

Consequences of migratory coupling of predators and prey when mediated by human actions

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Abstract

Aim: Animal migrations influence ecosystem structure, dynamics and persistence of predator and prey populations. The theory of migratory coupling postulates that aggregations of migrant prey can induce large-scale synchronized movements in predators, and this coupling is consequential for the dynamics of ecological communities. The degree to which humans influence these interactions remains largely unknown. We tested whether creation of large resource pulses by humans such as seasonal herding of reindeer *Rangifer tarandus* and hunting of moose, *Alces alces*, can induce migratory coupling with Golden Eagles, *Aquila chrysaetos*, and whether these lead to demographic consequences for the eagles.

Location: Fennoscandia.

Methods: We used movement data from 32 tracked Golden Eagles spanning 125 annual migratory cycles over 8 years. We obtained reindeer distribution data through collaboration with reindeer herders based on satellite tracking of reindeer, and moose harvest data from the national hunting statistics for Sweden. We assessed demographic consequences for eagles from ingesting lead from ammunition fragments in moose carcasses through survival estimates and their links with lead concentrations in eagles' blood.

Results: In spring, eagles migrated hundreds of kilometres to be spatially and temporally coupled with calving reindeer, whereas in autumn, eagles matched their distribution with the location and timing of moose hunt. Juveniles were more likely to couple with reindeer calving, whereas adults were particularly drawn to areas of higher moose harvest. Due to this coupling, eagles ingested lead from spent ammunition in moose offal and carcasses and the resulting lead toxicity increased the risk of mortality by 3.4 times.

Main conclusions: We show how migratory coupling connects landscape processes and that human actions can influence migratory coupling over large spatial scales and increase demographic risks for predators. We provide vital knowledge towards resolving human-wildlife conflicts and the conservation of protected species over a large spatial and temporal scale.

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KEY WORDS

conflict, lead poisoning, migration, predator-prey, reindeer, scale, scavengers, synchrony, toxicology

1 | INTRODUCTION

Species interact in diverse ways such as predation, parasitism, and symbiotic and competitive interactions (Tylianakis et al., 2008). These interactions have cascading effects that shape ecosystem structure and function (Estes et al., 2011). Human modification of ecosystems through land-use change, resource extraction and other ways can change the distribution and density of species and their resources (Oro et al., 2013; Robertson & Hutto, 2006). These modifications may affect species interactions at various scales, making them harder to predict (Tylianakis et al., 2008), and sometimes cause unexpected negative demographic consequences (Estes et al., 2011). We know relatively little about these indirect consequences of human actions on species interactions, distributions, movements and survival (see Allen & Singh, 2016; Tucker et al., 2018).

Predators are expected to track the movements and distribution of their prey in the environment (Barnett & Semmens, 2012; Furey et al., 2018; Laundré, 2010). Traditionally, predator-prey interactions have been studied using dietary information, population structure, and the relative abundances of predator and prey (Krebs et al., 2009; Middleton et al., 2013). When predator movements respond to migrant prey and extend beyond territories or home ranges, this response has been defined as “migratory or movement coupling” (Furey et al., 2018; Lima, 2002). When migratory coupling occurs, predators either adjust their migration timing and seasonal distributions to exploit migrant prey aggregations or movements to maximize duration of prey exposure (Furey et al., 2018). Such interactions have traditionally been studied between a single predator species and the distribution of its prey (Wolf and Elk, Fortin et al., 2005; Basking shark and Zooplankton, Sims et al., 2006). Although very informative, such an approach does not necessarily account for other simultaneous and potentially important interactions in the ecosystem.

In highly seasonal environments, peaks of prey availability may occur periodically over space and in time, and, if coupled, predator movements should respond to such variation (Deacy et al., 2016). For some predators and scavengers, humans create predictable peaks of prey density by providing food subsidies (Oro et al., 2013). These subsidies arise from supplementary feeding, agriculture, hunting and dumping of offal or indirectly through livestock husbandry that provides relatively easily accessible prey in high concentrations (Rodewald et al., 2011). Human-generated food subsidies can be attractive food sources that vary in space and time and that can ultimately affect predator movement behaviour, and even survival and reproduction (Leroux & Loreau, 2008; Rodewald et al., 2011). For generalist predators and scavengers, such peaks in human-generated food subsidies may define their seasonal and year-round movement behaviour and possibly even their population dynamics (López-López et al., 2014; Selva et al., 2014).

Generalist predators and scavengers that range over large areas are appropriate for testing the migratory coupling hypothesis (Furey et al., 2018). This hypothesis predicts that migration of prey attracts large-scale movements of predators and that this coupling has ecosystem-level consequences. The migratory coupling hypothesis also predicts the coupling potential to be highest in systems with low but variable productivity, occurrence and aggregation of migratory prey populations, and in presence of highly mobile predators.

The boreal forest landscape of Fennoscandia supports predatory Golden Eagles (*Aquila chrysaetos*) that are strongly associated with seasonally migrating ungulates including moose (*Alces alces*) and semi-domestic reindeer (*Rangifer tarandus*) (Moss et al., 2014; Sandström, 2015; Singh et al., 2012). Golden Eagles are both a predator and a scavenger in the Fennoscandian boreal ecosystem and may hold territories as well as undertake seasonal long-distance movements (Singh et al., 2016, 2017; Tjernberg, 1981). Juvenile and subadult birds are often observed to migrate south late September or October and return to the north in spring (Singh et al., 2017). Diet of eagles indicates that they rely on seasonally abundant prey; grouse species and mountain hare are dominant components of their diet in the breeding season (Melin, 2020; Tjernberg, 1981), while human-generated food subsidies may be important at other times. In Fennoscandia, the pattern of human activity and land use generates two major peaks of prey density and foraging opportunity, both of which could potentially be influential for Golden Eagles. The first peak occurs when thousands of migratory semi-domesticated reindeer aggregate to give birth in their seasonal calving areas. This provides eagles opportunities to hunt and scavenge on newborn calves and afterbirths. The second peak is through the availability of offal from hunting moose during autumn (Singh et al., 2014). This hunting-generated resource pulse is unnatural and increases lead exposure of eagles when ammunition fragments are accidentally ingested from offal, which may result in poisoning that alters their movement rate and flight altitude (Ecke et al., 2017).

Here, we test three predictions (P) stemming from the migratory coupling hypothesis.

P1: Movements of Golden Eagles match regional spatial and temporal variation of ungulate prey density peaks over their annual movement cycle. Given the spatial and temporal nature of availability of moose offal, reindeer prey and known large-scale mobility of Golden Eagles, we expect seasonal herding of reindeer to calving aggregations and hunting of moose to translate into food subsidies.

P2: We expect eagles to select for reindeer calving areas during the calving season and to select for areas with higher moose harvest density during the hunting season.

P3: As a consequence of this coupling with moose hunting areas and season, and in line with Ecke et al. (2017), we expect reduced survivorship in eagles as a consequence of lead poisoning.

2 | MATERIALS AND METHODS

2.1 | Study area

We studied the movements of the Golden Eagle in Fennoscandia (Figure 1). Golden Eagles are protected in Sweden, as well as in the European Union, under the EU Bird and Habitat Directives (European Commission, 1979, 1992). The northern Swedish landscape is dominated by coniferous forests in the lowlands, while in the mountains coniferous forest gradually changes to birch forest and open habitats with heaths, meadows, fens and snow beds. Local elevation ranges from sea level to 1,590 m and snow depths in winter can reach 120 cm (Raab & Vedin, 1995).

2.2 | Golden eagle data

During 2010–11 and 2014–15, we equipped 74 Golden Eagles in the northernmost Swedish counties of Västernorrland, Jämtland,

Västerbotten and Norrbotten with backpack-type global positioning system (GPS)–GSM (Groupe Spécial Mobile) telemetry units from three different manufacturers (Vectronic GmbH 135 g, Microwave Inc., and Cellular Tracking Technologies Inc. 70 g) (Figure 1). We included in this study individuals which had moved over area >100 Km² (i.e. an area greater than their home range size, Singh et al., 2017), and which had daily continuous data from March to November in at least 1 year. These individuals have been tracked and the data archived in the Wireless Remote Animal Monitoring database infrastructure (Dettki et al., 2013). Adult eagles (>5 years, identified based on plumage) were trapped with bow-nets during autumn (Bloom et al., 2015); and juveniles (here includes individuals from 0–5 years) were tagged in the nest during ringing events following their birth (Sandgren et al., 2014). We considered a minimum of six GPS positions per day per eagle for our analyses for March to November months. Doing this, we had a consistent fix frequency across all transmitters, sufficient to understand landscape scale and seasonal movement patterns (Singh et al., 2016). The number of eagle-years included in the analyses varied among analyses, depending upon the relevance and the adequacy of data for the time periods of analyses appropriate for each research question (see Appendix S1, Figure S1).

Permissions to trap and tag eagles were obtained from the Swedish Ethical Committee on Animal Research in Umeå

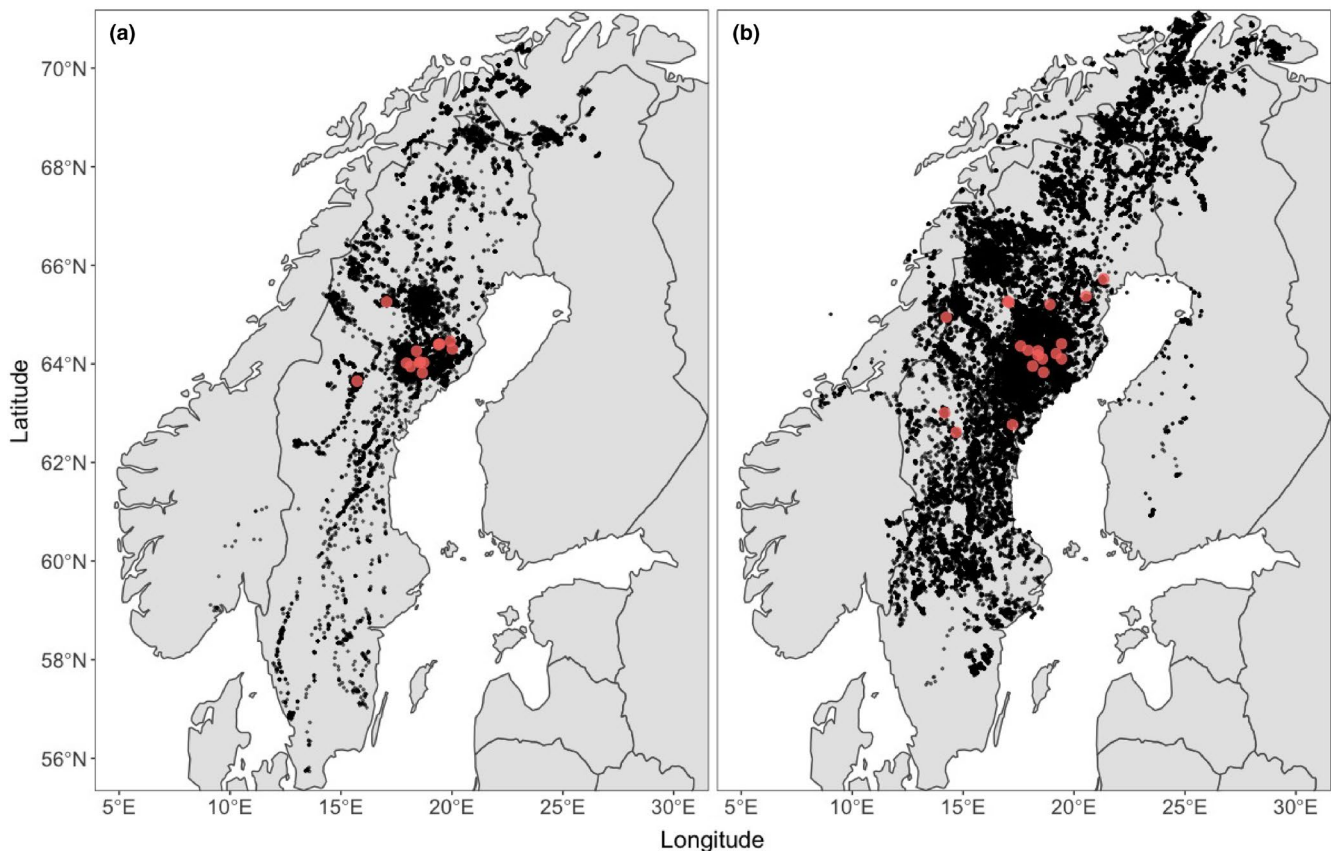


FIGURE 1 Study area and extent of annual range of (a) adult and (b) juvenile tagged Golden Eagles included in the study. Black dots represent locations of 32 GPS tracked Golden Eagles (125 eagle-years) tagged in northern Sweden. Movements during the months from March to November are presented. Red dots represent the capture locations

(Dnr A57-10, A58-10, A40-14 and A42-14) and the Swedish Environmental Protection Agency, Stockholm (Dnr 412-2994-10 and NV-04092-14).

2.3 | Reindeer calving distribution and timing

In Sweden, the Reindeer Husbandry Act (1971:437) gives the indigenous Sami people exclusive grazing rights in the northern 55% of Sweden, an area which constitutes the majority of the land within the boreal and alpine biomes (Sandström et al., 2003, 2016). This region is geographically divided into 51 reindeer herding communities, and each is managed independently. Within each reindeer herding community, the reindeer undertake yearly seasonal long-distance migrations between summer ranges in the west and winter ranges to the east. The maximum number of reindeer is fixed by the state, totalling at about 250,000 before calving. Based on their traditional knowledge, reindeer herders delineate calving areas, important summer and winter ranges as well as the timing of main life cycle events for each reindeer herding community in a participatory Geographic Information System platform (Renbruksplan, Sandström, 2015; Sandström et al., 2003). This Renbruksplan platform is further supported by data from several thousand reindeer equipped with GPS collars. We used this information from Renbruksplan to identify reindeer calving areas for all 51 reindeer herding communities (Figure 2).

Reindeer calving occurs between 01 May and 20 June, when thousands of female reindeer aggregate to give birth. Golden Eagles are regarded as predators and scavengers on reindeer calves and calving remains, and herders receive partial compensation for eagle predation on reindeer in Sweden (Source: The Sami Parliament; <https://www.sametinget.se/rovdjur>). There is an ongoing dispute about, whether this compensation is sufficient, on the total amount of calves lost to eagle predation, and on the proportion of the golden eagle population that visits the calving areas.

2.4 | Moose harvest data

Moose are distributed over all of mainland Sweden (Allen et al., 2016). Sweden is divided into moose management areas (MMA) in which multiple hunting teams lease and use hunting areas (Ericsson & Wallin, 1999). The moose hunt begins on the first Monday of September and most quotas are filled during the first 6–8 weeks, that is in September and October. In Sweden, annually, about 80,000–90,000 moose are shot during the hunting season (Singh et al., 2014). Hunting data are publicly available (<https://rapport.viltdata.se/statistik/>), and from these, we extracted and mapped information on number of moose taken in each MMA. We then estimated an MMA-specific average number of harvested moose per 1,000 ha (between 2012 and 2016). We used these numbers on a raster grid of 1 × 1 Km pixel size, as an index of potential offal availability over space during the hunting period at the eagle position.

This index turns to zero outside the hunting season. Note that the annual figure of harvest does not change dramatically over time as the harvest quotas are set so as to keep a stable huntable moose population (Singh et al., 2014).

Both the reindeer presence/absence and moose harvest data were used as prey distribution and availability index for subsequent data analysis. No reliable density estimates were available for reindeer.

2.5 | Blood samples

Blood lead concentrations link demographic consequences to the coupling of eagles' movement with moose hunting season. This is because eagles are exposed to lead primarily through consumption of offal from the hunted moose. As such, we considered in this study blood lead concentrations from 46 eagles captured during the moose hunting season (in 2014 and 2015) and followed them to the next spring (data from Ecke et al., 2017, Table S1 and Figures S2 and S5).

2.6 | Data analyses

We first tested the general probability of being migratory (undertaking long-distance movements) as a function of age (adults and juveniles). We evaluated the probability of being migratory by interpreting maximum net squared displacement (NSD—Km²) at an annual scale (Singh et al., 2012). To do this, we used a binomial generalized mixed-effects model with yearly migratory status, classifying NSD > 100 Km² as migratory and < 100 Km² as non-migratory, as the response variable, and age class as the predictor (Figure S3). We included individual eagle ID as a random effect due to repeated observations for each individual.

To test whether Golden Eagles associated themselves with the locations of ungulate prey subsidies over their annual movement cycle (P1 and P2), we estimated spatial and temporal synchrony of adult and juvenile eagles relative to reindeer calving and moose hunting.

To investigate spatial and temporal synchrony between eagles and reindeer, we first classified the eagle locations into four categories. Eagles could occur within or outside of calving areas (spatial synchrony) and they could occur during or outside the calving period (temporal synchrony). We used a binomial generalized linear mixed-effects model with the location of the eagles relative to the calving areas (within/outside) as the response variable and calving period (during/outside) along with eagle age class (adult/juveniles) as predictors (Bolker et al., 2009). Because we had multiple observations on each day, and we had multiple years of data for several individual eagles, we included the observation day and individual identity as random effects. We tested for improvement of model fit by incorporating a first-order autocorrelation structure, but these more complex models did not converge to a solution.

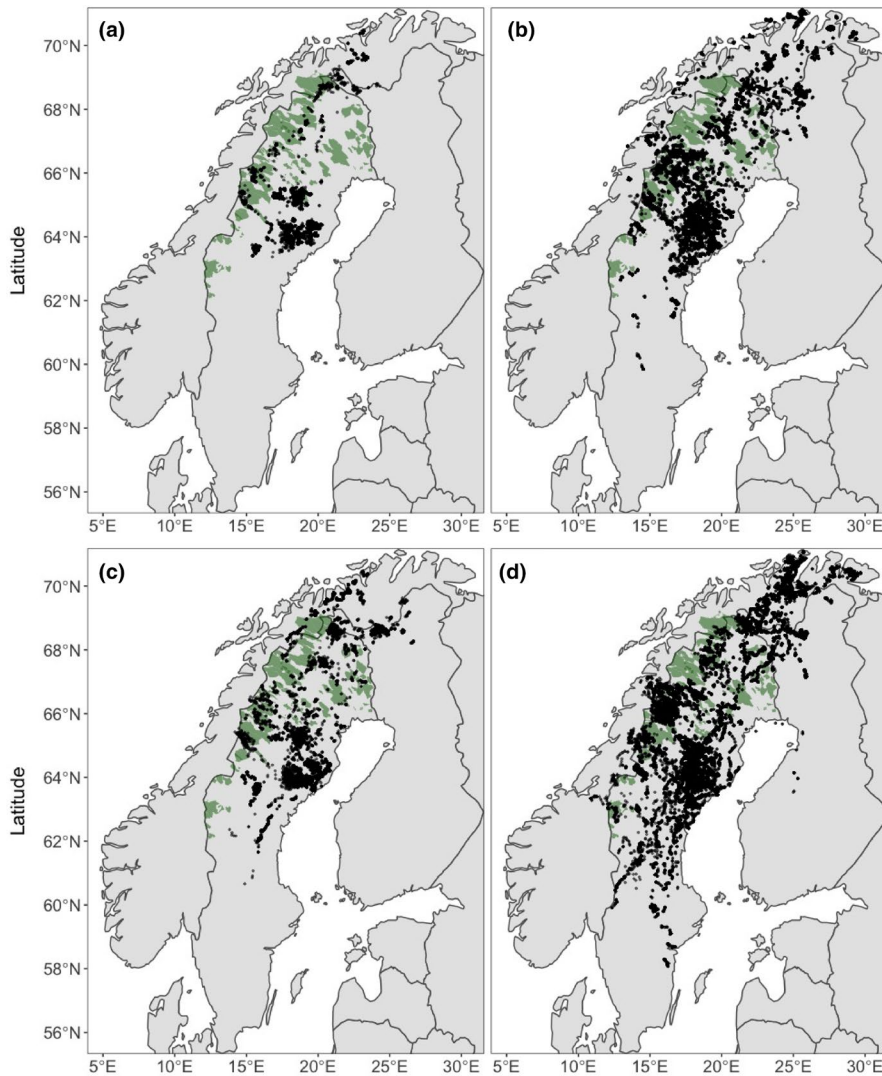


FIGURE 2 Maps of the study region, showing the Swedish reindeer calving grounds in green and movements of adult (a & c) and juvenile (b & d) Golden Eagles ($N = 32$), during the calving period (a & b, May–June) and outside the calving period (c & d, July–October)

To investigate spatial and temporal synchrony between eagles and moose hunt, we first extracted the values of moose harvest density (harvest/1,000 ha) observed at the 1 Km grids in which each of the eagle locations occurred. Since the moose harvest variable is a count, the aim here was to determine whether the eagles were attracted to high moose harvest density areas especially during the hunting season. The moose harvest value becomes zero outside the hunting season, we therefore classified the eagle locations into those occurring during (months of September–October) and outside the hunting season (other months). In this way, we created a binary variable—eagle presence during the hunting season (during/outside) that is similar to the temporal parameter for the reindeer models. To analyse these data, we again used a generalized linear mixed-effects model (family—Gaussian, Bolker et al., 2009) with moose harvest density as the response variable and eagle presence during the hunting (during/outside) season along with eagle age class (adult/juveniles) as predictors. We again included the observation day (day of the year) and eagle ID as random effects to account for repeated observations.

Finally, we tested if the spatial and temporal synchrony of eagles with the moose hunt had consequences for eagle demography (P3).

For this, we evaluated potential change in their blood lead concentration during the hunting season (Ecke et al., 2017; and Figure S3), and the subsequent survival probability of eagles after feeding on moose offal until the next spring. For this analysis, we used a dataset of 46 eagles sampled during the moose hunting season from Ecke et al. (2017). We also included data on the status of each individual eagle, recorded as “alive,” “dead” or “unknown” (see SI for identity and blood lead values for each individual, Figure S2). Out of these 46 samples, two were excluded from the survival analyses due to transmitter failure after installation. Of the 46 eagles with lead measurements, 13 individuals were also used in our analyses for P1 and P2.

We used proportional hazards regression to model the incidence of exposure, that is the number of individuals per population at-risk per unit time (Andersen & Gill, 1982; Cox, 1972). We tested the effect of blood lead concentration on survival probability using “Survival” package in R (Therneu & Lumley, 2015). We used “probability of death” as the response variable represented by a combination of the status of the event (0: survival or 1: death) and end time (calculated as difference between the last known date in spring following lead value estimation, and the capture date) and

lead concentration in the blood during capture, as the predictor (Kay, 1977). All individuals with “unknown” fate were assigned a zero and considered alive. Out of the 46 individuals in the study of Ecke et al. (2017) the study, 11 were dead, 12 were alive, and 23 were unknown in our dataset (Figures S4 and S5). We created models using blood lead concentrations both as a categorical (<25 ppb and >25 ppb; 25 ppb suggested sublethal lead concentration threshold) and as a continuous variable (Ecke et al., 2017). A positive effect would indicate increased risk of mortality with blood lead concentration, and a high hazard ratio estimated as the exponent of the coefficient, would indicate a high risk of mortality related to lead concentration. All analyses were conducted in R statistical software (version 3.2.0) (R Core Team, 2015).

3 | RESULTS

Of the 74 birds we considered, only 32 met our standards for inclusion in this study (SI Table S1); these included 13 adults and 19 juveniles. We tracked eagles for, on average, 288 data-days per eagle-year, across 125 eagle-years.

Adult and juvenile Golden Eagles ranged over vast areas covering large parts of Fennoscandia during their annual cycles (Figure 1). Eagles ranged over $532 \pm 446 \text{ Km}^2$ ($\bar{x} \pm SD$) annually, with maximum displacement between seasonal ranges as small as 212 Km^2 and as large as $3,261 \text{ Km}^2$ (Figure S3). Juvenile eagles had a higher probability of migration than did adults (1.46 ± 0.49 ($\bar{x} \pm SE$), z statistic = 2.95, $p < .01$, $n = 125$, Table 1). The odds of juvenile eagles being migratory were 4.34 times higher than adults (CI: 1.63–11.5). The variation among individuals explained about 21% of the variation in the model.

The timing of the reindeer migration and calving in these areas occurred between 1 May and 20 June (days of year 121–171, Figure 3). Data from the participatory GIS suggest that after the calving period, the reindeer usually move further west and stay in

the mountains the entire summer. At the end of the summer, they are herded or transported to winter ranges about 200–300 Km to the east, close to the coast of the Bothnian Bay.

The harvest statistics show that a higher number of moose were hunted in the eastern coastal MMAs (3–5 Moose/1,000 ha) compared to the west where the reindeer calving areas are located (0–2 Moose/1,000 ha, Figure 4).

3.1 | Migratory coupling

Eagles appeared in calving areas on average around 02 June (day of the year: 153 ± 18 days) and the arrival dates of individuals ranged from 15 May to 20 June (Figure 3). Eagles had a significantly higher probability of occurrence inside calving areas during the reindeer calving period than during other times (estimate \pm S.E.: 0.95 ± 0.10 , z statistic = 9.40, $p < .01$, $df = 766,130$, Table 2—odds ratio = 2.60, CI = 2.13–3.17). Moreover, juveniles were 3.39 times more likely to match their movements to reindeer calving than were adults (juveniles—estimate \pm S.E.: 1.22 ± 0.14 , $z = 8.4$, $p < .01$, Table 2—odds ratio = 3.39 [CI: 2.55–4.5]).

In autumn during the moose hunting period, the distribution of eagles was spatially synchronized to areas with higher moose harvest density (Table 3) within the hunting period (moose harvest density—estimate \pm S.E.: 0.21 ± 0.02 , t statistic = 10.04, $p < .01$, $df = 652,476$). Adults were more likely to occur in areas of higher moose harvest density than were juveniles (Table 3; juveniles—estimate \pm S.E.: -0.47 ± 0.2 , t statistic = -2.31 , $p < .01$).

3.2 | Demographic consequences

As a consequence of this synchrony between eagle movements and moose hunt (P3), the probability of mortality significantly increased with lead concentration, regardless of whether we

TABLE 1 Summary of binomial generalized linear mixed-effects model showing the differences in the probability of migration, that is to undertake long-distance movements (>100 Km², see also Table S1), between age classes

Predictors	Migratory		Test statistic	p
	Odds ratio	C.I.		
Intercept	1.63	0.89–2.99	1.58	.114
Age class (Juveniles)	4.34	1.63–11.50	2.95	.003
Random effects				
Variance	3.29			
Eagle ID	0.21			
N (eagles)	32			
Observations	125			
Marginal R ²	0.13			
Conditional R ²	0.19			

Note: Response variable is the maximum annual net squared displacement. “Adult” age class is the reference. Model AIC = 134.8.

Timing of entry and exit of calving areas

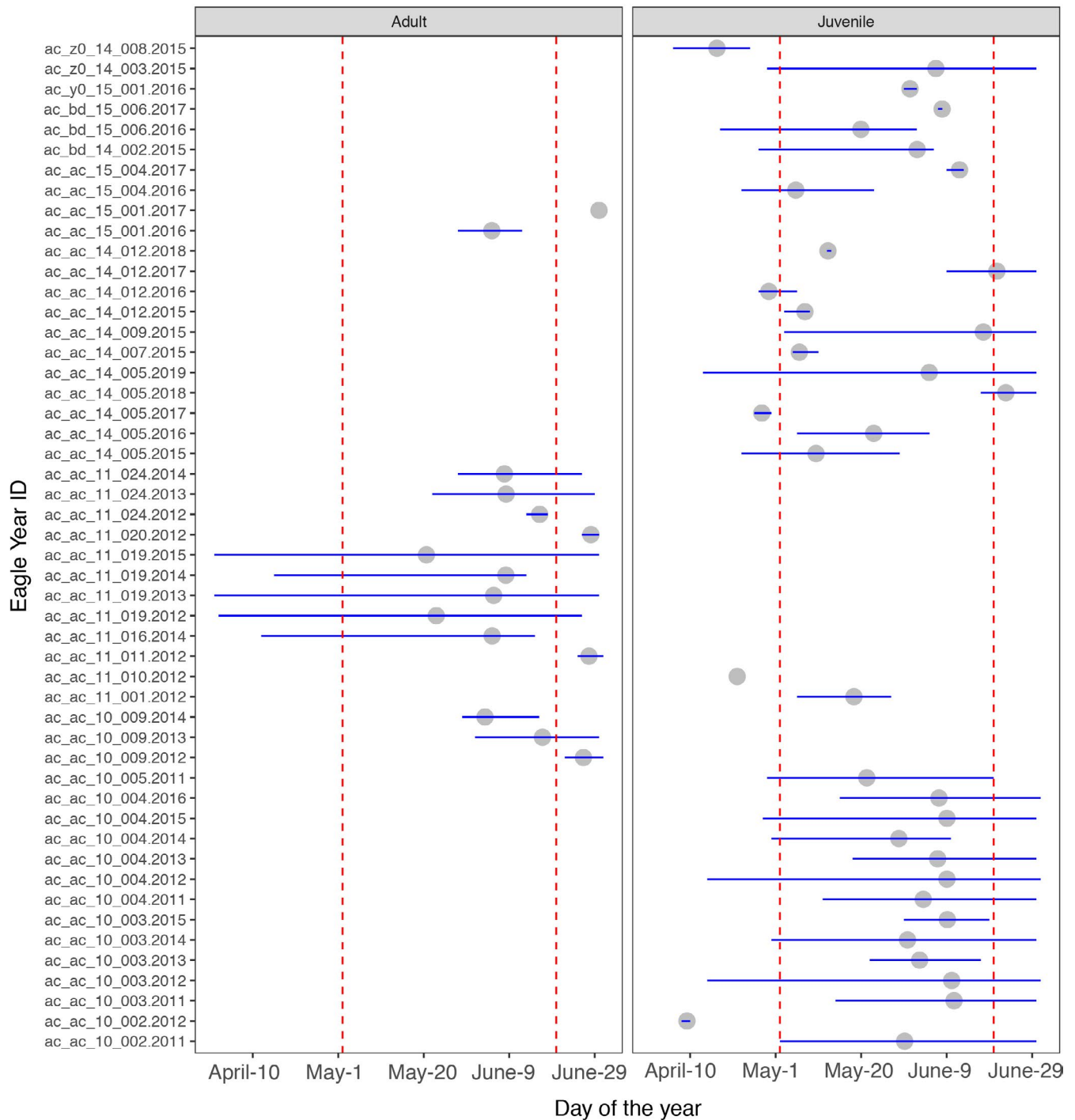


FIGURE 3 The date of the first and last known position of individual adult and juvenile Golden Eagles ($N = 23$) in different years, in the reindeer calving areas in Sweden. Dates of the first and last position are shown through the day of the year and are represented as the edges of the segments. Grey dots representing the mean date of presence within the calving areas taken as average from all positions within calving areas per individual eagle-year. Vertical red lines show the average start and the end of the calving period, respectively

considered lead concentrations as a categorical or a continuous variable (Table 4). When used as a categorical variable, the risk of death increased by 4.2-fold (hazard ratio) when lead concentrations were >25 ppb (estimated as %: $1 - \exp(\text{coef}) * 100$, Est \pm S.E.:

1.43 ± 0.62 , $\exp(\text{coef}) = 4.21$, $z = 2.31$, Table 4). When blood lead concentration was used as a continuous variable, the risk of death increased 3.4-fold with each unit increase in blood lead concentration (Table 4).

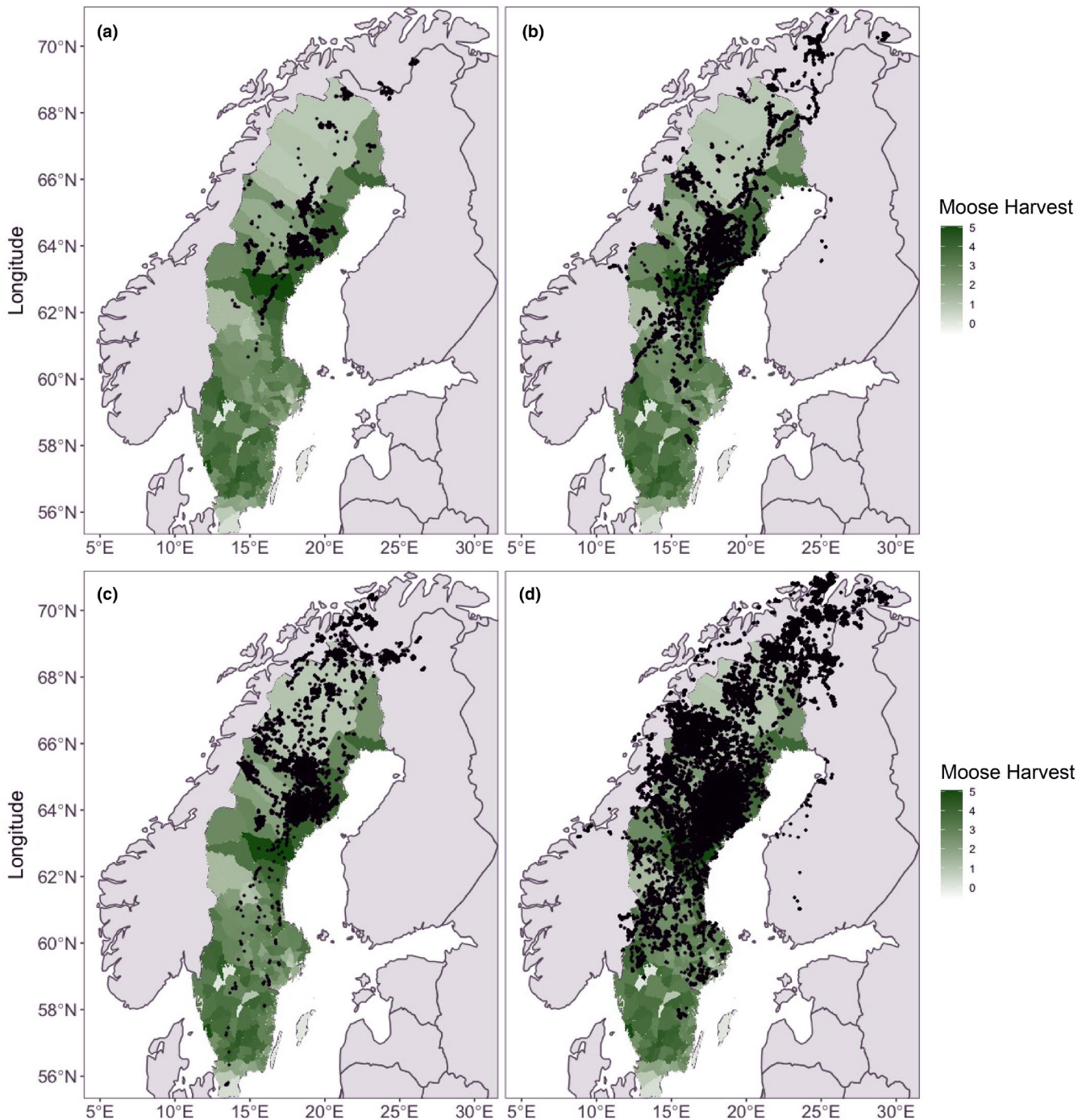


FIGURE 4 Maps of the study region showing the Moose Harvest gradient (moose shot/1,000 ha) in Sweden, represented as shades of green, and movement tracks (black dots) of adult (a & c) and juvenile (b & d) Golden Eagles ($N = 32$) during the main moose hunting period (a & b, September–October) and outside this period (c & d, March–August)

4 | DISCUSSION

Consistent with the migratory coupling hypothesis, Golden Eagles matched peaks of subsidies provided by migratory ungulate prey over their annual movement cycle. Eagles moved as the availability of these resources changed in the landscape. However, the synchrony with moose hunting season and high harvest density areas exposed the eagles to higher risk of mortality from lead poisoning.

As apex predators and scavengers, eagles can benefit from resource pulses from a wide variety of potential prey. However, capitalizing on resources distributed across a large landscape scale requires eagles to be in the right place at the right time. Behavioural patterns of predators typically develop in response to natural patterns of animal migration (e.g. caribou in Alaska, Furey et al., 2018; Hebblewhite & Merrill, 2007; White et al., 2014). Here, we demonstrate that behavioural patterns can also develop in response to the

Predictors	Inside calving area		Test statistic	p
	Odds ratio	C.I.		
Intercept	0.00	0.00–0.00	–59.83	<.001
Calving or not (Inside calving period)	2.6	2.13–3.17	9.41	<.001
Age class (Juveniles)	3.39	2.55–4.50	8.41	<.001
Random effects				
Variance	3.29			
Day of the year	14.83			
Eagle ID	10.34			
N (eagles)	32			
N (days)	3,077			
Observations	766,135			
Marginal R ²	0.01			
Conditional R ²	0.88			

TABLE 2 Summary of binomial generalized linear mixed-effects model showing the spatial and temporal synchrony of eagles with reindeer calving during the calving period

Note: Odds ratios are presented alongside their 95% CI. Response variable is individual eagle presence “inside” and “outside” calving area. Adult group is used as reference for age class. Individual eagle ID and observation day are random effects.

TABLE 3 Summary of the generalized linear mixed-effects model showing the spatial and temporal synchrony of eagles with moose hunt

Predictors	Moose harvest density		Test statistic	p
	Estimate ± S.E.	C.I.		
Intercept	0.53 ± 0.16	0.22–0.83	3.38	.001
Moose hunt or not (Inside hunting period)	0.21 ± 0.02	0.17–0.26	10.04	<.001
Age class (Juveniles)	–0.47 ± 0.20	–0.86 – –0.07	–2.32	.021
Random effects				
Variance	3.4			
Day of the year	24.1			
Eagle ID	31.2			
N (eagles)	32			
N (days)	3,071			
Observations	652,476			
Marginal R ²	0.03			
Conditional R ²	0.63			

Note: Response variable is moose harvest density (Moose shot/1,000 ha) at eagle position. Adult group is used as reference for age class. Individual eagle ID and observation day are random effects.

Abbreviation: C.I., 95% confidence interval.

density peaks generated by human land use and wildlife management practices.

This coupling between Golden Eagles, reindeer calving and moose hunting highlights important elements of human–wildlife conflicts and conservation. Potential risk of predation by eagles on semi-domestic reindeer calves raises concerns from the indigenous reindeer herding community about the actual losses and low compensation received (Nybakk et al., 1999). There are disagreements

between management's understanding of the impacts of eagle predation on reindeer and impacts claimed by the reindeer herding community based on their direct field observations. Information about the migratory coupling of visiting eagles can add essential knowledge to this issue. Locally, it is believed that eagles consuming calves are residents that merely converge in the calving areas. Our study suggests that some of these eagles are instead migratory. For management, an important question then becomes from where and

TABLE 4 Cox proportional hazard model for mortality of Golden Eagles ($N = 46$) in relation to blood lead concentrations (ppb)

	Estimate \pm S.E	Z	exp (Coef)	p-value
Lead concentration as categorical variable				
High lead concentration (>25 ppb)	1.43 \pm 0.62	2.31	4.21	.02
Lead concentration as continuous variable				
Lead concentration	1.23 \pm 0.52	2.35	3.42	.019

Note: The coefficients show the probability of mortality. For the first model, lead concentration is categorical; reference group is lead concentrations <25 ppb. The second model shows lead concentrations as a continuous explanatory variable; the values range between 0.46 and 600 ppb. Z–Wald statistic, exp(Coef) is the hazard ratio.

from how far away do the eagles aggregate. Resolving these questions will allow the development of a more accurate understanding of this human–wildlife conflict. On the other hand, the observed lead poisoning of eagles from consumption of moose offal contaminated with lead ammunition used for hunting is a direct threat to individual health (see also Ecke et al., 2017). Ecke et al. (2017) suggested that the sublethal threshold of lead poisoning can be as low as 25 ppb in comparison with the previous considerations of 200 ppb (Franson & Pain, 2011). Here, we show that the risk of death can be large even at these low background concentrations (which are eight times lower than previous considerations).

Coupling of eagle movements with reindeer calving and moose harvest may also have demographic consequences. For example, when calf losses to eagles become too high, reindeer herding communities may apply to the authorities for protective hunting. Likewise, lead exposure can result in lethal or sublethal effects with demographic consequences (Golden et al., 2016; Herring et al., 2020; Newton, 2021). There is irony in the fact that these demographic consequences likely stem from an evolved behavioural response by eagles to increased food availability (Cooper and Blumstein, 2015). As such, the reindeer calving and moose hunting we considered may be an “ecological trap” for these birds. The data we present here do not speak of demographic effects but they do suggest that this problem deserves additional study of the interface between ecological and human dimensions (Hale & Swearer, 2016; Robertson & Hutto, 2006; Schlaepfer et al., 2002).

We observed significant differences in behavioural responses for different age classes of eagles (Table 1). From an eco-evolutionary perspective, this is important. Reindeer calving is an event which has occurred for several millennia and often in the same areas as used today. It is likely that eagles have grown accustomed to this response over a long time period. In contrast, the moose hunt on this large and temporally restricted scale is fairly recent (since the 1980s). There may be several reasons that young eagles seem to be better synchronized to reindeer calving and undertake long-distance movements to access this food subsidy than adults. For example, this behaviour could be the result of nomadic movements

in search of foraging opportunities or it could stem from following other non-territory holding birds. Indeed, it is well established that subadult Golden Eagles tend to move at larger scales than adults (Miller et al., 2019; Oppel et al., 2015). Eagles are long-lived, and recent availability of offal from moose hunt has allowed adults to learn during their lifetime. This makes adults better synchronized with this food subsidy from the moose hunt, compared with juveniles. As young birds mature and settle into territories over time, their annual displacement may therefore decline with age, leading them to switch their diets to other local sources of food.

A recent study using the summer data from the eagles in our analysis shows that the strength of selection of linear infrastructure (roads and railroads) by juvenile eagles increased with age towards maturity (Etienne, 2020). This is an important aspect of life history, as young birds adapt and respond to predictable food sources with age. This would be visible in fine-scale investigations into fidelity to different potential sources of food during their life cycle. Eagles and vultures are already known to repeatedly visit feeding sites in Fennoscandia and elsewhere (<http://eagle72.se/>; Moreno-Opo et al., 2010).

We have only considered two main sources of prey in this study. However, there are potentially many other alternative prey species in the landscape as well as other food subsidies generated by humans. Other natural prey of eagles include migratory birds that pass through Sweden during their northward journeys in spring, such as cranes, swans, geese, other resident species such as grouse, mountain hare, voles, lemmings, and foxes (Larsson, 2020; Tjernberg, 1981). The distributions and densities of these prey along with other factors such as climate, weather patterns, human disturbance, and landscape infrastructure may also affect eagle behaviour in space and time. Moreover, there are other environmental drivers of species distribution and movements such as snow, photoperiod, and changes in greenness across the landscape. All of these are likely to influence eagle movements in concert with the migratory coupling that we have demonstrated here.

Whether the scavengers are avian, as in our study, or they are mammalian, humans almost universally protect their livestock and use lead ammunition to hunt. In fact, there is abundant evidence that when predators scavenge livestock or forage on hunter-provided offal, there are negative consequences to those predators (Cortés-Avizanda et al., 2010; Ecke et al., 2017). What is less clear, though, is whether predators and scavengers on other continents have developed similar behavioural responses to human-provided subsidies as we demonstrate here. Widespread existence of such responses would be indicative of greater connectivity of human actions, migratory coupling and ecosystem function than has been previously recognized.

5 | CONCLUSIONS

The implications of our results extend to other predators and scavengers in the boreal ecosystem and elsewhere. If the movement

behaviour and apparent survival of eagles are affected by food subsidies, then it is likely that other species such as brown bear (*Ursus arctos*) and fox (*Vulpes vulpes*) that also respond to these subsidies may also be similarly affected. The differences in the movement and ecology of space use, where being migratory, territorial or opportunistic may lead to differences in patterns of coupling, and reliance on food subsidies that have consequences for these species' demography (Lamb et al., 2017). Supplementary feeding of wildlife is a common practice across continents and has been shown to affect multiple aspects of species' biology including their behaviour (Oro et al., 2013; Pain et al., 2009). Such feeding places may also bring about unlikely interactions among species which may otherwise not overlap in nature. This suggests the potential relevance of studying multiple species interactions in landscapes that are dominated by humans. Such studies may reveal new and unexpected interactions with wide-ranging impacts on ecosystem structure and function.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data on eagle use of the reindeer and moose hunting areas are available as a supplementary file downloadable from <https://doi.org/10.5061/dryad.rbnzs7hbp>. Shapefile of reindeer calving areas is accessible at <https://ext-geodatakatalog.lansstyrelsen.se/GeodataKatalogen/> and moose harvest data are accessible at <https://rapport.viltdata.se/statistik/>.

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BIOSKETCH

Navinder J. Singh (<https://www.slu.se/cv/navinder-j-singh/>) is interested in the causes and consequences of animal movements and their implications on conservation and management of animal populations and their ecosystems. The author group is interested in studying the consequences of human modifications of ecosystems on biodiversity distribution and dynamics and developing innovations for conservation.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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