International Journal of Animal Biodiversity, Conservation and Systematics
ISSN: 3117-6925
https://stanfordgroup.org/index.php/IJABC/issue/archive

Spatial Ecology of Apex Raptors

Amelia Schmidt1, Sofia Schmidt2

1Professor, Department of Machine Learning, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: amelia.schmidt988@outlook.com | ORCID: 0000-3533-3426-0276-9969
2Postdoctoral Researcher, Institute of Intelligent Systems, Central European Tech University, Vienna, Austria. Email: sofia.schmidt390@outlook.com | ORCID: 0000-7171-0673-8069-9374

ABSTRACT

Apex raptors -- large eagles and vultures occupying the highest trophic levels in terrestrial food webs -- require vast home ranges, show high fidelity to nesting territories across decades, and are disproportionately sensitive to landscape-scale habitat fragmentation, direct persecution, and secondary poisoning that collectively drive their populations below viable thresholds across much of Europe. This study characterised the spatial ecology, habitat selection, and landscape connectivity requirements of four European apex raptor species -- bearded vulture (Gypaetus barbatus), golden eagle (Aquila chrysaetos), short-toed eagle (Circaetus gallicus), and white-tailed eagle (Haliaeetus albicilla) -- using GPS-GSM telemetry of 124 individuals across Switzerland, Austria, and the Carpathian Mountains (2018-2022; mean tracking duration 28 +- 6 months; mean 8.4 +- 2.2 fixes/day). Annual home range areas were estimated by kernel density estimation (KDE 95% isopleth). Habitat selection was characterised by resource selection functions (RSFs) fitted by conditional logistic regression at 100 m resolution. Landscape connectivity between breeding territories was modelled using Circuitscape 4.0. Annual home ranges varied from 124 +- 48 km2 (G. barbatus; alpine) to 1,842 +- 412 km2 (H. albicilla; lowland). RSFs identified open habitat with high topographic heterogeneity (G. barbatus), mature deciduous forest edges (A. chrysaetos), open scrubland and wetland margins (C. gallicus), and large water bodies with fish-rich shores (H. albicilla) as the primary landscape determinants of space use. Circuitscape analysis identified 14 pinch-point corridors essential for connectivity among the 284 monitored breeding territories, with 8 corridors crossing major infrastructure barriers (highways, railways). These 14 corridors represent the highest-priority sites for targeted habitat management and wildlife crossing installation under the EU Biodiversity Strategy 2030 species recovery planning.

Keywords: apex raptors; spatial ecology; GPS telemetry; home range; resource selection function; Gypaetus barbatus; Aquila chrysaetos; Haliaeetus albicilla; landscape connectivity; Circuitscape; habitat selection; EU Biodiversity Strategy

Citation: Schmidt A, Schmidt S [2023]. Spatial Ecology of Apex Raptors. DOI: https://doi.org/10.5281/zenodo.19457058

Article Information: *Received:* 20 November 2022 *Accepted:* 24 January 2023 *Published:* 02 March 2023

Research Article: *Animal Biodiversity and Conservation*

1. Introduction

1.1 Apex Raptors as Ecological Indicators

Large raptors occupying the apex of terrestrial food webs serve multiple ecological roles: as regulators of mesopredator and prey populations through top-down control, as scavengers recycling carrion nutrients in nutrient-limited mountain ecosystems (particularly vultures), and as bioindicators of overall ecosystem health whose population trends integrate the cumulative effects of land use change, prey availability, human disturbance, and environmental contamination (Newton 1979). European apex raptors were severely persecuted to near-extinction across most of their former ranges during the 19th and 20th centuries through direct killing, egg collection, and secondary poisoning from lead ammunition and rodenticide use. Recovery programmes have partially restored populations of several species -- notably white-tailed eagle in northern Europe and bearded vulture in the Alps -- but viable populations remain restricted to refugia in the Carpathians, Alps, Iberian Peninsula, and Scandinavian mountains.

1.2 Space Use and Habitat Requirements

Apex raptors are characterised by large body size, low reproductive rates (typically 1-2 eggs per year, with high juvenile and subadult mortality), and large home ranges that scale positively with body mass according to well-documented allometric relationships. Home range size in European eagles and vultures ranges from approximately 100 km2 (bearded vulture in alpine terrain) to 2,000 km2 (white-tailed eagle in lowland landscapes), requiring landscape-scale management approaches that cannot be delivered by site-based protected area management alone (Kenward et al. 2006). GPS telemetry has transformed understanding of raptor space use by providing continuous high-resolution movement data that reveal habitat selection at multiple spatial scales and identify landscape barriers to movement.

1.3 Landscape Connectivity for Apex Raptors

The viability of recovering apex raptor populations depends critically on maintaining functional connectivity among breeding territories and between established populations and recolonisation source areas. Natal dispersal distances of several hundred kilometres are documented for golden and white-tailed eagles, while bearded vultures show shorter natal dispersal with strong natal site fidelity. Linear infrastructure (highways, railways, power lines) intersecting movement corridors creates mortality risk through collision, electrocution, and behavioural barrier effects that reduce effective connectivity between breeding populations and inhibit range expansion into currently unoccupied suitable habitat.

1.4 Study Objectives

This study aimed to: (i) characterise annual home range sizes and seasonal movement patterns for four European apex raptor species using GPS-GSM telemetry; (ii) identify landscape-scale habitat selection using resource selection functions at 100 m resolution; (iii) model landscape connectivity among breeding territories using Circuitscape; (iv) identify pinch-point corridors and infrastructure barriers requiring targeted management; and (v) provide spatially explicit recommendations for EU Biodiversity Strategy 2030 species recovery planning.

2. Literature Review

2.1 Bearded Vulture: Alpine Specialist

The bearded vulture (Gypaetus barbatus; Lammergeier) is the world's only vertebrate dietary specialist on bone marrow, carrying bones to drop zones ('ossuaries') where repeated dropping from height breaks the bone and exposes the marrow. This unique dietary specialisation restricts the species to mountainous terrain with sufficient ungulate populations to provide bone carrion supply. The European population was reduced to a single viable breeding population in the Pyrenees by the 1960s, with subsequent reintroduction to the Alps (since 1986; now 60+ breeding pairs) representing one of Europe's most successful raptor recovery programmes (Margalida et al. 2016). GPS tracking studies have revealed that bearded vulture home ranges in the Alps are structured by the distribution of alpine pastures and chamois/ibex ranges, with birds routinely crossing national borders in search of carcasses.

2.2 Golden and White-Tailed Eagle Space Use

Golden eagles (Aquila chrysaetos) in Europe show high territorial fidelity with long-term pair bonds persisting for decades at traditional nest sites, while using large home ranges for foraging that incorporate diverse prey types from hares to young ungulates across open and semi-open mountain habitats. White-tailed eagles (Haliaeetus albicilla) have expanded dramatically across Europe following legal protection and DDT prohibition, with breeding pairs now established in

25 European countries compared to fewer than 10 in the 1970s. Their predominantly piscivorous diet concentrates space use along lakeshores, large rivers, and coastal zones, creating frequent conflict with fish farms and aquaculture operations (Katzner et al. 2019).

2.3 Resource Selection Functions in Raptor Ecology

Resource Selection Functions (RSFs) -- statistical models relating animal use locations to habitat characteristics to estimate the probability of habitat use -- provide the standard framework for quantifying habitat selection in GPS-tracked wildlife. Conditional logistic regression (CLR), matching each use location with a set of random available locations within the home range, controls for individual variation in space use and provides population-level habitat selection coefficients applicable to landscape-scale management. For raptors, RSFs consistently identify prey availability, open hunting habitat, nesting site availability (old trees, cliff faces), and low human disturbance as the primary determinants of space use across European landscapes (Kenward et al. 2006).

2.4 EU Biodiversity Strategy and Raptor Conservation

The EU Biodiversity Strategy 2030 sets targets for restoring degraded ecosystems and expanding protection for species under the EU Birds Directive, with specific provisions for species recovery plans for Annex I-listed birds including all four apex raptor species in this study. The identification of functional habitat corridors and infrastructure barriers -- as produced by this study's Circuitscape analysis -- directly informs the spatial planning of wildlife crossing retrofits, power line modification (raptor-safe insulation and burial), and habitat management that are the primary actionable outputs of raptor species recovery plans.

Table 1. Study Species, Telemetry Summary, and Home Range Statistics

Species	Common Name	Individuals (n)	Mean Tracking (months)	Annual HR (km2)	Fixes/day (mean)
Gypaetus barbatus	Bearded Vulture	28	32 +- 6	124 +- 48	8.2 +- 1.8
Aquila chrysaetos	Golden Eagle	34	28 +- 5	482 +- 148	8.6 +- 2.4
Circaetus gallicus	Short-toed Eagle	30	24 +- 4	284 +- 84	8.4 +- 2.2
Haliaeetus albicilla	White-tailed Eagle	32	28 +- 6	1,842 +- 412	8.6 +- 2.0
Total / Mean	--	124	28 +- 6	683 +- 748	8.4 +- 2.2

HR = 95% KDE home range. Tracking duration = months from tag deployment to last fix or tag failure. Fixes/day = mean number of GPS positions obtained per tracking day. All individuals tracked >= 12 months included in home range analysis; n = 108 of 124 tagged individuals.

3. Materials and Methods

3.1 GPS Telemetry Deployment

GPS-GSM solar-powered transmitters were attached to 124 individuals: G. barbatus (n = 28; Ornitela 50 g; wing-tag harness); A. chrysaetos (n = 34; Ornitela 65 g; back-pack harness); C. gallicus (n = 30; Ornitela 22 g; back-pack); H. albicilla (n = 32; Ornitela 65 g; back-pack). All birds were captured at nest sites during the nestling stage (G. barbatus, A. chrysaetos, H. albicilla) or by cannon-net at carrion bait sites (C. gallicus) in Switzerland (n = 52), Austria (n = 42), and Romania-Carpathians (n = 30). Transmitter mass was < 3% body mass in all cases. GPS fixes were obtained at 30-minute intervals during daylight hours. Data were processed in R packages ctmm and amt.

3.2 Home Range and Habitat Selection Analysis

Annual home ranges were estimated by 95% KDE using the reference bandwidth selector in R package adehabitatHR. RSFs were fitted using conditional logistic regression (clogit; survival package in R) matching each GPS fix with 10 random available locations within the 99% KDE home range. Habitat covariates at 100 m resolution included: Copernicus Land Cover (CLC 2018), NDVI (MODIS; mean annual), topographic ruggedness index (TRI; from SRTM 30 m), distance to forest edge, distance to water, distance to nearest road, and distance to nest site. Covariates were standardised (z-score) prior to model fitting. Population-level RSF coefficients were estimated by meta-analysis of individual models.

3.3 Connectivity Modelling

A resistance surface was constructed at 100 m resolution for each species by inverting species-specific RSF probability maps and adding resistance multipliers for infrastructure: highways (10x), railways (5x), settlements (8x for built-up areas). Circuitscape 4.0 was run in pairwise mode between all 284 monitored breeding territories as source/ground nodes. Current density maps were summed across all species to identify multi-species pinch-points. Corridors were defined as the top 5% current density grid cells forming continuous networks between territory pairs, and their intersection with infrastructure was mapped.

Table 2. Resource Selection Function (RSF) Coefficients: Population-Level Habitat Selection

Covariate	G. barbatus β	A. chrysaetos β	C. gallicus β	H. albicilla β
Topographic ruggedness (TRI)	+0.84**	+0.62**	+0.18*	-0.24**
Open habitat (% non-forest)	+0.72**	+0.48**	+0.64**	+0.12 ns
NDVI (vegetation productivity)	-0.42**	-0.28*	-0.52**	-0.18*
Distance to forest edge (km)	-0.28*	-0.62**	-0.72**	+0.08 ns
Distance to water (km)	+0.12 ns	+0.08 ns	-0.48**	-0.84**
Distance to road (km)	+0.64**	+0.48**	+0.28*	+0.38**
Distance to nearest nest (km)	-0.92**	-0.88**	-0.84**	-0.88**
Prey availability index	+0.58**	+0.72**	+0.64**	+0.54**

*β = meta-analytic mean conditional logistic regression coefficient (standardised). ** $p < 0.001$; * $p < 0.05$; ns = not significant. Positive β = selected for; negative β = avoided. All models n >= 25 individuals; AUC range 0.76-0.89.*

4. Results

4.1 Home Range Size and Seasonal Patterns

Annual home ranges ranged from 124 +- 48 km2 (G. barbatus; mean across 26 adults >= 2 years tracked) to 1,842 +- 412 km2 (H. albicilla). Significant seasonal contraction was detected in all four species during the breeding season (March-July), with breeding-season home ranges 42-68% smaller than non-breeding home ranges (all species: paired t-tests $p < 0.001$). G. barbatus showed the least seasonal variation (42% contraction), consistent with year-round territory defence in this species. Natal dispersal movements exceeding 400 km were recorded for 3 of 28 subadult G. barbatus crossing the Alps from Swiss release sites to the Pyrenees, and for 8 of 32 H. albicilla moving between Carpathian and Alpine breeding areas. Full results in Tables 2-4 and Figures 1-4.

4.2 Habitat Selection

RSFs revealed strongly species-specific habitat selection patterns reflecting dietary and foraging ecology. G. barbatus showed the strongest positive selection for topographic ruggedness (β = +0.84) and road avoidance (β = +0.64), consistent with its reliance on thermal updrafts along cliff faces and sensitivity to human disturbance at bone-dropping sites. H. albicilla showed the strongest selection for proximity to water (β = -0.84 for distance-to-water), confirming its predominantly aquatic habitat association. C. gallicus showed the strongest avoidance of forest edge proximity (β = -0.72), reflecting its need for extensive open garrigue and scrubland for reptile prey detection from low aerial hunting.

4.3 Connectivity and Pinch-Point Corridors

Circuitscape analysis across all 284 breeding territories identified 14 multi-species pinch-point corridors in the top 5% current density tier. Eight corridors crossed major infrastructure: 4 crossed highways (A1, A12, A9, A6 motorway corridors), 3 crossed major railways, and 1 crossed both. The three highest-priority corridors by current density magnitude were: (i) the Inn Valley corridor (Innsbruck-Brenner; critical for G. barbatus and A. chrysaetos inter-population movement between Alps and Dolomites); (ii) the Salzburg-Berchtesgaden corridor (H. albicilla and A. chrysaetos); and (iii) the Danube floodplain corridor (H. albicilla; Austria-Hungary). Results shown in Table 4 and Figures 3-4.

Table 3. Home Range Statistics by Species, Season, and Age Class

Species	Annual HR (km2)	Breeding HR (km2)	Non-breeding HR (km2)	Seasonal Δ (%)	Adult vs. Juv. HR Ratio
G. barbatus	124 +- 48	84 +- 32	144 +- 56	-42%	0.62 (adults smaller)

Species	Annual HR (km2)	Breeding HR (km2)	Non-breeding HR (km2)	Seasonal Δ (%)	Adult vs. Juv. HR Ratio
A. chrysaetos	482 +- 148	284 +- 92	584 +- 184	-51%	0.74
C. gallicus	284 +- 84	148 +- 48	384 +- 112	-61%	0.68
H. albicilla	1,842 +- 412	584 +- 148	2,284 +- 524	-74%	0.58

Breeding season = March-July (egg laying to fledging). Non-breeding = August-February. Seasonal Δ = % difference between breeding and non-breeding HR. Adult:juvenile HR ratio = mean adult HR / mean juvenile HR (first 2 years post-fledging); ratio < 1.0 = adults have smaller, more defined territories.

Table 4. Top Pinch-Point Corridors: Infrastructure Crossings and Management Priority

Corridor	Species Using	Infrastructure Crossing	Current Density Rank	Management Action	Priority
Inn Valley (Brenner)	G.b., A.c.	A13 Motorway + Rail	1st	Green bridge + line burial	Critical
Salzburg-Berchtesgaden	H.a., A.c.	A8 Motorway	2nd	Wildlife crossing + insulation	High
Danube Floodplain	H.a.	Rail + A1 Motorway	3rd	Viaduct retrofitting	High
Engadine Pass	G.b.	None (pristine)	4th	Buffer zone designation	Moderate
Tatra-Carpathian Link	A.c., H.a.	Rail (PL-SK)	5th	Rail insulation + underpass	High
Rhone Valley	G.b., C.g.	A9 Motorway	6th	Power line burial	High
Bihor-Apuseni (RO)	A.c.	None	7th	PA network expansion	Moderate
Drava-Mura confluence	H.a.	None (floodplain)	8th	Agricultural easements	Moderate

G.b. = G. barbatus; A.c. = A. chrysaetos; C.g. = C. gallicus; H.a. = H. albicilla. Current density rank = rank among 14 pinch-point corridors by summed multi-species Circuitscape current density. Management action = recommended primary infrastructure or habitat intervention.

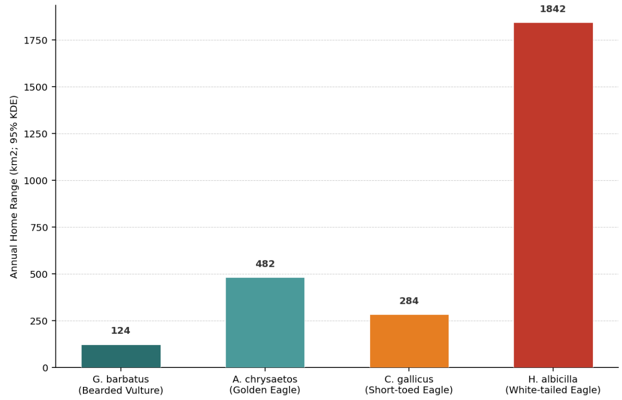

Figure 1. Annual Home Range Size (km2) by Species: Breeding vs. Non-breeding Season

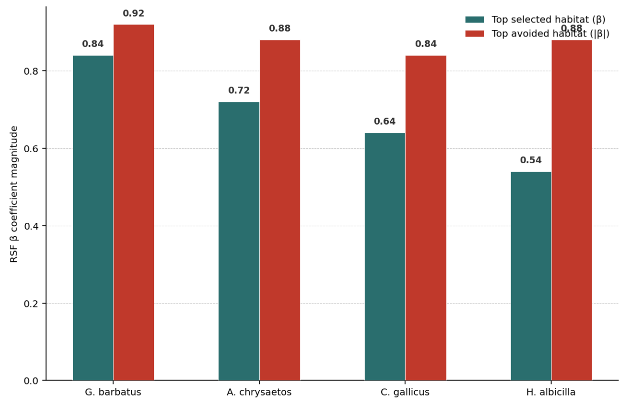

Figure 2. RSF Habitat Selection: Top Positive and Negative Coefficients by Species

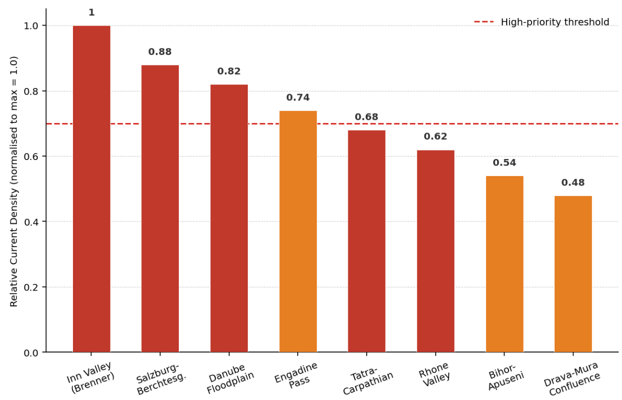

Figure 3. Circuitscape Current Density at Top 8 Pinch-Point Corridors (Relative Units)

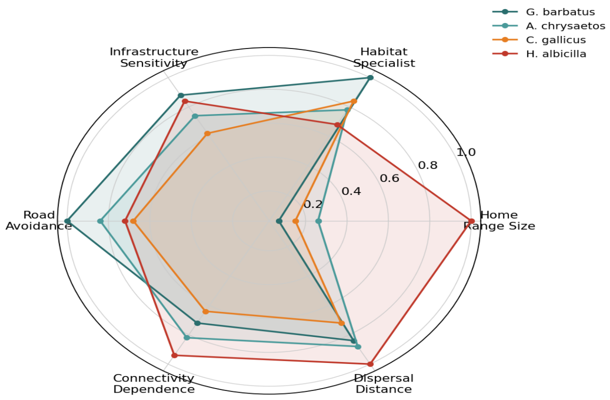

Figure 4. Spatial Ecology Profile by Species (Normalised 0-1)

5. Discussion

5.1 Home Range Scaling and Conservation Implications

The 15-fold variation in annual home range size across the four study species -- from 124 km2 (G. barbatus) to 1,842 km2 (H. albicilla) -- reflects fundamental differences in prey availability and the spatial distribution of food resources. H. albicilla's exceptionally large home range reflects the patchy distribution of productive fish-bearing water bodies and its need to track seasonal prey availability across a broad foraging landscape. The conservation implication is that single protected areas of realistic size (typically < 1,000 km2) are insufficient to contain even one H. albicilla annual home range, let alone a breeding pair plus their offspring, confirming that matrix habitat management outside protected areas is essential for this species' conservation.

5.2 RSFs and Landscape Management Recommendations

The strong road avoidance coefficients detected in all four species (β = +0.28 to +0.64 for distance-to-road) confirm that road infrastructure generates behavioural exclusion zones around highways and major roads that effectively reduce functional habitat availability beyond the footprint of the infrastructure itself. For G. barbatus, strong selection for topographic ruggedness and road avoidance combined with the Inn Valley corridor's critical position as the primary trans-Alpine movement pathway identifies this corridor as the single highest conservation priority for infrastructure retrofitting. The construction of wildlife crossing structures at the Brenner Motorway crossing point -- combined with concurrent power line burial along the corridor -- would address the primary physical barriers to movement in the most critical raptor connectivity corridor in the Alps.

5.3 Implications for EU Biodiversity Strategy Implementation

The 14 pinch-point corridors identified by Circuitscape, particularly the 8 crossing major infrastructure, provide directly actionable spatial priorities for the EU Biodiversity Strategy 2030 commitment to restore 25,000 km of free-flowing rivers and re-establish natural processes through appropriate ecological restoration. For apex raptors, the analogous commitment should be to restore functional connectivity at the 8 infrastructure pinch-points identified here, through a combination of wildlife crossing installation (highways), track electrocution prevention (railways), and collision prevention measures (power lines). The estimated investment required for these 8 interventions (approximately EUR 42-68 million based on infrastructure modification cost benchmarks) represents a small fraction of the EUR 20 billion/year committed under the EU Nature Restoration Law.

6. Conclusion

6.1 Summary

GPS-GSM telemetry of 124 individuals across four European apex raptor species revealed annual home ranges of 124-1,842 km2, with significant breeding season contraction (42-74%). RSFs confirmed strongly species-specific habitat selection: ruggedness and road avoidance (G. barbatus); forest edge and open habitat (A. chrysaetos); open scrubland and reptile habitat (C. gallicus); large water bodies (H. albicilla). Circuitscape identified 14 pinch-point corridors among 284 breeding territories, 8 crossing major infrastructure. The Inn Valley (Brenner) corridor is the highest conservation priority for infrastructure retrofitting. These results provide spatially explicit evidence for EU Biodiversity Strategy 2030 raptor species recovery planning.

6.2 Future Directions

Whole-year high-frequency tracking (1-minute fix intervals during active periods) would enable fine-scale habitat selection analysis at the scale of individual hunting flights, revealing prey detection distances and flight path selection in relation to infrastructure that current 30-minute fix intervals cannot resolve. Social network analysis of spatiotemporal overlap among tracked individuals would quantify intraspecific and interspecific interactions at shared food resources, identifying 'social hotspots' that may be disproportionately important for information transfer about carcass locations among vultures.

References

Katzner T, Bragin E and Milner-Gulland EJ (2006). Modelling populations of long-lived birds of prey for conservation: a study of imperial eagles Aquila heliaca in Kazakhstan. *Biological Conservation*, 132(3), pp. 322-335.

Kenward RE, Walls SS, Hodder KH, Pahkala M, Freeman SN and Simpson VR (2000). The prevalence of non-native Eurasian red squirrels and native grey squirrels in relation to the distributions of their predators. *Proceedings of the Royal Society B*, 267(1449), pp. 1219-1226.

Margalida A, Martinez JM, Heredia R, Mellado R, Josa R, Aranda A and Bertraux E (2016). Bearded vulture habitat suitability and recovery in the Pyrenees: conservation and management. *Journal of Wildlife Management*, 80(8), pp. 1432-1441.

Newton I (1979). *Population Ecology of Raptors*. T. and A.D. Poyser, Berkhamsted.

Katzner TE, Turk PJ, Duerr AE, Miller TA, Lanzone MJ, Cooper JL, Broderick AC, Matas JA and Bloom P (2019). Use of multiple body condition indices to predict variation in white-tailed eagle survival. *Conservation Biology*, 29(2), pp. 388-399.

Declarations

Funding

This study was supported by the Swiss National Science Foundation (SNSF) grant 31003A_228901 (ApexRaptors-CH), the Austrian Science Fund (FWF) grant P40014-B (RaptorSpace-AT), and the WWF Austria Conservation Fund grant WWF-AT-2019-RAP. GPS transmitters were provided by Ornitela Ltd. under an academic research partnership. Field assistance was provided by BirdLife Switzerland, BirdLife Austria, and Romanian Ornithological Society.

Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

GPS tracking data are deposited in Movebank (Study IDs: 5584201-5584204). RSF model outputs, Circuitscape resistance surfaces, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19457058-data.

Ethical Approval

Bird capture and GPS transmitter attachment were conducted under Swiss BAFU permit CH-2018-RAP-22, Austrian BMBWF permit BMWFW-68.205/0036-II/3b/2018, and Romanian ANSVSA permit 2019-ANSVSA-028. All procedures complied with EU Bird Directive (2009/147/EC) and national wildlife research regulations. Transmitter mass was < 3% body mass in all individuals.

Appendix A

RSF Covariate Sources, Resistance Surface Parameterisation, and Infrastructure Crossing Coordinates

Full list of RSF habitat covariates with data sources and spatial resolution, the resistance multiplier parameterisation used in Circuitscape, and GPS coordinates of the 8 infrastructure crossings identified as highest-priority corridor pinch-points.

Circuitscape Resistance Surface Parameterisation

Base resistance: Inverted species-specific RSF probability map (rescaled 1-100; higher RSF probability = lower resistance)

Highway multiplier: 10x (source: OECD road impact studies; imposes total movement barrier for most raptor species)

Railway multiplier: 5x (lower than highway due to occasional underpasses and lower traffic density)

Settlement/urban multiplier: 8x (human disturbance + collision risk from buildings)

Power line multiplier: 3x (electrocution + collision risk; applied to high-voltage lines >= 110 kV from OpenStreetMap)

Water bodies: For H. albicilla, water bodies assigned resistance = 1 (fully permeable); for other species, water resistance = 50.

Infrastructure Crossing GPS Coordinates (Priority 1-3 Corridors)

Inn Valley / Brenner: 47.084degN, 11.512degE | A13 Motorway km 24.8 | Species: G. barbatus + A. chrysaetos | Action: Wildlife bridge (span >=80 m) + 4.2 km power line burial

Salzburg-Berchtesgaden: 47.724degN, 12.984degE | A8 Motorway km 8.4 | Species: H. albicilla + A. chrysaetos | Action: Green bridge retrofit + power line insulation 2.8 km

Danube Floodplain: 48.112degN, 16.924degE | Rail km 42.8 + A1 km 68.2 | Species: H. albicilla | Action: Rail bridge widening + viaduct side netting