Research article

Continental scale light-temperature extremes reveal key behavioural trade-offs

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Abstract.

Daily rhythms determine ecological interactions, but we rarely know how animals convert activity schedules into movement and space use across extreme light–temperature regimes. Using multi-annual GPS data from 76 Golden Eagles (*Aquila chrysaetos*) tracked across Scandinavia and Iberia (spanning 35° latitude), we quantified diel activity and displacement to test how photoperiod and temperature reshape time budgets and movement. Activity was strongly diurnal with a midday peak, but its relationship with daylight was non-linear and latitude-specific: Scandinavian eagles shifted south in winter and remained active near freezing, whereas Iberian eagles were nomadic and reduced activity during long, hot days. Displacement peaks diverged from activity peaks, showing interactive light–temperature effects, greater movements by immatures, reduced movements during breeding, and winter maxima despite limited daylight. This partial decoupling reveals latitude-dependent movement–activity trade-offs: temperature alters the match between available active time and conditions for efficient travel, reshaping displacement and space use.

Keywords: climate change, daylength, energy landscape, migration, plasticity, space use.

Introduction

Species and their populations that are distributed across latitudes experience vastly different photoperiods. For example, near the poles, they may face continuous daylight in summer and extended darkness in winter, whereas near the equator, day length stays fairly stable year-round (Saikkonen et al., 2012). This provides a natural experiment to study how species adapt their biological activity to extreme light conditions as well as seasons (Steiger et al., 2013). Importantly, these adaptations are unlikely to involve timing of activity alone: for wide-ranging species, changes in the available time to be active can translate into compensatory changes in how much space they use and how far they move while active, creating potential activity–movement trade-offs across latitudes. Some species exhibit strong endogenous (internal) rhythms that persist regardless of external light cues, while others adjust their clocks dynamically (Eriksen & Wabakken, 2018; Pokrovsky et al., 2021). Comparing populations across latitudes can reveal how much of their circadian control is genetically hardwired versus how much is shaped by local environmental conditions (Ensing et al., 2014).

Differences in light exposure across latitudes could influence migration timing, breeding cycles, metabolism, hunting strategies and predator avoidance strategies (Ashley et al., 2013; Eriksen & Wabakken, 2018; Heurich et al., 2014; Sockman & Hurlbert, 2020; Steiger et al., 2013; Sunde et al., 2024). Investigating these adaptations can shed light on how environmental constraints shape biological patterns and processes such as behaviour, life history and demography (Ensing et al., 2014; Eriksen & Wabakken, 2018; Heurich et al., 2014). However, wide latitudinal distribution also implies diverse temperature conditions. In the Northern Hemisphere, higher latitudes are typically associated with colder climates, while lower latitudes are more frequently subjected to extreme heat. Temperature can constrain not only when animals are active, but also the cost of movement and the distance travelled per unit time, potentially forcing individuals to balance energy intake with thermoregulatory demands. As global temperatures shift due to climate change, species with a wide latitudinal range may face altered seasonal cues in different daylight regimes (Ensing et al., 2014; Heurich et al., 2014). Studying their plasticity can help predict which populations may be more resilient or vulnerable to these changes (Heurich et al., 2014; Steiger et al., 2013).

Most raptors are diurnal organisms, meaning they are active during the day and rest at night. These patterns align with the availability of prey, optimal hunting conditions (e.g., thermals for soaring species), and vision-dependent predation (Alarcón et al., 2017; Potier et al., 2018; Vidal-Mateo et al., 2022). Raptors, however, remain underrepresented in chronobiology studies, despite their ecological importance and the wide range of environmental conditions they experience. Moreover, because many raptors are wide-ranging, understanding their responses to photoperiod and temperature requires linking diel activity to movement behaviour. Individuals may respond to constraints by compressing activity into shorter windows with higher movement intensity, by spreading activity over longer periods with lower displacement rates, or by shifting both timing and space use to match favourable “energy landscapes.” In addition, species or populations may adopt different movement strategies, including migration, nomadism, or territoriality, depending on environmental conditions, prey availability or age class (Bourbour et al., 2024; Chaubet et al., 2025; Poessel et al., 2022; Singh et al., 2021). Changes in daylight duration and weather regulate key seasonal behaviours in raptors, such as migration, breeding, and molt cycles, but may also alter the distances travelled and areas used to meet energetic demands under different environmental constraints.

Many migratory birds use photoperiod cues to initiate migration timing, with some species showing circannual rhythms that persist even in controlled lab conditions (Fusani et al., 2009; Zuo et al., 2023). Large soaring raptors like eagles, vultures, and kites depend on thermals (rising warm air) for energy-efficient flight, increasing their activity to midday hours when thermal updrafts are strongest (García-Jiménez et al., 2018; Krone et al., 2009). This coupling of time-of-day and flight subsidies implies that avoiding unfavourable conditions (e.g., darkness, cold, or heat) may carry movement consequences: shifting activity away from thermal peaks could reduce soaring opportunities and change the energetic cost per kilometre moved, potentially affecting displacement and space use. However, similar species could have different responses to extreme climate events (Naves-Alegre et al., 2025). Wind conditions also play a role, with some species adjusting their flight times based on weather conditions rather than strict internal rhythms (Lanzone et al., 2012; Yates et al., 2001). Although the effects of weather and temperature on raptor behaviour have been studied (Braham et al., 2015; Nägeli et al., 2022; Naves-Alegre et al., 2025), important gaps remain regarding diel activity patterns and—crucially—how these patterns translate into movement and space-use trade-offs across latitudes (Bohrer et al., 2012).

We studied multiannual activity and daily displacement of adult and immature Golden Eagles across Scandinavian and Iberian peninsulas, spanning ~35° latitude (~3,900 km). We predicted stronger seasonal shifts in the north, where extreme photoperiods should drive high summer flexibility (potentially extending activity under prolonged daylight) but sharply constrain activity in winter, whereas southern eagles should show comparatively stable annual patterns (Pokrovsky et al., 2021). We further tested how temperature interacts with daylight to shape both activity and movement: we expected northern eagles to remain active at sub-zero temperatures but reduce activity during the coldest conditions, while at lower latitudes high temperatures should suppress activity, potentially shifting it toward cooler (crepuscular) periods (Bohrer et al., 2012). We also expected age-specific strategies, with territorial adults in both regions and contrasting immature behaviour—more migratory in the north and more nomadic in the south—yielding latitude-dependent movement–activity trade-offs in how individuals balance *when* to be active with *how far* to travel (Masello et al., 2021; Padró et al., 2025). Finally, we anticipated seasonal resource demands to modulate displacement, with adults increasing space use during breeding and immatures showing peak displacement during migration in the north and more weather- or resource-driven peaks in the south.

Material and Methods

Study species and sites

The Golden Eagle (*Aquila chrysaetos* Linnaeus, 1758) is a widely distributed raptor across the Northern Hemisphere, ranging from North America and Eurasia to North Africa, with highly variable daylight cycles (Watson, 2010). It occupies diverse habitats, from tundra and boreal forests in the north to mountainous regions, open grasslands, steppe habitats and deserts further south (Watson, 2010). In Scandinavia they thrive in rugged landscapes with abundant prey (Singh et al., 2016). Forestry is the main land use across the Golden Eagle range in Scandinavia. The boreal forest landscape is dominated by Norway Spruce (*Picea abies*) and Scots Pine (*Pinus sylvestris),* managed primarily by clear-cutting and even-aged silvicultural practices (Ecke et al., 2013; Esseen et al., 1997). The remaining landscape consists of a mosaic of forests interspersed with wetlands, including lakes, streams and mires, and patches of agricultural land (Helmfried, 1996). In the Iberian region, the subspecies *Aquila chrysaetos homeyeri* Sewertzow, 1888 live from rugged mountain territories to open dried areas, adapting to a wide variety of habitats and elevations (López-Peinado et al., 2024). In Iberia Golden eagles habitat varies from mountain areas to forests and shrublands mixed with agricultural land (López-Peinado et al., 2024). The southern areas are characterized by typical mediterranean landscape, with oaks evergreen (e.g. *Quercus ilex, Q. suber*) and pines (e.g., *Pinus halepensis, P. pinaster, P. nigra*). The Atlantic region, especially the northern areas, is normally composed of deciduous forests with broadleaf trees such as *Quercus robur*, *Fagus sylvatica* or *Betula sp*.

Golden eagles are opportunistic and their diet varies regionally, consisting primarily of mammals like lagomorphs, but they also take birds, ungulates, reptiles, and carrion (Clouet et al., 2017; Sánchez-Zapata et al., 2010; Singh et al., 2024). Breeding pairs are territorial and maintain large home ranges, while immatures adopt a range of movement strategies from nomadism to seasonal migration (Miller et al., 2016; Sandgren et al., 2014; Soutullo et al., 2006). In northern regions, their ecology is shaped by seasonal prey availability, extreme weather, and long migration routes, with some populations migrating south during winter while others remain year-round (Singh et al., 2021, 2024). In contrast, in southern regions, adults stay in their territories all year while immatures are vagrants until they settle in their own territory (Chaubet et al., 2025; Fernández-Gil et al., 2023).

Data collection

We tracked 76 Golden Eagles (40 adults and 36 immatures) across Scandinavia and Iberia between 2010 and 2025. Adults were captured using remote-controlled bownets or automatic folding net traps following established protocols (Bloom et al., 2007, 2015; Jackman et al., 1994) and fitted with solar-powered, backpack-mounted GPS/GSM transmitters attached with Garcelon harnesses (García et al., 2021). In Sweden, transmitters included 75g Microwave Telemetry Inc. (USA), 140g VectronicAerospace GmbH (Germany) and 70g Cellular Tracking Technologies Inc. (USA), with location errors ranging from 10–18 m. In Spain, eagles were tagged with 50g and 42g e-obs GmbH (Munich, Germany) devices, with location errors ranging from 2–10 m. Immature individuals in both countries were tagged as nestlings, approximately two weeks before fledging in Sweden (Sandgren et al., 2014) and at around 45 days old in Spain. Tracking periods ranged from six months to eight years, with a minimum of 750 recorded locations per bird. Eagles were distributed across latitudes 55°–71°N and longitudes 10°–29°E in Scandinavia, and 36°–43°N and –6°–1°E in Iberia (Figure 1). For Spain movement data were stored and downloaded from Movebank using the R package *move* (Kranstauber et al., 2024).

In both countries, immatures were classified as individuals <5 years old, based on plumage patterns (Table 1). All GPS tagging procedures were carried out in accordance with relevant ethical and legal regulations. In Sweden, the work was approved under Ethical Permit Nos. A57-10, A58-10, A57-10A, A33-13, and A11-2019 issued by the Swedish Board of Agriculture (Jordbruksverket), and Research Permit No. NV-07710-19 issued by the Swedish Environmental Protection Agency (Naturvårdsverket). In Spain, permissions were granted by the respective regional administrations, including: Madrid (14/149250.9/20 and 10/488052.9/24), Toledo (AUT TO 09-23 and 20-24), Soria (202210700009438, 20231070000100, and AUES/CYL/204/2024), Álava (22-014/11 and 24/013-7), and Murcia (AUF/2024/0092).

Temperature data for each eagle location was downloaded from Copernicus Data Store (CDS) using *ecmwfr* (Hufkens et al., 2019) and ncdf4 (Pierce, 2019) R packages (R Core Team, 2024). We obtained information on daylight period, including sunrise and sunset times, from the *suncalc* R package (Thieurmel & Elmarhraoui, 2024).

Data processing and analyses

Firstly, we prepared and filtered GPS location data to accurately assess Golden eagle activity and movement patterns. All locations from both countries were referred to Coordinated Universal Time (UTC). Because Golden eagles are diurnal animals, we selected only those locations recorded from 1 hour before sunrise to 1 hour after sunset. To ensure data quality, especially given the differences in GPS recording schedules between countries and challenges in recording during the Swedish winter, we included only days with at least 1 location every 2 hours. For immatures, we also removed the first month of data to ensure that all locations were recorded after fledging. This filtering resulted in a dataset of 2,021,659 GPS records. We then determined the threshold speed to classify an individual as in motion (i.e active periods) by analyzing GPS accelerometer speeds corresponding to confirmed stationary individuals captured by camera traps at perches or nests. A speed threshold of 0.5 m/s was used to classify an individual as active vs. stationary (mean speed during stationary periods = 0.15 m/s; 95% of values ≤ 0.5 m/s). Accordingly, each GPS location was classified as either active (1) or stationary (0) based on the speed threshold.

Using this processed database, we calculated several activity metrics: Proportion of day Active (hereafter PA), Total Active Hours (TAH), and Maximum Straight-line Distance (MSD) travelled per day. PA represents the percentage of the active time by an individual in relation to specific temperature and daylight hours, while TAH was the number of hours spent active by an individual in relation to temperature and daylight hours. MSD corresponds to the straight-line distance between the two furthest locations of an individual within a day. Therefore, Proportion of day active normalises activity relative to specific day lengths or temperatures, so it reflects temporal allocation rather than absolute time. On the contrary, total active hours and MSD reflect behavioural flexibility in exploiting available daylight or temperature ranges. We estimated the

PA as the mean of moving (1) or stationary (0) locations for each individual, latitude, temperature and daylight hours. The TAH was estimated as the PA multiplied by the total number of daylight hours. We estimated the Maximum Straight Distance for each individual id and day using the package *geosphere* in R studio.

To examine how eagle activity responds to temperature and daylight variation across latitudes, we fitted Generalized Additive Mixed Models (GAMMs) using the *mgcv* package (Wood, 2017) in RStudio. We modelled each response variable separately (PA, TAH, and Maximum Straight Distance), using a logit link for PA (Beta family) and Gaussian families for TAH and Maximum Straight Distance. The numeric explanatory variables, temperature (ºC), daylight (hours) and latitude were rounded to the unit. We used the dredge function from the *MuMIn* package (Kamil, 2016) to select the best-fitting model (i.e., with the lowest AIC) from a full model that included all pairwise interactions among the three predictor variables: Temperature × Daylight, Daylight × Latitude, and Latitude × Temperature, including individual id as random effect.

In order to test whether the movement of the individuals was affected not only by natural conditions (temperature, daylight hours) but also by age class, we performed a fourth model with Maximum Straight Distance as response variable using temperature, daylight hours and age class as predictors for the three response variables. Similarly, we used the dredge function to select the best-fitting model for the pairwise combination of predictors, with individual id as a random effect. We selected the best model using AIC.

We used Variance Inflation Factor (VIF) to assess multicollinearity among our variables, considering VIF above 2 as indicative of potential multicollinearity issues. To visualize how response variables vary across the temperature (-11 to 42ºC for Iberia and -24 to 31 ºC for

Scandinavia) and daylight hours gradients (8 to 16 hours for Iberia and 3 to 24 hours for Scandinavia), we generated prediction grids using 1-unit increments for temperature and latitude and 1-hour increments for daylight, using the *expand.grid* function in R. We used the function *predict* to estimate the value for each response variable according to the best-fitting model. Finally, we represented the response variable across predictors while fixing all other variables at their median values. Graphs were created using the *ggplot2* package.

Results

At Northern latitudes, eagles ranged across the entire Scandinavian peninsula, although most activity was concentrated in Scandinavia (Figure 1). At Southern latitudes, eagles were mostly restricted to the eastern and central parts of the Iberian Peninsula, due to their breeding or natal territories (Figure 1). Most of the activity concentrated during daylight hours (between sunrise and sunset) and peaked at midday for most of the months and latitude ranges (Figure 2). In the Scandinavian peninsula they followed a clear migration pattern, especially immatures, abandoning northern latitudes (66-72) in the winter months (Figure 2), and spending time in the south, returning to northern latitudes again during the summer months (Figures 2 and S1). In contrast, in the Iberian Peninsula, they displayed a nomadic pattern. In both cases, the PA decreased during the summer months (June to August) and increased in March and April. Additionally, some adult individuals remained within their territories (Figure S1). This could explain why some individuals did not migrate and stayed between latitudes 62-66 (Figure 2). Together, these spatial patterns show that latitude-driven constraints affect both activity timing and realized space use, revealing trade-offs between how long individuals are active and how far they move (km) under different light and thermal regimes.

For both PA and TAH, the best-supported models (lowest AIC) included significant two-way interactions among temperature, daylight, and latitude, as well as significant random effects (Table 2). In Scandinavia, PA increased from ~17% at 3 h of daylight to a peak of ~37% at 13 h, then declined toward 24 h, whereas in Iberia PA peaked earlier (~44% at 11.5 h) and declined sharply to ~26% at 16 h (Figure 3A). TAH in Scandinavia rose from ~1.5 h at 3 h of daylight to nearly 5h at ~15 h, with a mid-summer dip and recovery by 24 h, while in Iberia TAH peaked at ~4 h around 12.5 h of daylight and declined to ~2 h at 16 h (Figure 3C). Notably, the daylight–activity relationships were not monotonic (Figure 3A&C), indicating that extreme photoperiods shift activity timing rather than simply increasing activity, with movement either tracking or compensating for these time constraints.

In response to temperature, eagles in Scandinavia were more active at colder temperatures than in Iberia. In Scandinavia, PA followed a typical gaussian curve in relation to temperature, peaking at 3ºC while in Iberia peaked at ~15 °C (Figure 3B). Although maximum TAH was similar between the two countries (~4 h), it occurred at markedly different temperatures around 0 °C in Scandinavia and 12 °C in Iberia (Figure 3D). Thus, Iberian eagles showed higher activity levels at warmer temperatures compared to their northern counterparts (Figure 3D).

Eagles also showed varied responses in terms of their movements. The best-supported MSD models (lowest AIC) included significant two-way interactions among temperature, daylight, and latitude/age class, as well as significant random effects. In both cases, all the interaction terms were significant (Table 2). Immatures from both countries consistently travelled greater distances than adults throughout the year (Figure 4A). Adults showed greater variability, flying the longest distances shortly before the breeding season in Scandinavia and after the breeding season in Iberia, whereas immatures covered their longest distances in spring. However, the absolute greatest distances for both adults and immatures occurred during the winter months (Figure 4A). At high latitudes, winter's short days and harsh temperatures create a movement–activity trade-off, with individuals maintaining displacement by concentrating movement into limited favourable windows and/or adjusting spatial strategy (e.g., migratory relocation).

In Iberia, both adult and immature eagles travelled the greatest distances at ~12 hours of daylight, declining as daylight increased or decreased (Figure 4B). In contrast, movement patterns in Scandinavia showed greater variability between age classes. Adults tended to travel more during two distinct periods: when daylight ranged between 14 and 20 hours, and during the shortest days with only 3 hours of daylight. Immatures, on the other hand, increased their distance travelled per day during the longest days and around 13 daylight hours, coinciding with the onset of migration. This divergence indicates that movement (km) does not simply mirror activity levels: at northern latitudes, both very short and very long days can be associated with elevated displacement, suggesting flexible spatial responses to seasonal constraints rather than a single monotonic relationship. As with activity levels, Iberian eagles covered longer distances at higher temperatures compared to their Scandinavian counterparts (Figure S2). Although immatures travelled more than adults in both regions, adults tended to move during warmer conditions (Figure 4C). The partial decoupling of activity and MSD peaks across temperature and daylight gradients suggests that eagles adjust space use and daily displacement to buffer environmental constraints, trading off activity duration against movement intensity depending on latitude, season, and age class.

Discussion

Here, we show that Golden Eagles express flexible activity and movement patterns shaped by photoperiod across latitudes and modulated by temperature and life-history constraints. Across the gradient, daylight emerged as a major structuring cue for activity, but responses were non-linear and differed between regions. In particular, activity increased from short photoperiods up to intermediate day lengths but did not scale proportionally under very long days. This pattern suggests behavioural flexibility in how eagles allocate time and effort across the 24-hour cycle, likely reflecting an interplay between internal rhythms, foraging opportunities, and environmental constraints.

Both PA and TAH were best explained by interactions among temperature, daylight, and latitude (Table 2), indicating that photoperiod effects depend on the thermal and latitudinal context. In Scandinavia, PA increased to a peak around 13 daylight hours before declining, while TAH generally increased with long photoperiods but showing non-linear patterns. This combination—declining PA but relatively high TAH under long days—suggests that longer photoperiods may allow activity to be spread more broadly across time (i.e., reduced concentration of activity in the day), rather than simply increasing the fraction of the day active. In Iberia, both PA and TAH peaked at intermediate day lengths (around the equinox period) and declined as days became longer, indicating that eagles did not benefit from increasing photoperiod in summer to the same extent as in the north. These results align with the broader idea that diurnal birds can exploit longer daylight for foraging and movement, but that the benefits of longer days are not uniform across latitudes and environments (Pokrovsky et al., 2021; Sockman & Hurlbert, 2020).

Temperature further mediated eagle activity. In Scandinavia, PA and TAH peaked near freezing, indicating that eagles remain active under very cold conditions despite limited daylight. In Iberia, activity peaked at warmer temperatures (PA around 15 °C; TAH around 12 °C) and declined as temperatures rose, consistent with heat-related constraints during extended summer daylight. Importantly, these temperature relationships point to a key mechanism for movement–activity trade-offs across latitude: when temperatures constrain activity (heat in the south, extreme cold in the north), individuals may either (i) reduce activity and displacement, or (ii) maintain necessary movement by concentrating travel into narrower favourable windows, thereby changing displacement per unit active time.

Movement (MSD) was also best explained by interacting effects of temperature and daylight (and either latitude or age; Table 2), but movement responses did not track activity in a simple way, supporting partial decoupling between "being active" and "how far to travel." In Iberia, both adults and immatures travelled greater distances at intermediate day lengths (~12 h), with reduced MSD under both shorter and longer days. In Scandinavia, responses differed more strongly by age class: adults showed two movement peaks—during long days (14–20 h) and also during the shortest days (~3 h)—while immatures increased distance travelled during the longest days, coinciding with migration onset. Notably, the greatest MSD occurred during winter for both age classes, despite winter being the most constrained period in terms of light and temperature. This winter peak is consistent with a movement–activity trade-off framework: when time available for foraging is compressed, individuals may still need to increase displacement (km)—either through broader ranging or migration—to meet energetic requirements under harsh seasonal conditions.

Immatures travelled farther than adults throughout the year, consistent with dispersal, exploratory behaviour, and (in Scandinavia) migratory movement, as seen in other raptors (García-Jiménez et al., 2018; Singh et al., 2017). Adults showed greater variability and tended to make longer movements outside the breeding season, including a post-breeding increase observed in both regions. While territoriality and parental duties likely constrain adults during breeding, the results suggest that adults may increase displacement when those constraints relax, and when seasonal conditions change the distribution or predictability of resources. In Scandinavia, adult movement peaks during winter likely reflect a combination of constrained light, thermal conditions, and seasonal shifts in prey/scavenging opportunities (Singh et al., 2021, 2024), whereas immatures showed movement patterns that align more strongly with seasonal transitions, including the migration period.

Temperature-driven movement patterns suggest that eagles move selectively under conditions that minimize transport costs. In both regions, MSD peaked at moderately warm temperatures (roughly 17–21 °C, differing by age class and country), and Iberian eagles generally moved longer distances at higher temperatures than Scandinavian eagles (Figure 4C, Figure S2). While this is consistent with the importance of flight subsidies and efficiency (e.g., thermals) for long-distance travel (Carrard et al., 2025; Lanzone et al., 2012), our findings highlight that movement intensity peaks under a narrower set of conditions than activity, suggesting that movement and activity are related but not interchangeable traits.

The seasonal redistribution of Scandinavian eagles away from the highest latitudes in winter indicates that migration is a major component of their spatial response to extreme photoperiod regimes. In contrast, Iberian eagles were more geographically restricted and exhibited nomadic movements, consistent with a strategy where shorter-term flexibility may be favored over long-distance seasonal relocation. Together, these patterns suggest that photoperiod may act as a seasonal “framework” for activity and movement—especially at high latitudes—while day-to-day expression of behaviour is strongly modulated by temperature and (likely) resource dynamics.

Climate change could alter the balance among light, temperature, and food availability that currently structures Golden Eagle activity and movement (Saikkonen et al., 2012). Warmer northern winters could reduce thermal constraints but would not change photoperiod, potentially reshaping the costs and benefits of migration and the movement–activity trade-offs observed under short days. If migratory or ranging decisions are strongly tied to photoperiod cues, behavioural schedules may remain similar even as prey phenology and availability shift, potentially creating mismatches with resources (Gilg et al., 2012; Kubelka et al., 2022). In Iberia, increasing summer heat could further compress favourable activity windows and reduce movement capacity during hot periods, potentially pushing individuals toward behavioural adjustments such as shifting activity toward cooler hours and/or using elevational refugia (Braham et al., 2015; Navarro-Serrano et al., 2020). Overall, our results suggest that plasticity in both activity timing and space use may provide resilience, but only within environmental limits—especially where temperature extremes increasingly interact with fixed photoperiod constraints.

Similar flexibility under extreme photoperiods has been documented across taxa, underscoring that daily schedules are often shaped by the interaction between internal timing and local environmental constraints. For example, some predators maintain diel-structured activity even when darkness is absent, whereas others redistribute activity across the 24-hour day under continuous daylight (Eriksen & Wabakken, 2018). In carnivorous mammals, activity patterns can shift with photoperiod and latitude and frequently track prey behaviour (Heurich et al., 2014), while in herbivores and other taxa endogenous rhythms may be weak and daily activity can respond strongly to external drivers such as temperature and disturbance (Ensing et al., 2014). These examples highlight a general principle: organisms can buffer photoperiod and thermal constraints by adjusting not only *when* they are active, but also *how intensively* they move and use space.

More broadly, species may compensate for short favourable windows by concentrating foraging and travel into brief periods ("time compression"), or by reducing movement costs through behavioural shifts such as using microclimates, changing habitat selection, exploiting wind or currents, or switching between sedentary and mobile tactics as conditions change. Such flexibility should be especially important for wide-ranging species, migrants, and central-place foragers, where meeting energetic demands depends on balancing time budgets against the distances required to access resources (Pokrovsky et al., 2021). In this context, our results suggest that Golden Eagles combine strong diurnality with flexible activity and movement, producing latitude, season, and life-stage-dependent movement–activity trade-offs.

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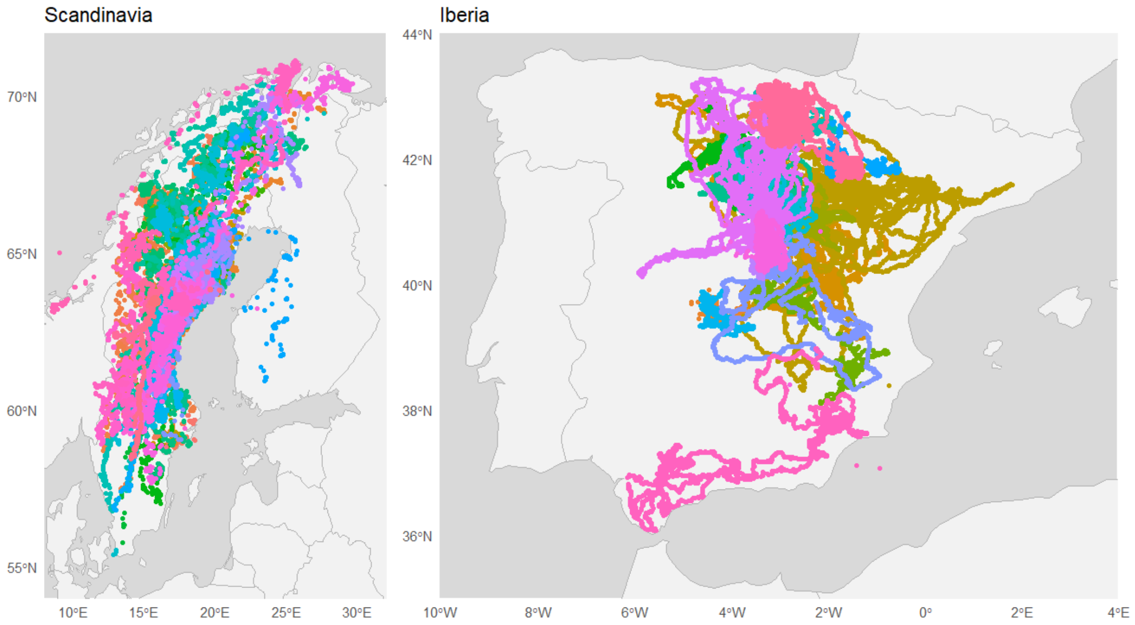

Figure 1. Locations for all the GPS tracked Golden eagles from Scandianvian and Iberian Peninsulas used in this study (n=76). Each color represents a different individual.

Figure 2. Golden eagles Proportion Active (blue ridgelines) for every month and hour of the day

558 by latitude ranges. Empty spaces (in white), mean there is no data for that month or hour.

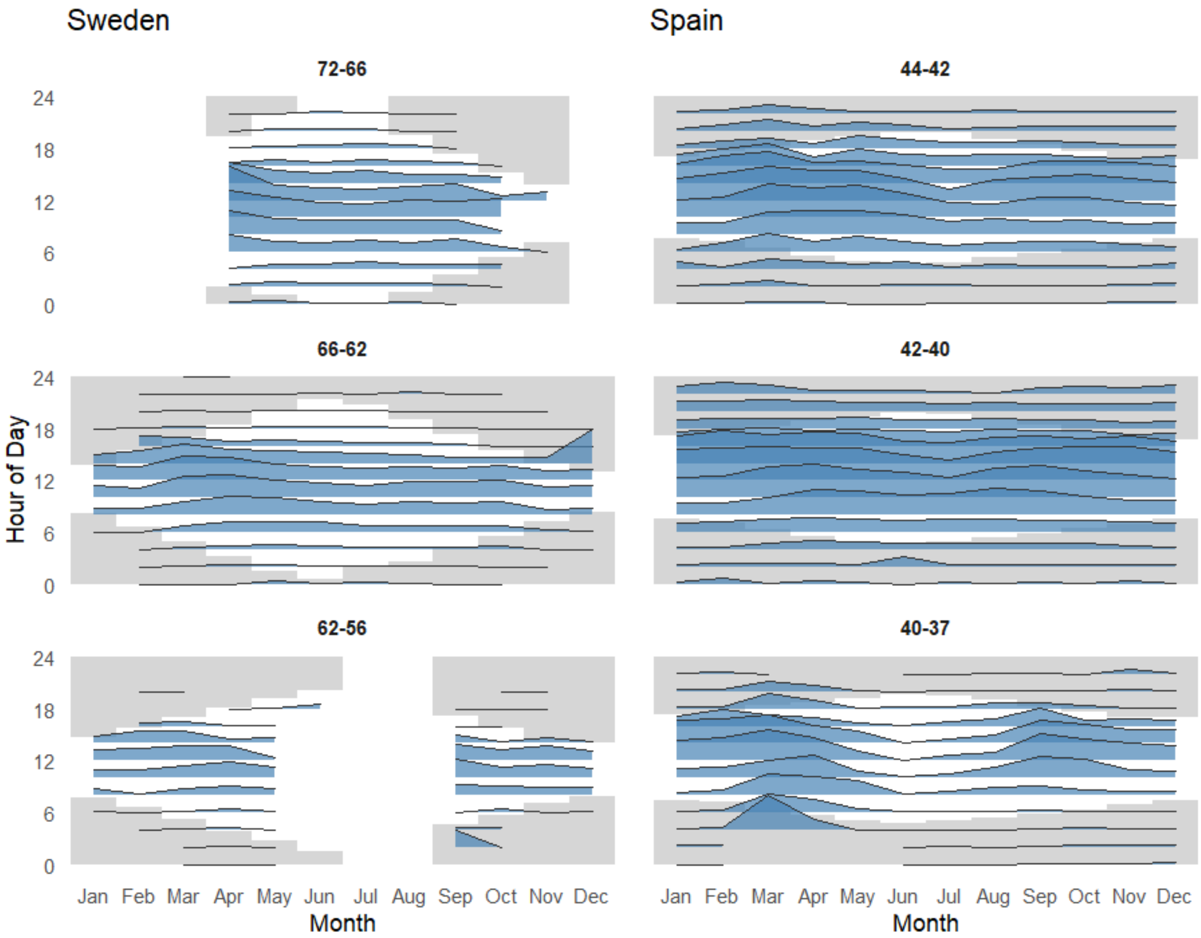

Figure 2. Golden eagles Proportion Active (blue ridgelines) for every month and hour of the day 558 by latitude ranges. Empty spaces (in white), mean there is no data for that month or hour.

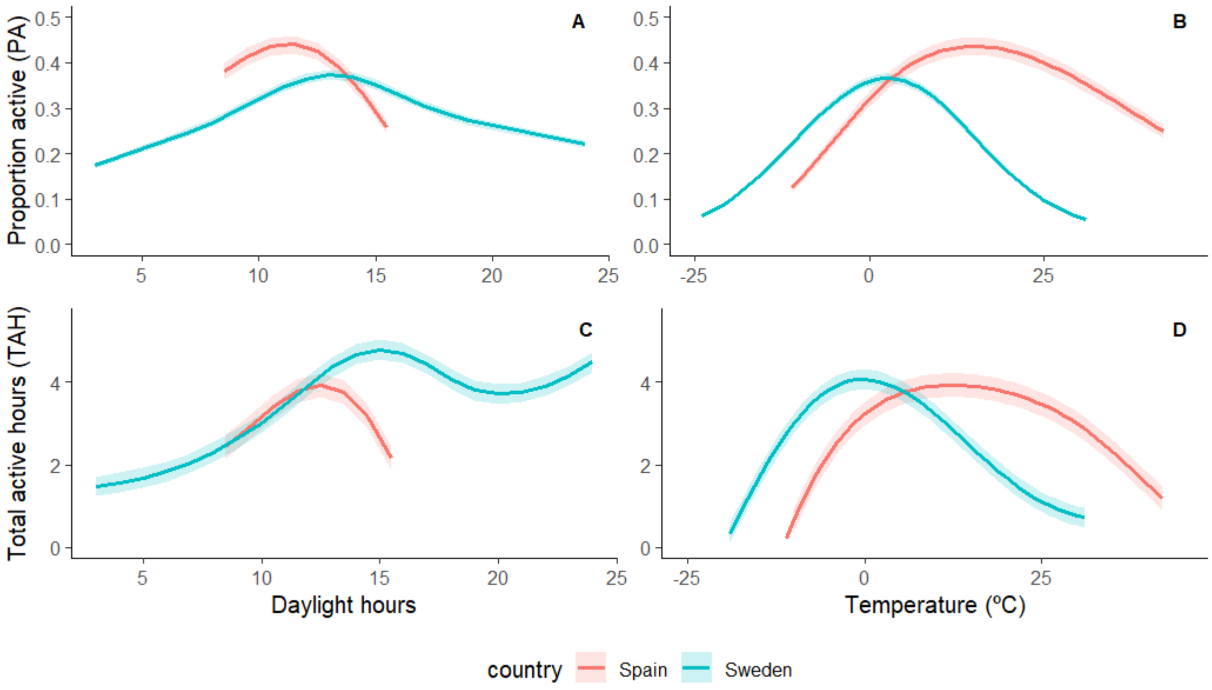

Figure 3. Golden eagles activity for Scandinavia and Iberia by daylight hours and temperature. Proportion Active (PA) in the upper row and Total Active Hours (TAH) in the lower row. Daylight hours in the left column and temperature in the right one. Lines in light blue for Scandinavia and red lines for Iberia. Plots are represented for the median values of the other predictor (15ºC and 3.5 ºC for Iberia and Scandinavia temperature respectively, and 12h daylight for both countries) and for Latitude 63ºN for Scandinavia and 40ºN for Iberia.

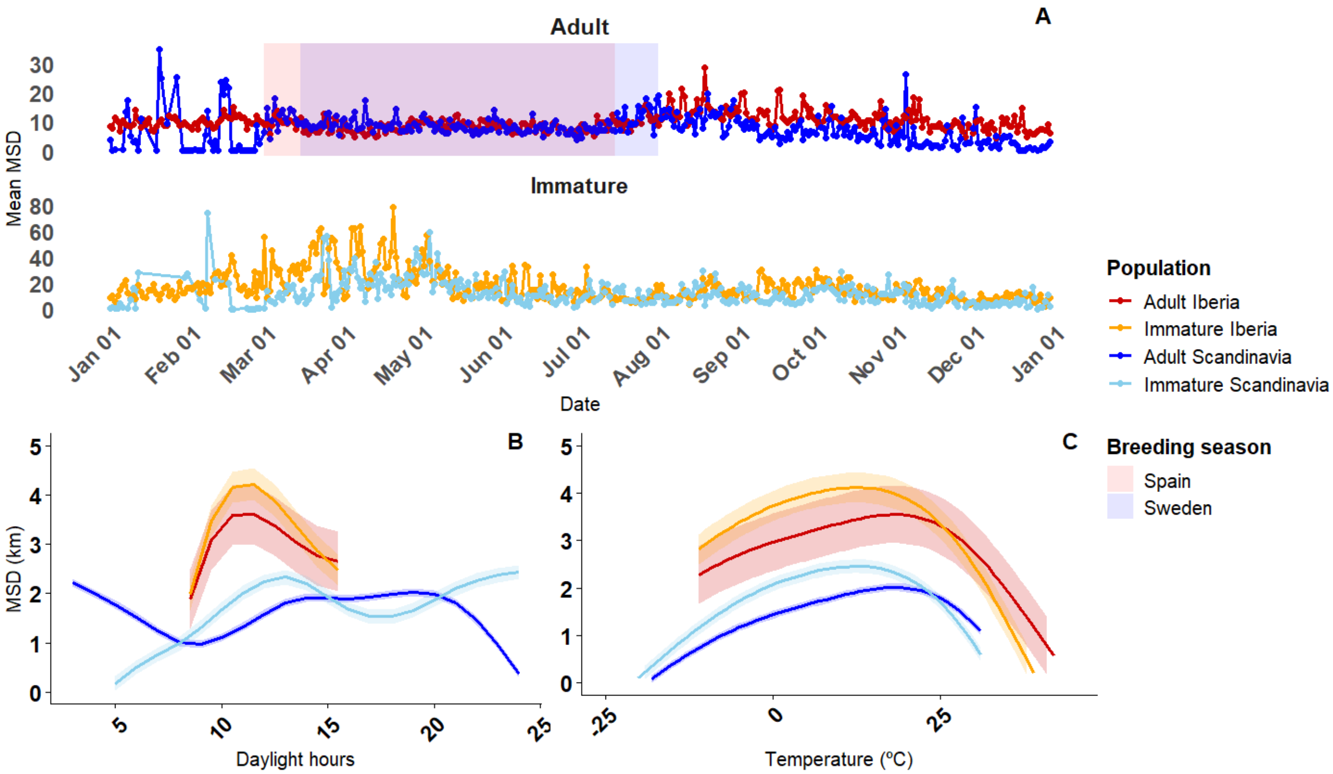

Figure 4. Maximum Straight Distance (in kilometres) travelled by Golden Eagles across countries and age classes, shown in relation to day of the year, daylight hours, and temperature. Plots are represented for the median values of the other predictors (12 h daylight for both countries; temperature and latitude of 3.5ºC and 63ºN for Scandinavia and 15 ºC and 40 ºN for Iberia. Estimates of the curves were calculated as the average for all the ids of each country and age class.

Table 1. Summary of GPS tracking data used for adult and immature Golden Eagles captured in Sweden and Spain. The table details sample sizes, study periods, tracking durations and other metadata, trapping methods and location accuracy. Coordinates indicate the approximate latitudinal and longitudinal range covered in each country.

Category	**Scandinavian Adults**	**Scandinavian Immatures**	**Iberian Adults**	**Iberian Immatures**
Number of Individuals	35	22	5	14
Study Period	2010–2020	2010–2020	2016–2025	2016–2025
Number of Locations	682,879	656,646	1,001,015	889,991
Coordinates (°N, °E)	55–71°N, 10–29°E	55–71°N, 10–29°E	36–43°N, –6–1°E	36–43°N, –6–1°E
Capturing Mode	Remote-controlled bow nets	Tagged as nestlings	Automatic folding net trap	Tagged as nestlings
GPS Transmitter Type & Weight	Microwave Telemetry (USA, 75g, 2010–11); Vectronic Aerospace GmbH (Germany, 140g, 2010–11); Cellular Tracking Technologies Inc. (USA, 70g, 2014)	Microwave Telemetry (USA, 75g, 2010–11); Vectronic Aerospace GmbH (Germany, 140g, 2010–11); Cellular Tracking Technologies Inc. (USA, 70g, 2014)	e-obs GmbH (Germany, 50g, 2016); e-obs GmbH (Germany, 2017–24)	e-obs GmbH (Germany, 42g, 2017–24)
Location Error	10–18 m	10–18 m	2–10 m	2–10 m

Table 2. Results of the models testing the effect of temperature, daylight and latitude/age class on activity and displacement of Golden Eagles. Table shows the summary of smooth terms for the models testing the lowest AIC. Models are referred to their response variable (Proportion Active (PA), Total Active Hours (TAH) and Maximum Straight Distance (MSD)). Estimate, standard error, Degrees of freedom (edf and Ref.df), Chi-square statistics/ F values, and p-values.

	Estimate	Std. Error	edf	Ref.df	Chi.sq/F	Pr(>IzI)/p-value
Model PA						
Intercept	-0.886	0.0424				<0.001
Temperature*Daylight			17.050	18.680	286.700	<0.001
Temperature*Latitude			10.390	12.390	241.100	<0.001
Daylight*Latitude			10.080	19.000	145.000	<0.001
s (id)			70.630	75.000	1618.900	<0.001
Model TAH						
Intercept	3.886	11.223				0.729
Temperature*Daylight			23.640	23.890	9145	<0.001
Temperature*Latitude			18.670	20.090	7387	<0.001
Daylight*Latitude			11.590	19.000	4241193	0.004
s (id)			20.46	76.000	59039	<0.001
Model MSD 1						
Intercept	-10410	11980				0.385
Temperature*Daylight			20.460	21.49	8136	<0.001
Temperature*Latitude			18.850	20.20	14712	<0.001
Daylight*Latitude			16.810	19.00	30642063	<0.001
s (id)			74.980	75.00	57757	<0.001
Model MSD 2						
Intercept	8534	1499				<0.001
Temperature*Daylight			21155	22.120	34.920	<0.001
Temperature*Latitude			2763	8.000	64.000	<0.001
Daylight*Latitude			6568	7.000	129.310	<0.001
s (id)			71777	75.000	72.110	<0.001