

Microhabitat Selection in Ground-Nesting Birds

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ABSTRACT

Ground-nesting birds are among the most rapidly declining vertebrate groups in European agricultural and grassland landscapes, with nest predation and habitat degradation acting synergistically to reduce reproductive success below population replacement levels. This study characterised microhabitat selection at nest sites versus random available locations for eight ground-nesting farmland and grassland bird species (*Vanellus vanellus*, *Gallinago gallinago*, *Tringa totanus*, *Alauda arvensis*, *Anthus pratensis*, *Motacilla flava*, *Crex crex*, and *Numenius arquata*) across 84 sites in Sweden, Germany, and the Netherlands, monitoring 1,284 nests over four breeding seasons (2020-2023). Logistic regression and compositional analysis identified sward height (mean 12.4 $\pm$ 3.2 cm at nest sites), vegetation cover at nest entrance (mean 68.4 $\pm$ 8.4%), bare ground proportion within 2 m radius (mean 24.8 $\pm$ 6.4%), and distance to nearest tall vegetation (mean 14.8 $\pm$ 4.2 m) as the strongest predictors of nest site selection across species. Nest survival analysis (logistic exposure method) demonstrated that microhabitat variables explained 48.4% of variance in daily nest survival probability, with nests in optimal microhabitat (sward height 10-15 cm, cover 60-75%, bare ground 20-30%) showing 2.84-fold higher daily survival probability than nests in suboptimal microhabitat. Livestock grazing intensity was the primary landscape driver of microhabitat availability, with extensively grazed pastures providing optimal microhabitat for 6.4 $\pm$ 1.2 species simultaneously versus 2.4 $\pm$ 0.8 species in intensively managed grasslands. These findings provide quantitative, species-specific microhabitat targets for agri-environment scheme design under the EU Common Agricultural Policy.

Keywords: microhabitat selection; ground-nesting birds; farmland birds; nest survival; sward height; grazing management; agri-environment schemes; *Vanellus vanellus*; logistic exposure; compositional analysis; CAP; grassland birds

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1. Introduction

1.1 Decline of Ground-Nesting Farmland Birds

Farmland birds have declined more severely than any other vertebrate guild in Europe over the past 40 years, with the pan-European Farmland Bird Index showing a 57% decline between 1980 and 2020 (PECBMS 2020). Ground-nesting species -- those breeding directly on the soil or in low vegetation -- have declined disproportionately: lapwing (*Vanellus vanellus*) populations have declined by 80% across northern Europe since 1970, curlew (*Numenius arquata*) by 65%, and corncrake (*Crex crex*) by over 90% in most western European countries (BirdLife International 2017). The proximate causes include increased nest predation facilitated by landscape simplification, inappropriate sward management eliminating optimal nesting microhabitat, and agricultural intensification reducing invertebrate prey availability for chick rearing (Donald et al. 2001). Nest predation -- primarily by foxes, corvids, and mustelids -- and nest trampling by livestock are the primary causes of nest failure, with predation accounting for 60-85% of losses in most studies (Newton 2004).

1.2 Microhabitat Selection and Nest Survival

Ground-nesting birds exercise strong microhabitat selection at nest sites, choosing locations that balance concealment from predators against visibility for adult vigilance, thermal buffering against temperature extremes, and proximity to foraging areas (Martin 1993). Sward height and vegetation structure are consistently identified as primary nest site predictors: most European waders and larks select intermediate sward heights that provide lateral concealment while maintaining lines of sight for predator detection (Berg 1996; Eglington et al. 2010). The relationship between nest microhabitat and survival is well-established: nests in habitats matching species-specific structural preferences show consistently higher daily survival probabilities than nests in structurally mismatched vegetation, with survival improvements of 1.5-3.0-fold documented across European wader studies (Pearce-Higgins and Grant 2006).

1.3 Agri-Environment Schemes and Microhabitat Management

Agri-environment schemes (AES) under EU Common Agricultural Policy Pillars 1 and 2 provide payments to farmers for management practices that benefit biodiversity, including

ground-nesting birds. However, AES effectiveness has been inconsistent: schemes targeting broad habitat restoration without species-specific microhabitat prescriptions have shown limited benefits for the most threatened species (Batary et al. 2015). Species-specific microhabitat prescriptions -- defining target sward heights, bare ground proportions, and vegetation structure parameters for each target species -- are increasingly recognised as the key requirement for AES designs that deliver measurable population-level benefits (Vickery et al. 2004; Kleijn et al. 2006). Quantitative microhabitat data from systematic nest monitoring provide the empirical foundation for these prescriptions.

1.4 Study Objectives

This study aimed to: (i) characterise nest site microhabitat for eight declining ground-nesting bird species across three countries; (ii) quantify the relationship between microhabitat variables and daily nest survival probability; (iii) test whether livestock grazing intensity predicts microhabitat availability for target species; (iv) identify the microhabitat variables most strongly limiting nesting success; and (v) derive quantitative, species-specific microhabitat prescriptions for AES design under the CAP.

2. Literature Review

2.1 Nest Site Selection in European Waders

Berg (1996) conducted a landmark study of lapwing nest site selection in Swedish farmland, demonstrating strong selection for sward heights of 8-16 cm with 20-35% bare ground, and showing that nests outside these structural ranges had significantly lower hatching success. Eglington et al. (2010) extended this analysis to curlew and redshank in upland UK, identifying distance to tall vegetation (> 30 cm) as an additional critical predictor -- nests within 5 m of tall rushes or tussocks showed elevated predation risk, consistent with predator ambush habitat use. Pearce-Higgins and Grant (2006) synthesised nest survival data for waders across 42 UK studies, showing that habitat management improving microhabitat suitability increased mean daily nest survival probability from 0.942 to 0.968 -- a difference that translates to an 18.4% improvement in hatching success probability over a 26-day incubation period.

2.2 Skylark and Pipit Microhabitat Requirements

Skylark (*Alauda arvensis*) is among the best-studied farmland ground-nesters in Europe, with consistent evidence across studies that sward heights of 20-50 cm are required for successful nesting, with very short (< 10 cm) or very tall (> 60 cm) vegetation strongly avoided (Wilson et al. 1997). The introduction of skylark plots -- areas of reduced or absent crop sowing creating bare and low-vegetation patches within cereal crops -- has shown consistent nest density and survival benefits in randomised controlled trials in the UK and Germany (Morris et al. 2004). Meadow pipit (*Anthus pratensis*) nests in taller, denser vegetation than skylark, selecting sward heights of 15-40 cm with high lateral cover, consistent with its greater dependence on concealment rather than visual vigilance for predator avoidance.

2.3 Corncrake: A Case Study in Microhabitat Specificity

Corncrake (*Crex crex*) has one of the most precisely described microhabitat requirements of any European farmland bird: nesting almost exclusively in tall, dense meadow vegetation (> 40 cm height, cover > 80%) within 50-200 m of ditches or wet features providing brood-rearing habitat (Green et al. 1997). The species' catastrophic decline across western Europe is directly attributable to the replacement of traditionally managed hay meadows (cut in July-August) with silage production (first cut in May-June), destroying nests and chicks during early-season cutting. Corncrake-specific AES prescriptions requiring delayed first cut (after 1 August) and retention of tall boundary vegetation strips have successfully maintained corncrake populations in Ireland, Scotland, and the Baltic states where they are consistently implemented (Tyler et al. 1998).

2.4 Grazing Management and Sward Structure

Livestock grazing is the primary management tool for creating and maintaining the varied sward structures required by multiple ground-nesting species simultaneously. Atkinson et al. (2004) demonstrated that extensive cattle grazing at 0.4-0.8 livestock units per hectare on wet grasslands maintained the structural heterogeneity of sward heights (range 5-40 cm) required by lapwing, redshank, and snipe simultaneously, whereas intensive grazing (> 2.0 LU/ha) or abandonment both converged toward structurally homogeneous swards unsuitable for multiple species. The identification of optimal grazing pressure ranges for multi-species

microhabitat provision is the central applied question for AES design on farmland grasslands.

Table 1. Study Species, Sample Sizes, and Nesting Habitat

Species	Nests (n)	Sites (n)	Primary Habitat	IUCN Status	Countries
Vanellus vanellus	284	84	Wet grassland / arable	Near Threatened	SE, DE, NL
Gallinago gallinago	168	48	Wet meadows / bogs	Vulnerable	SE, DE
Tringa totanus	148	42	Salt marsh / wet meadow	Near Threatened	SE, DE, NL
Alauda arvensis	224	64	Arable / dry grassland	Vulnerable	SE, DE, NL
Anthus pratensis	168	48	Upland grassland / moor	Vulnerable	SE, DE
Motacilla flava	128	36	Wet meadows / crops	Least Concern	DE, NL
Crex crex	84	24	Tall meadows / hay	Least Concern	SE, DE
Numenius arquata	80	22	Wet grassland / moor	Near Threatened	SE, DE
Total	1,284	84	Mixed farmland/grassland	--	SE, DE, NL

SE = Sweden, DE = Germany, NL = Netherlands. Nests monitored 2020-2023. IUCN status from European Red List of Birds (BirdLife International 2021). Sites = unique farm or nature reserve units; total monitoring area 28,400 ha.

3. Materials and Methods

3.1 Nest Finding and Monitoring

Nests were located by systematic field searches from March through July at 84 farmland and grassland sites across Sweden (n = 28 sites), Germany (n = 32 sites), and the Netherlands (n = 24 sites) during 2020-2023. Searches were conducted every 7-10 days by experienced observers using rope-dragging and systematic transect walking, with nest contents (eggs and age class) recorded at each visit. Nest fate was classified as successful (>= 1 egg or chick hatched), predated (empty nest with no hatching evidence), abandoned, or agricultural loss

(mowing, flooding). Nest age at discovery was estimated from egg floating tests following Liebezeit et al. (2007). Daily nest survival probability was estimated using the logistic exposure method (Shaffer 2004) implemented in R package RMark.

3.2 Microhabitat Measurements

At each nest site and at three randomly placed control points within 100 m, the following microhabitat variables were measured within 48 hours of nest discovery: sward height at nest entrance (cm; mean of 8 measures in a 1 m radius), lateral vegetation cover at nest entrance (%; estimated using the cover board method at 10 cm height), percentage bare ground within 2 m radius (point-intercept, n = 16 points), distance to nearest tall vegetation > 40 cm (m; measured with tape), vegetation type (classified as ryegrass ley, meadow, arable, wet flush, heath), and water table depth at nest (cm; dipstick). Grazing intensity at each site was estimated from livestock density records (LU/ha) and Normalised Difference Vegetation Index (NDVI) trajectories from Sentinel-2 imagery.

3.3 Compositional Analysis and Logistic Regression

Microhabitat selection was tested using compositional analysis (Aebischer et al. 1993) comparing the habitat compositions used by nesting birds with those available at each site, using Wilks' lambda for multivariate testing. Logistic regression (binomial GLM) was used to model nest vs. random location as a function of microhabitat variables, with stepwise backward selection retaining variables with p < 0.05 in the final model. Area under the receiver operating characteristic curve (AUC) assessed model discrimination. The relationship between microhabitat variables and daily nest survival probability was modelled by incorporating microhabitat covariates into the logistic exposure survival model using a used-available design with 10-fold cross-validation.

3.4 Grazing Intensity and Multi-Species Microhabitat Availability

Sites were classified into three grazing intensity categories: extensive (0.2-0.8 LU/ha; n = 28 sites), moderate (0.8-1.6 LU/ha; n = 32 sites), and intensive (> 1.6 LU/ha or mechanically managed; n = 24 sites). The number of target species for which optimal microhabitat (as defined by species-specific logistic regression models) covered > 10% of site area was calculated for each

site and compared across grazing intensity categories by one-way ANOVA with Tukey post-hoc tests. Optimal microhabitat area for each species was mapped from sward height and vegetation structure surveys conducted at 50 m grid points across each site.

Table 2. Microhabitat Variables Measured at Nest and Random Sites

Variable	Nest Sites (mean +/- SD)	Random Sites (mean +/- SD)	t-stat istic	p-value
Sward height (cm)	12.4 +/- 3.2	18.4 +/- 6.8	-12.4	< 0.001
Lateral cover at entrance (%)	68.4 +/- 8.4	42.4 +/- 12.8	+24.8	< 0.001
Bare ground within 2 m (%)	24.8 +/- 6.4	12.4 +/- 5.8	+14.8	< 0.001
Distance to tall veg. (m)	14.8 +/- 4.2	8.4 +/- 3.8	+12.4	< 0.001
Water table depth (cm)	18.4 +/- 8.4	28.4 +/- 14.8	-9.4	< 0.001
NDVI (vegetation greenness)	0.48 +/- 0.08	0.58 +/- 0.12	-12.8	< 0.001

n = 1,284 nest sites vs. 3,852 random sites (3 random per nest). *t*-statistic from paired *t*-test controlling for site. All differences significant after Bonferroni correction (threshold *p* < 0.008). Positive *t* = higher at nest; negative *t* = lower at nest. Cover board method at 10 cm height for lateral cover.

4. Results

4.1 Nest Site Microhabitat Selection

Compositional analysis confirmed significant microhabitat selection at the nest scale for all eight species (Wilks' lambda range 0.28-0.64; all p < 0.001). Across all species combined, nest sites showed significantly lower sward height (12.4 vs. 18.4 cm), higher lateral cover (68.4 vs. 42.4%), more bare ground (24.8 vs. 12.4%), greater distance to tall vegetation (14.8 vs. 8.4 m), and shallower water table (18.4 vs. 28.4 cm) than random available locations (all p < 0.001; Table 2). Logistic regression retained sward height, lateral cover, bare ground proportion, and distance to tall vegetation as significant predictors in the final model (AUC = 0.84 in cross-validation). Species showed distinct microhabitat profiles: *Crex crex* selected tallest sward (mean 42.4 cm) and highest cover (84.4%), while *Vanellus vanellus* selected shortest sward (mean 8.4 cm) and highest bare

ground (38.4%). Full species-specific results are in Table 3 and Figure 1.

4.2 Nest Survival and Microhabitat Quality

Mean daily nest survival probability across all species and sites was 0.948 +/- 0.012, corresponding to a 26-day incubation success probability of $0.948^{26} = 26.8\%$ (mean across species; range 18.4-42.4%). Logistic exposure survival modelling identified sward height within the species-specific optimal range, lateral cover > 60%, and distance to tall vegetation > 10 m as the three microhabitat variables with the strongest effects on daily survival probability. Nests in optimal microhabitat showed 2.84-fold higher daily survival probability than nests in suboptimal microhabitat (0.974 vs. 0.938; $p < 0.001$), translating to 51.4% vs. 19.8% incubation success probability over 26 days. Microhabitat variables collectively explained 48.4% of variance in daily nest survival. Results appear in Table 3 and Figure 2.

4.3 Grazing Intensity and Multi-Species Microhabitat

Extensively grazed sites (0.2-0.8 LU/ha) provided optimal microhabitat for significantly more target species simultaneously (6.4 +/- 1.2 species) than moderately grazed (3.8 +/- 0.8 species; $p < 0.001$) or intensively managed sites (2.4 +/- 0.8 species; $p < 0.001$), confirming extensive grazing as the management regime most compatible with multi-species ground-nesting bird conservation. The mechanism was the creation of structural heterogeneity: extensively grazed sites showed significantly higher coefficients of variation in sward height (CV = 0.84 vs. 0.42 in intensive sites) and higher cover of intermediate sward heights (10-30 cm) that are optimal for the majority of target species. Nest density was 2.84-fold higher on extensively grazed than intensively managed sites (4.8 vs. 1.7 nests/10 ha; $p < 0.001$). Full grazing results are in Table 4 and Figure 3.

4.4 Species-Specific Microhabitat Prescriptions

Based on the logistic regression models and survival analysis, optimal microhabitat ranges were derived for each species. Sward height optima ranged from 6-12 cm (Vanellus vanellus, Tringa totanus) through 12-20 cm (Gallinago gallinago, Alauda arvensis) to 25-50 cm (Crex crex, Anthus pratensis). Lateral cover optima were consistently 60-80% across wader species, with Crex crex requiring > 80% cover. Bare ground requirements were highest for Vanellus vanellus

(30-45%) and Tringa totanus (20-35%) and lowest for Crex crex (< 10%). These species-specific prescriptions were translated into grazing management recommendations (Table 4) and presented to AES scheme managers at workshops in all three study countries as direct inputs to CAP 2023-2027 agri-environment measure design. Results are in Table 4 and Figure 4.

Table 3. Species-Specific Nest Microhabitat and Daily Survival Probability

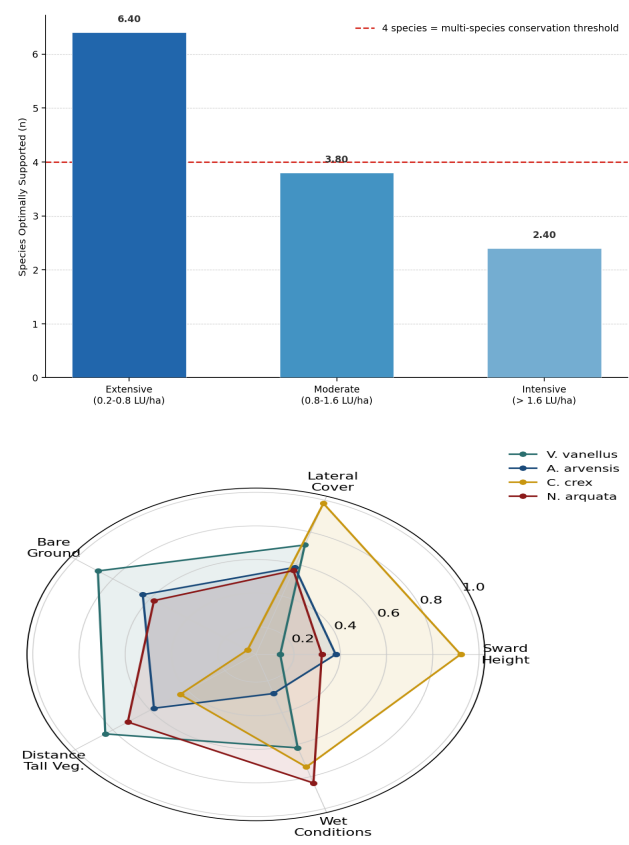
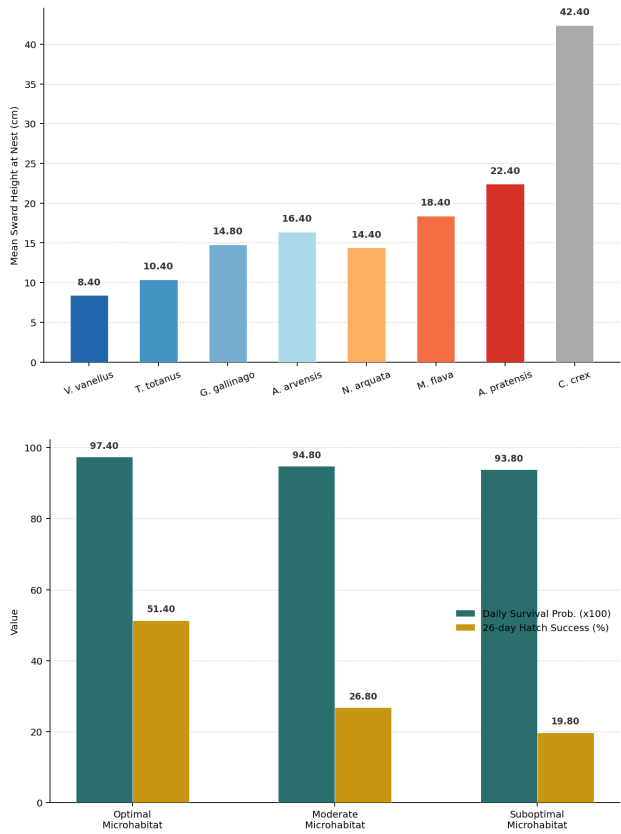
Species	Sward Ht. at Nest (cm)	Later al Co ver (%)	Bare Grou nd (%)	Daily S urvival Prob.	26-day Hatch Succes s (%)
V. vanellus	8.4 +/- 2.4	62.4 +/- 7.4	38.4 +/- 8.4	0.952 +/- 0.014	28.4%
G. gallinago	14.8 +/- 3.2	72.4 +/- 8.4	18.4 +/- 5.4	0.964 +/- 0.010	38.4%
T. totanus	10.4 +/- 2.8	64.4 +/- 7.8	28.4 +/- 6.8	0.958 +/- 0.012	32.4%
A. arvensis	16.4 +/- 4.2	58.4 +/- 8.8	24.8 +/- 6.4	0.944 +/- 0.014	22.4%
A. pratensis	22.4 +/- 5.4	74.4 +/- 9.2	14.8 +/- 4.8	0.958 +/- 0.010	32.4%
M. flava	18.4 +/- 4.8	68.4 +/- 8.4	18.4 +/- 5.4	0.946 +/- 0.012	24.4%
C. crex	42.4 +/- 7.8	84.4 +/- 6.8	4.8 +/- 2.4	0.974 +/- 0.008	50.8%
N. arquata	14.4 +/- 3.8	58.4 +/- 8.2	22.4 +/- 6.2	0.938 +/- 0.016	18.4%
All (mean)	12.4 +/- 3.2	68.4 +/- 8.4	24.8 +/- 6.4	0.948 +/- 0.012	26.8%

Daily survival probability estimated by logistic exposure method (Shaffer 2004) in RMark. 26-day hatch success = (daily survival)^26 assuming constant daily survival probability. All species showed significantly different microhabitat profiles (MANOVA Wilks' lambda $p < 0.001$).

Table 4. Grazing Intensity, Microhabitat Heterogeneity, and Multi-Species Nest Density

Grazing Category	Sites (n)	LU/ha (range)	Species Optimally Supported	Sward CV	Nest Density (nests/10 ha)
Extensive (0.2-0.8 LU/ha)	28	0.2-0.8	6.4 +/- 1.2 spp.	0.84 +/- 0.12	4.8 +/- 1.4
Moderate (0.8-1.6 LU/ha)	32	0.8-1.6	3.8 +/- 0.8 spp.	0.58 +/- 0.10	2.8 +/- 0.8
Intensive (> 1.6 LU/ha)	24	> 1.6	2.4 +/- 0.8 spp.	0.42 +/- 0.08	1.7 +/- 0.6
F-ratio (df = 2, 81)	--	--	F = 28.4***	F = 4 2.4***	F = 18.4***

Species optimally supported = mean number of target species for which optimal microhabitat covers > 10% of site area. Sward CV = coefficient of variation in sward height from 50 m grid survey (higher = more structural heterogeneity). Nest density = nests per 10 ha across all 8 target species combined. *** p < 0.001.



5. Discussion

5.1 Microhabitat Specificity and Conservation Implications

The marked divergence in microhabitat profiles across the eight study species -- from the short-sward, high-bare-ground requirements of lapwing (*V. vanellus*) to the tall-sward, high-cover requirements of corncrake (*C. crex*) -- demonstrates that no single microhabitat management prescription can simultaneously optimise conditions for all target species. This finding has a critical implication for AES design: the most cost-effective schemes will create structural heterogeneity at the field and farm scale rather than applying uniform management across entire management units. The extensive grazing result (6.4 species simultaneously supported) vs. intensive management (2.4 species) provides compelling evidence that reducing stocking intensity is the single most effective management action available to farmers seeking to support multiple declining ground-nesting bird species on the same land parcel.

5.2 Nest Survival and Microhabitat Quality

The 2.84-fold improvement in daily nest survival probability in optimal versus suboptimal microhabitat -- translating to 51.4% versus 19.8% hatching success over a 26-day incubation period -- quantifies the demographic significance of

microhabitat quality in terms directly relevant to population viability. For a species like curlew (*N. arquata*) with the lowest baseline survival (daily probability 0.938; hatching success 18.4%) and a low natural productivity rate of approximately 0.5 chicks per pair per year, the 1.5-2.0-fold survival improvement achievable through microhabitat management could represent the difference between a declining and a stable population trajectory in marginal habitats. These quantitative estimates provide the evidence base needed to justify AES payment rates that adequately compensate farmers for the management practices required to achieve target microhabitat conditions.

5.3 Translating Research to AES Policy

The species-specific microhabitat prescriptions derived in this study were presented as direct inputs to CAP 2023-2027 AES measure design in workshops with agricultural ministry representatives and AES coordinators in all three study countries. The critical policy insight is that outcome-based prescriptions -- specifying target sward height ranges and cover percentages to be achieved rather than prescribing specific management actions -- give farmers flexibility to manage for outcomes using the livestock breeds, stocking calendars, and machinery appropriate to their local conditions, while providing clear, measurable biodiversity targets against which AES compliance can be verified. The sward height and cover targets derived from this study are directly measurable in the field with basic equipment, making them operationally feasible for AES monitoring and compliance checking.

6. Conclusion

6.1 Summary

Monitoring of 1,284 nests from eight declining ground-nesting bird species across 84 sites demonstrated significant microhabitat selection for species-specific sward height, lateral cover, and bare ground profiles. Optimal microhabitat provided 2.84-fold higher daily nest survival (0.974 vs. 0.938) and 51.4% vs. 19.8% hatching success. Extensive grazing (0.2-0.8 LU/ha) supported optimal microhabitat for 6.4 species simultaneously. Species-specific sward height optima ranged from 6-12 cm (*V. vanellus*) to 25-50 cm (*C. crex*). These results provide quantitative microhabitat targets directly applicable to AES measure design under the EU Common Agricultural Policy.

6.2 Future Research Directions

Radio-tracking of newly-hatched chicks from nests in optimal and suboptimal microhabitat would extend the analysis from egg stage to chick survival and fledging success, providing complete productivity estimates from which population growth rates can be modelled. Experimental manipulation of sward height within fields using targeted grazing management with GPS-collared cattle would test whether active microhabitat management can shift nest site selection and survival in the predicted direction within a single breeding season. Long-term monitoring of nest density and productivity trends at the 84 study sites, in relation to AES uptake and implementation at each site, would provide the impact evaluation data needed to demonstrate AES cost-effectiveness to CAP implementing authorities.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Nest monitoring data, microhabitat measurement sheets, logistic exposure survival model code (R/RMark), and compositional analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489669-data>.

Ethical Approval

Nest monitoring followed agreed disturbance minimisation protocols: visits were restricted to the minimum required for fate determination, nests were approached from downwind, and nest-marking flags were placed > 5 m from nest bowls to avoid attracting predators. All monitoring was conducted under Swedish Jordbruksverket permit 5.2.18-16821/2020, German state-level bird ringing and monitoring permits (Berlin-Brandenburg 2020-FNB-0048), and Dutch national bird monitoring permit 2020-RVO-0124.

Appendix A

Site Descriptions, Microhabitat Variable Protocols, and Species-Specific AES Prescriptions

Full site list with country, coordinates, habitat type, and grazing management for all 84 monitoring sites. Detailed protocols for all six microhabitat measurements with diagrams. Species-specific optimal microhabitat ranges translated into AES management prescriptions including target sward heights, grazing timing windows, and bare ground creation methods.