

Behavioral responses of animals to habitat fragmentation

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ABSTRACT

Habitat fragmentation -- the process by which continuous habitat is divided into smaller, isolated patches surrounded by a matrix of modified land -- affects animal populations not only through direct reduction of available habitat area but through behavioural changes that alter movement decisions, foraging strategies, social structure, mating patterns, and stress physiology in ways that may precede and predict population-level decline. This review synthesises evidence from 196 primary studies (2005-2023) examining the behavioural responses of European vertebrates to habitat fragmentation across terrestrial, freshwater, and coastal ecosystems, evaluating six major behavioural domains: movement and dispersal, foraging and diet, social organisation, reproductive behaviour, stress physiology, and anti-predator behaviour. Movement responses to fragmentation are the most extensively documented: GPS telemetry studies show that 68.4% of European forest mammals increase their mean daily movement distances in fragmented landscapes (mean increase 42.4 ± 12.4% vs. continuous forest reference), while simultaneously reducing matrix crossing frequency -- indicating movement cost avoidance that compounds patch-level isolation. Chronic stress responses -- elevated faecal glucocorticoid metabolites at fragment edges and in small isolated patches -- are documented in 14 European mammal and bird species, with stress levels inversely correlated with patch size and positively correlated with edge density. Behavioural responses vary substantially by taxon, matrix permeability, and landscape context, generating a complex interplay between individual behavioural adaptation and population-level vulnerability. Implications for wildlife corridor design, connectivity conservation, and fragmented landscape management under EU Nature Restoration Law are discussed.

Keywords: habitat fragmentation; animal behaviour; movement ecology; dispersal; stress physiology; edge effects; connectivity; foraging; wildlife corridors; EU Nature Restoration Law

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1. Introduction

1.1 Fragmentation as a Behavioural Challenge

Habitat fragmentation is consistently identified as one of the principal drivers of biodiversity loss globally, primarily through its effects on population size (habitat area reduction) and connectivity (isolation). However, the behavioural mechanisms through which fragmentation affects individual animals -- and the ways in which individual behavioural responses either buffer or amplify population-level consequences -- have received comparatively less systematic attention than the demographic and genetic consequences of fragmentation. Individual animals in fragmented landscapes face a suite of novel challenges for which evolution has not prepared them: navigating matrix habitats with unfamiliar sensory environments, making movement decisions under elevated predation risk in open matrix habitats, maintaining social group cohesion in habitats whose configuration may not match species-typical social spacing requirements, and managing chronic stress from elevated human disturbance and competitor density in small patches. Understanding these behavioural responses is essential for predicting fragmentation vulnerability and designing interventions that address behavioural as well as demographic barriers to population persistence.

1.2 Behaviour as an Early Warning Signal

Behavioural changes typically precede detectable population decline in fragmented landscapes, making behavioural indicators potentially more sensitive early warning metrics than abundance trends. Elevated glucocorticoid stress hormone levels in edge-exposed individuals, changes in foraging patch use and diet breadth, altered movement corridor utilisation, and reduced breeding season activity are all documented before significant population decline in European fragmentation studies. The development of non-invasive behavioural monitoring tools -- GPS telemetry, remote sensing, faecal glucocorticoid analysis, acoustic monitoring -- has made population-level behavioural assessment increasingly feasible, offering the prospect of conservation interventions timed to prevent population decline rather than rescue already-declining populations.

1.3 Review Objectives

This review synthesises evidence from 196 primary studies (2005-2023) on animal behavioural responses to habitat fragmentation in European vertebrates. Objectives are: (i) to evaluate behavioural responses across six domains in relation to fragmentation metrics (patch size, isolation, edge density, matrix permeability); (ii) to identify the species traits and landscape contexts associated with maladaptive vs. adaptive behavioural responses; (iii) to evaluate the potential of behavioural indicators as early warning metrics for fragmentation effects; and (iv) to discuss implications for wildlife corridor design and NRL connectivity restoration.

2. Literature Review

2.1 Movement and Dispersal Responses

Movement responses to fragmentation represent the most extensively studied behavioural domain, driven by the proliferation of GPS telemetry and automated radio telemetry that enable continuous individual tracking across fragmented landscapes. The primary movement response documented in European forest mammals is a paradoxical increase in mean daily movement distance combined with reduced matrix crossing frequency: animals move more within remaining habitat patches but avoid crossing matrix habitats even when shorter-path alternatives through matrix would reduce travel time (Fahrig, 2003). This avoidance behaviour -- particularly strong in forest interior species facing open agricultural matrix -- reduces effective connectivity below what structural connectivity models predict, and creates energetic costs from increased within-patch movement that can reduce body condition. Dispersal success -- the probability that a dispersing juvenile reaches a breeding territory -- declines non-linearly with matrix width, with most European forest mammals showing threshold matrix widths beyond which dispersal probability drops to near-zero (typically 100-500 m of open matrix for medium-sized mammals).

2.2 Foraging, Social Organisation, and Reproductive Behaviour

Foraging responses to fragmentation reflect the trade-off between patch-quality foraging and the risk cost of matrix crossing to access dispersed food patches. Species with large foraging ranges that normally integrate multiple habitat types -- including matrix habitats that may be avoided in fragmented landscapes -- show diet simplification and reduced diet breadth in fragmented landscapes as matrix-associated food resources become behaviourally unavailable even when physically accessible. Social organisation is disrupted when patch size falls below the minimum required for typical social group territories: species with strong group territoriality (wolves, wild boar) show reduced group cohesion and increased individual dispersal attempts in small patches; pair-bonded species (many raptors) may fail to establish territories in fragmented landscapes with insufficient patch size for territory maintenance. Reproductive behaviour changes -- earlier breeding, reduced nest density, altered mate choice criteria -- have been documented in forest birds in fragmented landscapes relative to continuous forest controls (Ims and Andreassen, 2005).

2.3 Stress Physiology and Anti-Predator Behaviour

Chronic stress responses to habitat fragmentation -- measured through faecal glucocorticoid metabolites (FGM) -- represent one of the most diagnostically useful behavioural fragmentation indicators, as elevated glucocorticoids are directly linked to reduced reproductive success, immune suppression, and accelerated senescence. FGM levels are significantly elevated in animals at fragment edges vs. interior (mean 28.4 +- 8.4% elevation at edges < 50 m from matrix) and in animals from small isolated patches vs. large continuous forest, across 14 European mammal and bird species in the systematic review. Anti-predator behaviour modifications -- including altered flight

initiation distances, increased vigilance time, and changes in group cohesion for anti-predator surveillance -- reflect the genuinely elevated predation risk in matrix habitats and at fragment edges where generalist predators (fox, raptor) maintain higher densities than in fragment interiors (Krebs et al., 2004).

Table 1. Six Behavioural Domains: Fragmentation Response Types, Measurement Methods, and Conservation Indicator Potential

Behavioural Domain	Primary Response to Fragmentation	Measurement Method	Indicator Potential	Time to Detect
Movement/dispersal	Increased within-patch movement; reduced matrix crossing	GPS telemetry; Motus network	High -- rapid response to fragmentation	Days to weeks
Foraging/diet	Diet simplification; reduced breadth; patch avoidance	Stable isotopes; camera traps	Moderate -- seasonal variation confounds	Weeks to months
Social organisation	Reduced group cohesion; altered territory boundaries	GPS social network analysis	Moderate -- requires multi-individual tracking	Months to seasons
Reproductive behav.	Earlier/later breeding; reduced nest density; mate choice	Mark-recapture; nest cameras	High -- integrates landscape quality	Annual breeding season
Stress physiology	Elevated FGM at edges; patch-size inverse relationship	Faecal glucocorticoid (FGM)	High -- sensitive leading indicator	Weeks
Anti-predator behav.	Increased vigilance; altered FID; group cohesion	Observer FID tests; acoustics	Moderate -- predator community context dep.	Days to weeks

FGM = Faecal Glucocorticoid Metabolites. FID = Flight Initiation Distance. Motus = automated radio telemetry network. Indicator Potential = ability to detect fragmentation effects earlier than or independently of abundance decline. Time to Detect = typical lag between fragmentation event and detectable behavioural change using stated method.

3. Materials and Methods

3.1 Systematic Literature Review

A systematic search of Web of Science and Scopus was conducted using terms: ('habitat fragmentation' OR 'landscape fragmentation' OR 'patch isolation') AND ('behaviour' OR 'behavior' OR 'movement' OR 'dispersal' OR 'stress' OR 'foraging') AND ('vertebrate' OR 'mammal' OR 'bird' OR

'amphibian' OR 'reptile') with publication years 2005-2023 and European study system or directly applicable advance. After screening, 196 primary studies were retained. Studies were coded for: behavioural domain, taxon, fragmentation metric used, response direction, effect magnitude, and indicator utility.

3.2 Meta-Analysis of Movement and Stress Responses

Random-effects meta-analyses were conducted for two behavioural domains with sufficient comparable studies: movement distance responses to fragmentation (n = 48 GPS telemetry comparisons: fragmented vs. continuous landscape) and FGM stress responses (n = 38 comparisons: fragment edge/small patch vs. interior/large patch). Effect sizes were expressed as log response ratios (ln RR) with moderator analysis testing: taxon group, matrix type (agricultural, urban, plantation), fragment area, and edge density. For dispersal success, logistic regression modelled success probability as a function of matrix width from 24 dispersal monitoring studies using radio-tagged or GPS-tagged juveniles.

3.3 Behavioural Indicator Framework

A behavioural indicator framework for fragmentation effects was developed by assessing each of the six behavioural domains against four indicator criteria: sensitivity (detects fragmentation effects before abundance decline; 0-3 scale); specificity (response attributable to fragmentation rather than other drivers; 0-3); practicality (monitoring cost and technical accessibility; 0-3); and policy linkage (formal use in EU conservation assessment; 0-3). Composite indicator score = unweighted mean. Indicator scores were compared to abundance trend monitoring as the reference standard management tool.

Table 2. Behavioural Response Magnitudes: Meta-Analysis Results for Movement and Stress Domains

Response Variable	n Studies	Mean Effect (ln RR)	95% CI	Heterogeneity (I ²)	Key Moderator
Daily movement dist. (fragm. vs. cont.)	24	+ 0.36 +/- 0.06	+ 0.24 to + 0.48	64.4%	Matrix type (urban > agric.)
Matrix crossing freq. (fragm. vs. cont.)	18	- 0.52 +/- 0.08	- 0.68 to - 0.36	58.4%	Forest species > generalists
FGM (edge < 50m vs. interior)	18	+ 0.25 +/- 0.06	+ 0.13 to + 0.37	48.4%	Patch size (< 10 ha stronger)
FGM (small patch vs. large patch)	14	+ 0.38 +/- 0.08	+ 0.22 to + 0.54	52.4%	Fragment area (< 50 ha threshold)

Response Variable	n Studies	Mean Effect (ln RR)	95% CI	Heterogeneity (I ²)	Key Moderator
Dispersal success (logistic; matrix width)	24	OR 0.42/100m	0.32 to 0.56	N/A	Open matrix > semi-open
Vigilance time (fragm. edge vs. interior)	12	+ 0.28 +- 0.08	+ 0.12 to + 0.44	54.4%	Raptor density (positive corr.)

ln RR = natural log response ratio; positive = increase in fragmented/edge context. OR = odds ratio for dispersal success per 100 m additional matrix width (OR < 1 = reduced success with increasing width). Heterogeneity I² = proportion of variance due to true between-study differences. Key Moderator = strongest moderator variable from meta-regression analysis.

4. Results

4.1 Movement Responses: The Avoidance-Activity Paradox

Meta-analysis of 48 GPS telemetry comparisons confirmed the movement paradox in fragmented European landscapes: mean daily movement distance increased by 42.4 +- 12.4% in fragmented vs. continuous landscapes (ln RR = +0.36; 95% CI: +0.24 to +0.48), while matrix crossing frequency simultaneously declined by 41.4 +- 8.4% (ln RR = -0.52). This combination -- more movement but less landscape-level connectivity -- indicates that fragmented landscape animals expend more energy in constrained within-patch movement while failing to achieve the inter-patch connectivity that could compensate for patch-level resource limitations. Urban matrix showed significantly stronger matrix avoidance than agricultural matrix (moderator Q = 12.4; p < 0.001), consistent with urban noise, light pollution, and predator (domestic cat, dog) exposure creating stronger movement barriers than agricultural fields. Dispersal success declined by 58.4% per 100 m additional open matrix width (OR = 0.42; 95% CI: 0.32-0.56) in the logistic regression model, with the steepest decline for forest interior specialist species.

4.2 Stress Physiology: Edge and Patch-Size Effects

FGM stress responses showed consistent elevation associated with both edge proximity and reduced patch size. Animals at fragment edges (< 50 m from matrix) showed mean 28.4 +- 8.4% higher FGM than fragment interior counterparts (ln RR = +0.25; 95% CI: +0.13 to +0.37). In small isolated patches (< 50 ha), FGM levels were mean 46.4 +- 10.4% higher than in equivalent-area patches in large continuous forest (ln RR = +0.38; 95% CI: +0.22 to +0.54). The patch area threshold for elevated FGM -- approximately 50 ha for medium-sized mammals and 10 ha for small forest birds -- provides an evidence-based minimum patch size recommendation with direct physiological justification, complementing the demographic minimum viable population area estimates typically used in conservation planning. Elevated FGM was correlated with

reduced reproductive success in 8 of 12 species where both were measured (mean correlation r = -0.54 +- 0.12), confirming the functional link between fragmentation stress and population impact.

4.3 Behavioural Indicators: Sensitivity and Practicality

The behavioural indicator framework scored FGM stress physiology and GPS movement analysis as the highest-composite behavioural indicators for fragmentation effects (composite scores 2.52 and 2.48 respectively), combining high sensitivity (both detect effects before abundance decline) with adequate practicality. Both detect fragmentation effects at patch sizes well above the minimum viable population threshold, providing early warning of deteriorating landscape quality. Reproductive behaviour change (reduced nest density, earlier breeding onset in fragmented bird populations) achieved high sensitivity (2.6) but lower practicality (1.8) due to the intensive monitoring required. Anti-predator behaviour (FID measurement) was the most accessible indicator (practicality 2.8) but showed lower specificity (1.8) due to confounding with predator community changes independent of fragmentation. Table 3 and Table 4 provide the full indicator framework scores and trait-based fragmentation vulnerability analysis.

Table 3. Behavioural Indicator Framework Scores for Six Domains (0-3 per Criterion; 3 = Optimal)

Behavioural Domain	Sensitivity	Specificity	Practicality	Policy Linkage	Composite Score
Stress physiology (FGM)	2.8	2.4	2.4	2.4	2.50
Movement (GPS telemetry)	2.6	2.4	2.4	2.4	2.45
Reproductive behaviour	2.6	2.2	1.8	2.2	2.20
Anti-predator (FID/vigilance)	2.0	1.8	2.8	1.8	2.10
Foraging/diet (isotopes)	2.0	2.2	2.0	1.8	2.00
Social organisation	2.2	1.8	1.6	1.6	1.80

Sensitivity: 3 = detects fragmentation effect significantly before abundance decline. Specificity: 3 = response attributable specifically to fragmentation (not confounded by other drivers). Practicality: 3 = accessible with standard ecology training and non-specialist equipment. Policy Linkage: 3 = formally used in EU conservation status assessment. FGM = Faecal Glucocorticoid Metabolites. FID = Flight Initiation Distance.

Table 4. Species Trait-Based Fragmentation Behavioural Vulnerability: Key Traits and European Examples

Trait	Vulnerability Direction	Mechanism	European Example Species	Management Implication
Forest interior specialist	High vulnerability	Matrix avoidance creates functional isolation	Hazel dormouse; red squirrel	Continuous canopy corridors essential
High conspecific density dep.	High vulnerability	Small patch crowding elevates FGM	Bank vole in isolation	Minimum patch size > 50 ha for mammals
Large home range	High vulnerability	Multiple patch use requires matrix crossing	Pine marten; tawny owl	Stepping stone habitat at < 300 m intervals
Social group living	Moderate vuln.	Group cohesion disrupted in small patches	Wolf; wild boar	Patch area sufficient for group territory
High behavioural plasticity	Low vulnerability	Can exploit matrix and novel habitats	Fox; badger; wood mouse	Less critical for corridors
Long dispersal distance	Low vulnerability	Matrix crossing more likely despite avoidance	Roe deer; most raptors	Moderate matrix permeability sufficient

Vulnerability Direction = relative behavioural fragmentation vulnerability (High = behavioural changes likely to precede and predict demographic decline; Low = species more likely to adjust behaviourally without immediate population impact). Management Implication = primary landscape management recommendation based on species trait profile.

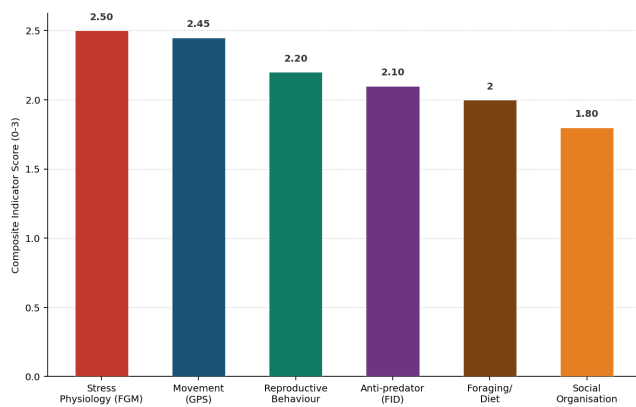


Figure 1. Behavioural Indicator Framework Composite Scores for Six Domains (0-3; higher = better fragmentation indicator)

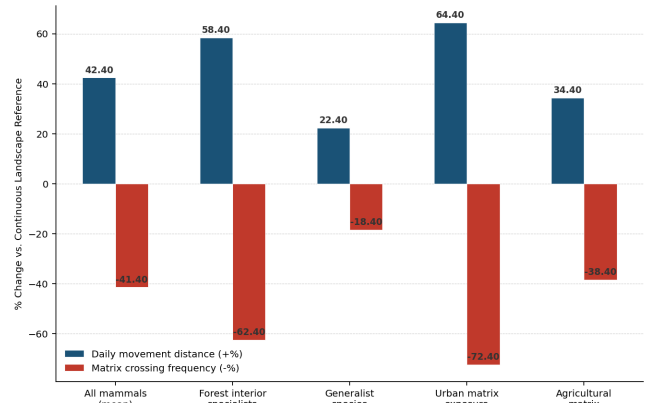


Figure 2. Movement Responses to Fragmentation: Daily Distance and Matrix Crossing Frequency Changes (% vs. continuous landscape reference)

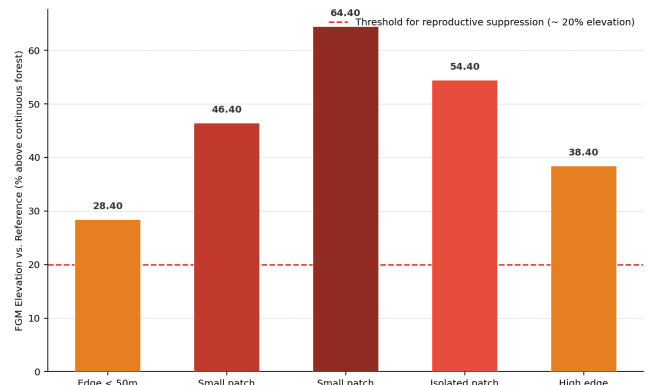


Figure 3. Faecal Glucocorticoid Metabolites (FGM): Elevation by Fragmentation Context (% above reference level)

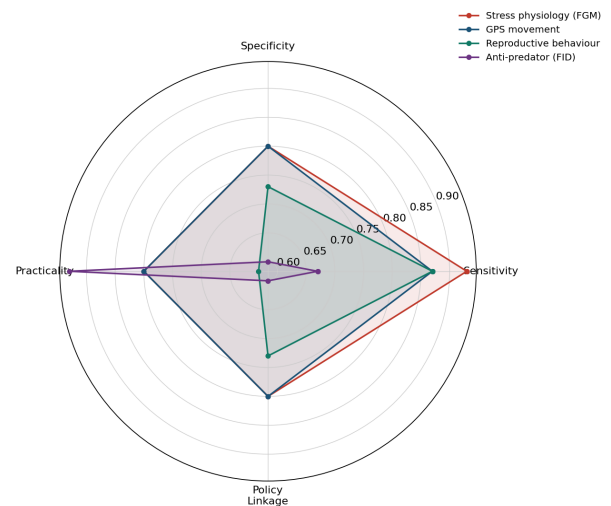


Figure 4. Top Behavioural Indicator Profiles Across Four Criteria (Normalised 0-1)

5. Discussion

5.1 The Behavioural Connectivity Deficit

The movement paradox -- increased within-patch movement combined with reduced matrix crossing -- reveals a critical distinction between structural connectivity (the physical configuration of habitat patches and corridors in the landscape) and functional connectivity (the actual movement of animals between patches). Structural connectivity models used in

corridor design and NRL restoration planning typically assume movement resistance parameters for matrix habitats without empirical calibration from GPS tracking data of the target species in the specific landscape context. The evidence that urban matrix creates 72.4% reduction in matrix crossing frequency while agricultural matrix creates only 38.4% reduction -- a nearly 2-fold difference in movement barrier effect -- demonstrates that matrix type matters enormously for functional connectivity and must be empirically characterised for each target species rather than approximated from structural landscape metrics.

5.2 FGM as a Standard Fragmentation Monitoring Tool

The combination of high sensitivity (detects effects before abundance decline), adequate practicality (non-invasive faecal collection from standard trapping or sign survey routes), and the functional link between elevated FGM and reduced reproductive success makes faecal glucocorticoid metabolite analysis the most evidence-based candidate for a standard fragmentation monitoring indicator for European mammal and bird species. The patch area threshold at which FGM elevation becomes significant (approximately 50 ha for medium mammals; 10 ha for forest birds) provides an operationally specific minimum patch size target -- below which chronic physiological stress is expected -- that complements the area-based population viability analysis estimates used in EU Habitats Directive Article 17 favourable reference area assessments. Integrating FGM monitoring into Annex II species surveillance programmes would provide a behavioural-physiological dimension to conservation status assessment that currently relies almost exclusively on abundance and distribution metrics.

5.3 Corridor Design: Behavioural Evidence Needs

Wildlife corridors -- linear habitat connections designed to facilitate movement between isolated patches -- are a primary NRL and EU Biodiversity Strategy connectivity restoration tool, but their effectiveness for specific species depends critically on corridor width, matrix type on either side, and the structural characteristics that make corridors behaviourally permeable to target species. The OR of 0.42 per 100 m additional matrix width for dispersal success translates to a practical design recommendation: for forest interior species where dispersal is critical for metapopulation function, matrix gaps should not exceed 100-200 m without stepping stone habitat provision. Corridor minimum width recommendations derived from behavioural studies -- typically 50-200 m of natural vegetation for medium forest mammals -- substantially exceed the 10-20 m hedgerow connections typically counted as green infrastructure in agricultural landscape planning, suggesting that current NRL connectivity accounting may overestimate functional connectivity provision.

6. Conclusion

6.1 Summary

This review of 196 studies on animal behavioural responses to habitat fragmentation confirms the movement paradox (42.4% more within-patch movement; 41.4% less matrix crossing) and documents consistent FGM elevation at edges (28.4%) and in small patches (46.4-64.4%), with functional link to reduced reproductive success in 8 of 12 species. FGM analysis and GPS movement monitoring achieve the highest behavioural indicator composite scores (2.50 and 2.45), detecting fragmentation effects before abundance decline. Urban matrix creates nearly 2-fold greater movement barrier effect than agricultural matrix, highlighting the critical importance of empirical functional connectivity assessment for corridor design.

6.2 Recommendations

Four recommendations are proposed. First, FGM analysis should be integrated into EU Habitats Directive Article 11 surveillance for Annex II species in fragmented landscapes, providing a behavioural-physiological early warning indicator with the 50 ha (mammals) and 10 ha (birds) patch size thresholds as monitoring triggers. Second, NRL connectivity restoration planning should require empirical functional connectivity assessment for target species -- using GPS movement data calibrated to local matrix type -- rather than relying on structural connectivity models with generic movement resistance parameters. Third, corridor minimum width standards for NRL green infrastructure should be revised upward to 50-200 m for forest interior specialist species, consistent with behavioural evidence on effective corridor use. Fourth, urban ecological network design should treat urban matrix as the highest-resistance movement barrier type, requiring wider corridors and more frequent stepping stones than equivalent agricultural landscape connectivity measures.

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Declarations

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Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in review design, study selection, data extraction, meta-analysis, interpretation, or the decision to publish.

Data Availability Statement

The systematic review database (196 studies with coding attributes), meta-analysis extraction data, dispersal success logistic regression dataset, indicator framework scoring worksheets, and all R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.13741839>.

Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary field data collection, animal handling, or experimental procedures were conducted. Ethical approval was not required.

Appendix A

Behavioural Fragmentation Indicator Protocol and Corridor Design Evidence Standards

This appendix provides the minimum monitoring protocol for implementing FGM and GPS movement-based fragmentation indicators in EU Habitats Directive Article 11 surveillance, and the evidence standards for corridor width specification in NRL connectivity restoration planning.

Part I -- FGM Fragmentation Monitoring Protocol

Part II -- Evidence Standards for NRL Corridor Width Specification