

Article

Touchdown Rate and Success in Vole Hunting by Wintering Hen Harriers (*Circus cyaneus*): Roles of Intrinsic and Extrinsic Factors

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Simple Summary

Hen Harriers hunt small mammals in open farmland during winter, when food is often scarce and weather conditions can be harsh. To understand how biological and environmental factors shape their hunting performance, we studied birds in Austria over five winters and analyzed more than 1800 hunting attempts. We compared males, territorial females, and non-territorial females. Males, which are smaller and more agile, achieved the highest success per hunting attempt. Territorial females, which defend vole-rich patches, made more hunting attempts per unit time but did not differ from males in the probability of a successful strike. Non-territorial females, lacking both the agility of males and the habitat access of territorial females, showed the lowest hunting success. Adult males tended to be more successful than other age–sex groups, although the effect was not statistically significant. Among weather factors, success increased under cloud cover, decreased with stronger wind, and was unaffected by temperature. These results show that both social status and weather conditions determine hunting success in wintering Hen Harriers. Males succeed through agility, territorial females through resource control, while non-territorial females remain most limited. Conserving open farmland together with small-mammal-rich core areas is crucial to support the different winter strategies of this raptor.



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Abstract

Raptors wintering in temperate regions face strong energetic constraints due to low temperatures and limited prey availability. Understanding how intrinsic traits and environmental conditions shape hunting performance helps to clarify the mechanisms underlying winter foraging efficiency. We studied wintering Hen Harriers (*Circus cyaneus*) in Austria over five consecutive winters (2020/21–2024/25) to quantify touchdown attempt rate and outcome in relation to sex, age, territorial status, and weather. Using generalized linear mixed models, we analyzed 1829 recorded touchdowns with individual identity as a random effect. Territorial females showed slightly higher attempt rates than males, whereas non-territorial females exhibited a tendency toward lower touchdown success. Adult males achieved the highest per-attempt efficiency, but age alone had no significant effect. Touchdown outcomes improved under cloud cover and declined with wind speed, while temperature showed no influence. Attempt rate was unaffected by any environmental variable. These results demonstrate that both intrinsic and extrinsic factors jointly determine winter foraging performance: males, with their smaller body size and agility, can persist even in vole-poor habitats by compensating through efficient flight and prey capture; territorial females benefit from stable access to vole-rich patches; and non-territorial females remain constrained by competition and limited access to prey. The findings highlight the need to maintain open farmland and vole-rich habitat to support diverse overwintering strategies.

Keywords: Hen Harrier; *Circus cyaneus*; winter ecology; hunting rate; hunting success; territoriality; reversed sexual dimorphism; environmental factors

1. Introduction

Raptors wintering in temperate zones are exposed to low temperatures and limited food availability [1,2]. To meet their daily food requirements and maintain energy balance, they must secure sufficient prey intake, which is determined by both encounter rate and capture success [3–8]. At constant predator search effort, encounter rate is primarily governed by prey availability, i.e., the fraction of the prey population that is active and detectable, shaped by activity, vigilance, and habitat structure [9,10]. Capture success, in turn, is driven by intrinsic predator traits and extrinsic environmental conditions. Among intrinsic parameters, age and sex are particularly important: under comparable habitat conditions and prey availability, capture success typically increases with age [11,12], and due to reversed sexual size dimorphism, smaller males are generally reported to outperform females [13–15]. Extrinsic factors such as wind [16], temperature [17], cloud cover [18], and snow cover [19] may further influence hunting outcomes independently of age and sex. For example, increased cloud cover may reduce visual contrast for prey and delay escape responses, while wind can modify flight energetics and hunting dynamics.

Harriers (genus *Circus*) are raptors adapted to open grasslands and wetlands, characterized by their distinctive low-altitude quartering flight [20] and well-developed, “owl-like” hearing [21]. The Eurasian Hen Harrier (*Circus cyaneus*) and its Nearctic vicariant, the Northern Harrier (*Circus hudsonius*) [22], predominantly hunt voles and small birds in regionally varying proportions [23–25]. For the population wintering in Central Europe [26], Common Voles (*Microtus arvalis*) constitute the primary winter prey, typically hunted in extensive, grassland-rich agricultural landscapes [24,27,28]. Voles are captured in rapid ground strikes [29,30]; rate and outcome of these “touchdowns” therefore provide a direct and clearly observable proxy for hunting efficiency in this species.

Several studies have investigated the winter ecology and hunting behavior of Hen and Northern Harriers [20,25,31–41]. While these works have provided important insights into prey spectra, hunting strategies, and seasonal adaptations, they share a number of limitations that constrain generalization, among others, the following five issues: First, there is no consistent terminology or classification of hunting methods, making cross-study comparisons difficult. Second, intrinsic groups are often insufficiently resolved: age and sex are not always distinguished, and brown female-type individuals—including juvenile males as well as females of all age classes—are frequently pooled and contrasted only with gray adult males. In addition, the distinction between non-territorial and territorial females, with the latter establishing and defending food-rich areas, has only rarely been considered. Third, extrinsic weather factors such as wind, cloud cover, or snow are only sporadically included, despite their potential relevance for hunting efficiency. Fourth, hunting outcomes are only partly differentiated by prey groups, although success and strategy may vary between mammals and birds. Fifth, many analyses fail to account for individual-level variation, as they do not incorporate random effects such as individual ID. Accordingly, studies integrating intrinsic, extrinsic, prey-specific, and individual-level factors are needed to better understand the determinants of hunting success in wintering Hen Harriers.

The present study addresses this need by quantifying touchdown attempt rate and success in wintering Hen Harriers in Austria, focusing on quartering flights directed at small mammal prey. Specifically, we considered intrinsic factors (social status and age) as well as extrinsic weather variables (wind, temperature, and cloud cover). We distinguished

three social groups, namely males, territorial females, and non-territorial females. Based on previous studies and identified knowledge gaps, we predicted the following:

Intrinsic factors

- (1) Males would show higher touchdown success due to their smaller size and greater maneuverability, but lower attempt rates because they are often displaced into suboptimal habitats.
- (2) Territorial females, benefiting from access to high-quality foraging grounds, would combine both high touchdown success and high attempt rates.
- (3) Non-territorial females, lacking both morphological advantages and access to high-quality habitat, would show low attempt rates and low touchdown success.
- (4) Adults would outperform juveniles in both attempt rate and touchdown success.

Extrinsic factors

- (5) Cloud cover would increase touchdown success, as reduced visual contrast may delay prey escape responses.
- (6) Temperature would have no effect on attempt rate or touchdown success.
- (7) Increasing wind speed would reduce touchdown success, by constraining flight control and strike precision.

Exploratory wind analysis

In addition to the above predictions on touchdown rate and success, we conducted three exploratory post hoc analyses addressing wind-related behavioral variation. First, we tested whether wind affected the proportion of time spent hunting. Second, we examined whether wind influenced the frequency of touchdown attempts per unit hunting time. Third, we tested whether males, territorial females, and non-territorial females differed in the wind conditions under which they were observed.

2. Materials and Methods

2.1. Study Areas

Fieldwork was conducted in two Austrian regions, Carinthia and Burgenland, during the winters 2020/21–2024/25 (Figure 1). Across all study areas, Hen Harriers occur exclusively as passage migrants and winter visitors [41–45].

In Carinthia, surveys focused on three lowland sections of the inner-alpine Klagenfurt Basin: the Krappfeld (46.832° N, 14.471° E; 600 m a.s.l.), the Glantal (46.729° N, 14.259° E; 500 m a.s.l.), and the vicinity of Sankt Jakob (46.564° N, 14.049° E; 470 m a.s.l.). Winters in this region are cold, with mean January temperatures of -1.6 ± 1.6 °C (2021–2025, Klagenfurt station, <https://www.geosphere.at/de/daten/datenzentrum/data-hub> (last accessed 19 August 2025)). The landscape consists mainly of intensively farmed cropland interspersed with grassland and winter catch crops, while structural elements such as hedgerows, solitary trees, or forest patches are scarce. All three areas represent relatively open agrarian islands embedded in a wider landscape dominated by forests and mountains.

In Burgenland, surveys were conducted on the Parndorf Plain near Nickelsdorf (47.938° N, 17.069° E; 130 m a.s.l.). Despite the low elevation, the continental Pannonian climate results in comparatively cold winters, with mean January temperatures of 2.4 ± 0.91 °C (2021–2025, Eisenstadt station, <https://www.geosphere.at/de/daten/datenzentrum/data-hub> (last accessed 19 August 2025)). The area is characterized by flat, treeless farmland forming part of the Little Hungarian Plain (~8000 km²), where Hen Harriers typically forage in meadow remnants, fallows, and catch crops.

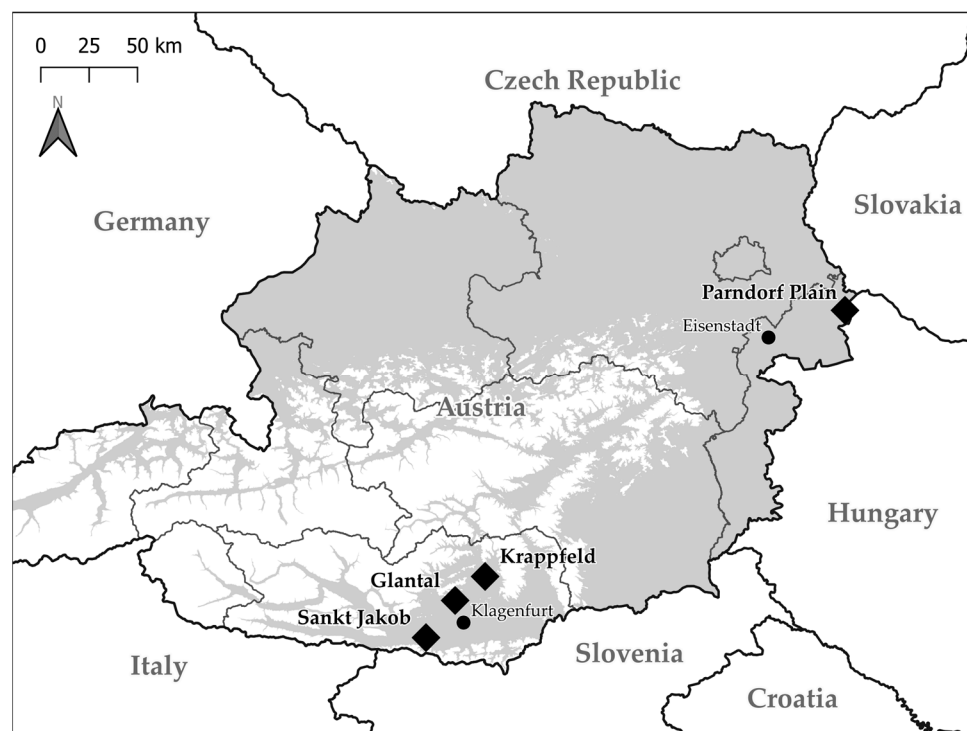


Figure 1. Locations of the study areas, shown as black diamonds, in the Austrian provinces of Carinthia (Glantal, Krappfeld, and Sankt Jakob) and Burgenland (Parndorf Plain). Meteorological reference stations in Klagenfurt and Eisenstadt are indicated by black circles. Areas shaded in grey represent elevations below 1000 m above sea level, which become less frequent towards the Alpine region in the west and correspond to the typical wintering grounds of the Hen Harrier (*Circus cyaneus*).

2.2. Field Methods

2.2.1. Age, Sex, and Individual Determination

Hen Harriers in their first winter, still carrying juvenile remiges, were classified as juveniles, while all older individuals were considered adults [46]. Ageing and sexing relied on a combination of general appearance (shape, size, flight style) and diagnostic traits such as plumage pattern, coloration, and eye color [47].

Individual recognition within a season was possible in female-type Hen Harriers, based on distinctive plumage features, molt limits, or occasionally damaged feathers [30]; see [35,36] for the very closely related Nearctic Northern Harrier. Adult males, however, are generally not individually identifiable [48]; they were treated as new individuals if no male had been recorded in the study area for two consecutive survey days. Because adult males are highly conspicuous in the open winter landscape, the absence of any male for two consecutive survey days reasonably indicates that the previously observed bird had moved on.

2.2.2. Grouping by Sex and Territorial Status

For reasons of comparability and consistency with earlier studies, we distinguished three intrinsic groups of Hen Harriers: (1) males, (2) non-territorial females, and (3) territorial females [41]. Territorial females were clearly recognizable in the field by characteristic behavioral displays. These included repeated chases and escort flights against non-territorial Hen Harriers and other raptors, territorial calls, and the distinctive aggressive “Kong position” on the ground (cf. [30,35,49]). Since female territories usually coincided with vole-rich hunting areas, they attracted frequent intrusions by conspecifics and other small-mammal predators. Accordingly, territorial females initiated daily conflicts,

typically averaging one displacement per hour and often engaging in prolonged guarding bouts lasting several minutes. Other female Hen Harriers in particular are not tolerated and are vigorously repelled. Importantly, individuals identified as territorial consistently emerged as winners in these encounters, confirming their dominant status. Males, in contrast, were not considered territorial (*sensu* [30]), even though some defended core areas against other males or occasionally attacked females.

2.2.3. Definition of Touchdowns

Several, partly non-congruent descriptions of the hunting behavior of Hen Harriers exist in the literature [29,31,32,37,38,40]. In the analysis presented here, only quartering flights, i.e., low cruising flights in search of voles, were considered as mammal-hunting behavior. This hunting method is clearly distinguishable from other flight types such as soaring, directional flight without foraging, or high-speed movements including territorial chases, mobbing, bird hunts, and predator escapes.

A touchdown was defined as a completed hunting attempt, i.e., a ground contact following a downstrike initiated from vole-directed quartering flight. The specific type of pounce type (hook, hover, straight, or low) was not considered relevant. Each touchdown was treated as an independent capture attempt, while potential effects of individual variation were addressed in the statistical analysis. A successful touchdown was defined as the capture of a small mammal, indicated by immediate handling or transport of prey. For all analyses, only touchdowns with a known outcome (>95% of cases) were included.

2.2.4. Recording of Extrinsic Factors

From the broader set of environmental variables, we focused on cloud cover, air temperature, and wind speed. All variables were recorded once per hour. Cloud cover was visually estimated in 10% intervals in the field, while air temperature (°C) and wind speed (km/h) were retrieved from the Geosphere Austria weather application, which provides interpolated model data for each location. During rare periods of moderate to heavy precipitation in winter, no data were collected. Snow cover was recorded upon arrival and considered potentially relevant, but continuous cover >5 cm occurred only very rarely; the few available records were excluded from the analysis due to insufficient sample size.

2.2.5. Field Protocols

We monitored Hen Harriers during five consecutive winters from 2020/21 to 2024/25 [41], following established protocols [35,36,40]. Observations were conducted primarily from a vehicle by two experienced observers using 10 × 42 binoculars or 20–60× spotting scopes. This minimally invasive approach was possible due to the open landscape with few visual barriers and the site fidelity of both territorial and stationary non-territorial individuals. Touchdown success was recorded through continuous focal observations, mostly in open grassland habitats where prey was readily visible. When hunting in tall vegetation, Hen Harriers often transported prey to open ground, presumably as an anti-predator strategy, which further facilitated identification.

2.3. Data Analysis

We analyzed touchdown attempt rate and touchdown success using generalized linear mixed models (GLMMs). Touchdown attempt rate was defined as the number of observed attempts per unit of active quartering time, derived from 20 min focal observation units (starting at sunrise) and calculated relative to the effective quartering time observed within each unit. Touchdown success was coded as 0 = failed attempt and 1 = successful capture. Fixed effects were intrinsic group (males [reference], territorial females, non-territorial

females), age (adult vs. juvenile), and the extrinsic covariates cloud cover (%), temperature (°C), and wind speed (km/h). Individual ID was included as a random intercept.

Attempt rate was modeled with a zero-inflated negative binomial GLMM (log link, offset = log(active quartering time); intercept-only zero-inflation). Touchdown success was modeled with a binomial GLMM (logit link). Results are reported as rate ratios (RRs) or odds ratios (ORs) with 95% confidence intervals and *p*-values. Inference was based on the combined interpretation of effect sizes, 95% confidence intervals, and *p*-values, with group-wise sample sizes and the distribution of touchdown attempts per individual explicitly considered when assessing uncertainty. Model adequacy was checked by assessing convergence, singularity, dispersion, DHARMA residuals, and collinearity.

Exploratory analyses focused on wind: (i) the effect on the proportion of time spent hunting (binomial GLMM), (ii) the effect on the rate of touchdown attempts per unit hunting time (negative binomial rate model with offset), and (iii) group differences in wind conditions (Gaussian model, ANOVA/*F*-tests). All exploratory analyses were conducted for interpretation only; their *p*-values are nominal and were not corrected for multiple comparisons.

All analyses were conducted in R 4.5.0 (x86_64-w64-mingw32) using glmmTMB (and lme4 where appropriate) for mixed models, DHARMA and performance for diagnostics, readr/dplyr for data handling, openxlsx/digest for reproducibility, and emmeans/ggeffects with ggplot2/patchwork for visualization.

Adult males could not always be individually identified in the field (see Section 2.2.1). The final dataset comprised 43 males, 14 territorial females, and 34 non-territorial females, each with repeated touchdown attempts. To assess whether uncertainty in male identity could influence model inference, we fitted two validation models in addition to the main GLMM: (i) a pooled-male model in which all adult males shared a single random-intercept level, and (ii) a female-only model including only individuals with fully reliable identities. Both validation models yielded effect sizes and confidence intervals that were highly consistent with the main GLMM, indicating that the conclusions are robust to potential male-ID uncertainty.

3. Results

3.1. Descriptive Results

Excluding periods with snow cover >5 cm, we observed Hen Harriers for 222.2 h, of which 57.2 h (25.8%) were devoted to quartering. During this vole-hunting time, we recorded 1829 touchdowns, corresponding to one every 1.88 min (overall: 10.66 per 20 min). By intrinsic group, males made 10.2 touchdowns per 20 min of quartering, non-territorial females 9.7/20 min, and territorial females 13.3/20 min. Raw touchdown success rate was 13.0% in males and 10.1% in both female groups. Expressed as minutes per capture during active quartering, territorial females, males, and non-territorial females required 15.5, 16.1, and 19.1 min capture^{−1}, respectively, consistent with [41].

Abiotic conditions during quartering ranged from −10 to 18 °C in temperature (median 3 °C, mean 3.4 °C), from 0 to 25 km/h in wind speed (median 2 km/h, mean 5.1 km/h), and from 0 to 100% in cloud cover (median 80%, mean 68.1%).

3.2. Model-Based Results

3.2.1. Attempt Rate

The model did not identify any statistically significant predictors of attempt rate (Table 1), and effects of age and extrinsic covariates (cloud cover, temperature, wind speed) were weak and inconsistent. However, relative to males (reference group), territorial females exhibited an estimated 18% higher attempt rate (RR = 1.18, 95% CI: 0.75–1.86,

$p = 0.467$), whereas non-territorial females showed an estimated 21% lower rate ($RR = 0.79$, 95% CI: 0.54–1.15, $p = 0.223$). This modeled pattern was consistent with the descriptive results presented above.

Table 1. Results of the zero-inflated negative binomial GLMM for attempt rate. Reported are rate ratios (RRs), 95% confidence intervals (CIs), and p -values.

Predictor	Rate Ratio (RR)	95% CI (Lower)	95% CI (Upper)	p -Value
Territorial Females vs. Males	1.18	0.75	1.86	0.467
Non-Territorial Females vs. Males	0.79	0.54	1.15	0.223
Adult vs. Juvenile	0.93	0.667	1.297	0.668
Cloud Cover (per 1%)	0.9973	0.9939	1.0006	0.108
Temperature (per °C)	1.0052	0.9980	1.0124	0.156
Wind Speed (per km h ^{−1})	1.0020	0.9787	1.0258	0.870

Random intercept variance for individual ID: 0.126 (SD = 0.355; $n = 100$ individuals). Model fit: Nakagawa's marginal $R^2 = 0.020$; conditional $R^2 = 0.084$.

3.2.2. Touchdown Success

The touchdown-success dataset comprised 1829 touchdown attempts, with 552 attempts from males, 517 from territorial females, and 760 from non-territorial females. Relative to males (reference group), territorial females were statistically indistinguishable from males ($OR = 0.80$, 95% CI: 0.48–1.34, $p = 0.401$), whereas non-territorial females showed lower hunting success ($OR = 0.67$, 95% CI: 0.42–1.06, $p = 0.084$; Table 2). Interpreted on the odds scale, this corresponds to $\approx 20\%$ lower odds for territorial females and $\approx 33\%$ lower odds for non-territorial females, neither statistically significant. Although raw per-attempt proportions and point estimates were lower for territorial females, uncertainty is substantial and the model supports no difference from males.

Table 2. Results of the binomial GLMM (logit link) for touchdown success. Reported are odds ratios (ORs), 95% confidence intervals (CIs), and p -values.

Predictor	Odds Ratio (OR)	95% CI (Lower)	95% CI (Upper)	p -Value
Territorial Females vs. Males	0.80	0.48	1.34	0.401
Non-Territorial Females vs. Males	0.67	0.42	1.06	0.084
Adult vs. Juvenile	1.19	0.793	1.777	0.405
Cloud Cover (per 1%)	1.0051	1.0008	1.0094	0.021
Temperature (per °C)	1.0069	0.9982	1.0157	0.119
Wind Speed (per km h ^{−1})	0.9633	0.9342	0.9934	0.017

Random intercept variance for individual ID: 0.118 (SD = 0.343; $n = 91$ individuals). Model fit: Nakagawa's marginal $R^2 = 0.023$; conditional $R^2 = 0.055$.

Age showed no detectable effect. To explore potential age–sex patterns, we additionally fitted a model including the full age $\times$ sex interaction (adult males as reference). Juvenile males ($OR = 0.70$, 95% CI: 0.33–1.49, $p = 0.53$), juvenile females ($OR = 0.62$, 95% CI: 0.31–1.28, $p = 0.29$), and adult females ($OR = 0.64$, 95% CI: 0.32–1.27, $p = 0.29$) all showed lower success odds. Although none of these contrasts reached statistical significance, the estimates suggest that adult males achieved roughly 30% higher touchdown success than the other groups.

Among abiotic covariates, success significantly increased with cloud cover ($p = 0.021$) and significantly decreased with wind speed ($p = 0.017$), while temperature showed no effect ($p = 0.119$; Table 2, Figure 2). Translated into biological terms, hunts were $\approx 10\%$ more successful with 20% more cloud cover, whereas an increase of 10 km/h in wind speed reduced hunting success by roughly one third.

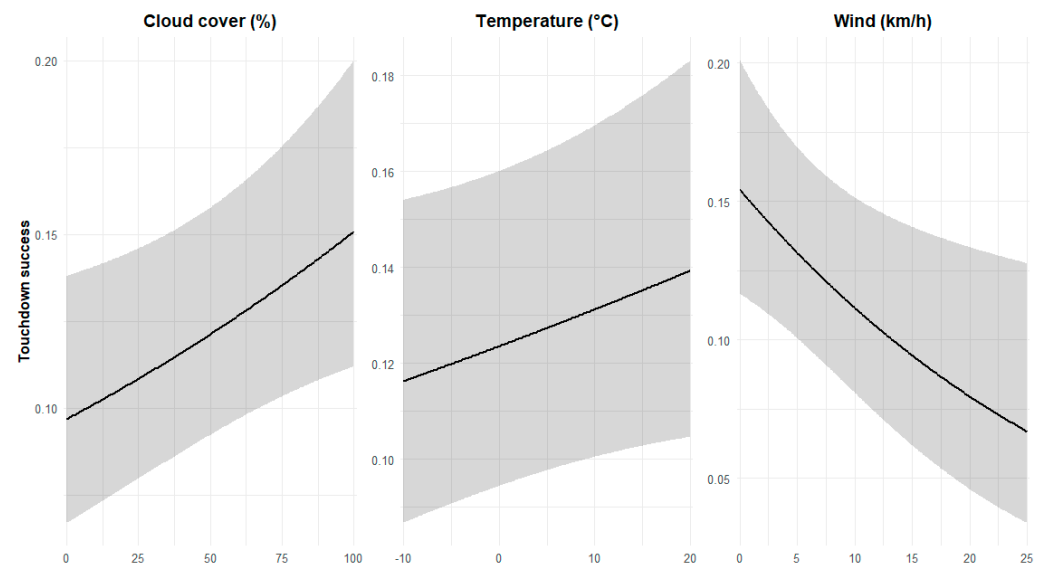


Figure 2. Effects of environmental factors on touchdown success probability in wintering Hen Harriers. Black lines show model-predicted probabilities from the generalized linear mixed model (binomial, logit), with shaded areas indicating 95% confidence intervals. Touchdown success increased with cloud cover (**left**) and decreased with wind speed (**right**), while temperature had no significant effect (**middle**).

3.3. Exploratory Analysis

Wind had no association with touchdown attempt rate in the main analysis (Table 1) but significantly reduced touchdown success (Table 2, Figure 2). Exploratory analyses of 20 min intervals indicated that wind increased the proportion of time spent hunting (OR = 1.01 per km h⁻¹, 95% CI: 1.01–1.02, $p < 0.001$) but did not affect the frequency of touchdown attempts per unit hunting time (RR = 1.01 per km h⁻¹, 95% CI: 1.00–1.02, $p = 0.214$).

In addition, wind conditions differed markedly among groups ($F(2,1826) = 135$, $p < 0.001$): territorial females were observed under substantially higher wind speeds (8.88 ± 7.95 km h⁻¹) than males (3.95 ± 5.89 km h⁻¹) or non-territorial females (3.35 ± 5.00 km h⁻¹).

4. Discussion

This study investigated touchdown attempt rate and touchdown success of wintering Hen Harriers in relation to intrinsic and extrinsic factors. We predicted higher success in males, combined high rate and success in territorial females, low performance in non-territorial females, and higher performance in adults compared to juveniles. We further predicted positive effects of cloud cover, negative effects of wind, and no effect of temperature. The results followed these expectations in part. Territorial females tended towards higher attempt rate and maintained success similar to males, while non-territorial females tended towards lower success. Age had no overall effect, although the interaction analysis indicated a tendency for adult males to be more successful than the other groups. Among the extrinsic variables, touchdown success increased with cloud cover and declined with wind speed, whereas temperature showed no influence, and none of these variables affected attempt rate. Because several contrasts, particularly those involving non-territorial females, showed effect sizes of biological relevance but confidence intervals overlapping zero, we base inference primarily on the joint interpretation of effect sizes and their uncertainty rather than on dichotomous significance thresholds. This explicitly acknowledges the limited precision arising from group-specific sample sizes and uneven numbers of repeated observations.

Concerning intrinsic factors, the contrasts among groups reflect two main mechanisms: sexual dimorphism and access to resources. Although not experimentally tested, the allometric male–female relationship suggests that smaller male body size translates into greater maneuverability [13,15,20,32], giving males an edge in per-attempt success when hunting the same prey in the same habitat. However, their frequent use of marginal habitats appears to have limited overall attempt rates. Territorial females did not exceed males in per-attempt success, but by securing vole-rich patches they increased encounter rates and thus compensated for morphological constraints, consistent with earlier findings of shorter capture times in this group [41]. Non-territorial females, lacking both advantages, combined reduced agility with restricted habitat access, explaining their tendency towards weaker performance. The exploratory age–sex analysis suggested a possible advantage of adult males, but overall age effects were negligible. This indicates that sex and social status, rather than age, govern hunting performance. Territories were established by both adult and juvenile females, showing that the benefits of territorial status were not restricted to older individuals.

Exploratory analysis further indicated that territorial females were more often observed under higher wind speeds, a condition that generally reduced success in our models. Because wind was modelled as acting equally across groups, this did not affect model-based contrasts. This highlights the need for caution when interpreting raw group differences and tentatively suggests that territorial females may offset unfavorable conditions through access to high-quality foraging sites.

Comparable evidence from other studies is scarce, and, to our knowledge, no previous work has simultaneously compared hunting success across all three intrinsic groups of wintering Hen Harriers. Existing studies differ substantially in design, behavioral definitions, prey type, and habitat, which complicates direct comparison across studies [31,32,35,37–39]. The role of social status, particularly territoriality, has received little attention in this context (but see [40]). These discrepancies concern not only success but also related parameters such as attempt rate, quartering time, or prey type, and they likely reflect a combination of ecological variation and methodologically driven divergences. Reported hunting success rates, used here as an example of such variation, range from 3.4% to 38%, with most studies clustering between 7% and 11%, illustrating the strong dependence of these measures on both study design and environment. The present study therefore provides the first standardized comparison among males, territorial females, and non-territorial females based on equivalent behavioral criteria and hunting effort restricted to vole-directed quartering flights.

In contrast to intrinsic characteristics, extrinsic factors represent environmental influences that affect all groups alike, shaping hunting performance through external conditions rather than individual morphology or social status. Extrinsic factors influenced touch-down success but not attempt rate. In line with [20] and consistent with Prediction 5, cloud cover exerted a significant positive effect on hunting success. While not tested experimentally, it is plausible that raptors become more conspicuous against a bright sky, thereby alerting potential prey earlier. Additionally, cloud cover also reduces overall glare conditions—including both direct brightness and surface reflections—which may influence predator–prey visibility to an unknown extent (comp. [50–52]). Considering that the interval between detection and access of a vole often falls below half a second [29], even a minimal advance in predator perception can shift the outcome of an encounter in favor of the rodent. Adult males, in addition to their experience and agility [39,53], may also benefit from their pale plumage, which reduces contrast against the sky; however, the relative importance of these mechanisms requires further investigation.

The predicted absence of a temperature effect (Prediction 6) was confirmed, with neither touchdown success nor attempt rate showing any response. This is consistent with findings from other harrier studies [20] and from the Snowy Owl (*Bubo scandiacus*), another vole specialist that frequently hunts diurnally in winter [54]. We assume that within the observed range of -10°C to 18°C , neither predator nor prey experienced major limitations to activity. The Common Vole, an ecological cold-steppe specialist, is particularly well adapted to low temperatures and, due to the poor nutritional quality of its food, maintains a polyphasic daily rhythm that requires regular surface activity [55]. Unlike *Apodemus* mice, which can enter torpor at very low temperatures, *Microtus arvalis* lacks this capability [56].

Wind, a key environmental factor in raptor foraging, can have both stabilizing and destabilizing effects [16,57]. Contrary to Prediction 7, touchdown success declined with increasing wind speed. Three aspects may explain this outcome. First, the metric itself matters: success, attempt rate, and quartering time must be distinguished. Our exploratory analyses showed that light headwinds can prolong quartering flights [31]. At the same time, the number of touchdowns per unit hunting time remained constant, while success per attempt declined under stronger winds [58]. This means that extended quartering time under moderate winds may not only offset reduced per-attempt success but even increase overall prey intake, whereas under stronger winds the destabilizing effects dominate and net gains decline. Second, although our study nominally covered 0–25 km/h, the distribution was strongly skewed, with calm conditions (median 2 km/h) dominating the dataset. Third, wind was obtained from hourly, interpolated model fields (~ 1 km resolution), which introduces unavoidable temporal and spatial mismatch to actual touchdown locations; such nondifferential measurement error typically attenuates estimated effect sizes. Interpretation therefore requires caution. Future work should combine multi-sensor telemetry [59] with on-site anemometry to test nonlinear wind effects and to quantify how quartering time, attempt rate, and per-attempt success integrate into overall prey intake.

Although our study provides robust evidence for the role of intrinsic and extrinsic factors in shaping hunting success, several important questions remain. Earlier work demonstrated that territorial females secure areas with substantially higher prey availability [41], yet it would be particularly informative to quantify vole activity patterns in real time [33,38] and to assess vegetation structure at fine spatial scales [35,60], both directly linked to actual touchdown sites. Addressing this requires simultaneous monitoring of vole surface activity and high-resolution spatial movement data of harriers. Previous analysis of the same study system showed that about 80% of successful hunts occurred in open habitats such as forage crops, pastures, and fields with vegetation below 20 cm, while roughly 20% took place in catch crops [41]. Such structurally more complex habitats may conceal frost-induced gaps with locally low vegetation that remain undetectable to observers but nevertheless provide profitable hunting opportunities. As the vast majority of touchdown events in our dataset occurred in open habitats across all groups, substantial habitat- or microtopography-related confounding of group contrasts appears unlikely; however, future work should quantify fine-scale structural variation directly at touchdown sites.

Finally, in alpine study areas, snow cover constitutes a potentially important additional extrinsic factor [50,61]. However, during our study winters, snow cover was largely absent, and sample size was insufficient to incorporate this variable into the analyses. Future winters with more consistent snow cover should allow testing this factor, and could further address open questions such as how voles are located under snow and whether hunting strategies shift when prey remains concealed beneath snow cover [19,62]. In a broader context, it also remains to be investigated whether Hen Harriers may use UV vision to support vole hunting [63,64], not least under critical conditions such as snow cover.

As with most behavioral field studies, our analyses are constrained by the spatial and temporal resolution of environmental data and by the limited observability of fine-scale processes at the exact moment of predator–prey interactions. These limitations do not affect the main conclusions but highlight that future work would benefit from approaches that integrate behavioral observations with high-resolution information on vegetation structure and local weather conditions, together with continuous tracking of both predators and prey. Such integrative designs would allow testing more specific, process-based hypotheses about predator–prey interactions that cannot be addressed directly with the present observational dataset.

5. Conclusions

By integrating winter energetics [41] with hunting success, we obtain a coherent picture of the three intrinsic groups of Hen Harriers as defined in this study. Males, all classified as non-territorial, are smaller, more agile, and have lower energetic demands (despite being regularly klepto-parasitized by females); these traits confer the highest per-attempt success and allow persistence even in vole-poor landscapes, partly compensated by hunting small birds. Territorial females are larger but reduce overall energetic expenditure through prolonged sitting and stable access to vole-rich patches, achieving the highest prey intake rates despite lower agility. Non-territorial females, lacking both morphological and territorial advantages, experience high energetic demands and limited access to profitable habitats; this combination constrains their foraging efficiency and results in the lowest hunting success.

Across groups, hunting success increases under cloud cover, decreases under wind (although wind may promote prolonged quartering), and remains unaffected by temperature. These findings demonstrate that males persist through morphological adaptation to marginal conditions, territorial females through resource control, and non-territorial females remain the most constrained intrinsic group. Conservation strategies should, therefore, secure both extensive open landscapes and vole-rich core areas to support the full spectrum of winter strategies.

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