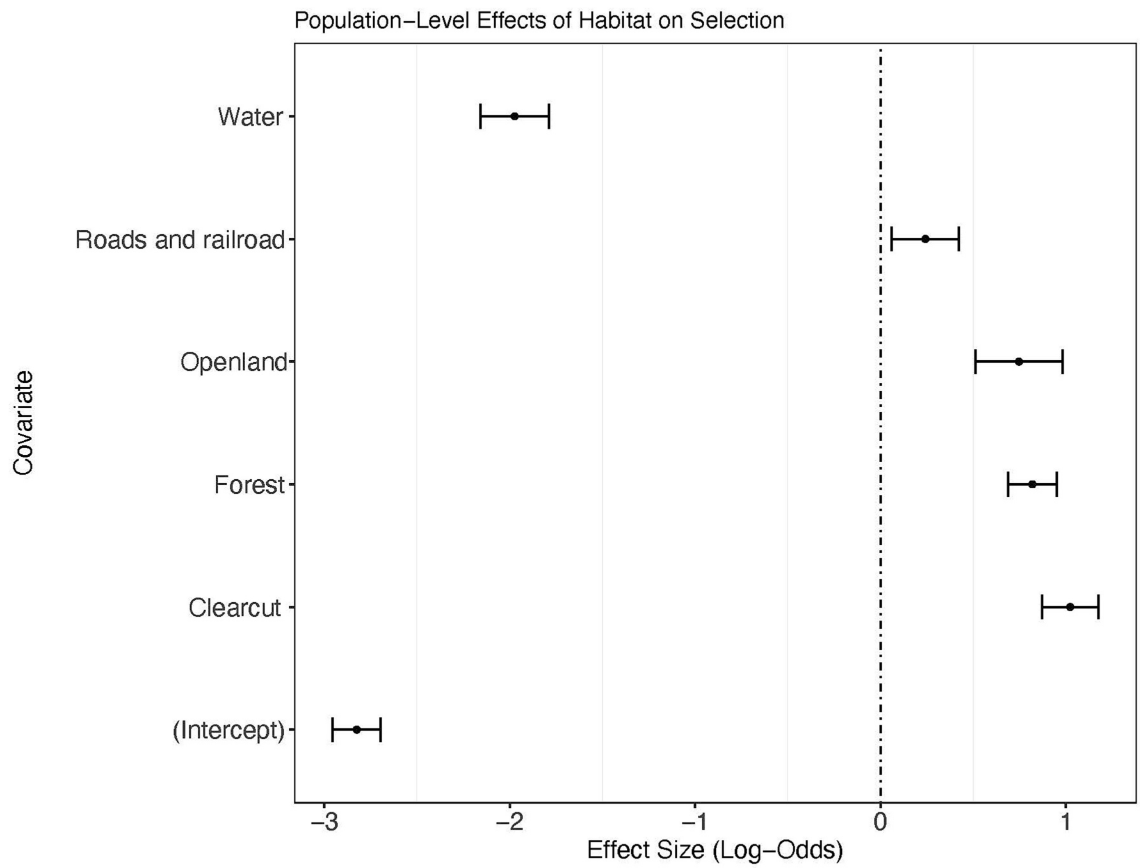

Fig. 2. Population level habitat selection coefficients for 63 Golden Eagles in Sweden using GPS tracking data ($n = 352{,}819$ locations). Individual eagle ID was the random effect. Positive effect sizes indicate selection and negative indicate avoidance. Wetland habitat is the intercept in the model.

Table 2
Summary of Step Selection Functions (SSF) modelling the effect of age on habitat selection of 36 adults and 37 immatures Golden Eagles in Sweden using GPS tracking data (36 adults and 37 immatures, N = 352,819 locations). Individual eagle ID was the random effect. Positive model coefficients for fixed effects indicate selection and negative indicate avoidance. Wetland habitat is the intercept in the model.

	Fixed Effect	Estimate	std.error	Statistic	p.value
1	(Intercept)	−2.91	0.04	−63.15	0
2	Open land	0.27	0.04	5.72	0.00
3	Roads and Railways	0.29	0.09	3.01	0.00
4	Water	−1.82	0.09	−19.47	0.01
5	Forest	0.99	0.03	25.70	0.01
6	Clearcut	1.28	0.04	31.93	0.01
7	AgeF	−0.25	0.08	−3.02	0.00
8	AgeM	0.24	0.07	3.17	0.00
9	Open land:AgeF	1.13	0.08	12.66	0.00
10	RoadsRailways:AgeF	0.14	0.17	0.82	0.40
11	Water:AgeF	0.09	0.17	0.55	0.57
12	Forest:AgeF	0.04	0.07	0.67	0.49
13	Clearcut:AgeF	0.09	0.07	1.31	0.18
14	Open land:AgeM	0.39	0.08	4.77	1.79
15	RoadsRailways:AgeM	−0.19	0.15	−1.27	0.20
16	Water:AgeM	−0.18	0.15	−1.19	0.23
17	Forest:AgeM	−0.38	0.06	−6.06	0.00
18	Clearcut:AgeM	−0.39	0.06	−5.87	0.00

the trap habitat, the risk of the event was much higher, reaching 93.75 % by four years (Fig. S4). The variance decreased over time, indicating more confidence in the cumulative incidence as time progressed (Fig. S4). Overall, the model output suggests that trap habitat was associated with a much higher risk of mortality, while clearcut and forest have lower, more consistent risks, and open land had no risk for the eagles in this dataset.

4. Discussion

In this study, using an extensive multi-annual dataset, we demonstrate that linear infrastructure creates an ecological trap for Golden Eagles. Both adult and immature eagles consistently selected areas closer to roads, railways, and power lines, with the strength of selection increasing for immatures during the first few years of their lives. In contrast, adults showed variation in their selection of trap habitats over time. The negative demographic consequences at the population level were confirmed through survival analyses, which showed that the highest mortality risk occurred in the trap habitats for both adults and immatures. Using national wildlife traffic accident statistics, we visualized the spatial and temporal extent of the habitat's attractiveness to eagles and their mortality patterns, showing that mortality was widespread across the landscape.

Golden Eagles are opportunistic predators and scavengers that range over large areas throughout the year, and require nesting sites and space for territories in old growth forests, and open areas and clear cuts for hunting (Singh et al., 2017). This is ascertained by our results where we observed a strong selection of forests, clear cuts and open land besides the roads and railways providing scavenging opportunities (Singh et al., 2017). Immature eagles are known to undertake long distance seasonal migrations and range extensively throughout the entire Scandinavian landscape (Singh et al., 2017). Their underdeveloped hunting skills, during early years of life, competition with adults and sub-adults for territories and food, nomadic and opportunistic behavior, and availability of predictable, easy and abundant food through traffic-killed wildlife may all contribute towards driving them to scavenge more

Table 3
Summary of Step Selection Functions (SSF) modelling the selection of linear habitat features - roads, railways, and powerlines by 63 Golden Eagles (36 adults and 37 immatures) in Sweden using GPS tracking data ($N = 388{,}066$ locations). Individual ID was the random effect. Negative model coefficients indicate selection of areas closer to a feature whereas positive signs of interaction terms indicate declining effect compared to the intercept. Immature age class is the intercept in all models.

Effect	Term	Estimate	std. error	Z statistic	p. value
Roads					
1	(Intercept)	−2.26	0.02	−95.62	0.00
2	scale(RoadsDistance)	−0.66	0.02	−38.62	0.00
3	AgeF	−0.05	0.04	−1.18	0.24
4	AgeM	0.00	0.04	−0.10	0.92
5	scale(RoadsDistance):AgeF	0.23	0.03	7.61	0.00
6	scale(RoadsDistance):AgeM	0.22	0.03	7.85	0.00
Railways					
1	(Intercept)	−2.20	0.02	−90.81	0.00
2	scale(RailwaysDistance)	−0.43	0.01	−37.39	0.00
3	AgeF	−0.08	0.05	−1.74	0.08
4	AgeM	−0.01	0.04	−0.25	0.80
5	scale(RailwayDistance): AgeF	0.09	0.02	3.86	0.00
6	scale(RailwayDistance): AgeM	0.23	0.02	11.86	0.00
Powerlines					
1	(Intercept)	−2.26	0.02	−107.34	0.00
2	scale(PowerlinesDistance)	−0.62	0.02	−37.11	0.00
3	AgeF	−0.06	0.04	−1.48	0.14
4	AgeM	0.02	0.04	0.51	0.61
5	scale(PowerlinesDistance): AgeF	0.18	0.03	5.84	0.00
6	scale(PowerlinesDistance): AgeM	0.27	0.03	10.26	0.00

than adults along linear infrastructure. This explains why the strength and consistency of selection of linear infrastructure was higher for immatures than adults, and during early years. Consequently, they are at higher risk of mortality due to accidents, as consuming large amounts of food can impair their ability to escape from fast-moving vehicles.

Powerline poles likely serve as perching sites for hunting and scanning for scavenging opportunities from electrocuted or collision-killed birds. This explains the electrocution risk faced by eagles, which has also been documented in other studies (Janss, 2000; Krüger et al., 2004; Slater and Smith, 2010; Slater et al., 2022). For e.g. Golden Eagle mortality due to electrocution is at very high levels in the United States (Ansell and Smith, 1980; Harness and Wilson, 2001). This is due to the kind of poles and material used for powerline poles and distance between the tops and the high-tension wires that facilitate a higher contact between the wires and the sitting perching birds (Simon et al., 2020). Alternatively, a higher food availability within the powerline corridors and resulting frequent use by the eagle drives these patterns (Bernardino et al., 2020). Powerlines also co-occur along the roads and railways (evident through a high spatial correlation between them, see methods) and hence these features potentially interact in affecting the habitat selection of eagles with resulting demographic consequences.

Our results indicate a 5.5 times higher risk of mortality in trap habitat compared to the others. Indeed, the majority (16 out of 22) of our deceased study individuals died along linear infrastructure, with deaths spread throughout the landscape (Fig. 3b). Moreover, the number of immature and adult birds that suffered mortality in the trap habitat were similar. This indicates that the mortality risk faced by both age classes is similar with potentially population wide serious demographic consequences. For example, attractive food subsidies through traffic accidents may keep the immature individuals within trap habitats and prevent dispersal, increase mortality, further reduce their ability to hunt

Table 4
Summary of Step Selection Functions (SSF) modelling the selection of linear habitat features - road, railway, and powerline by age and year for 63 Golden Eagles in Sweden using GPS tracking data (36 adults and 37 immatures, $n = 388{,}066$ locations). Individual ID was the random effect. Negative model coefficients indicate selection of areas closer to a feature whereas positive signs of interaction terms indicate declining effect compared to the intercept. Immature age class is the intercept.

	Effect	Term	Estimate	std. error	Statistic	p. value
Railway						
1	Fixed	(Intercept)	−2.08	0.04	−59.25	0.00
2	Fixed	scale(RailwayDistance)	−0.13	0.03	−5.30	0.00
3	Fixed	AgeF	−0.17	0.07	−2.49	0.01
4	Fixed	AgeM	−0.11	0.06	−1.72	0.08
5	Fixed	Year	−0.03	0.01	−4.93	0.00
6	Fixed	scale(RailwayDistance): AgeF	0.10	0.05	2.08	0.03
7	Fixed	scale(RailwayDistance): AgeM	0.08	0.05	1.69	0.09
8	Fixed	scale(RailwayDistance): Year	−0.05	0.00	−12.33	0.00
9	Fixed	AgeF:Year	0.02	0.01	1.60	0.10
10	Fixed	AgeM:Year	0.02	0.01	1.94	0.05
11	Fixed	scale(RailwayDistance): AgeF:Year	−0.01	0.01	−1.25	0.21
12	Fixed	scale(RailwayDistance): AgeM:Year	0.02	0.01	3.14	0.00
Road						
1	Fixed	(Intercept)	−2.22	0.04	−61.94	0.00
2	Fixed	scale(RoadDistance)	−0.53	0.04	−12.67	0.00
3	Fixed	AgeF	−0.16	0.07	−2.31	0.02
4	Fixed	AgeM	−0.05	0.07	−0.82	0.41
5	Fixed	Year	−0.01	0.01	−1.15	0.25
6	Fixed	scale(RoadDistance): AgeF	−0.04	0.07	−0.51	0.61
7	Fixed	scale(RoadDistance): AgeM	0.02	0.07	0.28	0.78
8	Fixed	scale(RoadDistance): Year	−0.02	0.01	−3.25	0.00
9	Fixed	AgeF:Year	0.02	0.01	1.87	0.06
10	Fixed	AgeM:Year	0.01	0.01	0.83	0.40
11	Fixed	scale(RoadsDistance2): AgeF:Year	0.04	0.01	4.27	0.00
12	Fixed	scale(RoadsDistance2): AgeM:Year	0.03	0.01	2.87	0.00
Powerline						
1	Fixed	(Intercept)	−2.15	0.03	−65.68	0.00
2	Fixed	scale (PowerlineDistance)	−0.37	0.04	−9.68	0.00
3	Fixed	AgeF	−0.17	0.06	−2.66	0.00
4	Fixed	AgeM	−0.05	0.06	−0.79	0.42
5	Fixed	Year	−0.02	0.01	−3.99	0.00
6	Fixed	scale (PowerlineDistance): AgeF	−0.03	0.07	−0.40	0.68
7	Fixed	scale (PowerlineDistance): AgeM	0.20	0.06	3.20	0.00
8	Fixed	scale (PowerlineDistance): Year	−0.04	0.01	−7.06	0.00
9	Fixed	AgeF:Year	0.02	0.01	2.03	0.04
10	Fixed	AgeM:Year	0.01	0.01	1.19	0.23
11	Fixed	scale (PowerlineDistance): AgeF:Year	0.03	0.01	3.07	0.00
12	Fixed	scale (PowerlineDistance): AgeM:Year	0.01	0.01	0.87	0.38

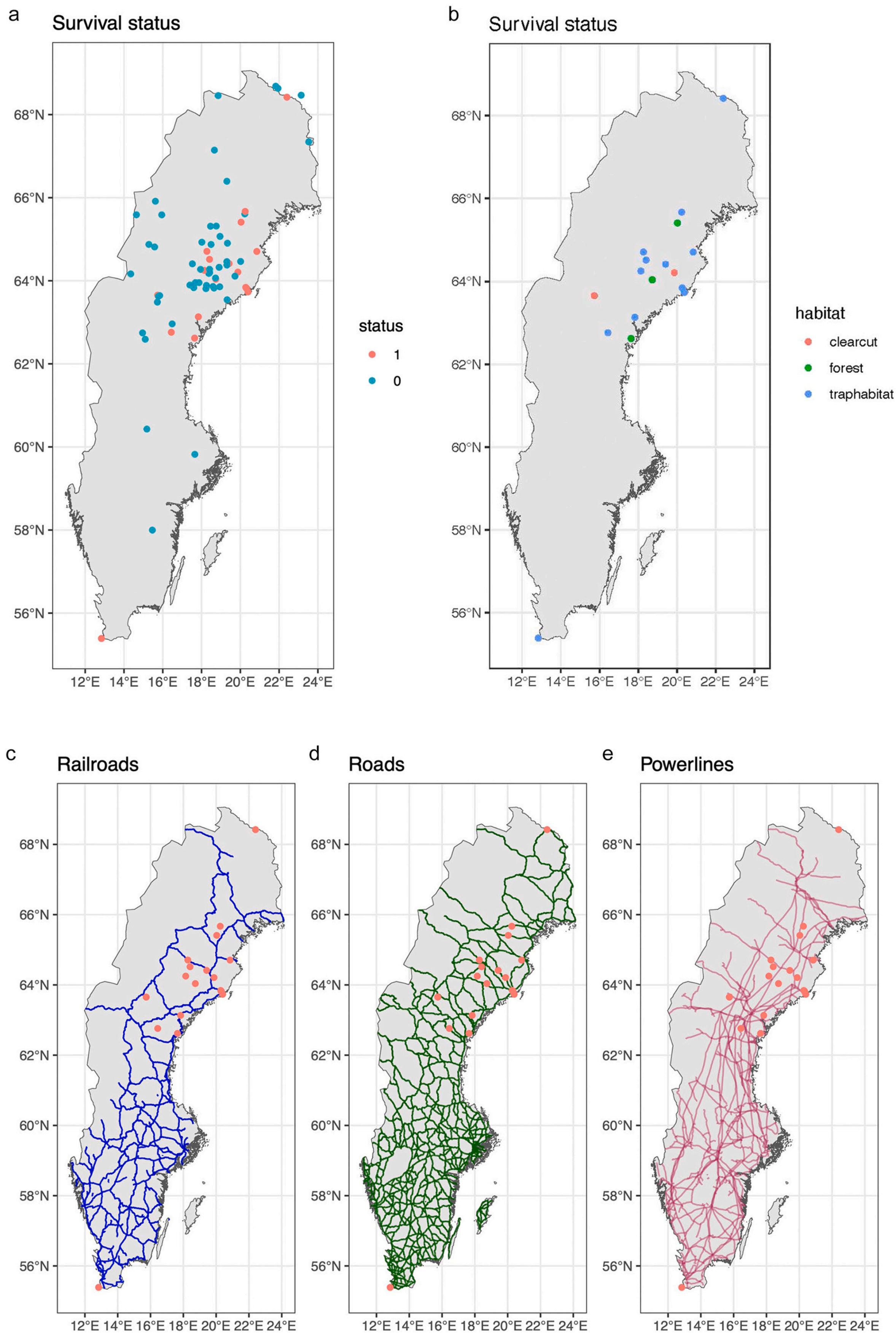

Fig. 3. a) Survival status (0 = alive and 1 = dead) and locations of the 74 Golden Eagles that are used in this study. b) locations of dead eagles used in this study and the respective habitats at those positions; dead eagles overlaid on c) railways d) roads and e) powerlines.

Table 5
Results of the cox proportional hazards model predicting hazard risk based on habitat type for 71 Golden Eagles in Sweden. The Clearcut is the reference habitat. N = 71, number of events = 22. Trap habitat is a combination of Roads, Railway and Power Lines. Estimates for Open land are irrelevant due to perfect separation i.e. no death events in this habitat. Positive values of estimates signify a higher risk. Model fit evaluations - Concordance 0.74 ± 0.05, Likelihood Ratio Test = 29.2 with df = 3, p < 0.01, Wald test = 15.65 with df = 3, $p < 0.01$.

	term	Estimate	std.error	Test-statistic	p.value
1	Forest	−0.31	0.87	−0.35	0.72
2	Open land	−18.5	6118.82	0	1
3	Trap habitat	1.7	0.75	2.26	0.02

or compete for mates, food and territories, thereby affecting future survival (Lamb et al., 2017). A high adult female mortality may first disrupt population growth directly, and indirectly when new females entering may be too young to reproduce leading to low recruitment in the population and low dispersal out of the trap (Proctor et al., 2012). We also observe that the risk of death became higher reaching 93.75 % by four years —around the time when immatures are beginning their transition to settling and finding mates and territories. This has likely serious implications for Golden Eagle population growth and its viability in the region.

Our findings suggest that other scavenger species, such as wolverines (*Gulo gulo*), ravens (*Corvus corax*), red foxes (*Vulpes vulpes*), and brown bears (*Ursus arctos*), may also face similar ecological traps from roads and railways. In fact, other human activities such as garbage creation, livestock rearing and other feed subsidies are creating similar situations elsewhere (Oro et al., 2013). Grizzly bears (*Ursus arctos*) in urban environments have been reported to be in an ecological trap due to their dependence on human created garbage dumps (Lamb et al., 2017). The vulture crisis in Asia caused by poisoning from diclofenac through livestock carcasses driving >95 % decline in populations is a prominent example of an ecological trap (Prakash et al., 2003). Pumas (*Puma concolor*) have been shown to kill livestock prey available through humans, and in retaliation face risk of being killed, due to a lower perception of risk from humans (Nisi et al., 2022). We also know that the other eagle species in the region, the White-tailed eagle, which has an even greater tendency to scavenge, is facing a similar situation, with 60 % of the mortality attributed to human related factors (Isomursu et al., 2018). Such diversity of examples indicates that even the same species might encounter multiple trap situations throughout its life cycle.

There are indeed other potential explanations for dependence of eagles on the carrion created by the linear infrastructure. Eagles in the boreal landscape are known to depend on cyclic prey species like mountain hare (*Lepus timidus*), grouse species (*Lagopus* spp.) and many species of medium sized and small mammals (Moss, 2015; Watson,

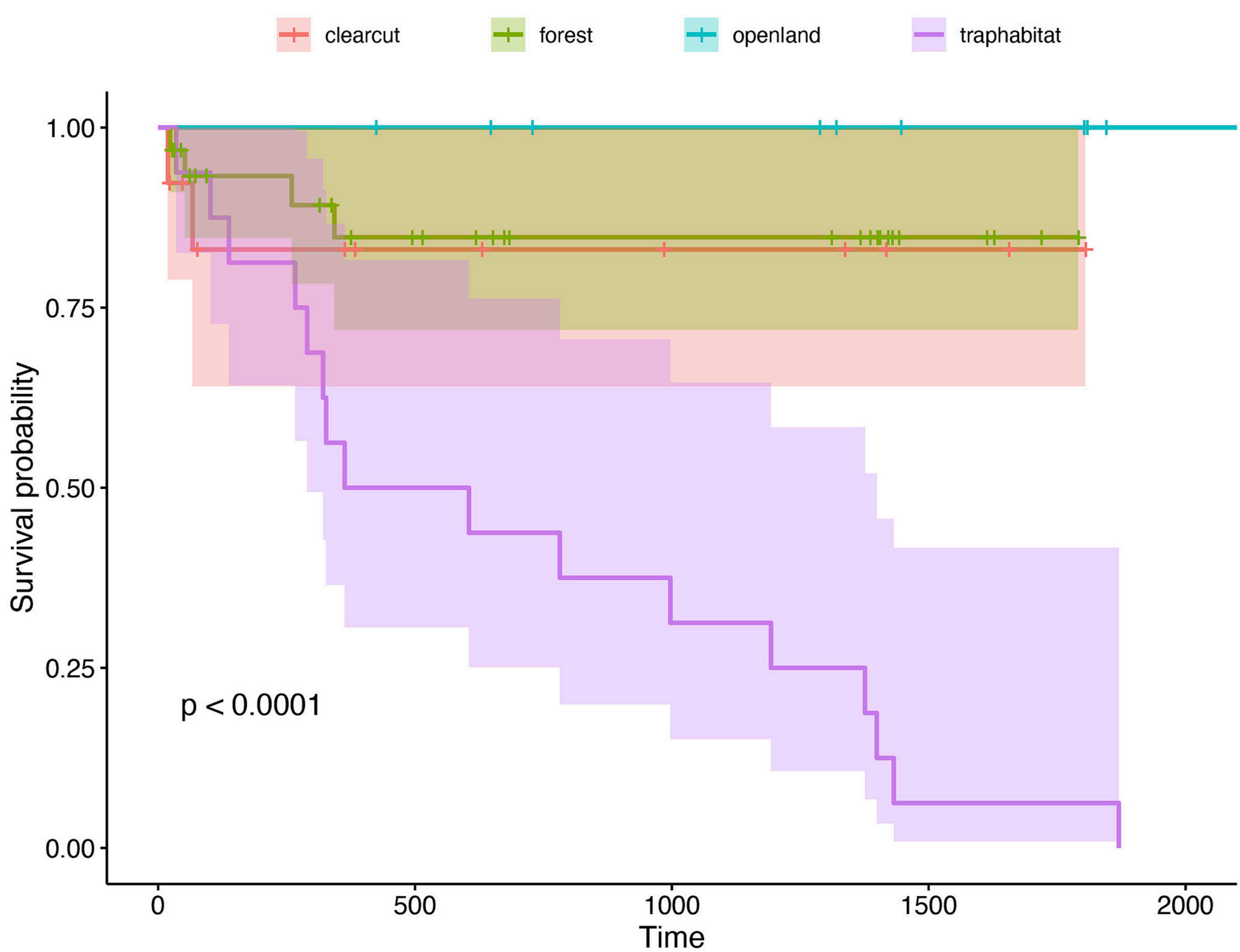

Fig. 4. Habitat specific survival curves for 71 GPS tracked Golden Eagles in Sweden obtained based on cox proportional hazard models. $n = 71$, 22 individuals died (10 adults, 5 males and 5 females, and 12 immatures), and 52 (26 adults and 23 immatures) survived or status unknown. Three individuals were removed from analyses. Trap habitat contains Railways, Roads and Powerlines. The p value shown is for the mortality rate in the trap habitat.

2010). These species are forest dwelling and are represented in the simultaneous selection of coniferous forests and clear cuts in our analyses (Singh et al., 2017). However, many of these species are currently suffering the negative impact of climate change, over harvesting and human modifications of landscapes, on their population demography and many are believed to have lost their cyclicity under the influence of these human driven changes in ecosystems (Cornulier et al., 2013). This likely has cascading impacts on eagle prey selection, behavior and demography through their increased dependence on carrion. We observed a consistent selection for trap habitats across the landscape and age classes, which implies that this is already occurring and eagles may be compensating for the lower abundances of prey species by switching to scavenging on carrion.

Eagles in our region are already exposed to other human induced rapid environmental changes that may create multiple ecological trap situations. These include ongoing rapid wind farm development, conflicts with reindeer and sheep husbandry through predation and retaliatory protective hunting, and lead poisoning from consumption of ammunition infested carcasses left over in the forest from annual moose and deer hunt (Ecke et al., 2017; Singh et al., 2017). Indeed, these all have been reported as main causes for eagle mortality in Sweden, besides the traffic collisions (Ecke et al., 2017; Helander et al., 2021). Another study showed the relationship between lead poisoning and consequent changes in eagle movement behavior and flight capacity, leading to a higher number of collisions and increasing the likelihood of death by more than three folds (Ecke et al., 2017; Singh et al., 2017; Isomursu et al., 2018). This shows many indirect interactions between human induced environmental changes and their cumulative impact on species populations potentially leading to a severe trap situation from combined mortality.

4.1. Conclusion and recommendations

Given that distribution of traffic accidents is widespread, hunting with lead ammunition is still common at the same scale, wind farm development is occurring throughout the country both on land and offshore, Golden Eagles are similarly exposed to these threats because of their migratory movements across a north-south latitudinal gradient (Singh et al., 2017). This presents a management challenge which requires careful national and regional coordination of mitigation measures such as carcass removal after accidents, careful monitoring and reporting of collisions, innovations in warning systems for both wildlife and humans. It also requires coordination between actors and stakeholders such as the traffic authorities, authorities responsible for wildlife management, hunting community, industry and other policymakers in the environmental sector. It is clear that there are certain wildlife traffic collision hotspots for eagles in Sweden which can be focused on for mitigation measures right away (Fig. 1c). This is also true for other involved species. The eagle populations have only recently recovered after the Europe wide ban in DDT and PCBs (Hailer et al., 2006; Korsman et al., 2012) but are now being exposed to high levels of novel emerging environmental contaminants (Dürig et al., 2022; Sturm and Ahrens, 2010). To conclude, there is an urgent need to eliminate the discussed threats while handling emerging ones simultaneously and enhancing population monitoring of key demographic parameters. We suggest that future studies should therefore incorporate multiple potential traps and other threats simultaneously to understand the impact of anthropogenic changes on species populations and ecosystems to ensure and improve their conservation.

CRediT authorship contribution statement

Navinder J. Singh: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Michelle Etienne:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Göran Spong:** Writing – review & editing, Supervision. **Frauke Ecke:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition. **Birger Hörnfeldt:** Writing – review & editing, Supervision, Resources, Funding acquisition, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.176934.

Data availability

The data that has been used is confidential.

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