Research article

Fixed photoperiod and extreme temperatures decouple activity from movement in wide-ranging species

Abstract

Aim: Animals facing environmental change must balance when they are active with how far they move. Yet activity and movement are often treated as interchangeable behavioural responses, even though animals may remain active without travelling far or may concentrate long-distance movement into short favourable windows.

Location: Scandinavia and Iberia, spanning approximately 35 degrees of latitude and contrasting sub-Arctic, boreal, temperate and Mediterranean light-temperature regimes.

Taxon: Golden Eagle (*Aquila chrysaetos*), used as a wide-ranging model species for testing how fixed photoperiodic constraints and variable thermal conditions shape realised movement.

Methods: We analysed multi-annual GPS data from 76 adult and immature Golden Eagles tracked between 2010 and 2025. We quantified the proportion of daylight spent active, total active hours and maximum daily straight-line displacement, and tested how these responses varied with photoperiod, temperature, latitude and age class using generalized additive mixed models with repeated observations accounted for by individual identity and year.

Results: Activity and movement were related but fundamentally non-equivalent responses to environmental constraints. Photoperiod and temperature shaped how active time was translated into movement, with activity peaking under intermediate day lengths and latitude-dependent temperatures, whereas displacement peaked under distinct seasonal and thermal contexts. This partial decoupling indicates that animals can respond to environmental variation either by adjusting time spent active or by modulating movement intensity within active periods.

Additionally, similar displacement peaks emerged from different movement strategies, including migration in Scandinavia and nomadism in Iberia.

Main conclusions: Environmental constraints reshape not only how much time animals spend active, but how effectively that active time is converted into movement. Climate warming may alter movement opportunities while leaving photoperiodic constraints unchanged, creating mismatches between behavioural schedules, energetic demands, and resource availability across wide-ranging species.

Keywords: activity budget; animal movement; behavioural flexibility; climate change; day length; energy landscape; migration; phenology; thermal constraint

Introduction

Animals must allocate limited time and energy among foraging, resting, reproduction, predator avoidance and movement. In ecological studies, however, activity and movement are often implicitly linked: an animal that is active is assumed to have greater opportunity to move, forage or range (Halperin *et al.*, 2018; Rafiq *et al.*, 2023). This assumption may be misleading. Active time describes when an animal is behaviourally available to move, whereas movement describes how that time is converted into spatial displacement (Mayer *et al.*, 2017; Bonnefond *et al.*, 2025). Environmental constraints may therefore affect these two processes differently. Animals may compensate for short favourable periods by moving farther or faster during compressed windows, or they may remain active for long periods while reducing displacement when movement is energetically costly. Understanding when activity and movement become coupled or decoupled is essential for predicting how animals respond to environmental change (Nathan *et al.*, 2008; Shaw, 2020).

Latitudinal gradients in photoperiod provide a powerful natural experiment for testing this activity-movement relationship. Near the poles, animals may experience continuous daylight in summer and extended darkness in winter, whereas near the equator, day length remains comparatively stable throughout the year (Saikkonen *et al.*, 2012; Steiger *et al.*, 2013). Photoperiod determines the seasonal envelope of light available for visually mediated behaviours, but unlike temperature it is not altered by climate warming (Saikkonen *et al.*, 2012; Heurich *et al.*, 2014; Sockman & Hurlbert, 2020). Temperature, by contrast, modifies thermoregulatory costs, atmospheric conditions, snow cover, vegetation structure, prey availability, and the energetic cost of movement (Peers *et al.*, 2020; Gonnerman *et al.*, 2023; Rafiq *et al.*, 2023; Carrard *et al.*, 2025; Cisneros-Araujo *et al.*, 2026). The same amount of active time may therefore produce very different movement outcomes depending on the thermal, seasonal and resource context (Cohen *et al.*, 2018; Forsman *et al.*, 2026).

This distinction is relevant across taxa. For large herbivores daily activity can respond strongly to external drivers such as temperature and disturbance (Ensing *et al.*, 2014). Carnivores may shift activity to track prey or avoid humans, whereas movement distances depend on prey dispersion and landscape permeability (Heurich *et al.*, 2014; Sunde *et al.*, 2024). Marine predators, seabirds and aerial species may spend long periods active but achieve large displacement only when winds, currents or prey concentrations reduce travel costs (Masello *et al.*, 2021). Migrants and nomads may also share similar displacement peaks despite different underlying mechanisms, including seasonal relocation, dispersal, prospecting or resource tracking (Shaw, 2020; Kubelka *et al.*, 2022). Activity measures alone may therefore overestimate behavioural flexibility if animals cannot convert active time into effective movement, or underestimate flexibility if animals maintain movement by compressing travel into short favourable windows.

Wide-ranging aerial predators provide a useful system for testing these ideas because their movement depends simultaneously on daylight, weather, energetic subsidies, prey availability and life-history stage (Alarcón *et al.*, 2017; Eriksen & Wabakken, 2018; Singh *et al.*, 2021; Vidal-Mateo *et al.*, 2022; Naves-Alegre *et al.*, 2025). Most raptors are diurnal, and their visual foraging, hunting and movement are strongly structured by daylight (Alarcón *et al.*, 2017; Potier *et al.*, 2018; Vidal-Mateo *et al.*, 2022). For soaring species, movement is not only a function of motivation or activity, but also of atmospheric conditions that determine the energetic cost of flight. Large soaring raptors can use thermals, orographic uplift and wind to subsidize movement, often increasing flight around midday when uplift is strongest (Bohrer *et al.*, 2012; Lanzone *et al.*, 2012; García-Jiménez *et al.*, 2018). Thus, activity and displacement may become decoupled when individuals are active under poor movement conditions, or when they concentrate long-distance travel into short periods with favourable uplift, temperature or wind.

Golden Eagles (*Aquila chrysaetos,* Linnaeus, 1758) are particularly suitable for testing this framework because they occur across strong latitudinal gradients, include territorial, migratory and nomadic strategies, and occupy environments ranging from Mediterranean heat to northern winter darkness (Watson, 2010). In Scandinavia, Golden Eagles encounter extreme seasonal variation in daylight and temperature, and some individuals migrate or redistribute southward during winter (Sandgren *et al.*, 2014; Singh *et al.*, 2021). In Iberia, adults are largely resident and immatures are more nomadic or prospecting, experiencing hotter summers and more moderate photoperiodic variation (Soutullo *et al.*, 2013; Fernández-Gil *et al.*, 2023). These contrasts allow us to ask whether similar activity or displacement patterns arise from shared environmental constraints or from different movement strategies.

We used multiannual GPS tracking data from adult and immature Golden Eagles across Scandinavia and Iberia to test how animals convert active time into movement under contrasting light-temperature regimes. We asked three general questions. First, does activity increase proportionally with available daylight, or do animals show non-linear responses when photoperiod becomes extremely short or long? Second, does movement track activity, or do displacement peaks occur under different light-temperature conditions than activity peaks? Third, do life-history stage and movement strategy alter this activity-movement relationship? We predicted that activity and movement would be partly decoupled: northern eagles should face strong time compression during short winter days but may maintain displacement through migration or concentrated movement, whereas southern eagles should experience heat-related constraints during long summer days, reducing the conversion of active time into movement. We further expected immatures to show larger displacements than adults because dispersal, exploration and migration should increase movement demand independently of daily activity levels.

Material and Methods

Study species and sites

The Golden Eagle 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, Golden Eagles occur in rugged mountains and forested landscapes with abundant prey (Singh et al., 2016). Forestry is the main land use across much of the Scandinavian range, where boreal forest landscapes are 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, lakes, streams, mires and patches of agricultural land (Helmfried, 1996). In Iberia, the subspecies *Aquila chrysaetos homeyeri* occupies habitats ranging from rugged mountain territories to open dry areas, forests, shrublands and agricultural mosaics (Gambra *et al.*, 2026). Southern Iberian areas are characterized by Mediterranean landscapes with evergreen oaks (e.g. *Quercus ilex, Q. suber*) and pines (e.g. *Pinus halepensis, P. pinaster, P. nigra*), whereas Atlantic areas include deciduous forests dominated by broadleaf trees such as *Quercus robur*, *Fagus sylvatica* and *Betula spp*.

Golden Eagles are opportunistic predators and scavengers. Their diet varies regionally and consists primarily of mammals such as lagomorphs, but they also take birds, ungulates, reptiles and carrion (Sánchez-Zapata *et al.*, 2010; Singh *et al.*, 2024; Gambra *et al.*, 2026). Breeding pairs are territorial and maintain large home ranges, whereas immatures can adopt movement strategies ranging from nomadism and prospecting to seasonal migration (Soutullo *et al.*, 2013; Sandgren *et al.*, 2014; Miller *et al.*, 2016; Poessel *et al.*, 2022). In northern regions, ecology and movement are shaped by seasonal prey availability, snow, extreme weather and long migration routes, with some populations migrating south during winter while others remain year-round (Singh *et al.*, 2021, 2024). In southern regions, adults generally remain within territories year-round, while immatures are vagrant or prospecting until recruitment into a territory (Fernández-Gil *et al.*, 2023; Chaubet *et al.*, 2025).

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 bow nets or automatic folding net traps following established protocols (Jackman *et al.*, 1994; Bloom *et al.*, 2007, 2015) and fitted with solar-powered, backpack-mounted GPS/GSM transmitters attached with Garcelon harnesses (García *et al.*, 2021). In Sweden, transmitters included 75 g Microwave Telemetry Inc. (USA), 140 g Vectronic Aerospace GmbH (Germany) and 70 g Cellular Tracking Technologies Inc. (USA) units, with location errors ranging from 10 to 18 m. In Spain, eagles were tagged with 50 g and 42 g e-obs GmbH (Munich, Germany) devices, with location errors ranging from 2 to 10 m. Immature individuals in both countries were tagged as nestlings, approximately two weeks before fledging in Sweden (Sandgren *et al.*, 2014) and at approximately 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 degrees N and longitudes 10-29 degrees E in Scandinavia, and 36-43 degrees N and -6 to 1 degrees E in Iberia (Figure 1). For Spain, movement data were stored and downloaded from Movebank using the R package move2 (Kranstauber *et al.*, 2024). In both countries, immatures were classified as individuals younger than five years based on plumage patterns (Table 1).

Temperature data for each eagle location were downloaded from Copernicus Data Store (CDS) using the 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

We prepared and filtered GPS location data to assess activity and movement patterns. All locations from both countries were standardized to Coordinated Universal Time (UTC). Given the diurnal behaviour of Golden Eagles and our aim to compare how available daylight was converted into activity and movement, we selected locations recorded from one hour before sunrise to one hour after sunset. To ensure data quality, especially given differences in GPS recording schedules between countries and challenges in recording during the Swedish winter, we included only days with at least one location every two hours. For immatures, we removed the first month of data to ensure that all locations were recorded after fledging. This filtering resulted in 2,021,659 GPS records.

We determined the threshold speed used to classify individuals as in motion by analysing GPS accelerometer speeds corresponding to confirmed stationary individuals observed by camera traps at perches or nests. A speed threshold of 0.5 m/s was used to classify an individual as active versus stationary (mean speed during stationary periods = 0.15 m/s; 95% of values $\leq$ 0.5 m/s). Each GPS location was accordingly classified as active (1) or stationary (0).

Using this processed database, we calculated three daily behavioural metrics: proportion of daylight active (PA), total active hours (TAH) and maximum straight-line distance travelled per day (MSD). PA represents the proportion of daylight locations classified as active. TAH was calculated as PA multiplied by the total number of daylight hours and therefore represents the absolute amount of active time available for movement or foraging. MSD corresponds to the straight-line distance between the two most distant locations of an individual within a day and was calculated using the geosphere package in R. Conceptually, PA and TAH describe temporal allocation, whereas MSD describes realised spatial output in terms of the maximum daily displacement of individuals. Comparing these metrics allowed us to test whether active time and movement were coupled or decoupled under different light-temperature regimes.

To examine how activity and movement responded 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, using a logit link for PA (Beta family) and Gaussian families for TAH and MSD. Temperature (degrees C), daylight (hours) and latitude were rounded to the nearest unit. Smooth terms were specified using tensor product smooths (te) and thin plate regression splines (bs = 'tp') when all predictors were continuous. We used the dredge function from the MuMIn package (Kamil, 2016) to select the best-fitting model, defined as the model with the lowest AIC, from a full model that included all pairwise interactions among temperature, daylight and latitude: temperature x daylight, daylight x latitude and latitude x temperature. To account for repeated observations and interannual variation, we included year nested within individual identity as a random effect in all models.

To test whether movement differed by life-history stage, we fitted an additional MSD model including temperature, daylight and age class as predictors. Smooth terms were again fitted using tensor product smooths. When interactions involved age class, we used tensor products with factor-smooth interaction bases (bs = c('tp', 'fs')) to allow group-specific smooths. We selected the best-fitting model using AIC and retained year nested within individual identity as a random effect.

We used variance inflation factors (VIF) to assess multicollinearity among predictors, considering VIF values above 2 as indicative of potential multicollinearity. To visualize how response variables varied across gradients of temperature (-11 to 42 degrees C for Iberia and -24 to 31 degrees C for Scandinavia) and daylight (8 to 16 h for Iberia and 3 to 24 h for Scandinavia), we generated prediction grids using 1-unit increments for temperature and latitude and 1-hour increments for daylight. We used the predict function to estimate each response variable from the best-fitting model, holding other variables at their median values where appropriate. Graphs were created using ggplot2.

Results

At northern latitudes, eagles ranged across the Scandinavian Peninsula, although most activity was concentrated in Sweden (Figure 1). At southern latitudes, eagles were mostly restricted to the eastern and central parts of the Iberian Peninsula because of their breeding or natal territories (Figure 1). Activity was concentrated during daylight hours and peaked around midday for most months and latitude ranges (Figure 2). In Scandinavia, especially among immatures, individuals showed clear seasonal redistribution, abandoning northern latitudes (66-72 degrees N) in winter, spending time farther south, and returning north during summer (Figures 2 and S1). In contrast, Iberian eagles displayed a more nomadic pattern. In both regions, PA decreased during summer (June to August) and increased in March and April. Some adult individuals remained within their territories throughout the year (Figure S1), explaining why some individuals did not migrate and remained between 62 and 66 degrees N (Figure 2). These spatial patterns show that latitude-driven constraints affected both activity timing and realised space use, revealing trade-offs between how long individuals were active and how far they moved under different light-temperature regimes.

For both PA and TAH, the best-supported models included significant two-way interactions among temperature, daylight and latitude, as well as significant random effects (Table 2). In Scandinavia, PA increased from approximately 14% at 3 h of daylight to a peak of approximately 35% at 13 h, then declined toward 24 h. In Iberia, PA peaked earlier, at approximately 45% at 11.5 h, and declined sharply to approximately 27% at 16 h (Figure 3a). TAH in Scandinavia rose from approximately 0.7 h at 3 h of daylight to approximately 4 h at 15 h, with a mid-summer drop to slightly more than 2 h at 24 h of daylight. In Iberia, TAH peaked at approximately 4.5 h around 13.5 h of daylight and declined to approximately 2.7 h at both 16 h and 8.5 h (Figure 3c). These daylight-activity relationships were not monotonic, indicating that extreme photoperiods altered the distribution and concentration of activity rather than simply increasing active time.

Temperature responses also differed between regions. Eagles in Scandinavia were more active at colder temperatures than eagles in Iberia. In Scandinavia, PA followed a unimodal relationship with temperature, peaking at approximately 3ºC, whereas in Iberia PA peaked at approximately 14ºC (Figure 3b). Maximum TAH was similar between regions (approximately 4 h) although it occurred at markedly different temperatures: around 0-2ºC in Scandinavia and 12-14ºC in Iberia (Figure 3d). Thus, the thermal conditions associated with activity were region-specific, suggesting that temperature modified the temporal opportunity for behaviour differently across latitudes.

Movement responses differed from activity responses. The best-supported MSD models included significant two-way interactions among temperature, daylight and latitude or age class, as well as significant random effects (Table 2). Immatures from both regions consistently travelled greater distances than adults throughout the year (Figure 4a). Adults showed greater variability, travelling 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 daily distances for both adults and immatures occurred during winter (Figure 4A), despite winter imposing strong constraints in terms of short daylight and low temperature at northern latitudes.

In Iberia, both adult and immature eagles travelled the greatest distances at approximately 12 h of daylight, with displacement declining as daylight increased or decreased (Figure 4b). In Scandinavia, movement patterns showed stronger age-dependent divergence. Adults tended to travel more during two distinct photoperiodic contexts: when daylight ranged between 14 and 20 h, and during the shortest days with approximately 3 h of daylight. Immatures increased daily displacement during the longest days and around 13 h of daylight, coinciding with the onset of migration. A clear autumn peak in immature displacement was not evident, despite expected migratory movement, suggesting that seasonal displacement cannot be inferred from migration status alone. Similar displacement patterns in Iberian immatures, which are predominantly nomadic rather than migratory, indicate that comparable movement outputs may arise from different behavioural mechanisms. In Scandinavia, displacement may reflect seasonal relocation under photoperiod and prey constraints; in Iberia, similar movement peaks may arise from nomadic exploration, territorial prospecting or spatial variation in prey and thermal conditions. Across temperature gradients, Iberian eagles covered longer distances at higher temperatures than Scandinavian eagles (Figure S2). Immatures travelled more than adults within the same region, while all individuals, regardless of region or age class, travelled farthest around 18º C (Figure 4c). That maximum displacement contrast with their low activity level for that same temperature in both regions. Overall, the partial decoupling of activity and MSD peaks across temperature and daylight gradients suggests that eagles adjusted space use and daily displacement to buffer environmental constraints, trading off activity duration against movement intensity depending on latitude, season and age class.

Discussion

Our study shows that activity and movement are related but non-equivalent behavioural responses to environmental constraints. Across a 35-degree latitudinal gradient, Golden Eagles did not simply become more active or move farther when more daylight was available. Instead, photoperiod and temperature altered how active time was converted into displacement. Activity peaked under intermediate light-temperature conditions, whereas displacement peaks often occurred under different seasonal, thermal and life-history contexts. This partial decoupling suggests that animals can respond to environmental constraints in at least two ways: by changing the amount of time spent active, or by changing the movement intensity achieved within that active time. Recognising this distinction is important because studies that analyse activity alone may miss how animals maintain, reduce or redistribute space use under environmental change.

Photoperiod acted as a temporal framework for behaviour, but it did not generate a simple linear increase in activity or movement. In Scandinavia, activity peaked at intermediate photoperiods and, although it declined under longer day lengths, individuals still spent more hours active than during winter. In Iberia, activity also peaked around intermediate day lengths, although it declined more abruptly 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 conditional on latitude, season and environmental costs (Sockman & Hurlbert, 2020; Pokrovsky *et al.*, 2021). Available daylight therefore defines the temporal opportunity for movement, but it does not determine how much that opportunity is translated into movement.

Temperature further mediated the conversion of active time into movement. In Scandinavia, activity peaked near freezing, indicating that eagles remained active under cold conditions despite limited daylight. In Iberia, activity peaked at warmer but moderate temperatures and declined as temperatures rose, consistent with heat-related constraints during extended summer daylight. However, in both regions maximum displacement occurred at warm temperatures related to low activity levels. These temperature relationships point to a key mechanism for activity-movement trade-offs: when thermal conditions constrain behaviour, individuals may reduce both activity and movement, or they may maintain necessary movement by concentrating travel into narrower favourable windows. Movement responses support the latter mechanism in some contexts, because maximum displacement did not simply track the activity maxima. Instead, displacement often peaked under conditions that likely combined sufficient daylight with favourable energetic or atmospheric movement conditions, which ultimately reduce active time needed.

Life-history stage and movement strategy further altered this activity-movement relationship. Immatures travelled farther than adults within regions, consistent with dispersal, exploration, prospecting and migration (Singh *et al.*, 2017; García-Jiménez *et al.*, 2018; Shaw, 2020; Poessel *et al.*, 2022). Adults were constrained by territoriality and breeding, showing lower displacement during breeding and increased movement when those constraints relaxed. Thus, maximum displacement occurred out of the breeding season and at similar temperature for both regions and age classes, suggesting a species optimum. Yet, the comparison between Scandinavia and Iberia is especially informative because similar displacement outcomes appeared despite different movement strategies. Scandinavian immatures are expected to show movement associated with migration, whereas Iberian immatures are largely nomadic or prospecting. The absence of a strong autumn displacement peak in Scandinavia, together with similar displacement peaks in Iberia, suggests that comparable movement distances can arise from different behavioural mechanisms. Thus, displacement should not be interpreted as a direct proxy for a single behavioural state; it is the realised spatial outcome of interacting constraints, motivation and opportunity.

The activity-movement distinction is relevant far beyond raptors. Across taxa, environmental change environmental change can alter how activity timing translates into movement distance. Large herbivores may change their active time under disturbance or heat (Ensing *et al.*, 2014). Carnivores might alter activity to elude humans or pursue prey, yet landscape permeability and prey dispersion determine the distances they travel (Heurich *et al.*, 2014; Sunde *et al.*, 2024). Marine predators and seabirds may spend long periods active but achieve large displacement only when winds, currents or prey fields reduce travel costs (Masello *et al.*, 2021). Migratory species may show strong photoperiodic schedules while the profitability of movement changes with temperature, snow cover, vegetation phenology or trophic mismatch (Cohen *et al.*, 2018; Kubelka *et al.*, 2022). In all these cases, activity measures alone may overestimate behavioural flexibility if animals cannot convert active time into effective movement, or underestimate flexibility if animals maintain movement by compressing travel into short favourable windows.

Climate change is likely to alter this activity-movement relationship because temperature is changing rapidly, whereas photoperiod is not changing. Warming may reduce cold constraints in northern winters, potentially making movement energetically easier, but animals will still face the same short-day temporal window. Conversely, in warmer regions, increasing heat may compress the periods during which movement is energetically profitable, even when daylight is abundant (Naves-Alegre *et al.*, 2025). This creates an important asymmetry: climate warming can change the cost and opportunity of movement without changing the light-based schedules that many animals use to organise daily and seasonal behaviour (Saikkonen *et al.*, 2012; Forsman *et al.*, 2026). Such decoupling may generate mismatches between behavioural timing, movement opportunity and resource availability, particularly for migrants, central-place foragers and species whose movement depends on atmospheric, thermal or trophic conditions.

For Golden Eagles, warmer northern winters could reduce thermal constraints but leave winter photoperiod unchanged, 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, 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, using elevational refugia or altering habitat selection (Braham *et al.*, 2015; Navarro-Serrano *et al.*, 2020). These contrasting regional outcomes illustrate a broader biogeographical point: the consequences of climate warming will depend not only on species' activity rhythms, but on whether animals can convert active time into effective movement under changing thermal and resource conditions. Our results therefore support a general principle: behavioural flexibility should be evaluated not only by asking whether animals can change when they are active, but by asking whether they can maintain the movement needed to access resources, avoid risk and complete seasonal life-history events. Activity defines the temporal opportunity for movement, but environmental conditions determine how much movement is performed within that opportunity. This distinction provides a more mechanistic basis for predicting vulnerability across wide-ranging species exposed to novel combinations of fixed photoperiod, changing temperature and shifting resource landscapes.

References

Alarcón, P.A.E., Morales, J.M., Donázar, J.A., Sánchez-Zapata, J.A., Hiraldo, F. & Lambertucci, S.A. (2017) Sexual-size dimorphism modulates the trade-off between exploiting food and wind resources in a large avian scavenger. *Scientific Reports*, **7**.

Bloom, P.H., Clark, W.S. & Kidd, J.W. (2007) *Techniques_Manual_Chapter-12*. *Raptor Research and Management Techniques*, pp. 193–219. Hancock House Publishers, Surrey, British Columbia, Canada.

Bloom, P.H., Kidd, J.W., Thomas, S.E., Hipkiss, T., Hörnfeldt, B. & Kuehn, M.J. (2015) Trapping success using carrion with bow nets to capture adult golden eagles in Sweden. *Journal of Raptor Research*, **49**.

Bohrer, G., Brandes, D., Mandel, J.T., Bildstein, K.L., Miller, T.A., Lanzone, M., Katzner, T., Maisonneuve, C. & Tremblay, J.A. (2012) Estimating updraft velocity components over large spatial scales: Contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters*, **15**, 96–103.

Bonnefond, L., Pinaud, D., Bollache, L., Schmidt, N.M., Lang, J., Hansen, L.H., Sittler, B., Moreau, J. & Gilg, O. (2025) Intraseasonal variations in the spatial behaviour of an Arctic predator. *Movement Ecology*, **13**.

Braham, M., Miller, T., Duerr, A.E., Lanzone, M., Fesnock, A., LaPre, L., Driscoll, D. & Katzner, T. (2015) Home in the heat: Dramatic seasonal variation in home range of desert golden eagles informs management for renewable energy development. *Biological Conservation*, **186**, 225–232.

Carrard, T., Nourani, E., Jansing, L., Zimmermann, T., Sumasgutner, P., Tschumi, M., Jenny, D., Wikelski, M., Safi, K., Sprenger, M. & Scacco, M. (2025) Golden eagles regularly use gravity waves to soar in the Alps: new insights from high-resolution weather data. *Journal of the Royal Society Interface*, **22**, 227.

Chaubet, T., Itty, C., Hemery, A., Duriez, O. & Besnard, A. (2025) Prospecting movements during the transit phase of immature eagles are driven by age, sex and season. *Movement Ecology*, **13**.

Cisneros-Araujo, P., Cubero, D., Pinto, D., Salinas, P., Jiménez, F., García, J., Martín, R., Salvador, V., Alonso, C., Gambra, D., García-Viñas, J.I., Gastón, A., Perea, R., San Miguel, A., Saura, S., Ezquerra, J. & Rodríguez de Rivera, Ó. (2026) Bearing the heat: Forest cover and human disturbance mediate brown bear behavior under thermal stress. *Biological Conservation*, **317**.

Cohen, J.M., Lajeunesse, M.J. & Rohr, J.R. (2018) A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, **8**.

Ensing, E.P., Ciuti, S., De Wijs, F.A.L.M., Lentferink, D.H., Hoedt, A., Boyce, M.S. & Hut, R.A. (2014) GPS based daily activity patterns in european red deer and North American elk (Cervus elaphus): Indication for a weak circadian clock in ungulates. *PLoS ONE*, **9**.

Eriksen, A. & Wabakken, P. (2018) Activity patterns at the Arctic Circle: nocturnal eagle owls and interspecific interactions during continuous midsummer daylight. *Journal of Avian Biology*, **49**.

Fernández-Gil, A., Lamas, J.A., Ansola, L.M., Román, J., de Gabriel Hernando, M. & Revilla, E. (2023) Population dynamics of recovering apex predators: Golden eagles in a Mediterranean landscape. *Journal of Zoology*, **319**, 99–111.

Forsman, A., Karimi, B. & Franzén, M. (2026) Contrasting phenological shifts in diurnal and nocturnal Lepidoptera under climate change. *Communications biology*, **9**.

Gambra, D., Navarro, E., Martel, J., Fernández-Pesquera, N., Ortega, P., San Miguel, A., Perea, R. & Peláez, M. (2026) Elevation, rather than land use, causes important dietary shifts in the Mediterranean golden eagle. *Journal of Zoology*.

García, V., Iglesias-Lebrija, J.J. & Moreno-Opo, R. (2021) Null effects of the Garcelon harnessing method and transmitter type on soaring raptors. *Ibis*, **163**.

García-Jiménez, R., Pérez-García, J.M. & Margalida, A. (2018) Drivers of daily movement patterns affecting an endangered vulture flight activity. *BMC Ecology*, **18**.

Gilg, O., Kovacs, K.M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., Ims, R.A., Meltofte, H., Moreau, J., Post, E., Schmidt, N.M., Yannic, G. & Bollache, L. (2012) Climate change and the ecology and evolution of Arctic vertebrates. *Annals of the New York Academy of Sciences*, **1249**.

Gonnerman, M., Shea, S.A., Sullivan, K., Kamath, P., Overturf, K. & Blomberg, E. (2023) Dynamic winter weather moderates movement and resource selection of wild turkeys at high-latitude range limits. *Ecological Applications*, **33**.

Halperin, T., Kalyuzhny, M. & Hawlena, D. (2018) How to use (and not to use) movement-based indices for quantifying foraging behaviour. *Methods in Ecology and Evolution*, **9**.

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson, J., Odden, J., Persson, J., Rauset, G.R., Schmidt, K. & Linnell, J.D.C. (2014) Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS ONE*, **9**.

Hufkens, K., Stauffer, R. & Campitelli, E. (2019) khufkens/ecmwfr: Ecmwfr.

Jackman, R.E., Hunt, W.G., Driscoll, D.E. & Lapsansk, F.J. (1994) Refinements to selective trapping techniques - a radio-controlled bow net and power snare for bald and golden eagles. *Journal of Raptor Research*, **27**.

Kranstauber, B., Safi, K. & Scharf, A.K. (2024) move2: R package for processing movement data. *Methods in Ecology and Evolution*, **15**, 1561–1567.

Kubelka, V., Sandercock, B.K., Székely, T. & Freckleton, R.P. (2022) Animal migration to northern latitudes: environmental changes and increasing threats. *Trends in Ecology and Evolution*, **37**.

Lanzone, M.J., Miller, T.A., Turk, P., Brandes, D., Halverson, C., Maisonneuve, C., Tremblay, J., Cooper, J., O'Malley, K., Brooks, R.P. & Katzner, T. (2012) Flight responses by a migratory soaring raptor to changing meteorological conditions. *Biology Letters*, **8**, 710–713.

Masello, J.F., Barbosa, A., Kato, A., Mattern, T., Medeiros, R., Stockdale, J.E., Kümmel, M.N., Bustamante, P., Belliure, J., Benzal, J., Colominas-Ciuró, R., Menéndez-Blázquez, J., Griep, S., Goesmann, A., Symondson, W.O.C. & Quillfeldt, P. (2021) How animals distribute themselves in space: energy landscapes of Antarctic avian predators. *Movement Ecology*, **9**.

Mayer, M., Zedrosser, A. & Rosell, F. (2017) Extra-territorial movements differ between territory holders and subordinates in a large, monogamous rodent. *Scientific Reports*, **7**.

Miller, T.A., Brooks, R.P., Lanzone, M.J., Brandes, D., Cooper, J., Tremblay, J.A., Wilhelm, J., Duerr, A. & Katzner, T.E. (2016) Limitations and mechanisms influencing the migratory performance of soaring birds. *Ibis*, **158**.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**.

Navarro-Serrano, F., López-Moreno, J.I., Azorin-Molina, C., Alonso-González, E., Aznarez-Balta, M., Buisán, S.T. & Revuelto, J. (2020) Elevation effects on air temperature in a topographically complex mountain valley in the Spanish pyrenees. *Atmosphere*, **11**.

Naves-Alegre, L., García-Mayoral, H., Morant, J., Pérez-García, J.M., Dias, A., Cano-Montes, E., Sánchez, Á. & García-Matarranz, V. (2025) Differential Flight Responses of Sympatric Raptor Species to Weather Conditions and Extreme Temperature Events. *Ecology and Evolution*, **15**.

Peers, M.J.L., Konkolics, S.M., Lamb, C.T., Majchrzak, Y.N., Menzies, A.K., Studd, E.K., Boonstra, R., Kenney, A.J., Krebs, C.J., Martinig, A.R., McCulloch, B., Silva, J., Garland,

L. & Boutin, S. (2020) Prey availability and ambient temperature influence carrion persistence in the boreal forest. *Journal of Animal Ecology*, **89**.

Pierce, D. (2019) ncdf4: Interface to unidata netCDF (version 4 or earlier) format data files. *R package version 1.17. https://CRAN.R-project.org/package=ncdf4*.

Poessel, S.A., Woodbridge, B., Smith, B.W., Murphy, R.K., Bedrosian, B.E., Bell, D.A., Bittner, D., Bloom, P.H., Crandall, R.H., Domenech, R., Fisher, R.N., Haggerty, P.K., Slater, S.J., Tracey, J.A., Watson, J.W. & Katzner, T.E. (2022) Interpreting long-distance movements of non-migratory golden eagles: Prospecting and nomadism? *Ecosphere*, **13**.

Pokrovsky, I., Kölzsch, A., Sherub, S., Fiedler, W., Glazov, P., Kulikova, O., Wikelski, M. & Flack, A. (2021) Longer days enable higher diurnal activity for migratory birds. *Journal of Animal Ecology*, **90**, 2161–2171.

Potier, S., Duriez, O., Cunningham, G.B., Bonhomme, V., O'Rourke, C., Fernández-Juricic, E. & Bonadonna, F. (2018) Visual field shape and foraging ecology in diurnal raptors. *Journal of Experimental Biology*, **221**.

Rafiq, K., Jordan, N.R., Golabek, K., McNutt, J.W., Wilson, A. & Abrahms, B. (2023) Increasing ambient temperatures trigger shifts in activity patterns and temporal partitioning in a large carnivore guild. *Proceedings of the Royal Society B: Biological Sciences*, **290**.

Saikkonen, K., Taulavuori, K., Hyvönen, T., Gundel, P.E., Hamilton, C.E., Vänninen, I., Nissinen, A. & Helander, M. (2012) Climate change-driven species' range shifts filtered by photoperiodism. *Nature Climate Change*, **2**, 239–242.

Sánchez-Zapata, J.A., Eguía, S., Blázquez, M., Moleón, M. & Botella, F. (2010) Unexpected role of ungulate carcasses in the diet of Golden Eagles Aquila chrysaetos in Mediterranean mountains. *Bird Study*, **57**, 352–360.

Sandgren, C., Hipkiss, T., Dettki, H., Ecke, F. & Hörnfeldt, B. (2014) Habitat use and ranging behaviour of juvenile Golden Eagles Aquila chrysaetos within natal home ranges in boreal Sweden. *Bird Study*, **61**.

Shaw, A.K. (2020) Causes and consequences of individual variation in animal movement. *Movement Ecology*, **8**.

Singh, N.J., Ecke, F., Katzner, T., Bagchi, S., Sandström, P. & Hörnfeldt, B. (2021) Consequences of migratory coupling of predators and prey when mediated by human actions. *Diversity and Distributions*, **27**.

Singh, N.J., Etienne, M., Spong, G., Ecke, F. & Hörnfeldt, B. (2024) Linear infrastructure and associated wildlife accidents create an ecological trap for an apex predator and scavenger. *Science of the Total Environment*, **955**.

Singh, N.J., Hipkiss, T., Ecke, F. & Hörnfeldt, B. (2017) *Betydelsen av kungs¨ornars hemområden, biotopval och r¨orelser f¨or vindkraftsetablering: Del 2.* ,.

Sockman, K.W. & Hurlbert, A.H. (2020) How the effects of latitude on daylight availability may have influenced the evolution of migration and photoperiodism. *Functional Ecology*, **34**.

Soutullo, A., López-López, P., Cortés, G.D., Urios, V. & Ferrer, M. (2013) Exploring juvenile golden eagles' dispersal movements at two different temporal scales. *Ethology Ecology and Evolution*, **25**.

Steiger, S.S., Valcu, M., Spoelstra, K., Helm, B., Wikelski, M. & Kempenaers, B. (2013) When the sun never sets: Diverse activity rhythms under continuous daylight in free-living arctic-breeding birds. *Proceedings of the Royal Society B: Biological Sciences*, **280**.

Sunde, P., Kjeldgaard, S.A., Mortensen, R.M. & Olsen, K. (2024) Human avoidance, selection for darkness and prey activity explain wolf diel activity in a highly cultivated landscape. *Wildlife Biology*, **2024**.

Thieurmel, B. & Elmarhraoui, A. (2024) suncalc: Compute sun position, sunlight phases, moon position and lunar phase.

Vidal-Mateo, J., Benavent-Corai, J., López-López, P., García-Ripollés, C., Mellone, U., De la Puente, J., Bermejo, A. & Urios, V. (2022) Search Foraging Strategies of Migratory Raptors Under Different Environmental Conditions. *Frontiers in Ecology and Evolution*, **10**.

Watson, J. (2010) *The Golden eagle*, second edi. (ed. by T&AD Poyser) A&C Black Publishers Ltd, 6 Soho Square, London W1D 3QY, London.

Wood, S.N. (2017) *Mixed GAM Computation Vehicle with Automatic Smoothness Estimation*,.

Tables and Figures

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.

Model PA						
Intercept	**-0.897**	0.0320				<0.001
Temperature*Daylight			18.360	19.990	448.9	<0.001
Temperature*Latitude			10.630	12.560	317.4	<0.001
Daylight*Latitude			10.850	19.00	448.6	<0.001
s (id/year)			178.660	202.00	3124.8	<0.001
Model TAH						
Intercept	**3.335**	0.107				<0.001
Temperature*Daylight			23.43	23.760	10.718	<0.001
Temperature*Latitude			18.330	19.760	9.392	<0.001
Daylight*Latitude			14.590	19.000	39.031	<0.001
s (id/year)			183.630	202.000	34.543	<0.001
Model MSD 1						
Intercept	**2.595**	0.108				<0.001
Temperature*Daylight			19.130	20.520	7.709	<0.001
Temperature*Latitude			21.670	22.360	10.013	<0.001
Daylight*Latitude			16.880	19.000	56.797	<0.001
s (id/year)			178.840	202.00	33.343	<0.001
Model MSD 2						
Intercept	**10.653**	1.385				<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/year)			71777	75.000	72.110	<0.001

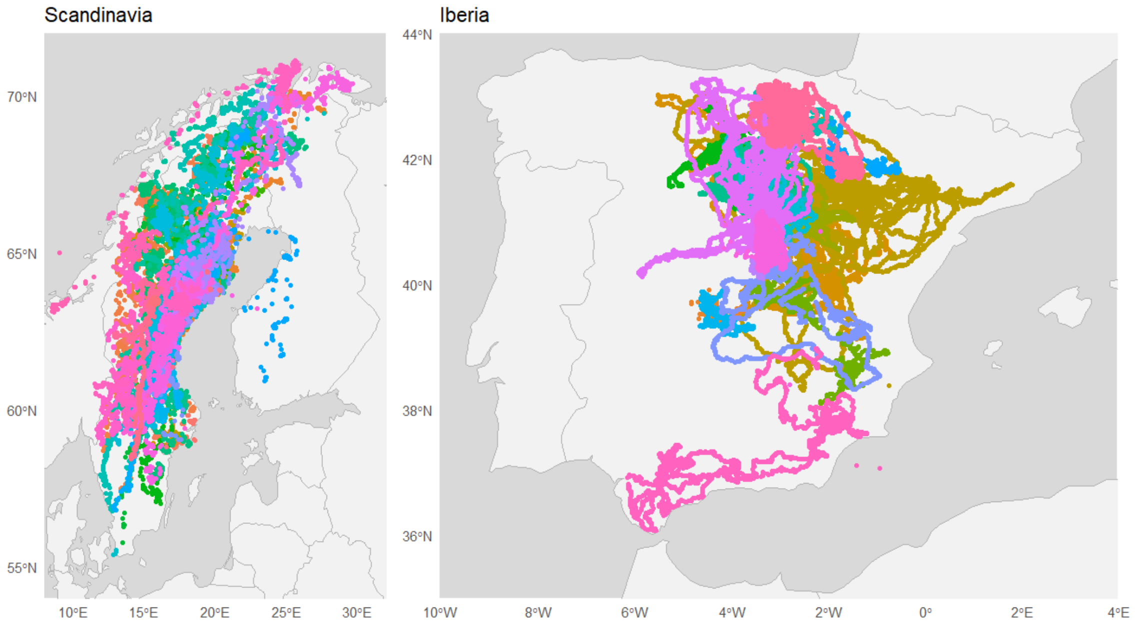

Figure 1. Locations for all the GPS tracked Golden Eagles from Scandianvian and Iberian Peninsulas used in this study (n=76). Each color represents a different individual.

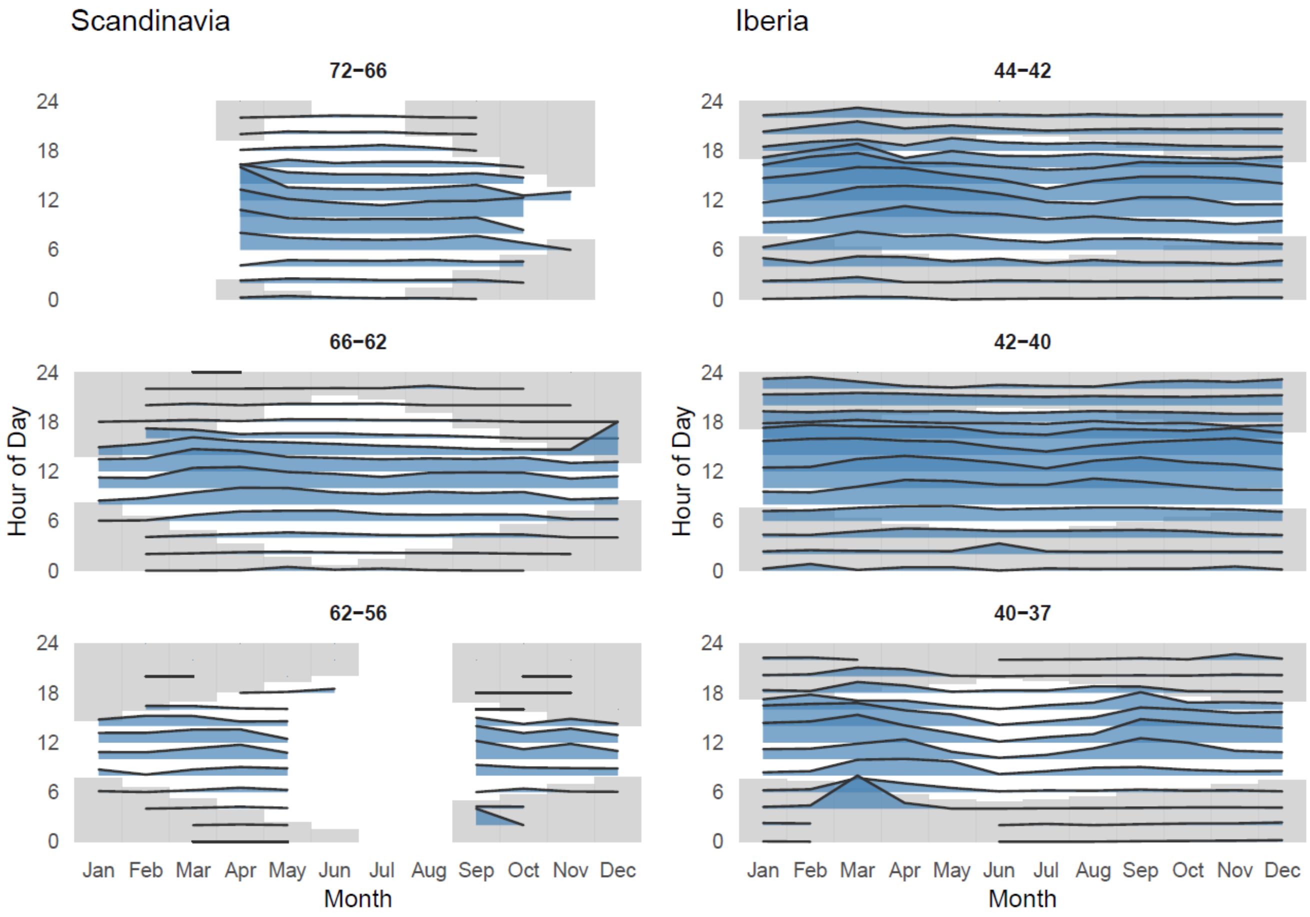

Figure 2. Golden Eagles Proportion Active (blue ridgelines) for every month and hour of the day by latitude ranges. Empty spaces (in white), mean there is no data for that month or hour.

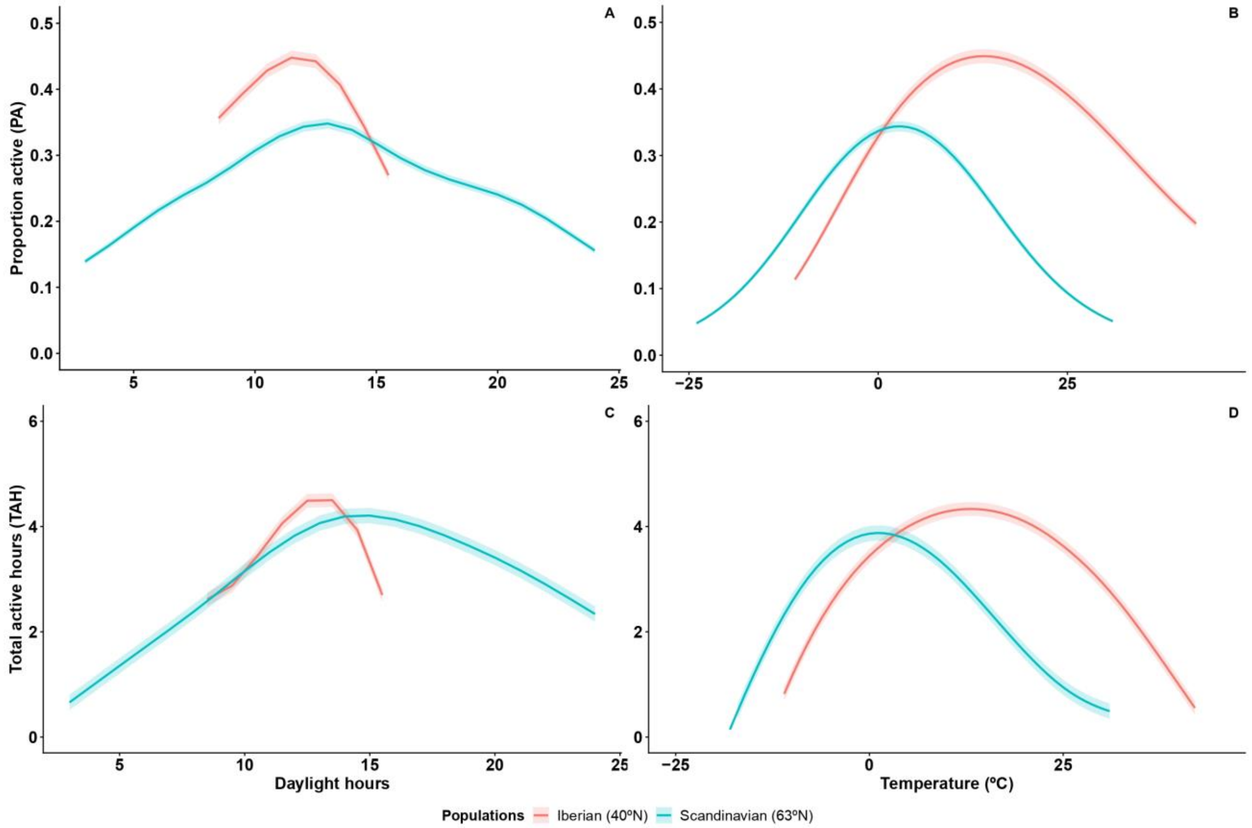

Figure 3. Golden Eagles activity for Scandinavia and Iberia by daylight hours and temperature. Proportion Active (PA) in the upper row and Total Active Hours (TAH) in the lower row. Daylight hours in the left column and temperature in the right one. Lines in light blue for Scandinavia and red lines for 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.

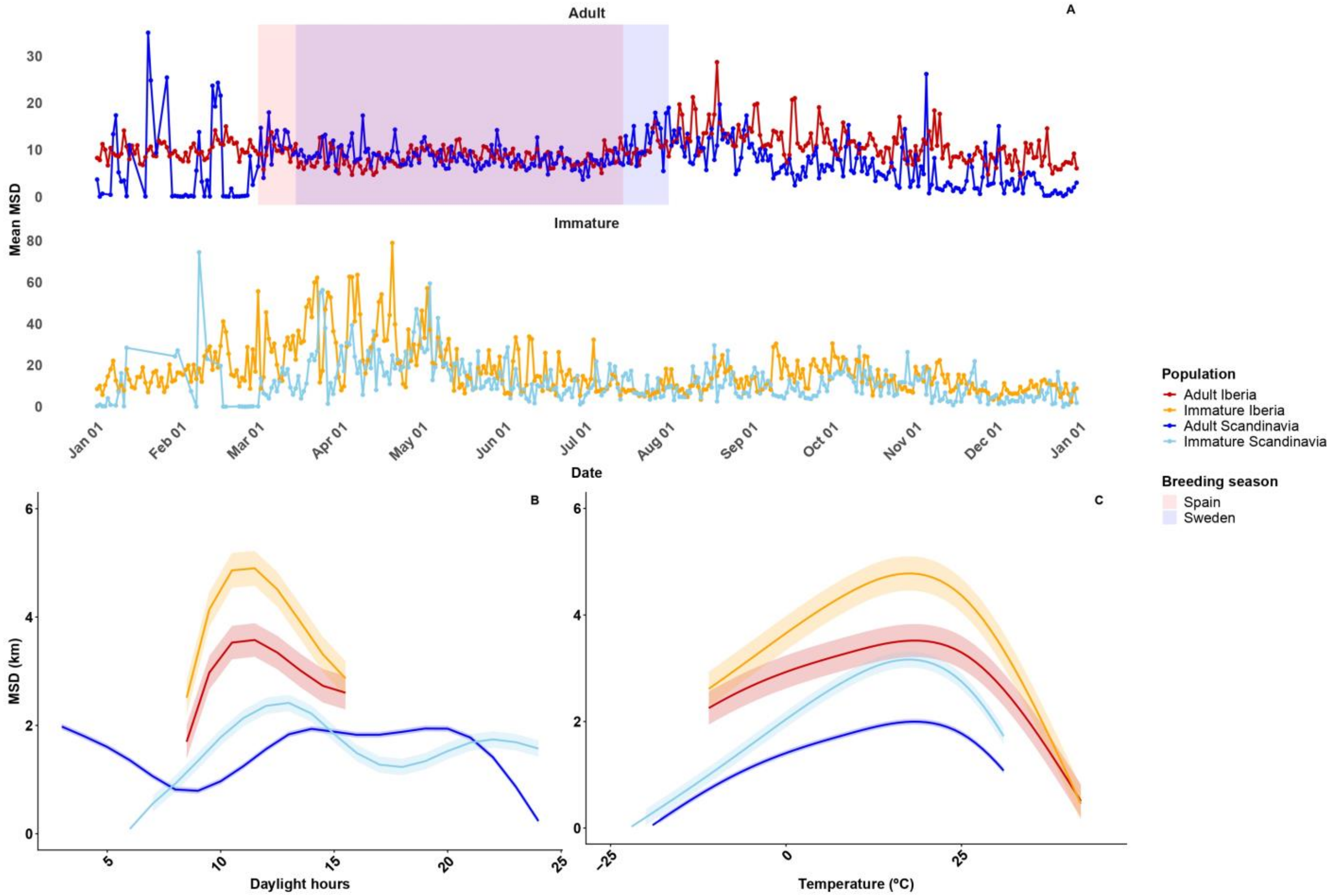

Figure 4. Maximum Straight Distance (in kilometers) travelled by Golden Eagles across countries and age classes, shown in relation to day of the year, daylight hours, and temperature. Plots are represented for the median values of the other predictors (12 h daylight for both countries; temperature and 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.