# Not everything that glitters is gold: Does linear infrastructure create an ecological trap for Golden Eagles?

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# Not everything that glitters is gold: Does linear infrastructure create an ecological trap for Golden Eagles?

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# Abstract

Animals can be caught in an “ecological trap” when they select for seemingly attractive habitats at the expense of their fitness. This maladaptive behaviour is often a consequence of human induced rapid changes in their natal environment, such as the development of linear infrastructure, where roads and railways create novel feeding conditions through traffic induced mortality of other species and powerline areas provide perching or nesting sites. In this study strong indication is demonstrated that linear infrastructure creates an ecological trap for the golden eagle (*Aquila chrysaetos*). This is illustrated using integrated step selection function for habitat selection and movement behaviour with ten years of data from 74 GPS-tracked golden eagles in Sweden. Eagles show high mortality at road and railway sites, which increase habitat attractiveness by providing scavenging opportunities on casualties from wildlife traffic accidents, while powerlines provide perching sites. Eagles selected for these habitats all year round; immature eagles were more consistent in their selection of roads and railway sites in comparison to adults and show learning behaviour through an increased selection with age. I discuss implications of these findings for the conservation and population ecology of eagles and other scavengers.

*Keywords:* HIREC, animal ecology, animal movement, animal behaviour, integrated step selection function, wildlife traffic accidents, maladaptive behaviour, fitness, habitat selection

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# Abbreviations

| | |
|---|---|
| ET | Ecological trap |
| HIREC | Human-induced rapid environmental change |
| iSSF | Integrated step selection function |

# 1. Introduction

In the Anthropocene, human pressure on nature is increasing and the need for improving conversation efforts becomes especially important. Animals rely on different cues for habitat selection, navigation, foraging, oviposition and mate choice with the aim to increase fitness (Darwin 1859). In a rapidly changing environment, many of these cues might be modified or new misleading cues develop that make animals select for a less suitable habitat even though habitats of higher quality are available. Evolutionarily, anthropogenic changes in the landscape are occurring fast at spatial and temporal scale (i.e. human-induced rapid environmental change, hereafter HIREC, Sih 2013). Hence, animals might not have the phenotypic plasticity to properly adapt and evaluate their decisions in the expense of their fitness.

Chosen habitats which seem attractive but lead to maladaptive behaviour are called 'ecological traps' (Gates and Gysel 1978, hereafter ET) and are often associated with HIRECs (Robertson et al. 2013). ETs have led to fitness costs in several animal groups such as reptiles (Hawlena et al. 2010), insects (Horváth et al. 2010), fish (Jeffres and Moyle 2012), birds (Remeš 2003) and mammals (Lamb et al. 2017). Sea turtle hatchlings for instance are driven by the reflected moonlight to move towards the ocean under natural circumstances, but might be caught in an ecological trap when attracted to the light polluted beach instead, thereby moving in the opposite direction, increasing risk and decreasing survival rate (Witherington 1997).

For an ET to exist, three criteria must be fulfilled: Comparing the trap habitat to surrounding source habitats (I) the trap habitat is preferred (severe trap) or animals are equally selecting both habitats (equal preference trap), (II) individual fitness is lower in the trap habitat, (III) animals actively move to the trap habitat (Hale et al. 2015; Robertson and Hutto 2006). Hawlena et al. (2010) demonstrated an equal preference trap where individuals of the lizard *Acanthodactylus beershebensis* equally selected for natural and a human modified trap habitat in which they were more exposed to predators, resulting in increased mortality rate. Moreover, a population of blackcaps (*Sylvia atricapilla*) selected a human-modified landscape with newly introduced plant species over their natural breeding habitat, resulting in a severe ET with lower breeding success (Remeš 2003).

A HIREC with high potential of forming ETs worldwide is linear infrastructure such as roads, railways and powerlines (Harris and Scheck 1991; Seiler 2001). Effects of linear infrastructure have been demonstrated mostly on mammals and birds, affecting movement (Jackson 2000; James and Stuart-Smith 2000; Prokopenko et al. 2017; Scrafford et al. 2018; Whittington et al. 2005), stress levels (Krone et al. 2019; Wasser et al. 2011) and other behaviours (Gibson et al. 2018; Slabbekoorn and Peet 2003; Tigas et al. 2002). Birds might use powerlines and poles as perching or nesting sites, where particularly large birds such as raptors or corvids show high mortality due to electrocution worldwide (Haas 2005; Janss 2000; Loss et al. 2014; Shobrak 2012; Tintó et al. 2010).

Wildlife traffic collisions are a major cause of mortality in birds (García et al. 2017; Loss et al. 2014) and mammals worldwide (Bruinderink and Hazebroek 1996; Gundersen and Andreassen 1998; Popp et al. 2018; Seiler et al. 2004). Carcasses attract predators and scavengers to roads and railway sites (Lambertucci et al. 2009; Prosser et al. 2008; Santos and Carvalho 2011), consequently increasing mortality risk by being exposed to traffic. Hence, linear features have a high potential of creating ETs, yet there is little evidence (Kriska et al. 1998).

Large scavenging birds such as eagles, corvids and vultures are especially vulnerable to ETs created by roads, railways and powerlines because they are long lived, have a strong ability to learn and move effectively over landscapes. Therefore, they have increased carrion detection and habitat accessibility compared to terrestrial predators.

A large raptor of conversation concern which is potentially vulnerable to ETs is the golden eagle (*Aquila chrysaetos*). The golden eagle is a long-lived, soaring bird of prey distributed across the Holarctic (Watson 2010). The species is listed as near threatened in Sweden (ArtDatabanken 2015) and as species needing special habitat conservation measures (Annex 1) in the EU Birds Directive (European Union 2009). Accordingly, golden eagles require protection measures. In Sweden adults establish home ranges in the north at ca. 60° - 66° latitude (Moss et al. 2014) while mostly immatures are migrating to the south of the country in late September to October and return north in late April to early May (Singh et al. 2017). The Swedish population uses old growth forests as breeding habitat and clear cuts and other open land with increased prey detectability for hunting (Singh et al. 2016), while also using scavenging opportunities (Watson 2010). As apex predators, golden eagles highly depend on naturally fluctuating abundances of mountain hares (*Lepus timidus*) and different grouse species in the boreal forest (Moss et al. 2012;

Tjernberg 1981). Considering the strong dependency on prey abundance, it is conceivable that eagles regularly use scavenging opportunities at infrastructure especially when prey abundance is low.

In 2019 there were ~ 65.000 reported fatal wildlife traffic collisions for animals on roads and railways in Sweden with numbers increasing (National Wildlife Accident Council, *Nationella Viltolycksradet*, www.viltolycka.se). According to the National Swedish News (SVT) with source from the National Traffic Management Agency (www.trafikverket.se), 104 golden eagles and white-tailed sea eagles (*Haliaeetus albicilla*) died of rail collisions in 2018[1]. Main causes of deaths in golden eagles recovered by the Swedish National Museum of Natural History, Stockholm, between 2003 - 2011 are attributed to collisions with trains (35,6 %), electrocution and powerline collisions (17,8 %) and starvation and other trauma (11,9 %), respectively, (Ecke et al. 2017). Other anthropogenic threats to eagles include windfarm development (Tjernberg 2010) and lead exposure by scavenging on leftovers of hunted game shot with lead ammunition. It has been shown that lead exposure alters flight behaviour in golden eagles, where the highest lead concentrations were found in individuals that died in traffic collisions (Ecke et al. 2017). Consequently, bioavailability and uptake of contaminants might alter behaviour and increase the use of road and railway sites as scavenging opportunities.

In this work, I study golden eagles on a populational level to investigate the hypothesis (i) that linear infrastructure creates an ET for eagles in Sweden. Therefore, I expect eagles to consistently select for and actively move to linear infrastructure since scavenging opportunities from wildlife traffic accidents increase attractiveness of road and railway habitats, while powerline areas increase attractiveness by providing perching sites, scavenging opportunities from electrocuted birds and increase visibility for eagles. Additionally, I investigate the national wildlife traffic accident database for the amount and spatial extent of scavenging opportunities for eagles as well as distribution of eagle mortalities.

To investigate the ecological trap on a local and seasonal scale, I further hypothesize that (ii) eagles actively search and sit in these habitats. Furthermore, I hypothesize that (iii) immature eagles are closer to roads and railways than adults because they scavenge more, as inexperienced juveniles have lower hunting success compared to adults (Kitowski 2009; Nadjafzadeh et al. 2016). I also hypothesize that (iv) immature eagles learn to use road and railway sites as scavenging opportunities i.e. closeness to these infrastructure increases with age.

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[1] https://www.svt.se/nyheter/lokalt/gavleborg/over-hundra-ornar-dodades-av-tag-i-fjol

I tested these hypotheses by formulating an integrated step selection function (iSSF, Avgar et al. 2016) investigating habitat selection and movement behaviour of GPS tagged golden eagles. Step selection functions have emerged as a widely used and powerful tool to investigate animal movement (Fortin et al. 2005; Prokopenko et al. 2017; Thurfjell et al. 2014), while integrated step selection functions allow to include movement parameters into habitat selection analysis (Avgar et al. 2016). Furthermore, I use national wildlife road and railway mortality statistics for eagles and other species (National Wildlife Accident Council, *Nationella Viltolycksradet*, www.viltolycka.se).

# 2. Methods

## 2.1. Study area and eagle data

Data comprises of 74 GPS-tagged golden eagles (36 adults, 38 immatures) within a study period of 10 years (07.07.2010 to 06.05.2020). Individual tracking periods ranged from one month to six years with minimum 500 relocations to ensure confidence in the model estimates (Figure 10 Supplementary material). Overall range included most of Sweden (55 – 68°N, 12. – 23°E, figure 9 Supplementary material). In northern Sweden where home ranges are established, main land use is commercial forestry. The heterogeneous landscape is dominated by clear felled areas and even-aged, even-height forest containing Norway Spruce (*Picea abies*) and Scots Pine (*Pinus Sylvestris*) (Esseen et al. 1997).

Adults were captured using remote controlled bownets (Bloom et al. 2007; Bloom et al. 2015; Jackman et al. 1994) and tagged with solar-powered, backpack mounted global positioning systems (GPS) in 2010-11 (75 g Microwave Telemetry Inc., USA and 140 g VectronicAerospace GmbH, Germany) and 2014 (70 g Cellular TrackingTechnologies, Inc., USA) with a maximum location error of ± 18 m. Sexes in adults were genetically identified through blood samples following the protocol by Fridolfsson and Ellegren (1999). Immatures were tagged as nestlings approximately two weeks prior to fledgling.

## 2.2. Habitat variables and traffic mortality

Road, railway, powerline, elevation and habitat data (100 m cell size, RT90) were based on raster layers in a geographic information system (GIS) provided by the Swedish National Land Survey (Lantmäteriet).

Monthly summaries of national wildlife traffic accidents at roads and railways for the years 2010-2019 were obtained from the National Wildlife Accident Council (Nationella Viltolycksradet). Species included were moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), wild boar (*Sus scrofa*), otter (*Lutra lutra*), eagle (golden eagle *Aquila chrysaetos* and white tailed sea eagle *Haliaeetus albicilla*), wolf (*Canis lupus*), brown bear (*Ursus arctos*) and lynx (*Lynx lynx*). Both white tailed and golden eagle are summarized as one species because of difficulties to correctly identify the two eagle species after collision. Six confirmed deaths of golden eagles that died in traffic accidents were obtained from GPS tagged individuals.

## 2.3. Statistical analysis

Data modification, spatial and statistical analysis were performed in R (R version 3.6.1, R Core Team 2019) and part of spatial data modification in QGIS (QGIS version 3.42, QGIS Development Team 2009).

### 2.3.1. Step selection function

I applied an integrated step selection function (Hereafter iSSF, Avgar et al. 2016), using the package *amt* for R (Signer and Fieberg 2019) to investigate golden eagle habitat selection and behaviour around linear infrastructure. Locations were treated as linear step between two consecutive relocations (Fortin et al. 2005; Thurfjell et al. 2014). Step selection functions test for habitat selection by conducting a conditional logistic regression comparing available to used habitat, while iSSFs allow to include movement parameters into habitat selection analysis (Avgar et al. 2016), which reduce inferential bias (Forester et al. 2009). Step lengths (m) were assumed to follow a gamma distribution. Eagle locations were resampled to an interval of 1 h ± 10 min to achieve a regular time interval and a set of random steps (n = 10) was created for each true step following the same distribution. A total amount of 437 217 true and random locations was analysed with 224 796 locations from immature eagles.

### 2.3.2. Selection of trap habitat

Habitat covariates extracted at step end were simplified in five categorical variables (‘water’, ‘open land’, ‘forest’, ‘road + railway’ and ‘clear cut’). I chose to use open land as the intercept in the model testing habitat selection (Model 1, table 1) as eagles regularly use and select forests and clear cuts and avoid water (Singh et al. 2016). The landcover ‘open land’ included open wetlands, arable land and other non-exploited open lands that are not clear cuts. For amount of locations for true and random steps falling in the different habitats see figure 12 - 13 in Supplementary material. Covariates for roads, railways and powerlines were extracted as continuous variable (Distance to the nearest feature in m) at the end of the step and tested in separate models due to correlation between the respective types of infrastructure.

Spring was defined between March and May, summer between June and August, autumn between September and November and winter between December and February. Summer was used as the intercept in the models testing selection consistency (Models 2 - 4, table 1; see figure 11 in Supplementary material for number of locations per season).

### 2.3.3. Behaviour in trap habitat

Number of eagle years were defined individually, where the first year was defined as the next 365 days after tagging. Height positions obtained from GPS locations were extracted and afterwards subtracted from elevation data to obtain the height above ground. Positions below 30 m above ground were assumed as ’sitting’ and above 30 m as ’flying’ based on maximal boreal forest height (Larsen 2013).

The cosine of the von Mises distributed turning angles reaches from -1 to 1 and can be used to describe movement direction, where positive values represent moving forwards from the previous location and negative values represent moving backwards (Benhamou 2006). I defined behaviour as ‘searching’ as cosine of the turning angle below zero and step length below 1000 m as eagles are soaring (backwards movement) taking smaller steps when performing searching behaviour, while travel movements are forwards with larger steps. Only flying positions were included in the models testing behaviour (182 044 flying locations, models 5 - 7, table 1) to minimize false positive results and movements other than ‘searching’ were treated as ‘travel’ to ensure model simplicity. The log of the step length was included in the models that tested behaviour and type of position (Models 5 - 10, table 1) as a modifier of the shape parameter of the underlying gamma distribution. As step length distribution differs between different behavioural modes, the log of the step length can be used to improve model efficiency (Avgar et al. 2016).

An overview about performed iSSF models is stated in table 1 with random or true step id (‘case’) as response variable. Positive model coefficients of categorical explanatory variables indicate selection, while for continuous explanatory variables, selection is indicated by a negative coefficient. The explanatory variables used in different models are as follows:

## Explanatory variables

### Continuous

| | |
|---|---|
| PowerD | distance to nearest powerline (m) |
| RailwayD | distance to nearest railway (m) |
| RoadD | distance to nearest road (m) |
| Log (sl) | log of step length |
| No.year | number of individual eagle years of immature eagles |

### Categorical

| | |
|---|---|
| Age | adult, immature |
| Behaviour | travel, searching |
| Habitat | open land, clear cut, forest, road+railway, water |
| Position | flying, sitting |
| Season | spring, summer, autumn, winter |

*Table 1. overview of different models testing the movement behaviour at linear infrastructure of golden eagles in Sweden, 'Case' indicates the response variable (true or random step id). For overview of explanatory variables see methods 2.3.3. Number of individuals in model 1 – 12: n = 74 (all eagles), model 13 – 14: n = 38 (immature eagles).*

| **Model** | **Formula** | **Intercept** |
|---|---|---|
| **1** | Case ~ Habitat | open land |
| **2** | Case ~ RoadD + RoadD:Season | summer |
| **3** | Case ~ RailwayD + RailwayD:Season | summer |
| **4** | Case ~ PowerD + PowerD:Season | summer |
| **5** | Case ~ RoadD + log (sl) + RoadD:Behaviour | travel |
| **6** | Case ~ RailwayD + log (sl) + RailwayD:Behaviour | travel |
| **7** | Case ~ PowerD + log (sl) + PowerD:Behaviour | travel |
| **8** | Case ~ RoadD + log (sl) + RoadD:Position | flying |
| **9** | Case ~ RailwayD + log (sl) + RailwayD:Position | flying |
| **10** | Case ~ PowerD + log (sl) + PowerD:Position | flying |
| **11** | Case ~ RoadD + RoadD:Age | adult |
| **12** | Case ~ RailwayD + RailwayD:Age | adult |
| **13** | Case ~ RoadD + RoadD:no.year | - |
| **14** | Case ~ RailwayD + RailwayD:no.year | - |

# 3. Results

## 3.1. Selection of trap habitat

Eagles selected for roads and railways, clear cuts and forest and avoided water relative to open land ($coef_{road+railway} = 0.13 \pm 0.06$, $coef_{clearcut} = 0.99 \pm 0.02$, $coef_{forest} = 0.67 \pm 0.02$, $coef_{water} = - 2.24 \pm 0.07$, table 2, figure 1).

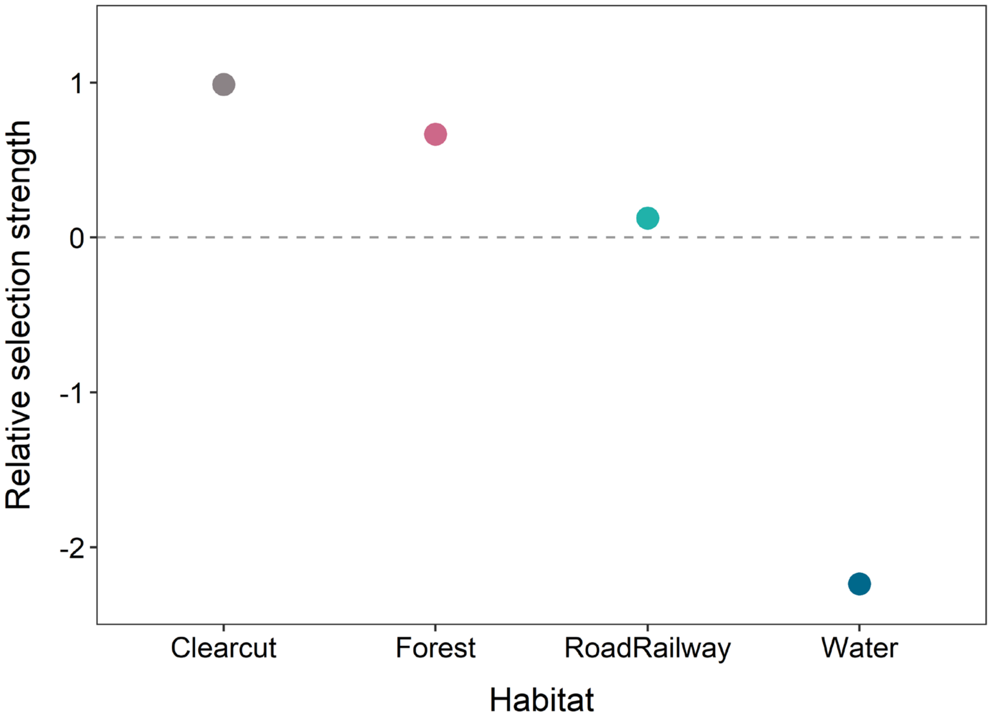

*Figure 1. Estimates of iSSF model 1 (coefficient ± SE, table 2) showing habitat selection for golden eagles in Sweden relative to open land. Positive values indicate selection and negative values avoidance.*

*Table 2. iSSF model 1 testing habitat selection in golden eagles in Sweden. Model explanation see table 1.*

| Model | Parameter | coef | se (coef) | Z | p-value |
|---|---|---|---|---|---|
| **1** | Road+Railway | 0.13 | 0.06 | 2.04 | < 0.05 |
| **1** | Water | -2.24 | 0.07 | -33.82 | < 0.001 |
| **1** | Forest | 0.67 | 0.02 | 34.65 | < 0.001 |
| **1** | Clear cut | 0.99 | 0.02 | 46.85 | < 0.001 |

Eagles were close to roads, railways and powerlines throughout autumn, winter and spring compared to summer ($road_{autumn}$: coef = - 0.38 ± 0.05, $road_{spring}$: coef = - 0.38 ± 0.04, $road_{winter}$: coef = - 0.42 ± 0.11, $railway_{autumn}$: coef = - 0.28 ± 0.03, $railway_{spring}$: coef = - 0.29 ± 0.03, $railway_{winter}$: coef = - 1.162 ± 0.13, $powerline_{autumn}$: coef = - 0.36 ± 0.05, $powerline_{spring}$: coef = - 0.25 ± 0.03, $powerline_{winter}$: coef = - 0.53 ± 0.12, table 3). Habitat selection for each year 2010 – 2020 using categorical variables is illustrated in figure 2.

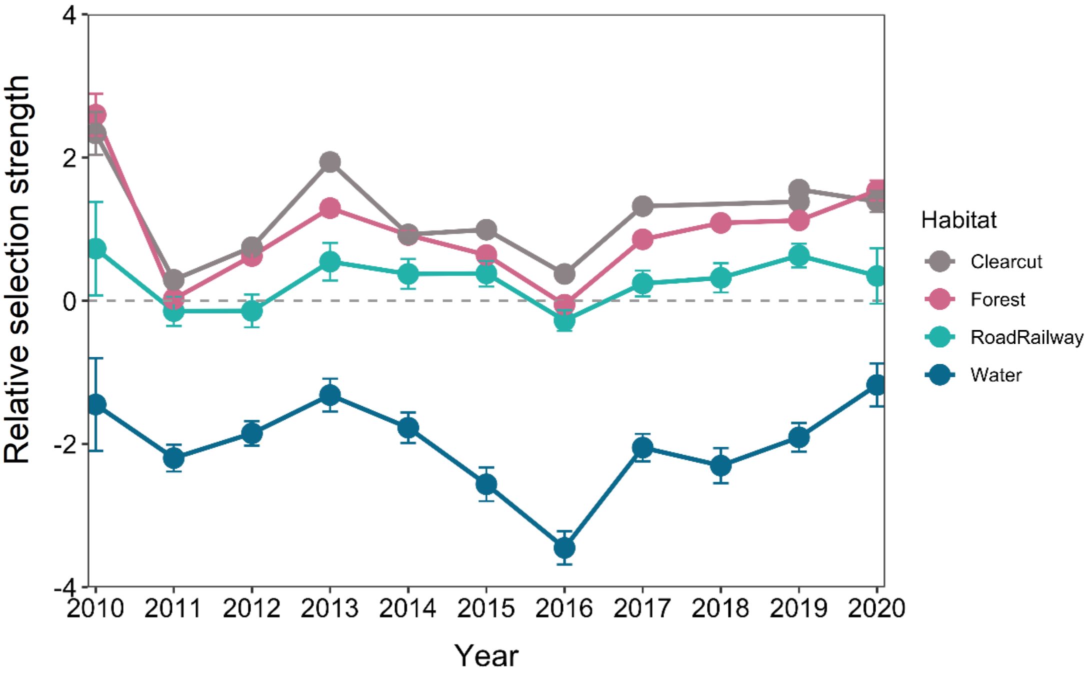

*Figure 2. Habitat selection (coefficient ± SE) per year 2010 – 2020 in golden eagles in Sweden relative to open land, $n_{2010}$ = 10, $n_{2011}$ = 27, $n_{2012}$ = 24, $n_{2013}$ = 15, $n_{2014}$ = 39, $n_{2015}$ = 41, $n_{2016}$ = 30, $n_{2017}$ = 20, $n_{2018}$ = 16, $n_{2019}$ = 14, $n_{2020}$ = 10. Positive values indicate selection and negative values avoidance. For more information on coefficients see table 14 Supplementary material.*

*Table 3. iSSF models 2 - 4 testing closeness to respective infrastructure in relation to seasons in golden eagles in Sweden. For model explanation see table 1.*

| **Model** | **Parameter** | **coef** | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|
| **2** | RoadD | -0.58 | 0.02 | -34.17 | < 0.001 |
| **2** | RoadD:Autumn | -0.38 | 0.05 | -8.13 | < 0.001 |
| **2** | RoadD:Spring | -0.38 | 0.04 | -10.76 | < 0.001 |
| **2** | RoadD:Winter | -0.42 | 0.11 | -3.82 | < 0.001 |
| **3** | RailwayD | -0.39 | 0.01 | -31.35 | < 0.001 |
| **3** | RailwayD:Autumn | -0.28 | 0.03 | -8.60 | < 0.001 |
| **3** | RailwayD:Spring | -0.29 | 0.03 | -11.35 | < 0.001 |
| **3** | RailwayD:Winter | -1.16 | 0.13 | -8.73 | < 0.001 |
| **4** | PowerD | -0.53 | 0.02 | -32.31 | < 0.001 |
| **4** | PowerD:Autumn | -0.36 | 0.05 | -8.13 | < 0.001 |
| **4** | PowerD:Spring | -0.25 | 0.03 | -7.88 | < 0.001 |
| **4** | PowerD:Winter | -0.53 | 0.12 | -4.56 | < 0.001 |

There is a consistent spatial trend that eagle traffic accidents are observed throughout Sweden (See figure 15 in Supplementary material for more information). This is also ascertained from the study eagles, where six individuals were killed by traffic (Figure 3).

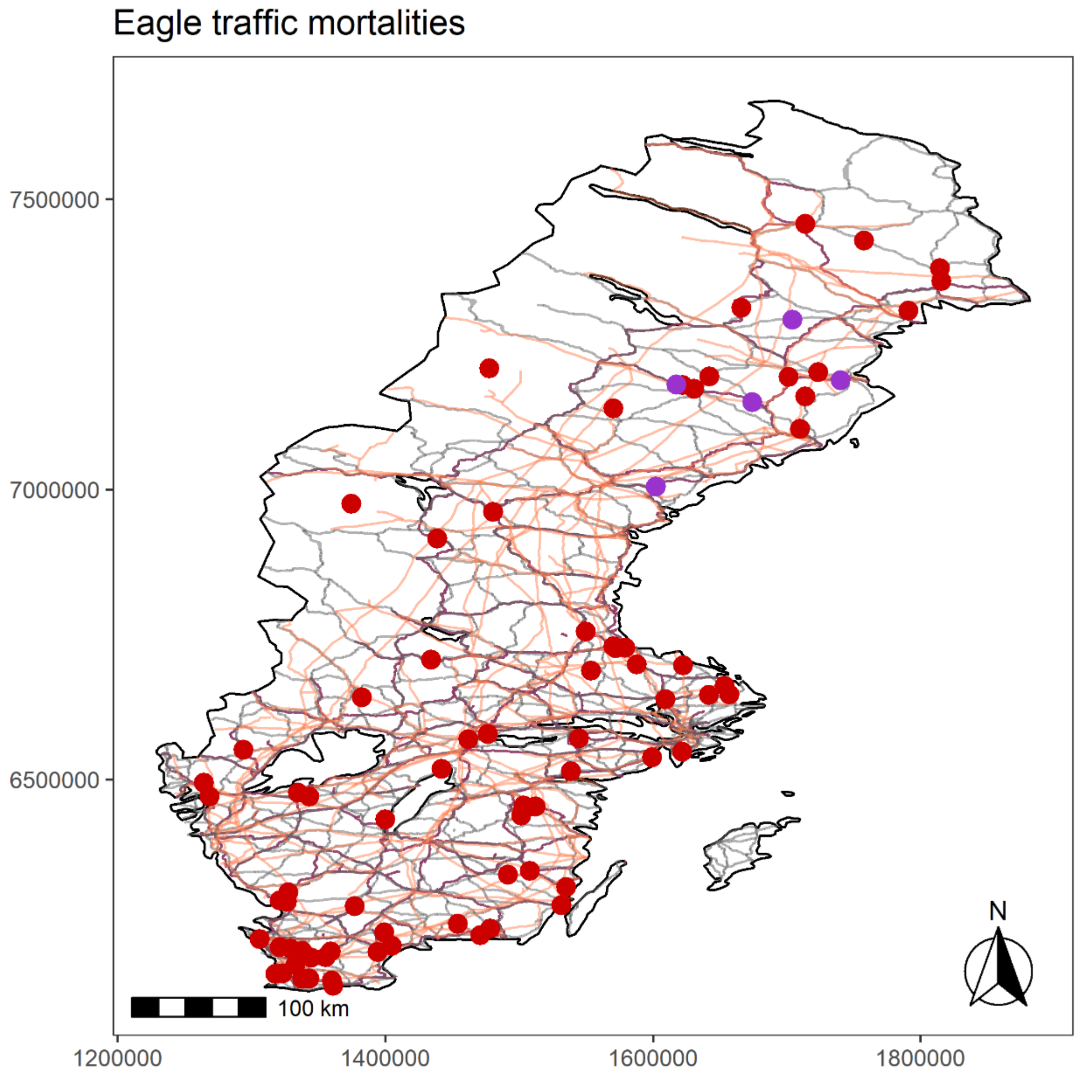

*Figure 3. Eagle traffic mortalities in Sweden. Red dots indicate location of death for eagles from national wildlife traffic accident database 2010 – 2016 (Golden eagle and white-tailed sea eagle, Nationella Viltolycksradet). Purple dots indicate location of death of five recovered GPS tagged golden eagles. The sixth confirmed death is not shown in the figure due to missing location data. X axis: Easting, Y-axis: Northing.*

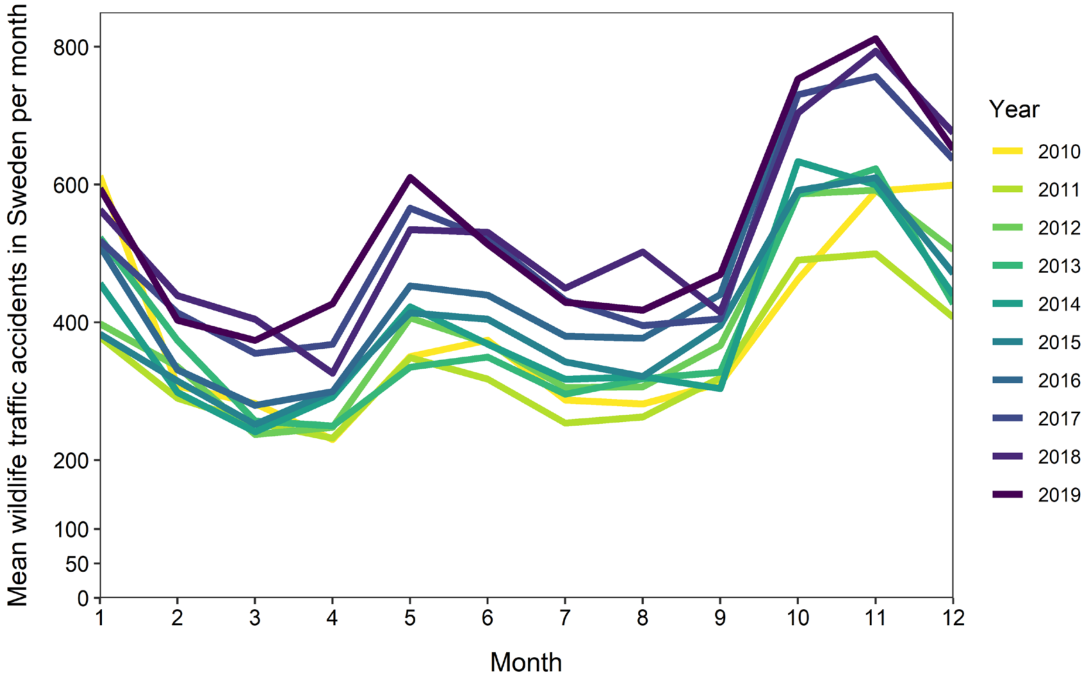

*Figure 4. Mean wildlife traffic accidents in Sweden per month. SD was not included in the figure due to high variation in mean number of accidents between species. Number of included species per year = 10, for more details see methods 2.2 and figure 14 in Supplementary material. Data obtained from National Wildlife Accident Council (Nationella Viltolycksradet).*

The temporal seasonal trend of wildlife accident reveals an increasing number of accidents since 2010 (See figure 14 Supplementary material) and annually towards winter, with two general peaks. One peak occurs in May and June and the other occurs during September to December. Overall, the trend provides a mean estimate of number of accidents per month as an index of attractiveness of roads and railways.

## 3.2. Behaviour in trap habitat

Close to roads and railways golden eagles performed more search than travel behaviour, while at powerline areas there was no indication for search movements (road: coef = - 0.50 ± 0.08 railway: coef = - 0.25 ± 0.06, powerline: coef = - 0.05 ± 0.04, table 4).

Additionally, eagles were sitting more frequently instead of flying close to linear infrastructure (road: coef = - 1.13 ± 0.05, railway: coef = - 0.84 ± 0.04, powerline: coef = - 0.95 ± 0.05, table 5).

*Table 4. iSSF models 5 - 7 testing searching behaviour in relation to closeness to linear infrastructure in golden eagles in Sweden. For model explanation see table 1.*

| Model | Parameter | coef | se (coef) | Z | p-value |
|---|---|---|---|---|---|
| **5** | RoadD | -0.27 | 0.01 | -23.38 | < 0.001 |
| **5** | Log (sl) | 0.11 | 0.00 | 30.29 | < 0.001 |
| **5** | RoadD:Searching | -0.50 | 0.08 | -6.43 | < 0.001 |
| **6** | RailwayD | -0.43 | 0.01 | -32.80 | < 0.001 |
| **6** | Log (sl) | 0.09 | 0.00 | 24.96 | < 0.001 |
| **6** | RailwayD:Searching | -0.25 | 0.06 | -4.07 | < 0.001 |
| **7** | PowerD | -0.14 | 0.01 | -13.29 | < 0.001 |
| **7** | Log (sl) | 0.11 | 0.00 | 30.53 | < 0.001 |
| **7** | PowerD:Searching | -0.05 | 0.04 | 1.22 | 0.22 |

*Table 5. iSSF models 8 – 10 testing sitting positions in relation to closeness to linear infrastructure in golden eagles in Sweden. For model explanation see table 1.*

| Model | Parameter | coef | se (coef) | Z | p-value |
|---|---|---|---|---|---|
| **8** | RoadD | -0.89 | 0.04 | -24.96 | < 0.001 |
| **8** | Log (sl) | 0.03 | 0.00 | 14.08 | < 0.001 |
| **8** | RoadD:Sitting | -1.13 | 0.05 | -23.16 | < 0.001 |
| **9** | RailwayD | -0.98 | 0.04 | -36.51 | < 0.001 |
| **9** | Log (sl) | 0.02 | 0.00 | 8.06 | < 0.001 |
| **9** | RailwayD:Sitting | -0.84 | 0.04 | -20.93 | < 0.001 |
| **10** | PowerD | -0.48 | 0.04 | -13.41 | < 0.001 |
| **10** | Log (sl) | 0.03 | 0.00 | 13.71 | < 0.001 |
| **10** | PowerD:Sitting | -0.95 | 0.05 | -19.57 | < 0.001 |

Figure 5 shows the location of death of four GPS tagged golden eagles and illustrates eagle positions around linear infrastructure. In most figures, based on flying and sitting locations, it can be seen that eagles tend to visit linear features quite frequently and sit along these.

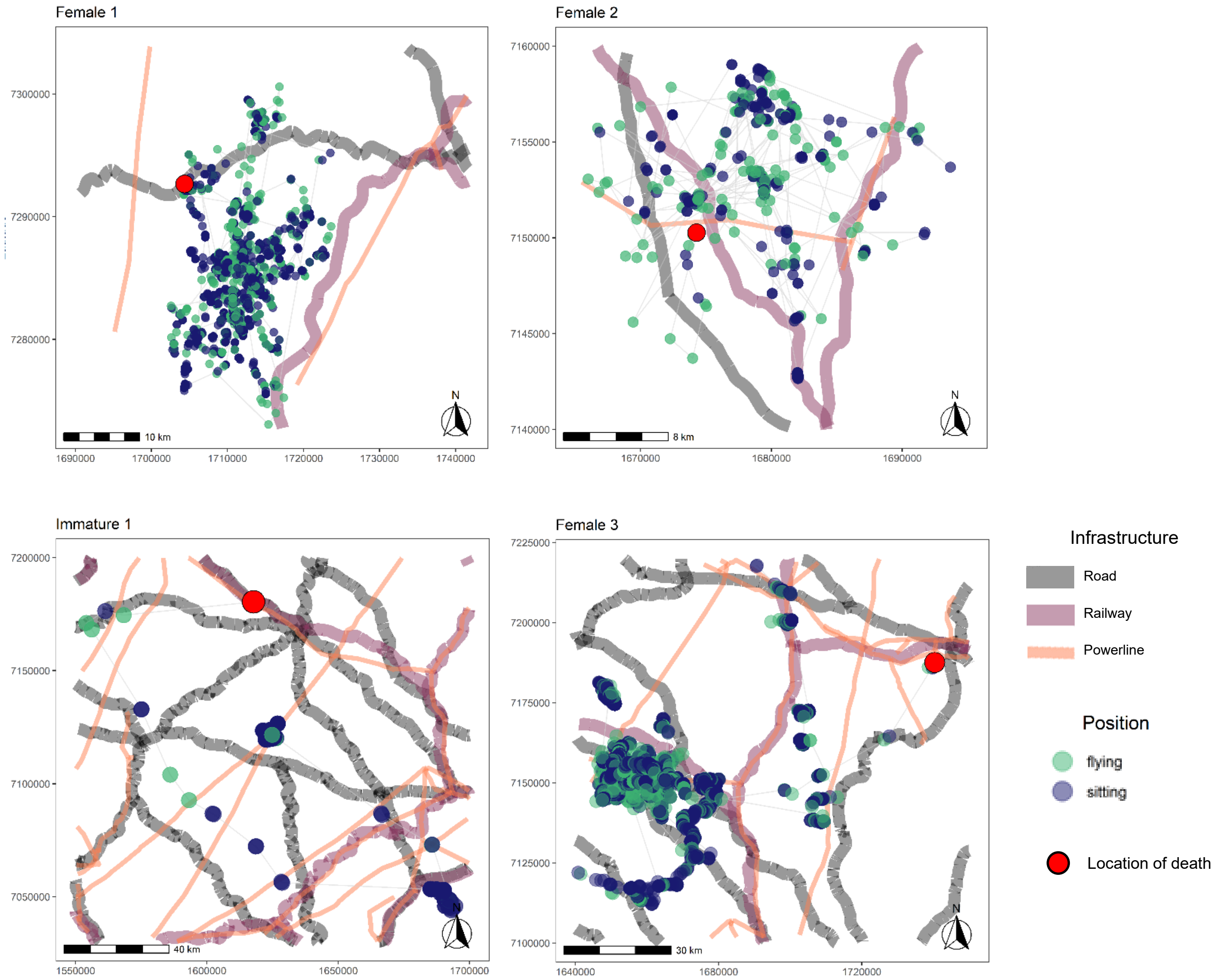

*Figure 5. Movement of four GPS tagged eagles (one individual per plot) in Sweden at individual temporal and spatial scale around linear infrastructure (roads = grey, railways = pink, powerlines = orange). Blue dots indicate sitting and green dots indicate flying locations. Location of death is illustrated as red dot for each individual. X axis: Easting, Y-axis: Northing.*

## 3.3. Selection of trap habitats by immatures

Immature eagles were closer to roads and railways than adults (road: coef = - 0.41 ± 0.03, railway: coef = - 0.42 ± 0.02, table 6). Examples of movement close to linear infrastructure of two immature eagles are illustrated in figure 6 showing consistent reocurring movements along the infrastructure across years.

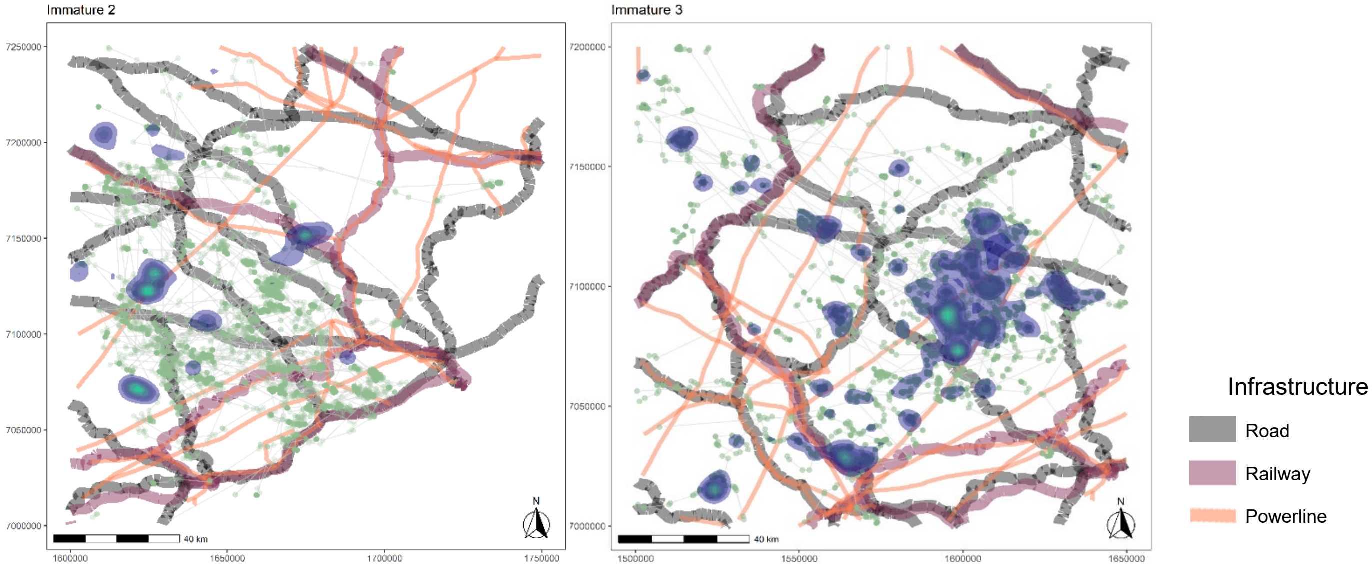

*Figure 6. GPS Locations of Immature 2 amd 3 (green) and smoothed density of positions indicating revisited areas at Infrastructure in an area in Sweden (high density= light blue, roads = grey, railways = pink, powerlines = orange). Data includes locations in the shown areas within a period of 5 years for immature 2 and 6 years for immature 3. X axis: Easting, Y-axis: Northing.*

*Table 6. iSSF models 11 – 12 testing differences in closeness to roads and railways between adults and immature golden eagles in Sweden. For model explanation see table 1.*

| **Model** | **Parameter** | **coef** | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|
| **11** | RoadD | -0.53 | 0.02 | -29.88 | < 0.001 |
| **11** | RoadD:Age I | -0.41 | 0.03 | -15.15 | < 0.001 |
| **12** | RailwayD | -0.29 | 0.01 | -22.00 | < 0.001 |
| **12** | RailwayD:Age I | -0.42 | 0.02 | -21.68 | < 0.001 |

Figure 7 shows an example of the range of trap habitat encountered at a landscape scale including type of positions of one immature. It is clear how eagles encounter linear features multiple times across their annual movements and face the risk of collisions.

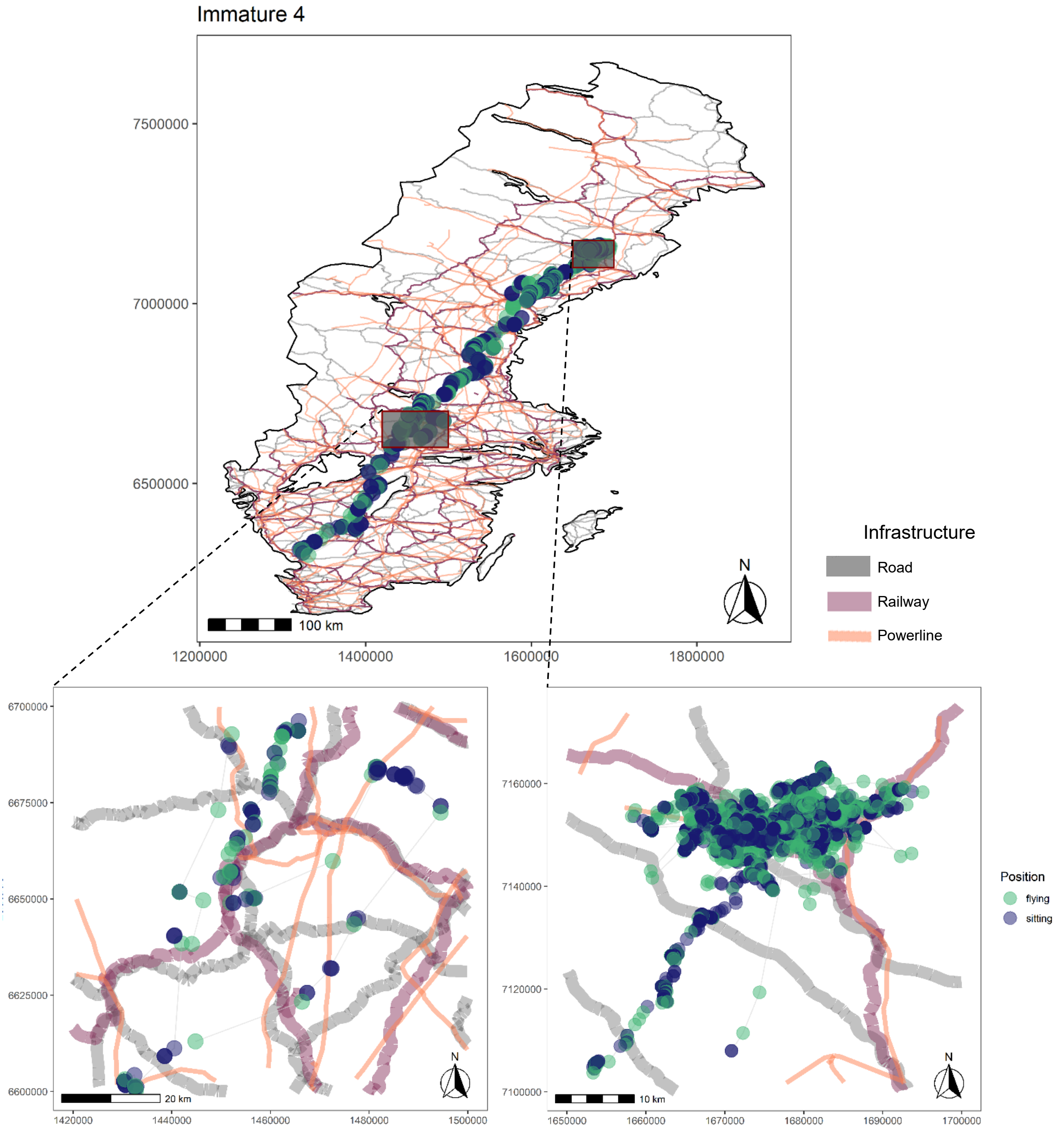

*Figure 7. GPS locations of one year of immature 4 throughout Sweden with sitting and flying positions showing probability of trap encounter at landscape scale, roads = grey, railways = pink, powerlines = orange. X-axis: Easting, Y-axis: Northing.*

## 3.4. Learning in immatures

As immature eagles got older, they moved closer to roads and railways (road: coef = - 0.05 ± 0.02, railway: coef = - 0.16 ± 0.01, table 7). General selection for these areas by immatures is illustrated in figure 8 using categorical habitat variables.

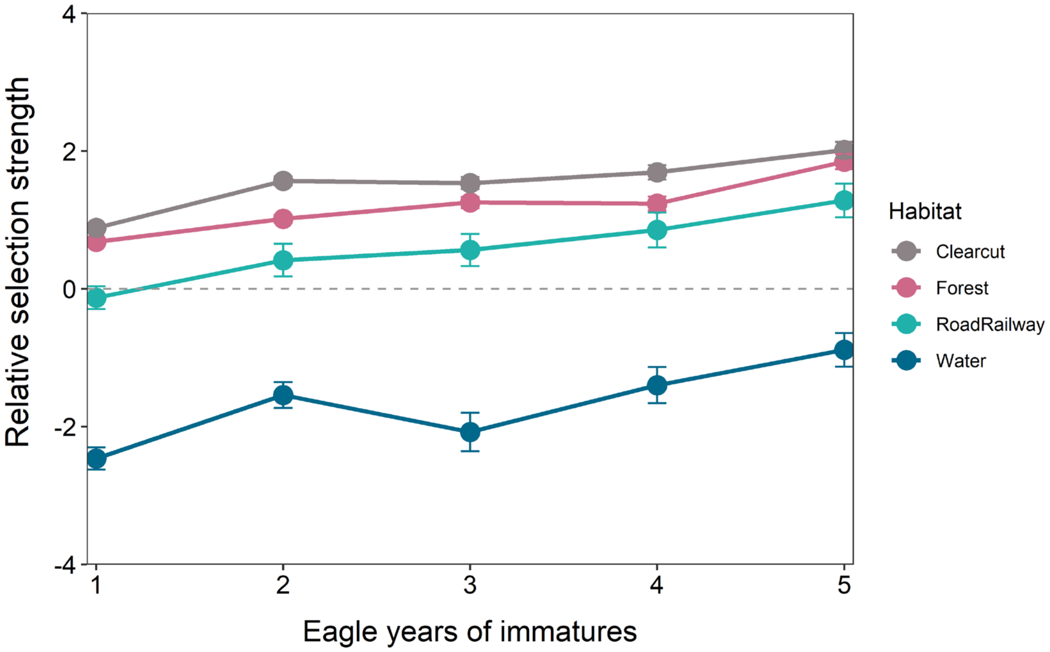

*Figure 8. Habitat selection (coefficients ± SE) per individual eagle years (age) in immature eagles in Sweden relative to open land.* $n_{year\ 1} = 38$, $n_{year\ 2} = 15$, *nyear 3 = 10,* $n_{year\ 4} = 9$, $n_{year\ 5} = 8$. *Year 6 was excluded due to low sample size. Positive values indicate selection and negative values avoidance. For more information on coefficients see table 15 Supplementary material.*

*Table 7. iSSF models 13 – 14 testing the effect of age i.e. number of individual eagle years in immature golden eagles in Sweden in relation to closeness to roads and railways. For model explanation see table 1.*

| Model | Parameter | coef | se (coef) | Z | p-value |
|---|---|---|---|---|---|
| **13** | RoadDI | -0.85 | 0.04 | -20.57 | < 0.001 |
| **13** | RoadDI:no.year | -0.05 | 0.02 | -3.12 | < 0.01 |
| **14** | RailwayDI | -0.44 | 0.03 | -14.44 | < 0.001 |
| **14** | RailwayDI:no.year | -0.16 | 0.01 | -12.17 | < 0.001 |

# 4. Discussion

In this study through an extensive and unique multi-annual dataset, I am able to demonstrate strong indication that linear infrastructure creates an ecological trap (ET) for golden eagles across space and time. Among the conditions that need to be fulfilled to demonstrate an ecological trap, I demonstrated that eagles consistently selected, searched and sat frequently closer to roads and railways, called 'trap habitats' here, across seasons, years and throughout their range in Sweden. The condition about the negative demographic consequences at the population level, could be inferred through the death of six of the study eagles and published studies (e.g. Ecke et al. 2017). The national wildlife accident database includes the observed instances of dead eagles ascertaining the demographic costs of foraging in these habitats.

Immature eagles selected these habitats due to their attractiveness and possibly due to a lack of hunting experience and showed an increased selection of these habitats over time. This demonstrates and fulfils another condition for an ET, that to have population level persistent effects, animals should move from source into the trap habitats.  Settling in the habitat where an animal was born (i.e. natal) habitat is an important life history decision in animals (Davis and Stamps 2004). It has been shown that when animals may select natal-like habitats, it can reduce their fitness (Fletcher et al. 2015; Piper et al. 2013). Hence, natal environments can have long-term and populational level effects, especially when HIRECs (human induced rapid environmental change, Sih 2013) reduce the quality and quantity of available settlement and breeding habitat. Here, through increased selection of road and railway sites as the young eagles mature, I demonstrate strong indication that ETs influence the selection of natal habitats, which most likely results in negative consequences for eagles through high mortality risk in the trap habitat.

Lamb et al. (2017) in a study on grizzly bears showed, how bears face an ET produced by human-caused mortality in an area of high human density and rich food resources for bears. This trap caused population declines of approximately 8% per year in the trap habitat. There are no yearly numbers on population decline of golden eagles in Sweden available, but there are published estimates of the most known causes of death (Ecke et al. 2017) and reported cases of dead eagles that died in traffic collisions recovered by the police (See figure 3, figure 15 Supplementary material). I referred to these numbers and published studies here but also show through six instances of death of the study individuals. Furthermore, it is most often difficult to distinguish between adults and immatures in the collision databases to ascertain any age differences in dead eagles, unless an autopsy is conducted. The Swedish Veterinary Agency often is responsible for conducting such autopsies and sends out post-mortem reports. In these reports, 'trauma' signifying physical injuries is one of the most commonly reported cause of death for Swedish eagles (unpublished data). At the population level, which is where the ET response is measured, I believe that my results are convincing as the mortality of eagles through traffic collisions is observed throughout Sweden (Figure 3).

Due to a lack of natural predators, apex consumers lack capacity to perceive novel sources of risk, especially HIREC-induced (Ripple et al. 2014), which highly increases vulnerability to ETs. Golden eagles fit in this category and likely are not able to perceive the risks from oncoming traffic at high speeds. The results of this study show the failure in HIREC- associated risk assessment by apex predators. Other reasons for eagles to collide with traffic might be that after feeding on carrion, eagle body weight is too heavy to allow them to gain enough height, and also lead poisoning is likely to alter flight behaviour and increase traffic-induced mortality risk (Ecke et al. 2017). It remains to be tested how the contaminants in eagles affect their behaviour by altering their sensory perception, and the relationship with linear infrastructure.

I report the national wildlife traffic accident statistics which show the level of traffic caused mortality at spatial and temporal scales as a measure of attractiveness of habitat to eagles. Habitat attractiveness can be modelled in other ways based on the distribution density and frequency of accidents observed and potential food availability from carcasses. However, how much new information that would provide on mechanisms for eagles selecting these linear habitats is questionable, unless one is interested in fine scale patterns and the proportion of scavenge in the eagle diet. Otherwise, it is also important to note that eagles are known to rely on cyclic prey species like mountain hare (*Lepus timidus*), grouse species and small mammals (Watson 2010), which is likely to affect their scavenging frequency.

Furthermore, numbers on wildlife traffic accidents are likely to be much higher than the listed cases as many incidents remain unreported (Seiler et al. 2004). Nevertheless, the wildlife traffic accidents occur all year around in high numbers across Sweden, adding to the high predictability of this large food subsidy and resulting foraging opportunities (See figure 4, figure 14 Supplementary material).

The mechanisms underlying the selection of linear infrastructure are, that such features of the landscape provide open habitats and cues for foraging opportunities, which encourages eagles to conduct search in these habitats, as is seen through the eagle movement data and extensive observation of search behaviour throughout. Moreover, sitting to feed on the carcasses is another behaviour also observed in the movement data.

Additionally, eagles selected and were sitting more frequently at powerline areas, but in contrast to roads and railways, eagles did not show indication of searching behaviour. This suggests that powerline areas were selected for providing attractive perching sites to hunt and look for scavenging opportunities from remains of other electrocuted birds. Thus, eagles face higher electrocution risk as shown in other studies (Janss 2000; Kruger et al. 2004; Slater and Smith 2010). Golden eagle mortalities due to electrocution have been shown to be very high in the United States (Ansell and Smith 1980; Harness and Wilson 2001) and numbers in Sweden are mostly unknown (Ecke et al. 2017).

Eisaguirre et al. (2019, under review) found that roads and railways can alter the movement patterns of golden eagles in Alaska. Areas near roads and railways were selected during spring and fall migration and slower movements were performed indicating searching behaviour. It was also suggested that eagles spend more time close to roads and railways compared to other habitat during spring and that infrastructure is also likely to attract eagles to scavenge. Although selection consistency over time, measures of traffic accidents i.e. habitat attractiveness and mortality has not been tested, these results support the results of my study. Moreover, golden eagles in Sweden might not only use linear infrastructure to scavenge, as immature eagles are migrating it is likely that these habitats also contribute as orientation points during migration periods. Hence, linear infrastructure serving multiple purposes could even increase mortality risk through traffic collisions for migrating individuals and therefore increase the severity of the ET.

Morelli et al. (2014) reviewed several of the effects of linear infrastructure on birds as positive. Besides providing scavenge, perching and nesting sites, they can prolong diurnal activity through streetlights and provide warm surface. This might have a positive effect in a short term, but increased mortality risk through traffic collisions and electrocution, as well as severe anthropogenic interference in the natural environment leading to possible behavioural changes should not be underestimated, especially when HIRECs act as an ET on a populational level.

As suggested by Hale et al. (2015) ETs are most severe when they cover a large proportion of the habitat which is given in this study as the probability to encounter linear infrastructure i.e. the trap habitat for eagles is very high throughout the whole landscape as well as consistent trough time (Figure 7).

It is therefore likely that other scavengers and opportunistic predators in the boreal landscape are also affected by the trap habitat. Ravens and red foxes for instance have been observed to also scavenge on road kills (Schwartz et al. 2018) and the national wildlife traffic accident database documents frequent collisions in other apex predators such as bears, wolves and wolverine.

Conclusively, there is need to eliminate this ET to improve conservation for eagles and other scavengers. The easiest way to remove the trap would be to lower attractiveness. Fenced areas around roads result in decreased wildlife traffic accidents, yet exclusive fencing can increase habitat fragmentation for terrestrial and other non-target species (Seiler 2001). I suggest that faster road and railway site clearing would be the most effective and cost-efficient method to decrease attractiveness of the trap habitat. More studies are needed to estimate the response time of eagles in relation to an accident or the spotting of a carcass. These would aid the managers in identifying the optimal time needed to remove the carcass before it is spotted and discovered by scavengers. General public needs to be educated about circumstances in case of a wildlife accident on the response required to handle carcasses with the help of police and other agencies and authorities involved with traffic.

In this study I demonstrated strong indication that linear infrastructure creates an ET for golden eagles at a populational and landscape scale. It is likely that other HIRECs like windfarm development and uptake of offal from hunting with lead ammunition causing poisoning of eagles, could exacerbate the effects of the trap, thereby further threatening the eagle population. Examples of such effects have been shown in a population of cape vultures (*Gryps coprotheres*) in Africa, which suffered high numbers in mortality induced by electrocution, poaching and poisoning independently, resulting in population decline (Mundy 1983). Future studies should therefore incorporate multiple traps and other threats simultaneously to understand holistically, the impact of anthropogenic changes and hence improve conservation.

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# Appendix 1

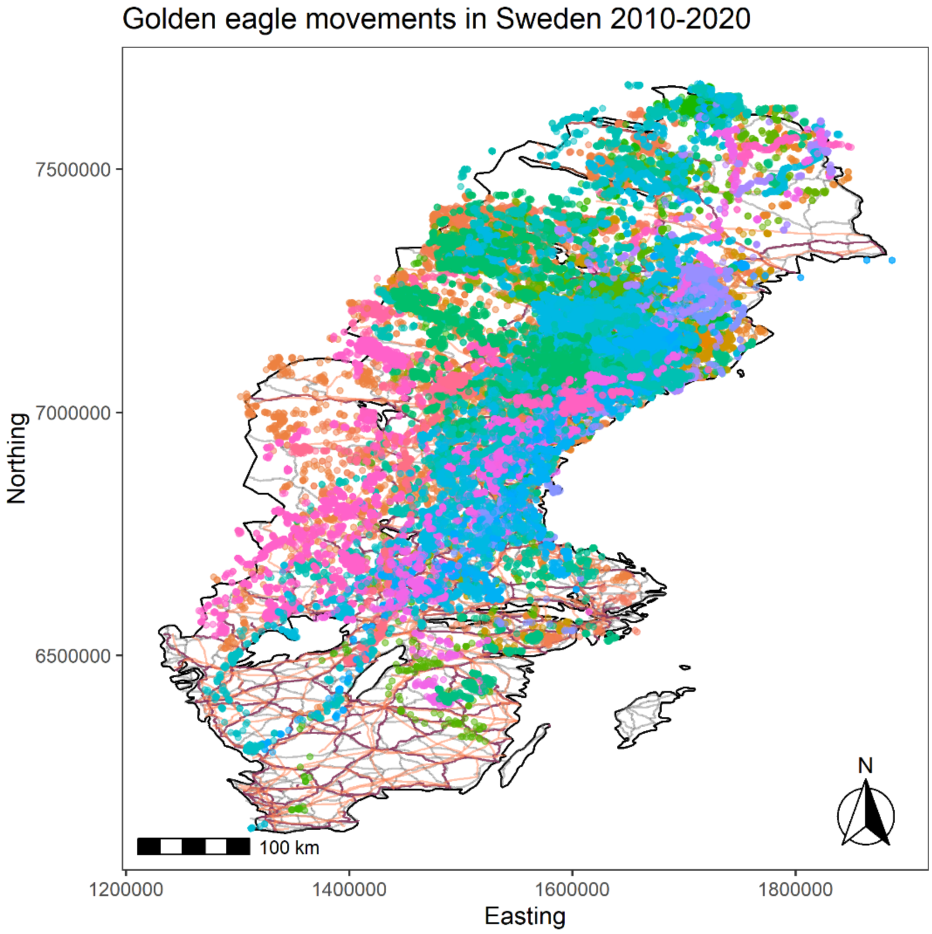

*Figure 9. Locations of 74 GPS tagged golden eagles in Sweden 2010-2020. Different colors indicate different individuals.*

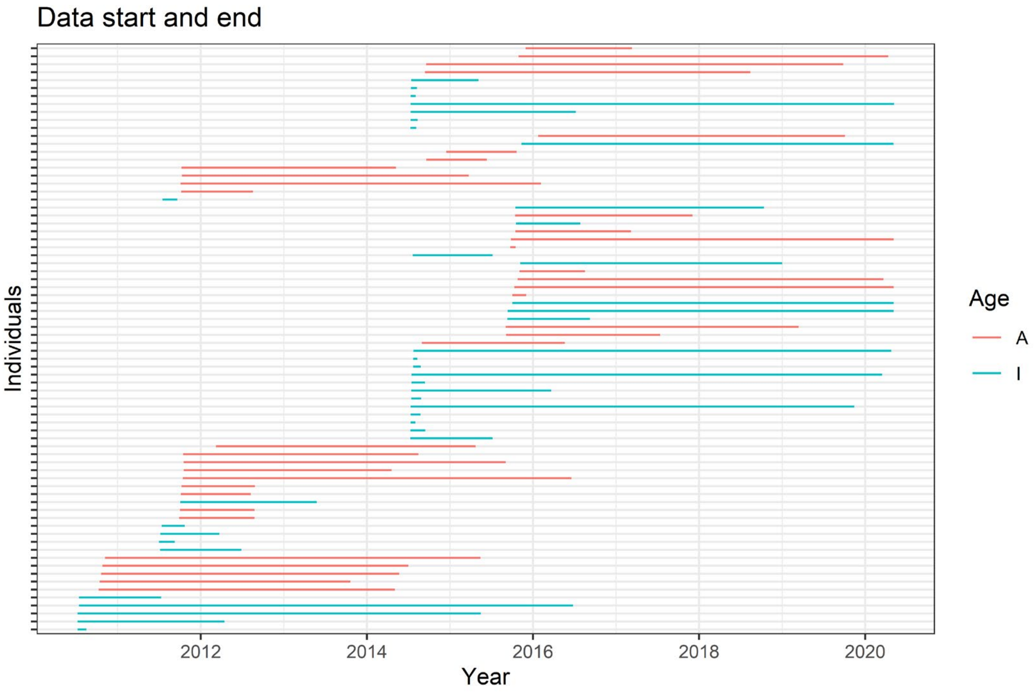

*Figure 10. Individual tracking periods of 36 adult golden eagles (A, red) and 38 immatures (I, blue). Each line indicates one individual.*

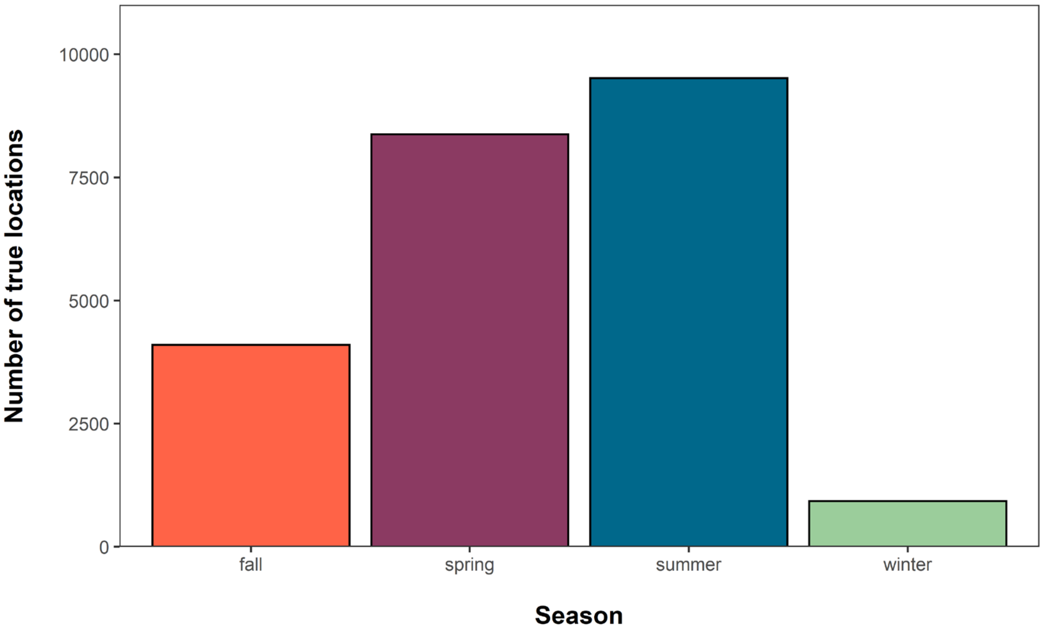

*Figure 11. Number of true GPS tagged golden eagle locations falling in different seasons (fall, spring, summer, winter).*

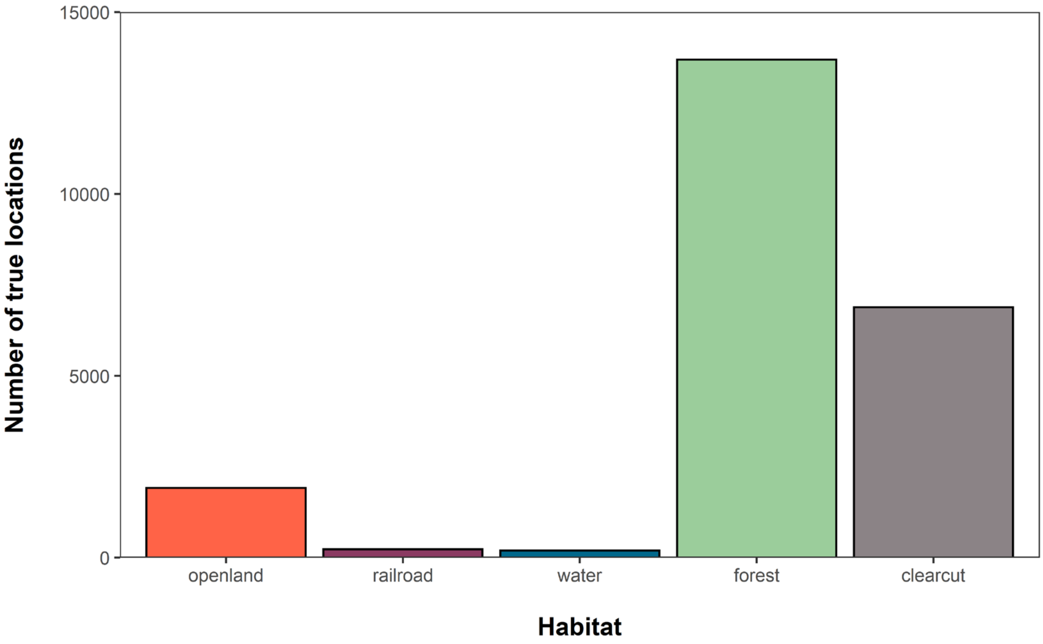

*Figure 12. Number of true golden eagle locations falling in different habitats (Open land, road+railway, water, forest, clear cut).*

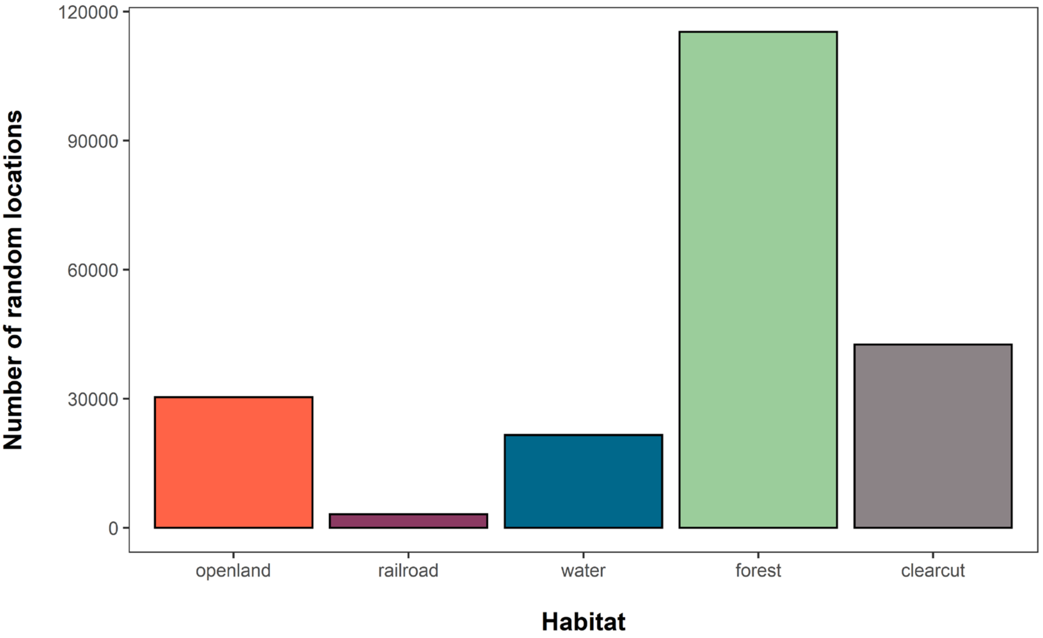

*Figure 13. Number of random golden eagle locations falling in different habitats (Open land, road+railway, water, forest, clear cut).*

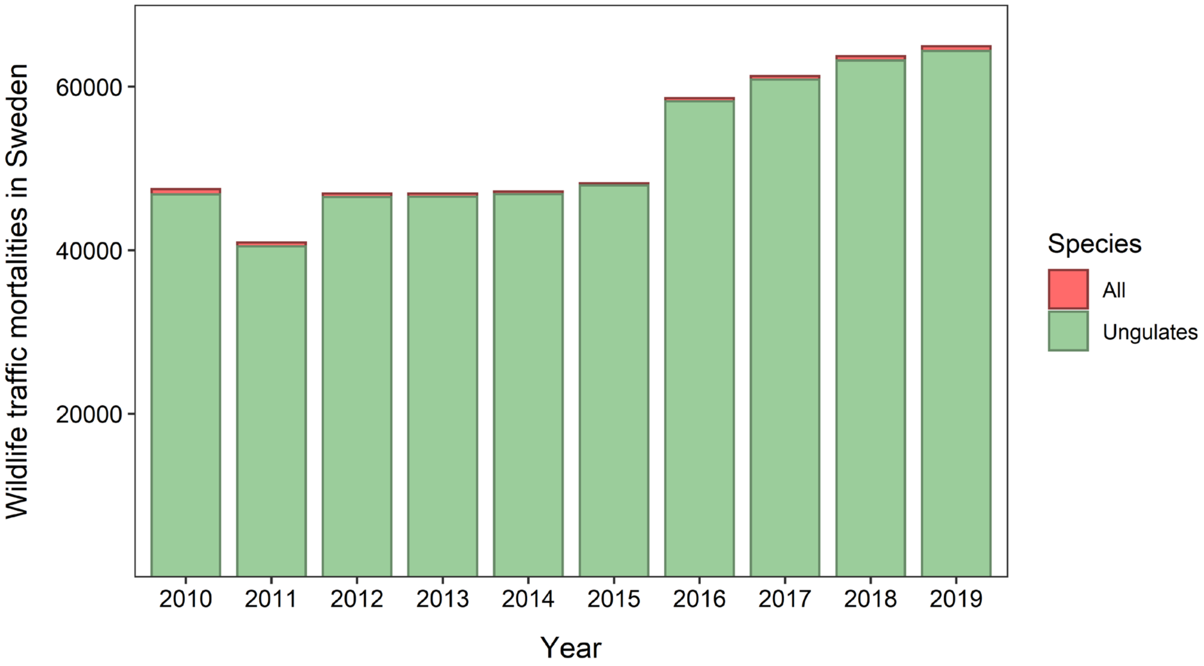

*Figure 12. Number of wildlife traffic accidents in Sweden 2010 – 2019. Number of accidents (n):* $n_{2010}$ *=47 475,* $n_{2011}$ *= 40 951,* $n_{2012}$ *= 46 928,* $n_{2013}$ *= 46 944,* $n_{2014}$ *= 47 167,* $n_{2015}$ *= 48 190,* $n_{2016}$ *= 58 579,* $n_{2017}$ *= 61 282,* $n_{2018}$ *= 63 750,* $n_{2019}$ *= 64 931. Number of included species per year = 10, for more details see methods 2.2. Data obtained from National Wildlife Accident Council (Nationella Viltolycksradet).*

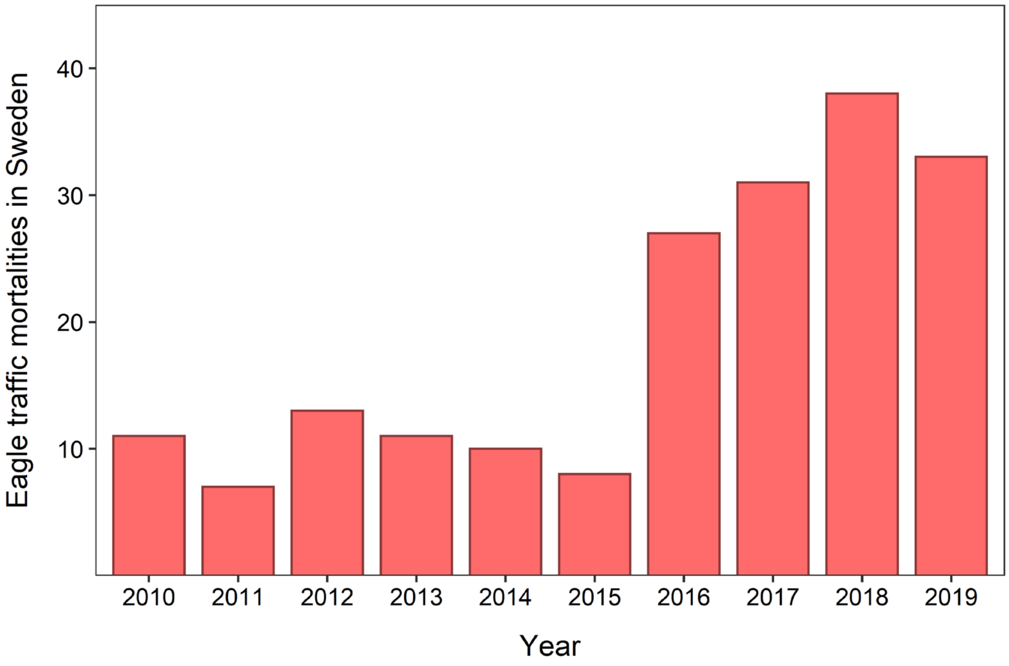

*Figure 13. Number of reported eagle traffic collisions in Sweden 2010 – 2019. Number of accidents (n):* $n_{2010}$ *= 11,* $n_{2011}$ *= 7,* $n_{2012}$ *= 13,* $n_{2013}$ *= 11,* $n_{2014}$ *= 10,* $n_{2015}$ *= 8,* $n_{2016}$ *= 27,* $n_{2017}$ *= 31,* $n_{2018}$ *= 38,* $n_{2019}$ *= 33. Data includes the species golden eagle (*Aquila chrysaetos*) and white-tailed sea eagle (*Haliaeetus albicilla*). Data obtained from National Wildlife Accident Council (Nationella Viltolycksradet).*

*Table 8. full iSSF model 1 testing habitat selection in golden eagles in Sweden. Model explanation see table 1.*

| **Model** | **Parameter** | **coef** | **exp(coef)** | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|---|
| **1** | Railway+Road | 0.13 | 1.13 | 0.06 | 2.04 | < 0.05 |
| **1** | Water | -2.24 | 0.11 | 0.07 | -33.82 | < 0.001 |
| **1** | Forest | 0.68 | 1.95 | 0.02 | 34.65 | < 0.001 |
| **1** | Clear cut | 0.99 | 2.69 | 0.02 | 46.85 | < 0.001 |

*Table 9. full iSSF models 2 - 4 testing closeness to infrastructure in relation to seasons in golden eagles in Sweden. For model explanation see table 1.*

| **Model** | **Parameter** | **coef** | **exp(coef)** | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|---|
| **2** | RoadD | -0.58 | 0.56 | 0.02 | -34.17 | < 0.001 |
| **2** | RoadD:Autumn | -0.38 | 0.69 | 0.05 | -8.13 | < 0.001 |
| **2** | RoadD:Spring | -0.38 | 0.68 | 0.04 | -10.76 | < 0.001 |
| **2** | RoadD:Winter | -0.42 | 0.66 | 0.11 | -3.82 | < 0.001 |
| **3** | RailwayD | -0.39 | 0.67 | 0.01 | -31.35 | < 0.001 |
| **3** | RailwayD:Autumn | -0.28 | 0.76 | 0.03 | -8.60 | < 0.001 |
| **3** | RailwayD:Spring | -0.29 | 0.75 | 0.03 | -11.35 | < 0.001 |
| **3** | RailwayD:Winter | -1.16 | 0.31 | 0.13 | -8.73 | < 0.001 |
| **4** | PowerD | -0.53 | 0.59 | 0.02 | -32.31 | < 0.001 |
| **4** | PowerD:Autumn | -0.36 | 0.70 | 0.05 | -8.13 | < 0.001 |
| **4** | PowerD:Spring | -0.25 | 0.78 | 0.03 | -7.88 | < 0.001 |
| **4** | PowerD:Winter | -0.53 | 0.59 | 0.12 | -4.56 | < 0.001 |

*Table 10. full iSSF models 5 - 7 testing searching behaviour in relation to closeness to linear infrastructure in golden eagles in Sweden. For model explanation see table 1.*

| **Model** | **Parameter** | **coef** | **exp(coef)** | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|---|
| **5** | RoadD | -0.27 | 0.77 | 0.01 | -23.38 | < 0.001 |
| **5** | Log (sl) | 0.11 | 1.11 | 0.00 | 30.29 | < 0.001 |
| **5** | RoadD:Searching | -0.50 | 0.61 | 0.08 | -6.43 | < 0.001 |
| **6** | RailwayD | -0.43 | 0.65 | 0.01 | -32.80 | < 0.001 |
| **6** | Log (sl) | 0.09 | 1.09 | 0.00 | 24.96 | < 0.001 |
| **6** | RailwayD:Searching | -0.25 | 0.78 | 0.06 | -4.07 | < 0.001 |
| **7** | PowerD | -0.14 | 0.87 | 0.01 | -13.29 | < 0.001 |
| **7** | Log (sl) | 0.11 | 1.11 | 0.00 | 30.53 | < 0.001 |
| **7** | PowerD:Searching | -0.05 | 0.95 | 0.04 | 1.22 | 0.22 |

*Table 11. full iSSF models 8 – 10 testing sitting positions in relation to closeness linear infrastructure in golden eagles in Sweden. For model explanation see table 1.*

| **Model** | **Parameter** | **coef** |  | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|---|
| **8** | RoadD | -0.89 | 0.41 | 0.04 | -24.96 | < 0.001 |
| **8** | Log (sl) | 0.03 | 1.03 | 0.00 | 14.08 | < 0.001 |
| **8** | RoadD:Sitting | -1.13 | 0.32 | 0.05 | -23.16 | < 0.001 |
| **9** | RailwayD | -0.98 | 0.37 | 0.04 | -36.51 | < 0.001 |
| **9** | Log (sl) | 0.02 | 1.02 | 0.00 | 8.06 | < 0.001 |
| **9** | RailwayD:Sitting | -0.84 | 0.43 | 0.04 | -20.93 | < 0.001 |
| **10** | PowerD | -0.48 | 0.62 | 0.04 | -13.41 | < 0.001 |
| **10** | Log (sl) | 0.03 | 1.03 | 0.00 | 13.71 | < 0.001 |
| **10** | PowerD:Sitting | -0.95 | 0.39 | 0.05 | -19.57 | < 0.001 |

*Table 12. full iSSF models 11 – 12 testing differences in closeness to road and railways between adult and immature golden eagles in Sweden. For model explanation see table 1.*

| **Model** | **Parameter** | **coef** | **exp(coef)** | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|---|
| **11** | RoadD | -0.53 | 0.59 | 0.02 | -29.88 | < 0.001 |
| **11** | RoadD:Age I | -0.41 | 0.66 | 0.03 | -15.15 | < 0.001 |
| **12** | RailwayD | -0.29 | 0.75 | 0.01 | -22.00 | < 0.001 |
| **12** | RailwayD:Age I | -0.42 | 0.66 | 0.02 | -21.68 | < 0.001 |

*Table 13. full iSSF models 13 – 14 testing the effect of age i.e. number of individual eagle years in immature golden eagles in Sweden in relation to closeness to roads and railways. For model explanation see table 1.*

| **Model** | **Parameter** | **coef** | **exp(coef)** | **se (coef)** | **Z** | **p-value** |
|---|---|---|---|---|---|---|
| **13** | RoadDI | -0.85 | 0.42 | 0.04 | -20.57 | < 0.001 |
| **13** | RoadDI:no.year | -0.05 | 0.95 | 0.02 | -3.12 | < 0.01 |
| **14** | RailwayDI | -0.44 | 0.64 | 0.03 | -14.44 | < 0.001 |
| **14** | RailwayDI:no.year | -0.16 | 0.86 | 0.01 | -12.17 | < 0.001 |

*Table 14. Habitat selection coefficients for golden eagles in Sweden per year. Open land was used as the intercept.*

| **Year** | **Coefficient** | **S.E.** | **Habitat** |
|---|---|---|---|
| 2010 | 0.73 | 0.65 | RoadRailway |
| 2010 | -1.45 | 0.65 | Water |
| 2010 | 2.60 | 0.29 | Forest |
| 2010 | 2.34 | 0.30 | Clearcut |
| 2011 | -0.14 | 0.21 | RoadRailway |
| 2011 | -2.20 | 0.19 | Water |
| 2011 | 0.02 | 0.06 | Forest |
| 2011 | 0.29 | 0.07 | Clearcut |
| 2012 | -0.14 | 0.23 | RoadRailway |
| 2012 | -1.85 | 0.17 | Water |
| 2012 | 0.62 | 0.06 | Forest |
| 2012 | 0.75 | 0.07 | Clearcut |
| 2013 | 0.55 | 0.26 | RoadRailway |
| 2013 | -1.32 | 0.23 | Water |
| 2013 | 1.29 | 0.10 | Forest |
| 2013 | 1.94 | 0.11 | Clearcut |
| 2014 | 0.38 | 0.21 | RoadRailway |
| 2014 | -1.77 | 0.21 | Water |
| 2014 | 0.92 | 0.07 | Forest |
| 2014 | 0.93 | 0.08 | Clearcut |
| 2015 | 0.38 | 0.18 | RoadRailway |
| 2015 | -2.56 | 0.24 | Water |
| 2015 | 0.64 | 0.05 | Forest |
| 2015 | 0.99 | 0.06 | Clearcut |
| 2016 | -0.27 | 0.15 | RoadRailway |
| 2016 | -3.45 | 0.23 | Water |
| 2016 | -0.05 | 0.04 | Forest |
| 2016 | 0.37 | 0.05 | Clearcut |
| 2017 | 0.24 | 0.18 | RoadRailway |
| 2017 | -2.05 | 0.19 | Water |
| 2017 | 0.86 | 0.06 | Forest |
| 2017 | 1.32 | 0.06 | Clearcut |
| 2018 | 0.32 | 0.20 | RoadRailway |
| 2018 | -2.30 | 0.25 | Water |
| 2018 | 1.09 | 0.07 | Forest |
| 2019 | 1.38 | 0.07 | Clearcut |
| 2019 | 0.63 | 0.17 | RoadRailway |
| 2019 | -1.91 | 0.20 | Water |
| 2019 | 1.12 | 0.07 | Forest |
| 2019 | 1.55 | 0.07 | Clearcut |
| 2020 | 0.35 | 0.39 | RoadRailway |
| 2020 | -1.17 | 0.30 | Water |

| | | | |
|---|---|---|---|
| 2020 | 1.54 | 0.14 | Forest |
| 2020 | 1.39 | 0.15 | Clearcut |

*Table 15. Habitat selection coefficients for immature eagles for each individual number of eagle year (no.year). Open land was used as the intercept.*

| **no. year** | **Coefficient** | **S.E.** | **Habitat** |
|---|---|---|---|
| 1 | -0.1 | 0.16 | RoadRailway |
| 1 | -2.5 | 0.16 | Water |
| 1 | 0.7 | 0.04 | Forest |
| 1 | 0.9 | 0.05 | Clearcut |
| 2 | 0.4 | 0.24 | RoadRailway |
| 2 | -1.5 | 0.19 | Water |
| 2 | 1.0 | 0.06 | Forest |
| 2 | 1.6 | 0.07 | Clearcut |
| 3 | 0.6 | 0.23 | RoadRailway |
| 3 | -2.1 | 0.28 | Water |
| 3 | 1.3 | 0.08 | Forest |
| 3 | 1.5 | 0.09 | Clearcut |
| 4 | 0.9 | 0.25 | RoadRailway |
| 4 | -1.4 | 0.26 | Water |
| 4 | 1.2 | 0.10 | Forest |
| 4 | 1.7 | 0.11 | Clearcut |
| 5 | 1.3 | 0.24 | RoadRailway |
| 5 | -0.9 | 0.24 | Water |
| 5 | 1.8 | 0.11 | Forest |
| 5 | 2.0 | 0.12 | Clearcut |

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