

Faculty of Forest Science

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-Synchronous movements in a boreal ecosystem

Rörelseekologi hos kungsörn och ren i ett borealt ekosystem

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Abstract

The golden eagle Aquila chrysaetos in Sweden are believed to be rather sedentary. Hence, studies in Norway suggest the opposite with a diurnal pattern with seasonal migrations to e.g. south Sweden during the winter – distances of thousands of kilometers. Almost 90 percent of the eagles in Sweden are distributed in the northern parts and occur only in scattered patches in the southern parts of the country. Still, there are reports of eagles visiting feeding ground in these parts of the country during the winter although their origin so far has been unknown. In these boreal ecosystems there are reports that the semi-domesticated reindeer Rangifer tarandus L. constitutes the main prey base for native large carnivores. Here, studies on nesting eagle's food preferences have reviled it to be an important scavenger on reindeer although its extent to prev is concealed. Still, interactions between the species effect ecosystem functions and thus, its resilience. Today, there are few studies on golden eagle movement behavior and there is no study in relation to the movement of the semidomesticated reindeer. On a landscape level, identification of such behaviors enables us to quantify the extent, duration and the timing of the movement dynamics. It gives us understanding to what level these movements are synchronized or not - movement behaviors depending on different life stages, e.g. age, environmental factors and food resources. In Northern Sweden, the ecosystem is characterized by high seasonality causing periods with limited access to food for both predators and prey causing population fluctuation and seasonal migrations. This seasonal movement behavior gives rise to large reindeer migrations twice a year: from the boreal forest in the winter (the winter feeding range) to the alpine tundra in the summer (calving- and summer feeding range). Due to eagles tracked with GPS --transmitters, I had the opportunity to test for spatio-temporal synchronization on the timing of the movement of golden eagle (n = 43) and reindeer migration during two consecutive years (2011) and 2012). My results suggests that both juvenile- and adult golden eagles migrate often over 1000 km. Further, a behavioral change points analyses suggested that individuals likely synchronized the timing of migration to those of the reindeer's in spring. Hence, the synchronism was less significant during the autumn indicating several factors participating. Hopefully, this study will help to increase our knowledge on movement patterns of golden eagles in Scandinavia, and also, rise questions for further studies of both eagles and reindeers and thereby develop the management of both species in the future.

Introduction

Movement is a primal reaction of an organism to its environment (Sugden and Pennisi 2006) and is essential for it to increase fitness. Analyzes of movement gives us understanding of where animals move, when they move and why they move. Ultimately, movement studies give us opportunities to explain animal behaviors and interactions (Nathan et al. 2008) which reshape ecosystems and affect their resilience (Lundberg and Moberg 2003). Identifying these movements enables us to analyze spatio-temporal behavior. Due to enhanced computing capacity and emergence of new tracking technologies, studies on animal's movement are increasing rapidly (Nathan et al. 2008). Here, Nathan et al. (2008) suggest considering movement at multiple scales. The smallest scale of movement is 'steps' which are displacement between successive steps (Time_i-Time_{i+x}). The intermediate scale is a set of steps (a phase) also called 'phases of movement' and refers to behaviors such as feeding, predating or escaping. The largest scale is the 'tracks of a life-time' which is a movement from birth to death and often includes both dispersal and migration. Further, animal movements can be classified into four main classes (Mueller and Fagan 2008): *i*) sedentary or home range behavior; *ii*) dispersal *iii*) migratory and *iv*) nomadic. However, the pattern of movement is sometimes less clear with a mixture of two or more behaviors. For example, the populations might be partly migratory, see for example Bunnefeld et al. (2011), depending on different life stages (e.g. age), sex and environmental factors, e.g. food, landscape characteristics, snow depth etc. (Singh et al. 2012).

In the northern hemisphere, where ecosystem are characterized by high seasonality, the food base for predators is often limited and may be available for short periods when migratory prey species arrive and other species fluctuate in abundance (Hörnfeldt 1978, Oksanen and Oksanen 1992). Changing food availability may force predators to respond to this variability in prey densities. Some predators may hence decide to synchronize their movement to their prey to maximize the benefits of short term subsidies and also synchronize their timing of breeding. These movements may take any form depending upon the movements of prey, ranging from unpredictable nomadic movements to seasonal migrations. Eberhardt and Hanson (1978) report long-distance nomadic movement patterns of arctic fox in Alaska (via ear tagging) driven by food shortage due to fluctuating lemming populations. Killer whale *Orcinus orca*, an apex predator, is also making seasonal movements in response to changes in prey abundances (Barrett-Lennard et al. 2011, Ford et al. 2013). There are numerous other such examples from across the globe. However, predator populations have suffered throughout the globe during the past two centuries (Estes et al. 2011).

In some countries of Europe, the conservation policy of large carnivores has shifted from lethal persecution towards landscape-level conservation (Bengtsson et al. 2003) resulting in an increase in their populations (Danell 2000, Pape and Löffler 2012). These increasing populations are now causing conflicts with local land-use practices (Heikkinen *et al.* 2011, Jonsson *et al.* 2012) – while also having cascading effects on other flora and fauna (Polis et al. 1997, Elmhagen et al. 2010, Schmitz et al. 2010, Killengreen et al. 2012, Ripple et al. 2014). In the northern boreal ecosystems, the semi-domesticated reindeer *Rangifer tarandus* L. (hereafter just 'reindeer') comprises the main prey base of many large carnivores (Bjärvall et al. 1990, Heikkinen et al. 2011, Karlsson 2011) such as brown bear (Persson et al. 2001), wolverine, lynx

(Andrén et al. 2011, Mattisson et al. 2013) and golden eagle *Aquila chrysaetos* (Nybakk et al. 1999, Thompson-Hobbs et al. 2012) with depredation rates on reindeer sometimes equaling the harvest (Andrén et al. 2011). This predation creates challenges for both reindeer production (Danell *et al.* 2009) as well as conservation practices of wildlife managers (Pape and Löffler 2012). Therefore, there is an urgent need for more in-depth knowledge about this socio-ecological system and how the predator-prey dynamics work.

The golden eagle is widely distributed in the northern hemisphere and scavenging by golden eagle on semi-domesticated reindeer is reported all over the Sami reindeer herding areas in Finland (Norberg et al. 2006), Norway (Nybakk et al. 1999), and Sweden (Hjernquist 2011). Previous studies suggest that the predation rate is high enough to require attention from wildlife management authorities. A successful management of this conflict requires understandings of both their distribution and movement (Bull et al., Mueller and Fagan 2008) of both species (Heikkinen et al. 2011, Hipkiss et al. 2013). As these movements are dynamic in space and time, it requires focus on the timings, durations and extents of movements and whether the golden eagles synchronize their landscape level movements, especially migration, to the movements of reindeer. Little is known about the movement of golden eagles in Scandinavia (Hipkiss et al. 2013), and especially little in reindeer herding areas. Reindeer husbandry is present over almost whole northern Scandinavia (CAB 2014). In Sweden, reindeer herding is an exclusive right for Sami people where approximately 900 of the Samis are managers of a reindeer herding company (Jordbruksverket 2003, SOU 2006). Today's extensive reindeer husbandry - with large herds of semi-domesticated reindeers – is about 300-400 years old (Lundmark 2006, Moen 2006). Within every reindeer herding area, the herders use different pastures depending on the reindeer's need (Horstkotte et al. 2011, Inga and Danell 2012). In spring, the majority of the calving areas are in the alpine region whereas the reindeer's winter-feeding ground is mainly inland and sometimes almost at the coast (Lundmark 2006, Skarin et al. 2008). This seasonal movement behavior gives rise to large reindeer migrations twice a year: from the boreal forest in the winter (the winter feeding range) to the alpine tundra in the summer (calving- and summer feeding range).

Only a few quantitative studies have investigated the movement patterns of golden eagle and none in relation to the movement of reindeer (Kochert and Steenhof 2002, Bunnefeld et al. 2011, Sandgren et al. 2013). In North America, golden eagles in the south generally migrate less than eagles from the north (approximately from 60°N and above). These migrating individuals shows a diurnal (spring- and autumn) migratory behavior (Kochert and Steenhof 2002) sometimes reaching over long distances e.g. from interior Alaska to North-Central Mexico (McIntyre et al. 2008). McIntyre (2008) studied juvenile golden eagles and identified a diurnal migration pattern. Their autumn migration started in mid-September or beginning of October flying eastwards or to the southeast with duration of the migration reaching over 31-86 days. Their movement was more intensive in the beginning (>50 % of the individuals) than it was at the end of the migration period. The cumulative tracking distance of the autumn migration varied between c. 800 – 4800 km (75-c. 700 km in direct distance). Here, they did not discover any differences in timing or distance between cohorts or sexes. Furthermore, most birds stopped more than once (1-7 times) during the migration with a mean stopover duration time of 2-19 days; stop that lasted longer for those with multiple stops. No correlation was found between distance and duration of the spring migration. Their spring migration started in late March and mid-April heading to the northwest – a migration that lasted between 32-51 days – (shorter duration of movement than during the autumn migration). The cumulative distance varied between c. 2000-4500 km (87-c. 650 km in direct distance). Mean duration for the stopovers during the spring migration varied between 3-6 days; a shorter stopover duration than during the autumn migration, and also, with a smaller amount of stops (84 % made only 1-2 stops). Over all, they found an increase in their rate of movement early in the period of the autumn migration.

In Scandinavia, movement studies from Finnmark in northernmost Norway (Systad et al. 2007, Jacobsen et al. 2011) suggest a similar diurnal pattern with seasonal movements during the winter. Here, it was primarily young eagles that moved where some moved to the west (the Lofoten area) or to the east (Russia) although the majority moved to the south (Finland and Sweden). The movement to the south generally took place in October and varied between 400-900 km in distance from the place of birth, hence, males moved a longer distance and later (females: 13 October; males: 22 October). The movement back to their natal range occurred around March. During their first year, half of the individuals (11 of 22) moved >10 km from the nest with mean date the 11th of September, a dispersal (*i.e.* date of independence) sometimes reaching over 200 km in distance (Systad et al. 2007). However, a permanent movement out of their natal area occurred between September 7 to January 8; mean date October 18. In Sweden, the golden eagle is believed to be less migratory (Hjernquist 2011, Hipkiss et al. 2013) although individuals have been observed during winter on feeding grounds in southern parts of the country (Hjernquist 2011).

Status of Golden Eagles

In the end of the 1800s and the beginning of the 1900s, the golden eagle was almost extinct from Sweden due to direct persecution. The species was totally protected in 1924 in Sweden. Today, the population has slowly increased to c. 500 pairs (Hjernquist 2011) and almost 90 percent of the eagles are distributed in the north and occur only in scattered patches in the southern parts of the country (Tjernberg 2006). In the Arctic- and mountainous regions of Europe, the Golden Eagle favor habitats with thin forest stands and it nests at cliffs or in old trees. It is a day active hunter with a relatively large body-size, it seems to prefer rural- and undisturbed landscapes through open- and hilly terrain (Watson 2010), e.g. clear-cuts in Swedish forests, but see Sandgren et al. (2013). In Scandinavia, it primarily preys on birds, *i.e.* Ptarmigan species (Lagopus spp.) and small mammals as mountain hares Lepus timidus (Nyström et al. 2006, Jacobsen et al. 2011, Moss et al. 2012). In winter, it prefer to prey on carcasses of larger ungulates and domesticated sheep Ovis aries, goats Capra aegagrus hircus, cattle Bos primigenius (Watson 2010) and reindeer (Jacobsen et al. 2011). In northern Sweden in the eighties, Tjernberg (1981) did a study on nesting eagles prey preferences. He found remnants from reindeer fawns in 65 % of the nests (17 % of the total biomass), a significant contribution to the total amount of reindeer in the prey. Later, Nyström et al. (2006) made a diet-study in the alpine region of Sarek-Padjelanta. They found that reindeer contributed to 11.4 % of the prey species, a finding also supported by Johnsen et al. (2007) in Finnmark, Norway. Here, they found reindeer remains in almost half of the nests with golden eagles making up 8.5 % of all prey items. Thus, there are studies trying to quantify the predation by eagles

on reindeer. Between 1995 and 1996, Nybakk et al. (1999) estimated the predation on reindeer to almost 7 % (10 individuals where 6 of them where calves). In a study on reindeer calf mortality in Finland, Norberg (2006) estimated average amount of predation to 2.2 % (0.0 to 4.4 % between years and areas) of all reindeer calves. Highest predation was observed in years with harsh winters and in years when parasitic infestations was severe. There was also a pattern with higher predation with increasing latitudes. In central Norway, Nybakk et al. (1999) claimed that the eagles is an important thing to consider for reindeer mortality – estimating the total loss due to golden eagle predation to 5.3 % (9 calves; 3 female adults). Except for rough calculations based on indirect studies (Tjernberg 1981, 2006) there are few attempts trying to estimate the predation on reindeers by golden eagle. Still, there are reports indicating similar behavior on golden eagle predation – both from scientists (Bjärvall et al. 1990), reindeer herders (Fjällås 2014) and authorities (Jonsson et al. 2012).

Considering the importance of the issue of species interactions in the boreal north, and lack of knowledge on the movements of these, I designed this study to answer the question: if eagles synchronize their long distance movements with the movements of the reindeers. I use high resolution GPS tracking data from multiple years for both juveniles- and adult eagles. I further test if the migratory movements of the eagles are timed with the arrival of the reindeer to their summer calving and feeding areas in northern Sweden. This study will help to increase our knowledge on movement patterns of golden eagle and provide valuable insights of further studies to enhance the management of both the eagles and the reindeers. To address the above question, I made the following predictions:

- 1. The direction of eagle movements should match the direction of reindeer movements.
- 2. The timing of eagle migrations to the reindeer calving and summer grounds should match that of the reindeer
- 3. The timing of return migrations of the eagles should match that of the reindeer return migrations.

Further, I discuss these findings in a broader context of large carnivore-reindeer management, and thus, suggestions on further studies and management implications today in Sweden and in Scandinavia.

Materials and methods

Study area

The study area covers the north of Sweden between 62–69°N (figure 1). The landscape of the region is characterized by coniferous forest, lakes and rivers with great mire complexes and montane birch forests closer to the alpine zone. The elevation spans to almost 2000 meters above sea level. The boreal forest is dominated by the coniferous trees Norwegian spruce *Picea abies* and Scots pine *Pinus Sylvestris* with the deciduous trees birch *Betula* spp., aspen *Populus tremula*, willows *Salix spp.* and rowan *Sorbus aucuparia*. The wildlife comprises of moose *Alces alces*, reindeer *Rangifer tarandus* and scattered populations of roe deer *Capreolus capreolus*. Large predators besides the golden eagle are the Scandinavian brown bear *Ursus arctos*

European lynx *Lynx lynx* and wolverine *Gulo gulo* with occasional visits by wolf *Canis lupus*.

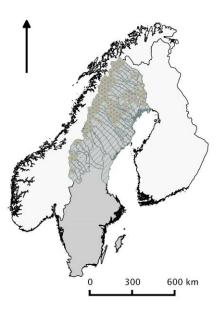


Figure 1. Map over the study area with Sweden (gray) and the Swedish reindeer herding areas (lined diagonally) and reindeer's summer calving- and feeding areas (dotted brown). Black arrow shows the north. Country maps is downloaded from diva-gis.org/datadown. All reindeer herding areas and reindeer summer areas (polygons) are sampled with permission from Per Sandström via renGIS 2013.

Movement data from 29 adult and 14 juvenile golden eagles ($n_{\text{eagles}} = 43$) comes from the ongoing research program VINDVAL at the Swedish University of Agricultural Sciences (SLU) in Umeå. All eagles were equipped with a GPS- (global positioning system) transmitter by experienced personnel from both Sweden (SLU) and from people with high catching expertise from Bloom Biological Inc., California, USA. The birds were marked in the county of Västerbotten during 2010 and 2011. Two different transmitters were used, both partly solar driven; the Vectronic Aerospace 135 g GPS PLUS Bird; and Microwave Telemetry's 70 g Solar Argos/GPS PTT-100. The transmitters were set to automatically enter positions from every ten minutes to one position per hour. All data was automatically transferred via GPS (Vectronic) or Argos satellite system (Microwave Telemetry) to the Wireless Remote Animal Monitoring database system on SLU (WRAM 2013). All positions were determined with Argos- and GPS satellites with a horizontal precision of 18 m. GPS positions consist of latitude and longitude in the Swedish national coordinate system RT 90 2.5 gon V together with altitude, although the altitude was excessive and therefore excluded from this study.

Reindeer Migrations and space use

To compare the eagle's use of reindeer calving- and summer feeding areas in the Northern Sweden, I have used polygons for those areas in ArcMap (ESRI 2013) and Q-gis (Q-GIS 2014). These reindeer habitat have been mapped in the field based on

information from the reindeer herders. These maps are stored in renGIS (reindeer geographic information system) – a participatory GIS (pGIS) environment developed in collaboration between scientists at SLU and reindeer herders (Sandström et al. 2003). For detailed information on when the reindeers migrate to the west in spring (for calving, summer feeding and rutting) and to the east in autumn (for winter feeding), a representative from a sami village was interviewed (Anders-Erling Fjällås, telephone interviews 2013-11-25 and 2014-01-08).

Movement analyses

Identification- and quantification of changes in animal movements started with studies on the species absence or presence within an area or mark recapture. Today, studies on structural shifts in species behavior have developed via tagging and marking, *e.g.* ear tagging (Eberhardt and Hanson 1978) to much more detailed- and threedimensional positioning features. This is a great progress giving us opportunities to study species behavior in detail and also, this gives us opportunities to search for links between multiple animals' behavior and the environment (Edenius 1997, Costa et al. 2012, Mysterud 2013). A common technique to analyze movement is by calculating the square of the distance between an animal's first- and current position, a key parameter called the 'net squared displacement'; NSD (Börger and Fryxell 2012). The NSD -parameter was first developed by Turchin (Turchin 1998) and has gained ground during the last decade within animal movement research such as in the studies of movements by moose (Singh et al. 2012), red deer (Mysterud 2011), ducks (Beatty et al. 2013) and buffalo (Naidoo et al. 2012). More recent advancements include methods to identify structural shifts in movements, called as 'behavioral change point analysis' (bcpa) which identify shifts in behaviour using a sweeping window through estimates of speeds and turnings.

Eagle data preparation and analyses

The data used in the analyses was first prepared for the analyses using the steps shown in figure 2. Data from both juveniles- and adult golden eagles were used in the study (WRAM 2011). The raw data consisted of 43 golden eagles. If data for one individual were available for more than one year, each individual were divided into one year per eagle (hereafter 'eagle years'). Accordingly, the 43 eagles were divided in 96 eagle years between 2011 and 2012 (table 1).

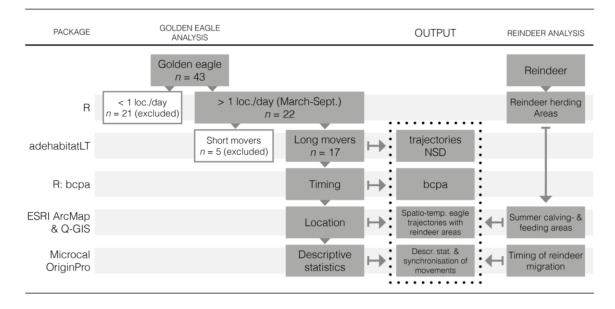


Figure 2. Flow chart showing analyzed data (*Golden eagle* and *Reindeer*) and output from respectively analysis: trajectories (NSD), behavioral change point analysis (BCPA), maps and timing of movements (descriptive statistics).

Net Squared Displacement (NSD)

I focused on eagle movements at a landscape scale. This is their movements outside that of their home-range. The net squared distance was calculated using the package 'adehabitatLT' (see further explanation of this parameter below) (n = 17) for 23 eagle years using the package 'adehabitat' in R (Calenge et al. 2009). I calculated length of displacement; ' R^2N ' (recalculated from km² to km) and the direction of the movement; 'abs.angle' (calculated in radians). To meet the satisfaction for line trajectories with regular time lag (*i.e.* time lag of 'type II') between relocations, trajectories need a constant time lag (Calenge 2006, 2011, 2013). Therefore, if there were more than one positions a day and individual, these positions were aggregated into one mean location per day. Also, one mean angle per day and individual was calculated (mean abs.angle) if there were more than one location per day for analysis of the eagles seasonal directions. I separated short distance movers (who did not travel outside their home range) from long movers by defining a criterion for minimum distance that they had traveled. This criterion was set to 200 km (after clear inspection of home range size).

Behavioral change point analyses (BCPA)

To analyze the timings and durations of changes in golden eagle movement, I used the behavioral change point analysis; 'bcpa' (Gurarie et al. 2009) using R. It is a novel and robust method for detection of discrete- and suddenly behavioral changes over time. These structural shifts can otherwise be easy to over look in movement data at a large scale (shifts in movement behavior due to dispersal and/or migration). Looking at longer movements, *e.g.* migration, where multiple behaviors are to be expected within an individual movement path, it is important to identify shifts in movement

behaviors. Here, one example is when movements change from goal-oriented-(discrete behavior; e.g. migration) to a more disruptive mode (suddenly behavior, e.g. feeding mode). In BCPA, speed (velocity; V), and compass directions (turning angle, Ψ) are calculated over time (T; Julian days). The output is either the propensity- and extent of movement to continue (V_p) or the tendency to change direction (V_t) . Estimates of the velocity (V) are described as mean (μ), standard deviation (σ) and autocorrelation (ρ). Here, high autocorrelation can be seen as the tendency to move in a particular direction; if something moves at one direction, it is also likely that this movement will continue at the same direction. In this study, I used the Vp function; also called the 'V*cos(Theta)' function within the bcpa package (Gurarie et al. 2009). When one is analyzing the V_p function, an increase in μ , ρ suggests a more directed movement (e.g. a migratory behavior) whereas an increase in σ amplifies a more variable movement (e.g. a search /feeding behavior). Each individual data set (here one individual per year) must be worked through with different values of the parameters, which is set by the 'windowsweep' -function in the bcpa package (Gurarie 2013) which is the resolution of a step-wise estimation of the parameters (μ , $\sigma \rho$ of estimated velocity) of each re-location (*i.e.* time point). By using the V_p function to detect shifts in the animals movement behavior - the autocorrelation value determines the scale of movement with high values when migratory (directed movements) and low values when feeding. Thus, a high mean value of V_p (persistence velocity) indicates a more directed and faster movement. BCPA yielded a number of change points for each individual trajectory. These change points were then connected to the day of the year to identify when in time the behavior occurred. All the change points were then plotted and interpreted. The time difference between the change points was used to estimate the duration of the movement bouts.

All movement analyzes was performed in R (R Development Core Team 2013, R version 3.0.1 and 3.0.2) with reference to required packages therein: adehabitatLT (object class 'df' and 'ltraj') as well as the package 'bcpa'. For additional statistics, OriginPro 8.6 (Microcal 2013) was used (figure 2).

Results

Distance- and direction of the movement

I calculated movement extents for 17 golden eagle individuals between 2011-2012 which resulted in a total of 23 adult golden eagle years (10 males, 11 females and 2 with unknown sex) and 5 juvenile eagle years (table 1). Many studied eagles migrated towards the northwest (mountains) in spring (April-May) and southeast in autumn (August-September [figure 3]). They stayed in the west for the period between May and August (figure 4). Mean extent of movements during the two consecutive years 2011 and 2012 (both years pooled) ranged from $1 \pm 1 \text{ km} (\pm \text{SD})$ up to $1656 \pm 4 \text{ km}$ (table A1) within the group of long movers (table 3 and figure 4) with \geq location per day between March and September.

	Sample size (eagle years)													
	n ((NSD)		n (BCPA)										
	2011	2012	tot	2011 2012 tot										
Adults Juveniles	4 3	14 2	18 5	16 16 32 5 4 9										
tot	7	16	23	21 20 41										
or:														
Males	2	8	10	13 12 13										
Females	4	7	11	7 7 14										
Sex unknown	1	1	2	1 1 2										

Table 1. Sample size (n) of analyzed golden eagles (eagle years) between the years 2011 and 2012 in the NSD- and BCP - analysis.

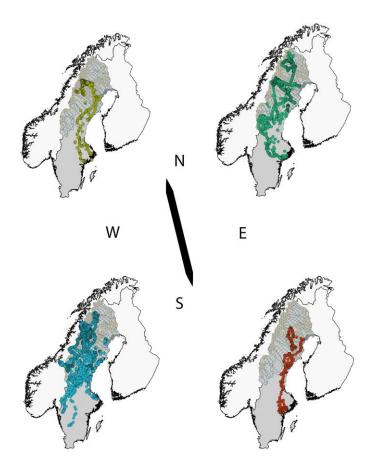


Figure 3. Approximated direction of eagle migration (black arrow) between their winter- (southeast) and summer ranges (northwest) in Sweden (gray) due to the line trajectory analysis in R (abs.angle in the ltraj package). The Swedish reindeer herding area is marked with diagonally lines and reindeer summer areas (calving- and feeding ground) is symbolized by brown dots. Each map is one individual golden eagle (here: four individuals randomly chosen) with trajectories from both 2011 and 2012.

Structural shifts

The behavioral change point analysis revealed two major periods of changes in golden eagle movement behavior: one in the spring and one in the autumn (table 3, figure 4 and 5 but see figure A2 for each individual). In spring, median date of movement for all eagle years (n = 23; table 1) was May 4th and first change point on 12th march (adults; males) and the last (max.) June 11th (adults; females): a span of three months, although half of the dates stretched less than a month between April 22nd and May 13th (*i.e.* dates within the lower- and upper quartiles). In spring, median dates for all categories were detected within 11 days: May 2nd (females, n = 11) – May 12th (males, n = 10). In autumn, the width of behavioral changes was greater than in the spring with the earliest change the 17th of June (juveniles; sex unknown, n = 2) and the latest change November 14th (males, n = 10) (figure 4; table 3). The duration of the eagles that stayed within the reindeer summer areas is consequently the period between the spring- and autumn migration (with the median dates May 4th to August 10th); an average stop-over period of 98 days (14 weeks).

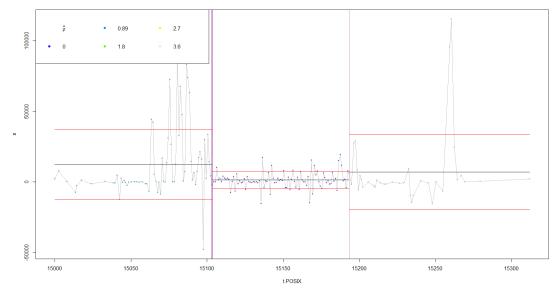


Figure 3. Example of a bcpa -plot for one individual. The analysis is executed with the window sweep function (median window size = 60) in R (bcpa package) to enable identification of the most likely behavioral change points over the study period where the x-axis shows time (t.POSIX) and the y-axis shows $V_p(x)$. The time period ranges from March (t.POSIX \approx 15000) to October (t.POSIX \approx 15300) in 2011. Each point refers to one location and day after calculation in the ltraj -package. Each behavioral change point denotes by purple vertical lines. Different phases of movement behavior are drawn by horizontal lines showing mean- (black line) and st. dev. (red line) between the change points. Autocorrelated movement (^p) is value-colorized (see legend) from low- (blue dots) to high (yellow dots) autocorrelation values. High autocorrelation (blue) means that there is big change in movement patterns and indicates a feeding behavior whereas low autocorrelation emphasizes a low change in movement pattern and denotes a more migratory behavior. Accordingly, this plot yields three different phases: one feeding phase in the middle during summer (between the two vertical behavioral change point lines) and two migratory phases: one in spring (on the left hand side) and one in autumn (on the right hand side). Notable is also that the higher mean values (black horizontal lines) in spring and autumn indicates a faster and more directed movement.

The figure above (figure 3) is an example of an average plot from the bcp -analysis. The structure of the autocorrelated values indicates a seasonal migration behavior. It reveals three phases of movement over a year: two migration phases (one in spring and one in autumn) with a more directed movement (high autocorrelation) and one feeding-like phase during the summer (low autocorrelation). During the summer the general pattern is more disruptive movement behavior with suddenly shifts on movement behavior. Within the studied eagle population, 78 % of the juvenile eagles shoved this seasonal movement structure whereas 40 % of the adult eagles showed the same structure. There was a tendency for more significant shifts in their movement behavior in spring with 89 % behavioral change points for juveniles and 54 % for adults whereas the same shift's in the autumn were 67 % for juveniles and 41 % for adults. To find most significant behavior change points, an average window sweep size of 60 was used (the window estimates the mean; μ , standard deviation; σ and autocorrelation; ρ for the velocity in each time-point) although the size ranged between 10 and 160.

Reindeer movement and calving areas

In 2011, the reindeer in the study area migrated to their calving areas to the west towards the mountains in the beginning of May with calving initiated around May 10^{th} – with an peak at the 20^{th} of May (approx. 75 % of all births) – ending around May 30^{th} . In 2012, the reindeer migrated in the end of April with initiation of calving around the 10^{th} of May – and a peak at the May 12^{th} (approx. 75 % of all births) – ending around May 30^{th} (figure 4). Here, the reindeer's autumn migration usually starts in the last weeks of September and ends during the month of October – usually coinciding with the first snow fall (Fjällås 2014). Accordingly, the duration of the stay of reindeer in these areas is 5 months; between April/May to October.

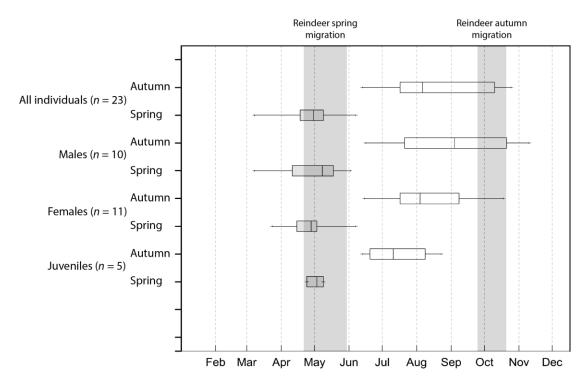


Figure 4. Box plots with dates of the Reindeer calving period in spring (vertical gray shadowed area to the left: end of April to the end of May) and reindeer's autumn migration (vertical gray shadowed area to the right: the end of September to the end of October) as well as golden eagle movement periods in spring (grey box plots) and in autumn (uncolored box plots). Median date (vertical line) and lower quartile (25 %) to the left and upper quartile (75 %) to the right. Whiskers shows max.- and min. dates of migration on the right- and left hand side of the box respectively. All dates are significant change points from the behavioral change point analysis (R: bcpa).

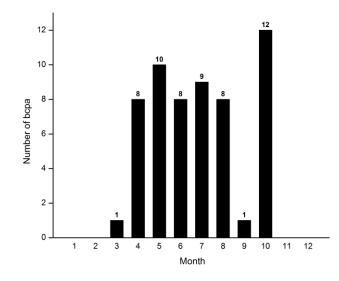


Figure 5. Stable-bar with number of behavioral change points; bcpa's on the y-axis due to month they appeared (between March and October) on the x-axis. All dates are significant change points from the behavioral change point analysis (R: bcpa).

Table 3. Dates with median; min; max; lower quartile (Q1) and upper quartile (Q3) for golden eagle migration sorted by all individuals (n = 23) and into groups by females (n = 11) and males (n = 10) and juveniles (n = 5). All dates derive from the behavioral change point analysis (R: bcpa) between March and September. Year 2011 and 2012 are pooled. All sample sizes are eagle years.

	Juve	niles	Fen	nales	Ма	ales	All				
	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn			
Max	13-maj	27-aug	11-jun	22-okt	06-jun	14-nov	11-jun	14-nov			
Q3	10-maj	05-aug	07-maj	12-sep	22-maj	25-okt	13-maj	14-okt			
Median	07-maj	15-jul	02-maj	08-aug	12-maj	08-sep	04-maj	10-aug			
Q1	02-maj	27-jun	19-apr	21-jul	15-apr	25-jul	22-apr	21-jul			
Min	28-apr 17-jun		28-mar	19-jun	12-mar	20-jun	12-mar	17-jun			

Discussion

Most studied individuals were classified as long movers (n = 17) and migrates with large extents of movement in both juvenile- and adult golden eagles. Further, the timing of eagle migrations synchronized closely with the reindeer migration in spring. The eagles that moved long distances showed a great range of displacement: from 1 km up to 1656 km between southern Sweden trough the Fennoscandian mountain range up to northernmost finish Lapland. Long movements were undertaken by both adults (males: n = 10; females: n = 11) and juveniles (n = 5). This is in line with the findings from golden eagles in North America (Kochert and Steenhof 2002, McIntyre et al. 2008, Watson 2010) as well as in Scandinavia (Systad et al. 2007). In Sweden, eagle movements were believed to be less migratory (Hjernquist 2011, Hipkiss et al. 2013) but my study proves otherwise. According to my study, displacement distances reached over 1600 km – a distance ranging over the whole Scandinavian peninsula (figure 3). This looks very much like the thousands of kilometers that migratory eagles traversed from Denali in Alaska to Mid-Western Canada (McIntyre et al. 2008) and also, as migrations distances discovered in Eastern Canada (Brodeur et al. 1996) with displacements up to 1650 km and in a Norwegian population that migrated to southern Sweden with distances up to almost 1500 km (Jacobsen et al. 2011). Hence, this in contrast to shorter movement behaviors (a more sedentary behavior) founded in eagles that origins from lower latitudes (<60°N) in North America (Kochert and Steenhof 2002). Long distance movements detected in the northern populations of golden eagle is also supported by studies in the Finnmark region in northern Norway (Systad et al. 2007, Jacobsen et al. 2011) who discovered long movements of both sub-adult- and adult golden eagles of both sexes - movements reaching between 400-900 km in distance between their summer- and winter ranges.

Many species in the northern hemisphere are migratory where the migrations are believed to depend on environmental factors. For eagles, amount of prey and daylight are reported to be the drivers (McIntyre and Collopy 2006) whereas for ungulates such as moose and reindeer, snow conditions are known to drive migrations (Singh et al. 2012). The majority (75 %) of the eagles in this study initiated their movement within a period of 3 weeks between April 22nd and May 13th with the median date 4th of May. For migratory golden eagles in North America (McIntyre and Collopy 2006), migrations were initiated between March and mid-April heading northwest. In Canada, 3 of their 4 studied eagles migrated north in March, although this is a small sample and should be carefully evaluated (Brodeur et al. 1996). The same pattern was reviled in Norway where Jacobsen et al. (2011) could see young eagles coming to the north (Finnmark) in March-April. However, the direction of spring migrations in northern Norway is reversed compared to the directions we have discovered in Sweden: in Norway the reindeers migrate to the east (to islands at the coast) with eagles migrated to the tundra in at Finnmark or eastwards). In Alaska, McIntyre et al. (2008) founded saw a less broad migration window (between 15 September and 5 October). In Norway, however, Jacobsen et al. (2011) estimated median date for autumn migration 18^{th} of October – a later initiation of migration than both my studied population here in Sweden, but also in the studied population in North America. My results suggest that mean off-set for autumn migration is earlier here than in both Norway and in Alaska. However, and due to the eagle's discrete autumn migration, the method I used to calculate migration dates (the bcp -analysis) was a possible factor for biased dates towards a prolonged migration period.

Eagle-reindeer interactions

This study clearly show that eagles move to mountains in synchrony with the reindeer and especially in spring. However, this does not necessarily prove that eagles primarily scavenge on reindeer. There are many possible reasons for the discrete migratory behavior that we are observing during the autumn, especially if the food is an important factor: if there is food in the area – why move so quickly? In these northboreal areas, the food resources have a high variation in time and space and the eagles can bee seen as both generalist- and specialist predators depending on prey abundance (Watson 2010). Thus, Nyström et al. (2006) found strong correlation between golden eagles nesting success and the density to its main pray Ptarmigan species and could indicate that nesting eagles in that area have a low preference for alternative prey. In Norway, Jacobsen et al. (2011) found the highest proportion of reindeer scavenges due to predation of nesting eagles within the reindeers wintering area in the eastern part of Finnmark (in the area between Kautokeino and Karasjokk). Moreover, there was few young eagles that killed reindeer within the reindeers calving- and summer area at the coast. Here, they discovered that most of the young eagles drifted around within the reindeers calving area in early summer but without paying any special attention for the calving areas. Notable here is that the study relied on VHFtransmitters, and although its robustness, small-scale movements (phases) as predation could have been overlooked. Still, this reversed movement pattern in Finnmark and thus potential predation where reindeer seems to be scavenged more in winter is contradicted by other studies on the eagle's favoring of reindeer in summer. Nevertheless, there are other potential species besides the reindeer which could contribute to explaining the eagle migrations. The migrating moose could be one

factor for eagle movement. Singh et al. (2012) founded that over 80 % of the moose did seasonal migration in May (eastwards) and October (westwards), see figure 6.

Data limitations

As we are re-making an animal's continuous movement into discrete data we are immediately dealing with uncertainties. How does our discretization (our models) of an animal's continuous movement affect our understanding of the animal's behavior (Nams 2013)? A possible factor for error in all spatial studies on tracking data is the precision of the transmitted data (*i.e.* coordinates). Here, Gurarie et al. (2009) tested the robustness of GPS -positioning due to the use of behavioral change point analyses. They saw that coarse filtering of the data (making the data less noisy) made the precision of the GPS –positioning less important – especially identifying structural shifts as migration vs. feeding-like movements.

Calculating the NSD was limited to the warmer period of the year, and thus, there was a lack of sufficient data (number of relocations) during the winter period (October to February). This shortcoming is probably due to solar powered transmitters – charged (or partly charged) with sunlight when this is insufficient.

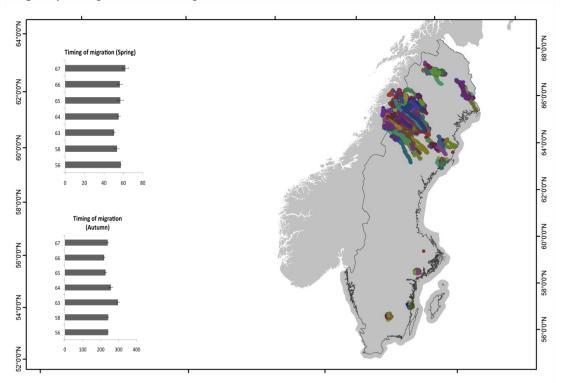


Figure 6. Map showing seasonal moose migration (colored paths at latitudes between $63-67^{\circ}N$) and moose nomadic movements (colored paths at latitudes between $56-58^{\circ}N$) in Scandinavia. Staple bars shows the timing of the migrations (spring- above autumn migration) where the y-axis shows latitude ($56-67^{\circ}N$) and the x-axis shows days from March 31^{st} . Figure with permission from Singh et al. (2012).

Consequently, there are advantages with VHF –transmitters although less sophisticated in delivery of spatio-temporal due to its robustness in transmitting. Yet, this problem was of less importance in this study where I looked at movement patterns at a large scale over a long time period and therefore, my analyses were not so sensitive in the resolution of the time period though I was able to identify structural shifts without year-around data. Therefore, the reported precision from the deliverer of the eagle transmitters, as well as gaps in the data-set from the winter period, has to be considered as irrelevant in this study. But still, and more critical, were the lack of positions within the study period between spring and autumn. This is a shortcoming that forced me to reject 22 individuals from further analysis, and thus, a majority of the juvenile golden eagles. This made statistical comparison between juvenile and adult eagles impossible. Hence, and to detect rapidly movements of eagles covering long distances per day, it is important to have a continuous data set with at least one location per day.

The bcp -analysis I used to detect behavioral changes has to bee considered as a relatively easy-to-use method with few parameters to prepare. Basically, the only needed information is ID, date and position. Still, the R -environment is guite demanding for inexperienced users and thereby also limiting the participating audience and thus, it is hard to look at the method more critically. Looking at the bcpa -analysis in this study, the average window sweep function (that estimates mean; μ , standard deviation; σ and autocorrelation; ρ for the velocity in each time-point) was set to 60 (ranging between 10 and 160). In the paper where Gurarie et al. (Gurarie et al. 2009) evaluates the method, they discuss that no smaller size than 30 should be chosen for the window sweep function. Yet, they interpret that a window size of 50 is more than good enough although this masked behavioral changes that occurred more than once a day (i.e. small-scale behavioral shifts). Basically, this function sets the coarseness of the step-wise estimation of velocities: in a spatial data with few positions (e.g. gappy data), a large window-size might over-look change points. Thus, my experiences from long time-data-sets – with homogenous sets of data points (here coordinates) – is that there are no changes in the timing of the change point selected due to the window size function. Still, using a large window size might underestimate the number of change points and consequently, a small window size maybe makes an overestimation. For example, a visual inspection of individual 10_003s bcpa -plot in 2011 (and perhaps also in 2012) yields that some significant change point/-s might bee missed due to the pattern of high autocorrelation in the autumn (Figure A2). Here, after visual inspection of the bcpa -plots, the use of a relatively large window size might be an explanation why I miss potential change points in the autumn and should therefore be additionally tested for similar analyses. Further, another experience is that the precision of the timing of the change point is ± 2 days and therefore enough for movement studies at a large scale. However, and although the robustness of the method to detect behavioral change point's, I was not able to detect more precise dates for start and stop days. The directed movement of the eagles showed variation within the timing of the change points (*i.e.* from low- to high autocorrelation). Still, the timing for every single change point is the most significant date where their movement behavior changed. These estimates can be improved by using more high resolution data, which was not regarded in this study due to computational and time limitations.

Eagle's movement and management

Our knowledge on eagle movement ecology is limited and it is a shortcoming for management. Today, it is also important that we don not study species as isolated populations and better try to quantify their behaviors. For better decision making, we need to define effects of actions (or inactions) – efforts that gives both ecological consequences as well as and economic ones, hence with different magnitude depending on interested party. This is something Redpath et al. (2013) also pinpoints as important. Here, they suggest that it is of most importance to let stakeholders integrate themselves in a social context and to be ware of the effects. Here, one example is the compensation scheme for golden eagles that builds on both ecological knowledge and local participation – a system which reindeer herders highly depends upon. Still, the base for the compensation scheme due to losses of golden eagle predation builds on the knowledge of nesting pairs breeding success and therefore, consequences of non-breeding eagles as free ranging and migratory juvenile eagles is possibly overlooked. Consequently, more research is needed to be able to better understand eagle movement over time. Future studies on e.g. large-scale movements (more studied individuals gives a more solid ground to build management upon) and eagle movement at a smaller scale (e.g. feeding-like behaviors with potential predation rate evaluations) are important – all studies that get the most credibility if executed by all parties. Increased understanding of the species, and better the synchronous between them, minimizes future surprises in an already unpredictable environment.

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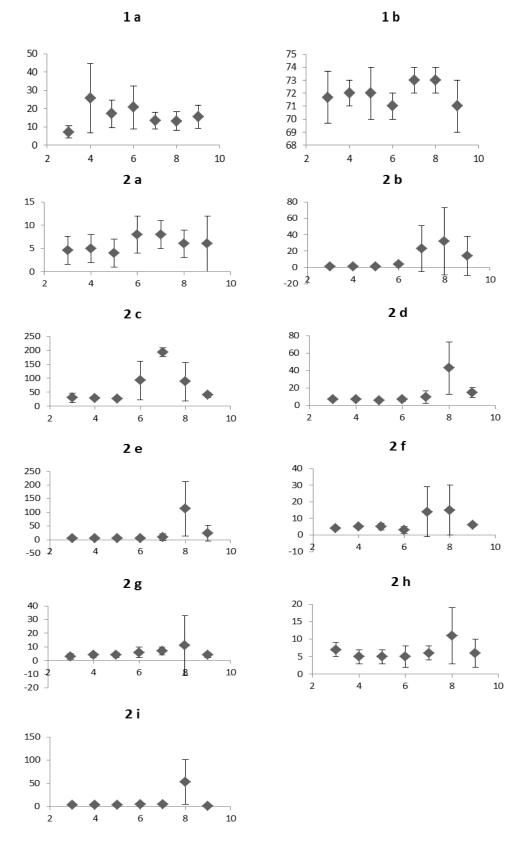
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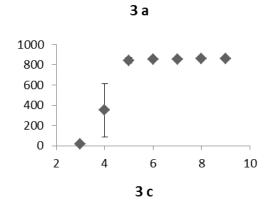
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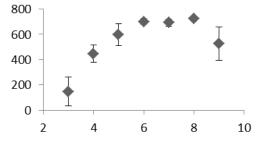
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Appendix

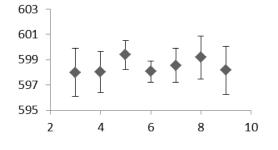
Figure A1. Net square displacement; NSD (y-axis; km) with mean (gray dots) and SD (black whiskers) calculated per month (x-axis) in 2011 (1a-b and 3a-e) and 2012 (2a-i and 4a-g).

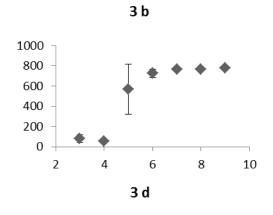


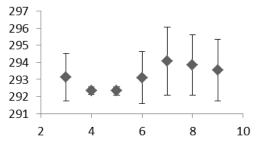


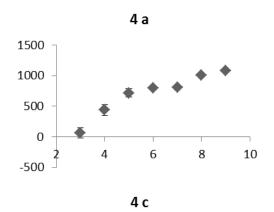


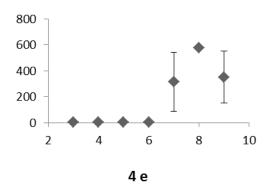


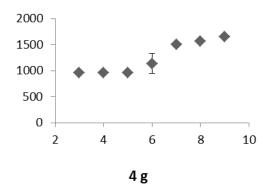


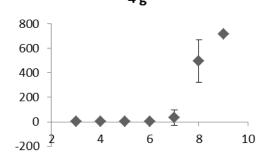


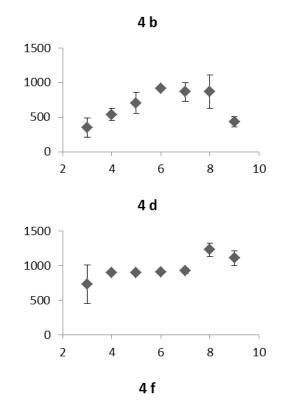


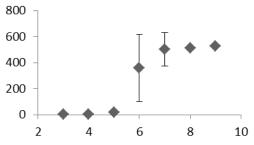






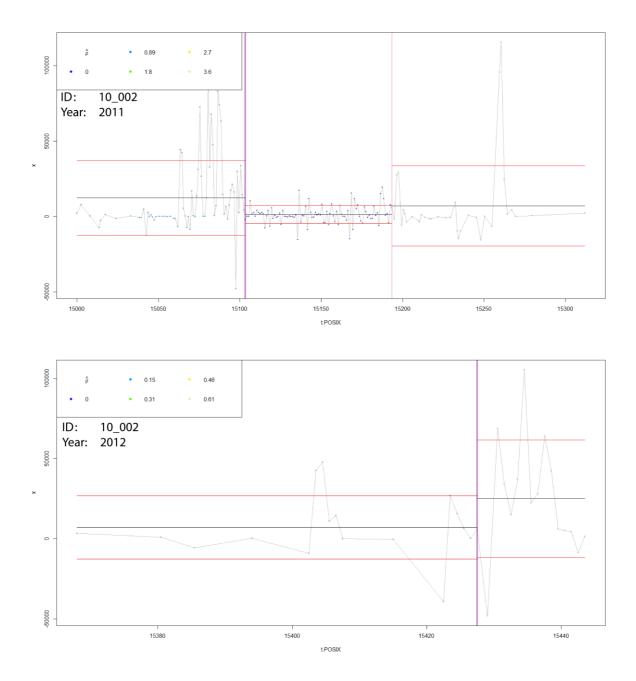


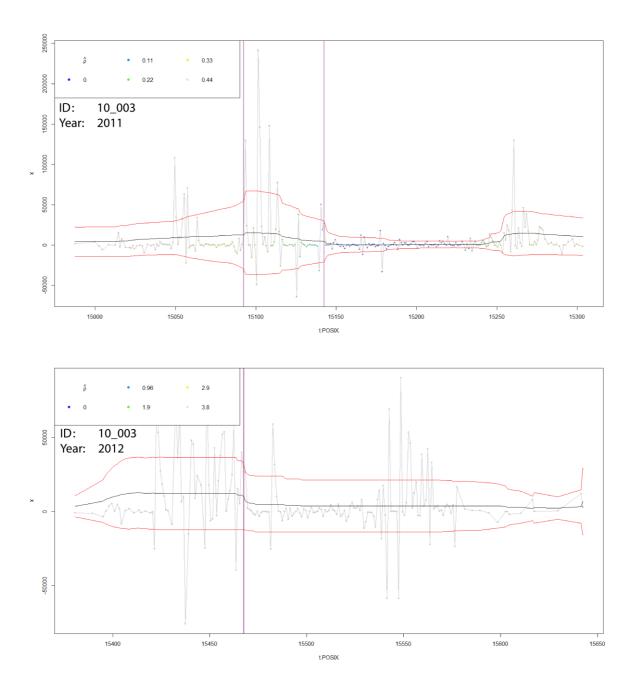


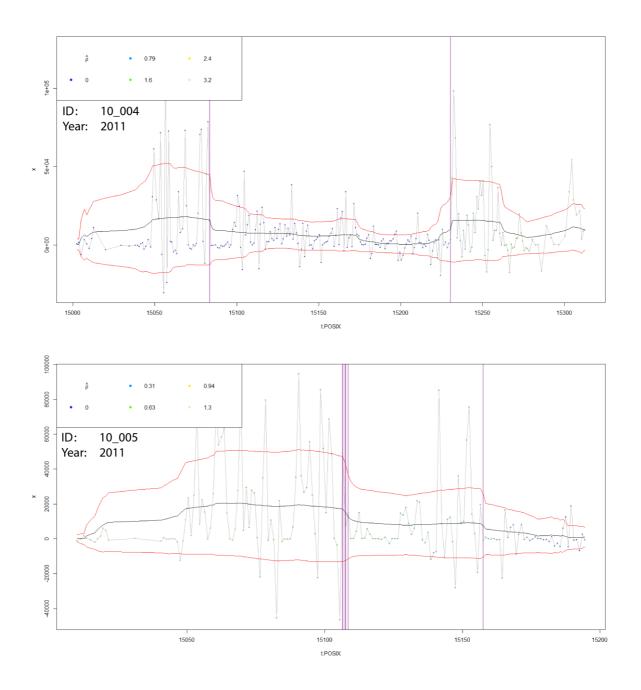


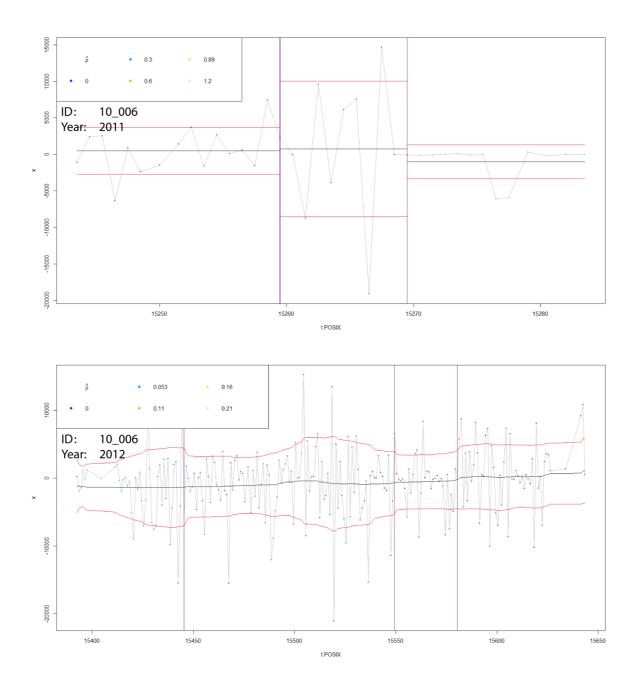
	Age	Sex	ID		NSD (mean ± SD [km²])																			
Year	class			Mar			Apr			May			Jun			Jul			Aug			Sep		
1	_	F	10_009	7	±	3	26	±	19	17	±	7	21	±	12	13	±	5	13	±	5	16	±	6
2011	Ad.	м	10_012	72	±	2	72	±	1	72	±	2	71	±	1	73	±	1	73	±	1	71	±	2
			10_006	5	±	3	5	±	3	4	±	3	8	±	4	8	±	3	6	±	3	6	±	6
			10_008	1	±	1	1	±	0	1	±	1	4	±	2	23	±	28	32	±	41	14	±	24
		F	10_009	30	±	17	29	±	5	27	±	2	92	±	69	194	±	16	88	±	70	40	±	9
			10_010	7	±	1	7	±	0	6	±	1	7	±	2	10	±	7	43	±	30	15	±	6
2012	Ad.		y0_11_006	4	±	2	4	±	2	4	±	3	5	±	2	5	±	2	53	±	48	2	±	2
N	-		10_012	6	±	1	5	±	1	5	±	1	5	±	1	10	±	12	113	±	99	23	±	29
		М	11_013	4	±	1	5	±	1	5	±	2	3	±	2	14	±	15	15	±	15	6	±	1
			y0_11_004	7	±	2	5	±	2	5	±	2	5	±	3	6	±	2	11	±	8	6	±	4
			y0_11_005	3	±	2	4	±	2	4	±	2	6	±	4	7	±	3	11	±	22	4	±	2
		F	10_002	19	±	11	352	±	262	842	±	29	854	±	5	851	±	3	861	±	12	857	±	5
	.vuč	м	10_004	147	±	113	447	±	69	597	±	87	700	±	21	691	±	27	721	±	18	525	±	131
2011	· ·	Uk	10_003	79	±	37	52	±	11	568	±	249	724	±	40	765	±	8	763	±	7	775	±	6
N	Ad.	F	10_008	293	±	1	292	±	0	292	±	0	293	±	2	294	±	2	294	±	2	294	±	2
	Ā	Г	10_010	598	±	2	598	±	2	599	±	1	598	±	1	599	±	1	599	±	2	598	±	2
	Υ.	м	10_004	346	±	138	537	±	86	703	±	153	915	±	18	867	±	134	869	±	238	431	±	76
	, vuć	Uk	10_003	64	±	85	436	±	86	715	±	69	797	±	5	808	±	46	1007	±	28	1075	±	12
N	-		11_020	961	±	21	964	±	2	964	±	2	1138	±	194	1505	±	47	1561	±	5	1656	±	4
2012		F	y0_11_003	3	±	1	4	±	2	2	±	1	3	±	2	35	±	64	496	±	172	715	±	4
	Ad.		11_016	2	±	2	4	±	2	3	±	2	4	±	2	315	±	229	575	±	6	351	±	200
		м	11_019	729	±	278	895	±	24	898	±	16	902	±	11	923	±	35	1227	±	96	1106	±	109
			11_024	4	±	2	3	±	2	17	±	15	358	±	258	503	±	127	515	±	5	527	±	7

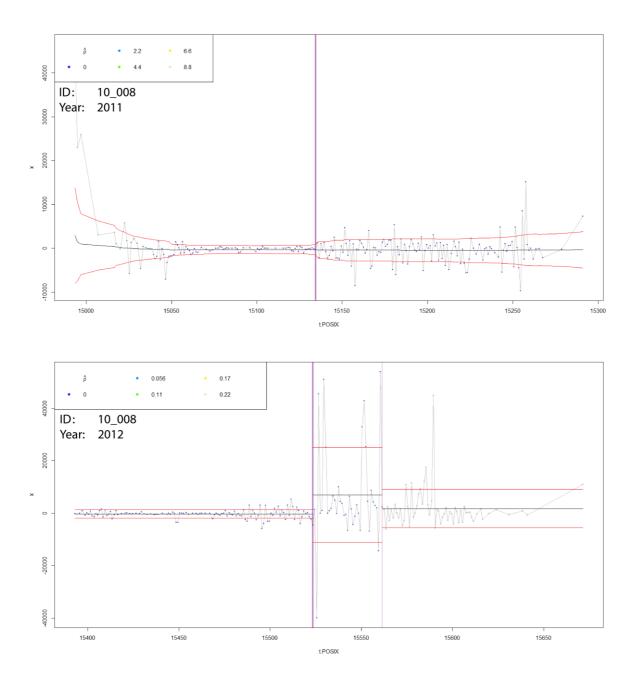
Table A1. Table showing net square displacement (NSD) means \pm st. deviations. (SD) per eagle (ID) and month within the study period (2011 and 2012).

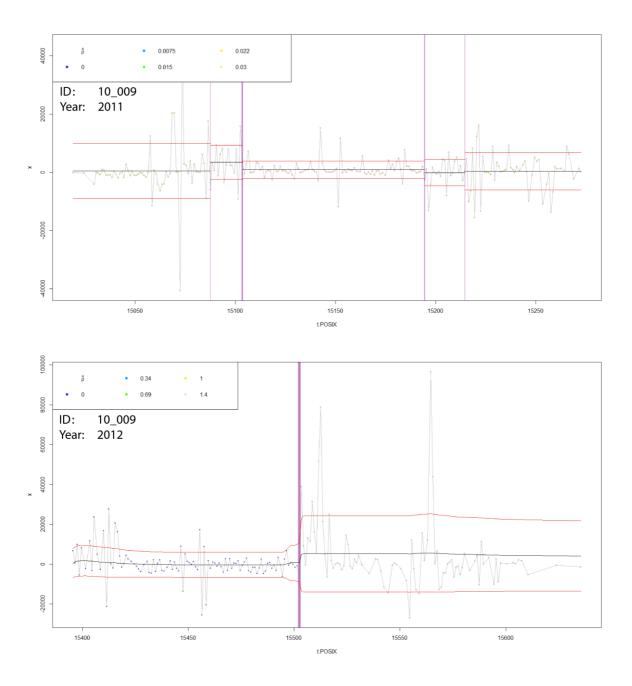


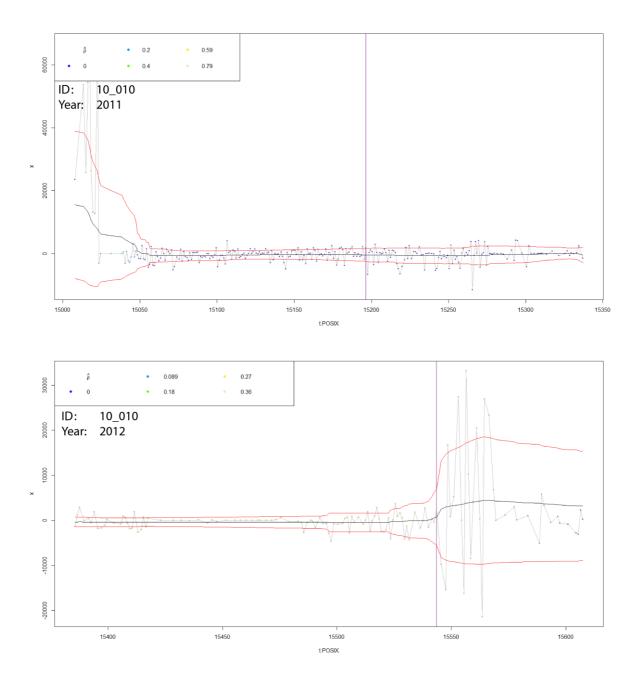


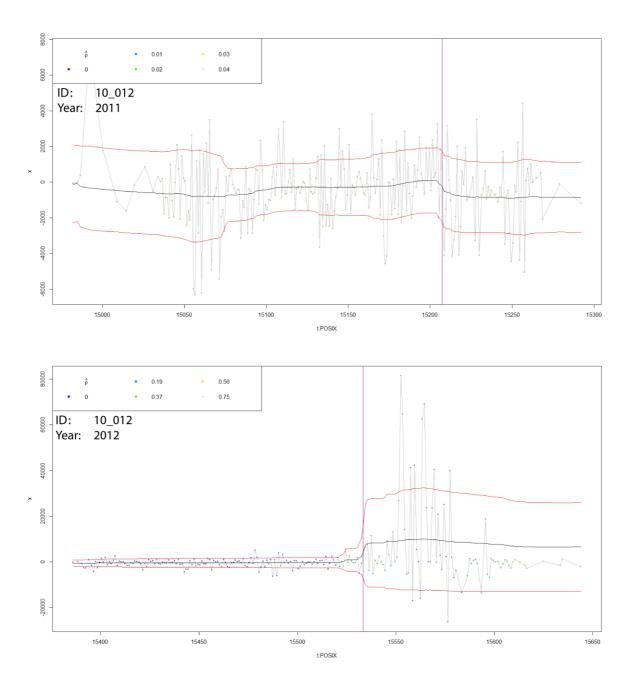


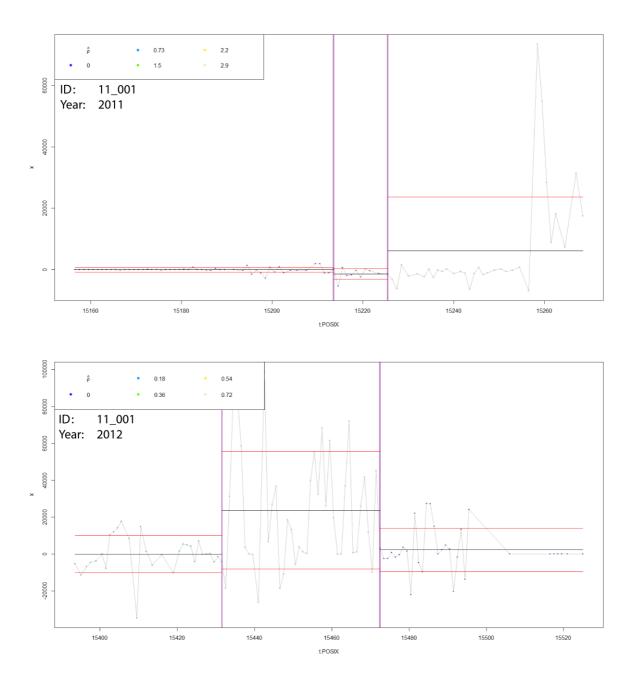


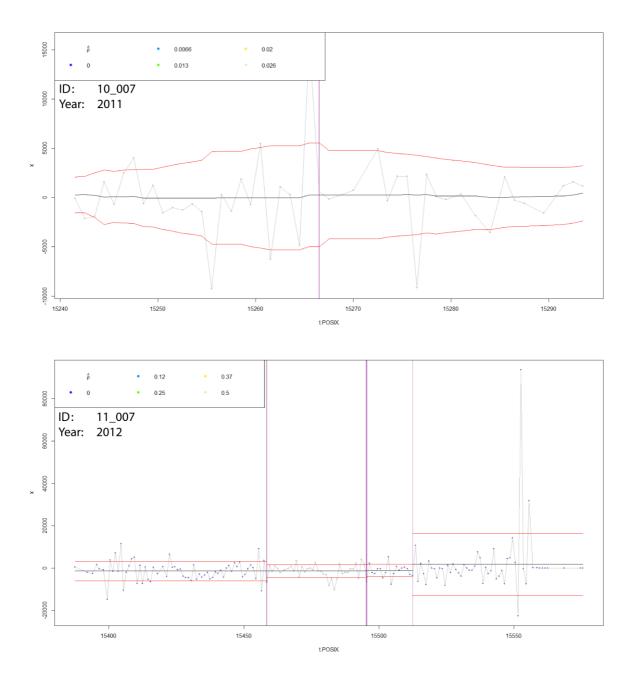


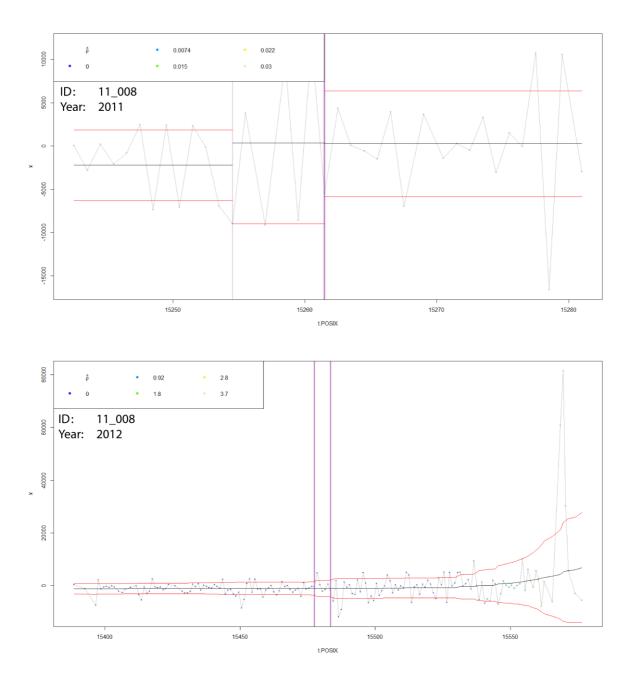


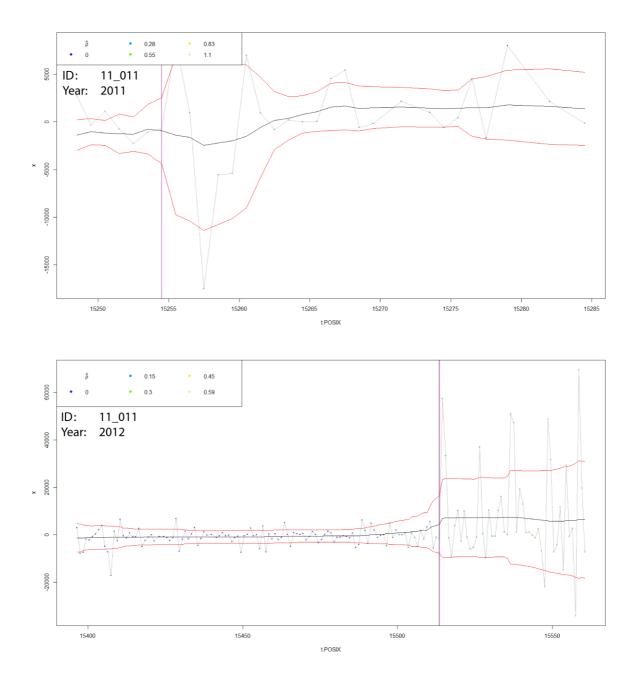


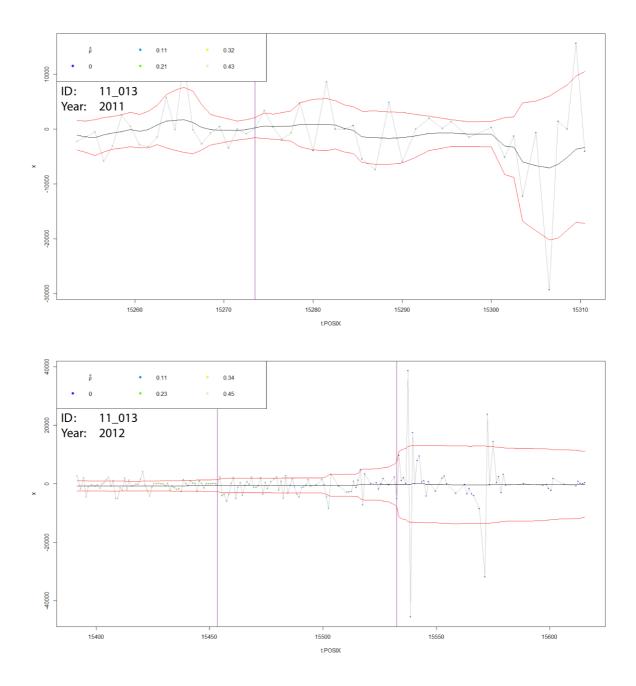


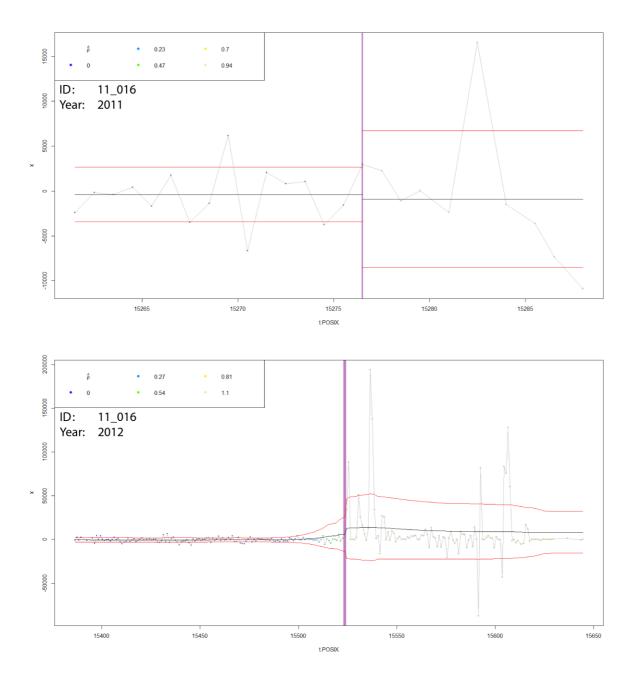


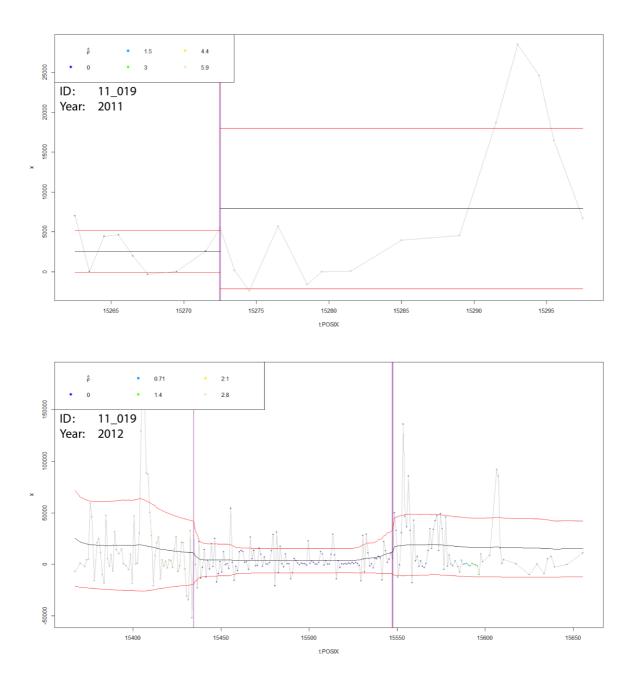


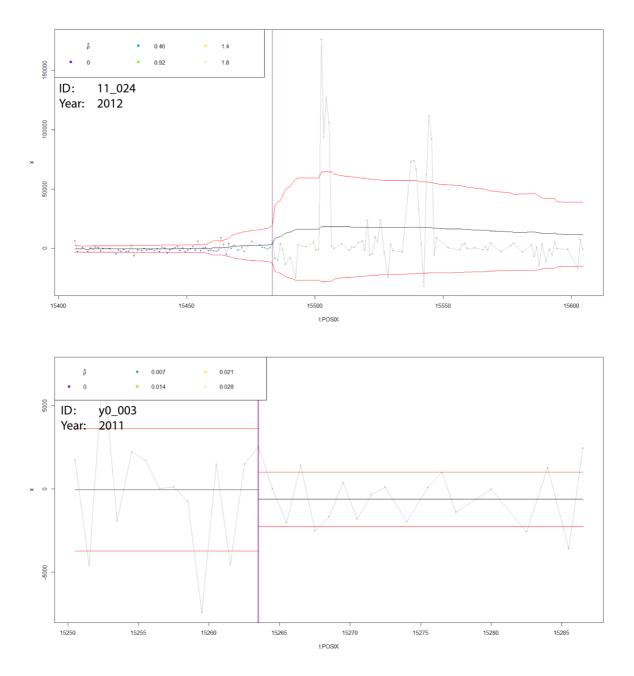


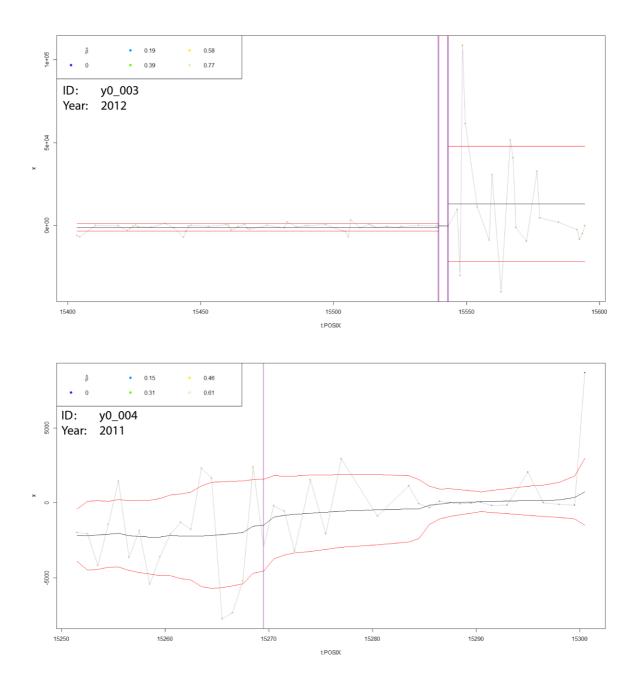


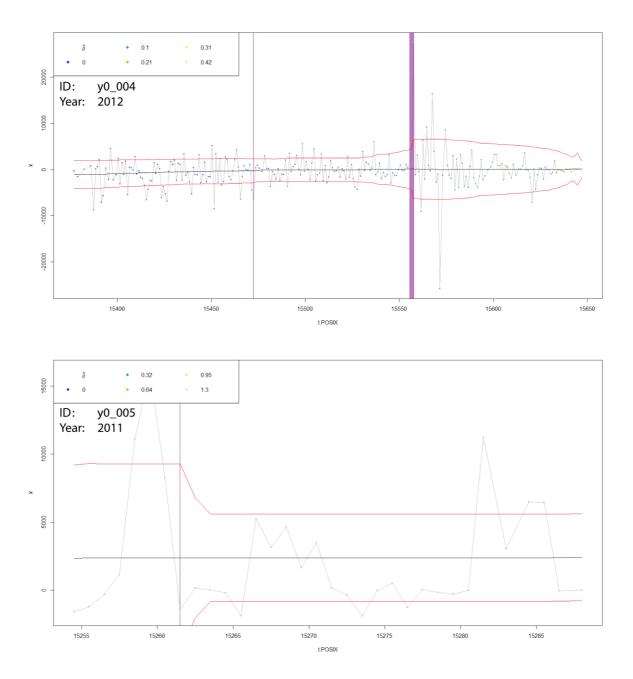


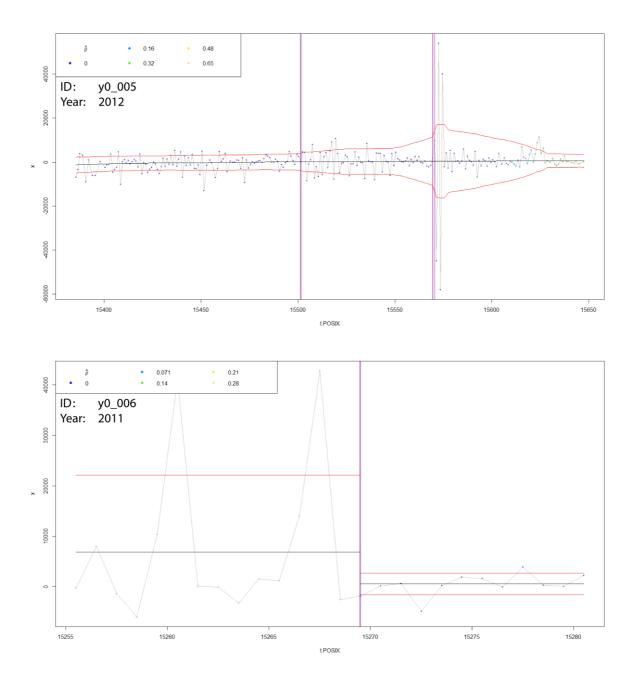












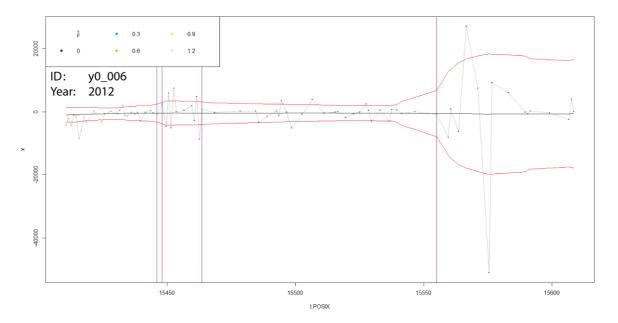


Figure A2. Figures showing output from the behavioral change point analysis (bcpa) for identification of the most likely behavioral change points (here, GPS locations) over the study period (x-axis: t.POSIX) from March to October in 2011 (t.POSIX: March \approx 15000 and October \approx 15300) and 2012 (t.POSIX: March \approx 15400 and October \approx 15550). Each point refers to one location and day. Each behavioral change point denotes by purple vertical lines. Different phases of movement behavior are drawn by horizontal lines showing mean- (black line) and st. dev. (red line) between the change points. Autocorrelated movement ^p is colorized from low- (blue dots) to high (yellow dots) where higher autocorrelation (here, denoted by light blue- [first phase] to yellow colors [last phase]) means a more directed movement (no account to the speed).

SENASTE UTGIVNA NUMMER

2013:8	Social and economic consequences of wolf (Canis lupus) establishments in Sweden. Författare: Emma Kvastegård
2013:9	Manipulations of feed ration and rearing density: effects on river migration performance of Atlantic salmon smolt. Författare: Mansour Royan
2013:10	Winter feeding site choice of ungulates in relation to food quality. Författare: Philipp Otto
2013:11	Tidningen Dagens Nyheters uppfattning om vildsvinen (Sus scrofa)? – En innehålls- analys av en rikstäckande nyhetstidning. Författare: Mariellé Månsson
2013:12	Effects of African elephant (<i>Loxodonta africana</i>) on forage opportunities for local ungulates through pushing over trees. Författare: Janson Wong
2013:13	Relationship between moose (<i>Alces alces</i>) home range size and crossing wildlife fences. Författare: Jerk Sjöberg
2013:14	Effekt av habitat på täthetsdynamik mellan stensimpa och ung öring I svenska vattendrag. Författare: Olof Tellström
2013:15	Effects of brown bear (<i>Ursus arctos</i>) odour on the patch choice and behaviour of different ungulate species. Författare: Sonja Noell
2013:16	Determinants of winter kill rates of wolves in Scandinavia. Författare: Mattia Colombo
2013:17	The cost of having wild boar: Damage to agriculture in South-Southeast Sweden. Författare: Tomas Schön
2013:18	Mammal densities in the Kalahari, Botswana – impact of seasons and land use. Författare: Josefine Muñoz
2014:1	The apparent population crash in heath-hares <i>Lepus timidus sylvaticus</i> of southern Sweden – Do complex ecological processes leave detectable fingerprints in long- term hunting bag records? Författare: Alexander Winiger
2014:2	Burnt forest clear-cuts, a breeding habitat for ortolan bunting <i>Emberiza hortulana</i> in northern Sweden? Författare: Cloé Lucas