Flexible Resource Use but Consistent Parental Care across Populations in a Nocturnal Raptor

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Abstract

Parental investment is often quantified by how much food offspring receive, yet parental behaviour throughout the breeding phase and the timing and composition of resource delivery may be equally important. We tested this by integrating behaviour, diet and activity rhythms in two populations of tawny owl (*Strix aluco*) in northern Europe. Parental behaviour followed conserved temporal patterns across populations, shifting from nest attendance before hatching to increased provisioning activity as chicks developed. In contrast, diet composition (the identity and relative abundance of prey types) varied geographically despite similar diet diversity and prey biomass, indicating flexible resource use while maintaining comparable overall dietary breadth and energy intake. Provisioning activity was strongly nocturnal and highly consistent between populations, although prey-specific timing reflected differences in prey ecology. Different components of parental investment were associated with different reproductive outcomes: diet diversity increased fledgling success, while provisioning effort was associated with earlier fledgling.

Together, these results show that behavioural and temporal patterns are conserved but diet composition remains flexible. This combination between flexibility and conserved traits allows consistent reproductive performance across environments and highlights that multiple, interacting components of parental investment underlie fitness variation.

Key words: parental care, parental behaviour, nest attentiveness, diet, activity rhythms, population variations.

Introduction

Life-history theory seeks to explain how organisms allocate limited resources among competing demands such as growth, reproduction and survival, and how these strategies vary along a life history continuum (S. C. Stearns 1989; Rose and Mueller 1993; Roff 1993; Stephen C. Stearns 2000; Zera and Harshman 2001; Ricklefs and Wikelski 2002a). A central challenge within this framework is understanding how variation in resource acquisition and allocation generates differences in reproductive strategies both within and between populations (Williams 1966; Van Noordwijk and De Jong 1986; Clutton-Brock 1991; De Jong and Van Noordwijk 1992; Boggs 1992). In species with parental care, resources acquired by adults are transferred directly to offspring, making reproductive success dependent not only on total investment but also on how parental effort is allocated over time and how resources are delivered (Clutton-Brock 1991). Classical theory predicts trade-offs in allocation that shape both total reproductive effort and per-offspring investment, ultimately influencing offspring growth, development and survival (Smith and Fretwell 1974; Lee et al. 2013; Ratikainen et al. 2018).

In birds, these predictions have been largely tested, as avian systems allow good quantification of parental care and reproductive output (Clutton-Brock 1991). Most research has focused on how variation in food acquisition and provisioning constrains reproductive success, with the assumption that total prey intake or biomass delivered to nests is the primary determinant of offspring performance (Skutch. 1949; Martin 1987; Ricklefs and Wikelski 2002b; Martin 2004). However, evidence suggests that parental investment cannot be fully understood from quantity alone, and resources are delivered, in particular considering dietary composition, may play a crucial role in shaping offspring outcomes (Espíndola-Hernández et al. 2017; González-Bernardo et al. 2025). Diet diversity may buffer nutritional constraints, reduce

64 temporal variability in prey availability and improve developmental stability, potentially
65 decoupling reproductive success from total provisioning effort.
66 Beyond resource quantity and composition, parental investment also has a strong temporal
67 dimension. Activity rhythms determine when resources are acquired and delivered,
68 influencing prey selection, hunting efficiency and energetic costs (Timewell and Mac Nally
69 2004; Santiago-Quesada et al. 2012; Grémillet et al. 2012; Militão et al. 2023; Capilla-Lasheras
70 et al. 2025). While activity patterns are often considered species-specific, there can also be
71 intraspecific variation in response to environmental conditions such as prey availability,
72 energetic demands and photoperiod (Lundblad and Conway 2021; Pires et al. 2022). In
73 nocturnal species, shifts in diel activity may allow parents to exploit different prey
74 communities, without necessarily changing overall provisioning rates (Zárybnická et al. 2012).
75 However, it remains unclear whether such temporal flexibility translates into differences in
76 reproductive outcomes, or whether populations maintain similar provisioning strategies
77 despite ecological variation.
78 The tawny owl (*Strix aluco*) provides an ideal study system to investigate these questions. This
79 widespread nocturnal raptor occupies a broad range of forest habitats across Europe and
80 relies on a diverse diet, based primarily on small mammals and birds (Obuch 2011; López-
81 Peinado et al. 2020; Pagaldai et al. 2023). Previous studies have shown that reproductive
82 success in tawny owls is influenced by prey availability, environmental conditions and parental
83 traits (Sasvári and Nishiumi 2005; Fanfani et al. 2008; Sasvári et al. 2008; Lehikoinen et al.
84 2011; Fanfani et al. 2015; Hoy et al. 2016; Luka and Riegert 2018). However, few studies have
85 simultaneously integrated parental behaviour, diet composition and activity rhythms across
86 populations to assess how these components shape together the reproductive performance.

Here, we adopt an integrative approach to investigate reproductive strategies in two northern European populations of tawny owls breeding in Finland and Sweden. These populations occur at similar latitudes but differ in forest structure and prey communities, providing a natural framework to investigate how ecological variation influences parental investment. We first quantify variation in parental behaviour across breeding phases, focusing on changes in time allocation inside and outside the nest as offspring develop. We then assess how these behavioural patterns relate to resource use by exploring diet diversity (number of prey taxa consumed), prey composition (relative contribution of mammals, birds and other prey categories), and total prey biomass. In addition, we investigate diel activity rhythms and prey-specific temporal patterns to determine how the timing of provisioning shape resource delivery. Within this framework, we explore how variation in parental behaviour, diet and activity patterns translate into differences in reproductive outcomes, specifically fledgling success and fledgling phenology.

Overall, we expect parental behaviour to vary consistently across breeding phases in both populations, while also being influenced by ecological conditions such as habitat structure and prey availability. In this context, we explore whether variation in diet composition and activity rhythms emerges between populations and whether these components are associated with differences in parental behaviour. Finally, we assess how behavioural, dietary, and temporal variation relates to reproductive performance, with the aim of understanding how ecological differences are reflected in parental strategies and their reproductive consequences.

Material and Methods

a) Study populations

This study was conducted over three consecutive breeding seasons (2022, 2023 and 2024) in two nestbox breeding populations of tawny owls located near the northern limit of the species' distribution. The study areas were situated in southern Finland (central point Siuntio: 60°15´N, 24°15´E; hereafter FI) and south-central Sweden (central point Undenäs: 58°39´N, 14°25´E; hereafter SW). Both populations occupy boreal forest landscapes dominated by spruce interspersed with agricultural land. The regions experience cold winters with prolonged periods of sub-zero temperatures and persistent snow cover, conditions that may influence prey availability during the subsequent breeding season.

b) Data collection

Parental behaviour, prey delivery and activity rhythms were monitored using infrared trail cameras (Victure HC200) installed in 60 nest boxes (FI: n = 30; SW: n = 30). Cameras were mounted on the inner face of the nestbox roof to minimise disturbance to the owls. Cameras were active year-round with an interval of two hours between pictures as part of a parallel study on nestbox use. Once a nestbox was confirmed to be occupied for the breeding season (i.e., presence of a breeding female and eggs), the sampling frequency was increased to one image every 15 minutes in 2022 and every 10 minutes in 2023 and 2024. Monitoring continued until mid/late summer when most of chicks have already fledge, after which pictures were downloaded and analysed. Occasionally, camera malfunctions or battery failures resulted in incomplete image series. Consequently, only nests with sufficient camera data for the relevant study period were included in the analysis. The number of nests included therefore varied slightly among analyses depending on data availability.

Images were analysed to extract female presence in the nest (inside/outside), timing of breeding events (laying, hatching, fledging), prey delivery events and prey identity.

Observations were ordered chronologically for each nest, and each image in which a new behavioural state (e.g. female inside or outside the nestbox) appeared was considered as the start of that behaviour. The behavioural state recorded in each picture was assumed to persist until a subsequent picture showed a different behavioural state. For example, if a female was recorded inside the nestbox in two consecutive pictures taken 10 minutes apart, but was absent in the third picture, we inferred that she remained inside the box during the 20 minute interval between the first and third picture. Because photographs were taken at relatively short intervals (15 minutes in 2022 and 10 minutes in 2023 and 2024), behavioural states lasting longer than these intervals were likely to be detected. However, brief events occurring entirely between two consecutive photographs may not have been captured.

To quantify parental time allocation, time intervals between consecutive observations were calculated and split at noon (period in which owls are less active) when crossing calendar boundaries. For each nest and day, we calculated total time spent inside and outside the nest (in minutes). Behavioural transitions were identified by comparing consecutive observations (outside → inside (entry); inside → outside (exit)). All observations were standardized relative to the hatching date of the first nestling, which was defined as day 0. The hatching day itself was excluded from analyses. Days were grouped into three biologically relevant phases: pre-hatching phase (days -10 to -1 before hatching), the early nestling phase (days 1 to 10 after hatching) and late nestling phase (days 11 to 20 after hatching). Tawny owls nestlings generally fledge at approximately 28 days of age, meaning that the late nestling phase represents the period immediately before fledgling.

Prey items delivered to nests were identified from images based on taxonomic identity and body size. Each prey item was recorded as a single provisioning event when it first appeared

in the nestbox and was not counted again in subsequent photographs if it was still there. Then, prey was classified into seven functional groups for the analysis of activity rhythms: small mammals (e.g. shrews and harvest mice), medium mammals (e.g. voles *Microtus* spp. and *Apodemus* mice), large mammals (e.g. water voles and leverets). Bird prey was divided into small birds (primarily passerines), medium birds (e.g. thrushes and nestlings of larger bird species) and large birds (e.g. magpies, jays and partridges). The category "other" included amphibians (e.g. frogs), reptiles (e.g. slow worms) and any non-avian or non-mammalian prey.

Diet composition was assessed independently by analysing prey remains left within the nest box. After the chicks fledged, nest material was collected from the bottom of each nest box and systematically sorted. Tawny owls regurgitate indigestible prey parts such as bones, fur and feathers, which are accumulated in the nest substrate. These remains were used to identify prey items and estimate prey numbers following established protocol (Brommer et al. 2003; Kekkonen et al. 2008). Total prey biomass per each nest was then calculated by summing the estimated biomass of all prey items identified from the nest remains, based on species or category specific mean body masses. For each taxon or functional group, we used average body mass values from Karell et al. 2021 and multiplied these by the number of prey items within that group.

Habitat composition was quantified within 1000 m buffer around each nestbox, corresponding to the typical home range of tawny owls (based on observed movement patterns, Passarotto et al. 2023). Land cover data were obtained from CORINE (land.copernicus.eu) and classified into coniferous, mixed, and deciduous forest.

c) Statistical analyses

All statistical analysis were conducted in R version 4.5.2. Prior to analyses, continuous predictors were standardized (z-scores) to facilitate comparison of effect sizes and improve model convergence. Model assumptions were assessed using residual diagnostics and multicollinearity was evaluated using variance inflation factors (VIF) through 'performance' package (version 0.13.0), with all values <5 indicating acceptable levels.

(i) Behavioural analysis

To quantify parental time allocation, we analysed daily time spent inside and outside the nest, as well as the number of entries and exits. Nest ID was included as a random factor in linear mixed-effects models (LMMs) to account for non-independence of multiple observations within the same nest across breeding phases. Response variables (daily average of minutes spent inside and outside the nest) were log-transformed to improve normality and homoscedasticity. Fixed effects included breeding phase (pre-hatching: days -10 to -1; early nestling phase: days 1-10; late nestling phase: days 11-20), country (FI and SW), year and habitat composition (proportion of coniferous, deciduous and mixed forest). Initial models included an interaction between breeding phase and country to test whether behavioural trajectories differed between populations. As this interaction was not significant and increased collinearity, it was removed from final models.

(ii) Diet analyses

Diet diversity was quantified using the Shannon diversity index calculated from prey counts per nest based on nest material. Total prey biomass delivered per nest was log-transformed prior to analysis. Linear models (LMs) were used to test whether diet diversity (Shannon index) and total prey biomass varied with country and habitat compositions. These models included country and habitat variables as fixed effects.

To assess differences in diet composition, permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity was run (package “vegan” version 2.7-2). Separate analyses were conducted for: prey counts (number of prey items, reflecting prey identity and frequency), total prey biomass (reflecting energetic contribution). Models included country and habitat composition as predictors, and significance was assessed using 999 permutations.

Multivariate patterns in diet composition among nests were visualized using non-metric multidimensional scaling (NMDS; package “vegan” version 2.7-2) based on Bray-Curtis distances calculated from prey count data (number of items per prey group). NMDS was performed in two dimensions (K=2) using multiple random starts to ensure stable convergence. Stress values were used to evaluate the goodness of fit.

(iii) Activity rhythm analyses

Temporal patterns of prey delivery recorded from the photographs were analysed using circular statistics and generalized linear mixed models (GLMMs). Differences in mean activity timing between populations were tested using the Watson-Williams test for circular data.

To assess whether prey deliveries were uniformly distributed across the 24-hour cycle, Rao’s spacing test was applied separately for each country. Temporal overlap in activity patterns between populations was quantified using the coefficient of overlap ($\hat{D}$), based on kernel density estimation. To test for differences in diel activity, a binomial generalized linear model (GLMM) was fitted with day/night (binary response) as the dependent variable, country as fixed effect, and nest identity as a random intercept to account for repeated observations. In addition, prey-specific diel patterns were evaluated with separate binomial GLMMs for each prey category (small, medium and large mammals; small, medium and large birds; other; see

Data collection). In these models, day/night was the response variable, with country as a fixed effect and nest ID included as a random factor.

(iv) Integrative analysis of reproduction and phenology

To investigate how behavioural, dietary and habitat variables jointly structure variation among nests, a principal component analysis (PCA) was performed with the 'FactoMineR' package (version 2.11). Continuous variables describing parental behaviour (pre-hatching time spent inside the nest, post-hatching time spent outside the nest), diet (total prey biomass and Shannon diversity index) and habitat composition (proportion of coniferous, deciduous and mixed forest) were included. All variables were standardized prior to analysis. The PCA was conducted using complete cases only, and the first two principal components were retained to describe major axes of variation.

To assess factors influencing reproductive success, a binomial generalized linear model (GLM) was fitted with fledgling success (number of fledglings relative to clutch size) as the response variable. Predictors included standardized behavioural variables (pre-hatching time spent inside the nest, post-hatching time spent outside the nest), dietary variables (log-transformed prey biomass and Shannon diversity), habitat composition, country and year.

To examine determinants of breeding phenology, fledgling timing was analysed using a linear model (LM) with fledgling date (expressed as day of year, DOY) as the response variable. This variable represents the calendar timing of fledgling (i.e. breeding phenology). All predictor variables were standardized (z-transformed) prior to analysis, whereas the response variable (DOY) was not.

Results

Behavioural patterns across breeding phases

Parental time allocation varied strongly across breeding phases (Fig.1 and Table 1). Time spent inside the nest differed significantly among phases (χ^2 = 78.83, df = 2, p < 0.001), increasing slightly from the pre-hatching phase to early nestling phase and decreasing markedly during late nestling phase. There was no effect of country on time spent inside the nest. Year significantly affected time spent inside the nest, suggesting inter-annual variation. Habitat composition did not have a significant influence. In contrast, the number of observed entries increased during the breeding phases highlighting the higher provisioning activity in the post-hatching phases (Fig.1 B).

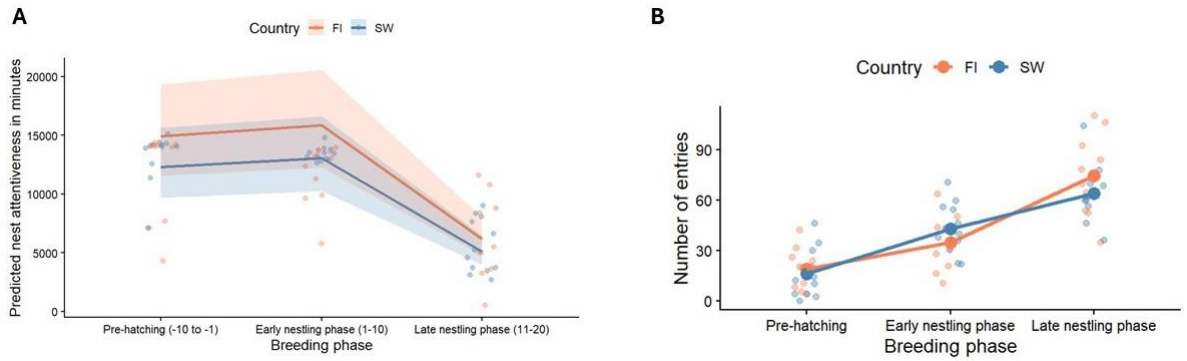


Fig.1 Parental behaviour: (A) nest attentiveness across breeding phases. (B) Number of observed entries across the breeding phases. In panel (A) lines indicate model predictions with shaded areas representing 95% confidence intervals.

Table 1 LMMs on nest attentiveness (time spent inside the nest) across breeding phases, country, year and habitat composition. Values in bold indicate statistically significant effects (p < 0.05).

Resp. variables	Ind. variables	Estim. β ± SE	t	p
Nest attentiveness (time	**Intercept**	566.44 ± 176.93	3.20	**<0.005**
spent inside the nest)	Early nestling phase (1–10)	0.06 ± 0.12	0.51	0.615

Late nestling phase (11–20)	-0.88 ± 0.12	-7.39	**<0.001**
Country (SW)	-0.19 ± 0.16	-1.18	0.258
Year	-0.28 ± 0.09	-3.15	**<0.01**
Coniferous forest	0.00 ± 0.00	1.18	0.258
Deciduous forest	0.01 ± 0.01	1.05	0.313
Mixed forest	-0.00 ± 0.00	-0.97	0.347

Diet diversity and composition

Diet diversity calculated from prey remains collected from nestbox material did not vary significantly with country or habitat composition. Total prey biomass did not differ between FI and SW or across habitat types.

In contrast, diet composition differed significantly among nests. PERMANOVA based on prey counts (number of prey items within each prey category per nest) showed a significant effect of country and habitat composition ($F = 2.06$, $R^2 = 0.29$, $p = 0.005$), indicating that variation in prey identity and relative abundance was affected by geographic and environmental context. However, PERMANOVA based on biomass was not significant, suggesting that compositional differences were driven by prey types and numbers rather than energetic contribution (Fig.2 B).

Non-metric multidimensional scaling (NMDS; stress = 0.17) showed partial separation between FI and SW with substantial overlap (Fig.2 A), indicating weak but consistent geographic differences in diet composition despite broadly similar dietary diversity and total biomass.

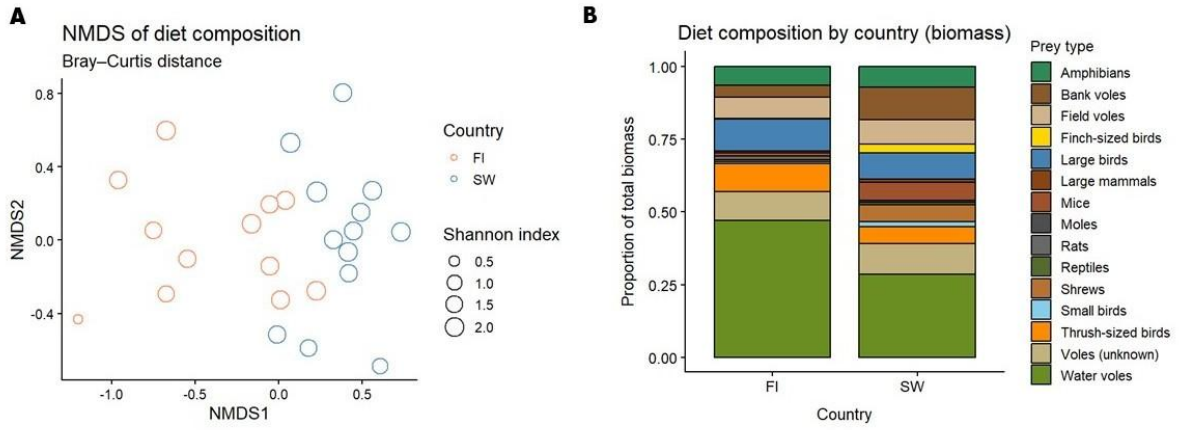


Fig.2 Diet composition across the study populations. (A) Non-metric multidimensional scaling (NMDS) ordination based on prey composition. Points represent individual nests and distances reflect dissimilarity in diet composition. (B) Diet composition by country based on prey biomass.

Activity rhythms

Prey deliveries were not uniformly distributed across the 24-hour cycle in either population, indicating strong diel structuring of provisioning activity (Rao's spacing test: FI, $T = 230.99$, $p < 0.001$; SW, $T = 206.29$, $p < 0.001$). Despite this temporal structuring, the overall activity patterns were highly similar between populations, with substantial temporal overlap ($\hat{D} = 0.87$).

At the population level, prey deliveries were significantly more likely to occur at night when analysed in a binary framework (binomial GLMM with day/night as response variable and nest ID as a random factor; Fig.3 A and C, and Table 2), while no significant effect of country was detected. This indicates that diel provisioning patterns are strongly nocturnal and consistent across geographic regions.

Prey-specific GLMMs showed pronounced variation in diel delivery patterns among prey types. Small mammals were significantly more likely to be delivered at night (Fig.3 B and Table 2), whereas medium-sized mammals showed no significant diel effect. Large mammals showed a marginal tendency towards daytime delivery (Fig.3 B and Table 2). Among birds, medium-sized birds showed a weak, non-significant tendency towards daytime delivery (Fig.3 B and Table 2). No significant effects of country or diel period were detected for large birds and other prey.

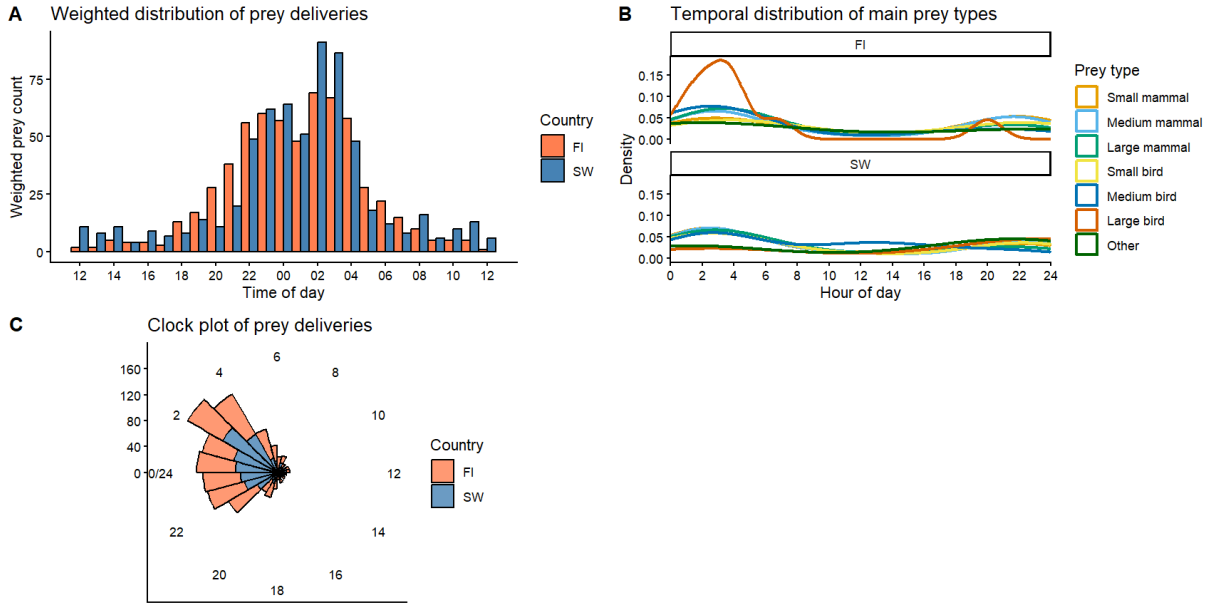


Fig.3 Activity rhythms of prey deliveries across 24-hour cycle. (A) Weighted distribution of prey deliveries. (B) Temporal distribution of the main prey types. (C) Circular (clock) plot of prey deliveries.

Table 2 Results of binomial GLMMs testing the effects of diel period (day vs night) and country (FI vs SW) on prey delivery patterns. Separate models were fitted for each prey category. Positive estimates indicate increased probability of the response variable: night delivery for

311 the overall model, and occurrence for the focal category. Values in bold indicate statistically
312 significant effects ($p < 0.05$).

Resp. variables	Ind. variables	Estim. β ± SE	Z	p
All deliveries (day/night)	**Intercept (night)**	1.07±0.21	5.16	**<0.001**
	Country (SW)	-0.12±0.29	-0.43	0.671
Small mammals	**Night**	0.31±0.16	1.99	**<0.05**
	Country (SW)	0.52±0.35	1.47	0.141
Medium mammals	Night	0.05±0.13	0.40	0.691
	Country (SW)	-0.19±0.16	-1.19	0.235
Large mammals	Night	-0.36±0.19	-1.94	0.052
	Country (SW)	-1.03±0.26	-3.91	**<0.001**
Small birds	Night	0.14±0.25	0.56	0.576
	Country (SW)	1.03±0.49	2.11	**<0.05**
Medium birds	Night	-0.36±0.19	-1.94	0.052
	Country (SW)	0.23±0.38	0.62	0.536
Large birds	Night	-0.45±0.67	-0.68	0.499
	Country (SW)	-1.33±0.87	-1.52	0.128
Other prey	Night	0.67±0.57	1.17	0.241
	Country (SW)	0.98±0.73	1.35	0.176

313

314 *Multivariate integration of parental behaviour, diet and habitat*

315 The first two principal components explained 57.1% of the total variance in behavioural,
316 dietary and habitat variables (PC1: 36.6%, PC2: 20.5%; Fig.4 and Supplementary Table 2 and
317 3). PC1 was mainly associated with habitat composition, with strong contributions from
318 coniferous, deciduous and mixed forests, together describing a habitat gradient among sites.
319 Pre-hatching time spent inside the nest also contributed substantially to PC1. PC2 was mainly
320 associated with parental behavioural variation, particularly post-hatching and pre-hatching

activity, with additional contributions from habitat structure. Multivariate ordination showed partial separation between FI and SW along PC1, reflecting systematic differences in habitat composition between populations. SW sites tended to align with higher proportion of coniferous forests, whereas FI sites showed greater association with mixed forest landscapes. Pre-hatching parental activity also contributed to the variation represented by PC1, whereas post-hatching activity was primarily associated with PC2

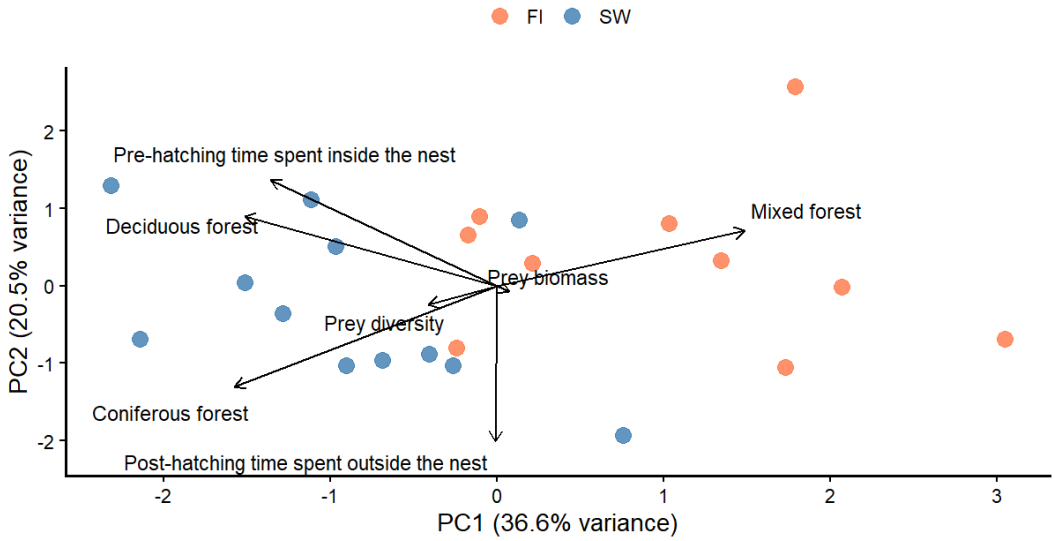


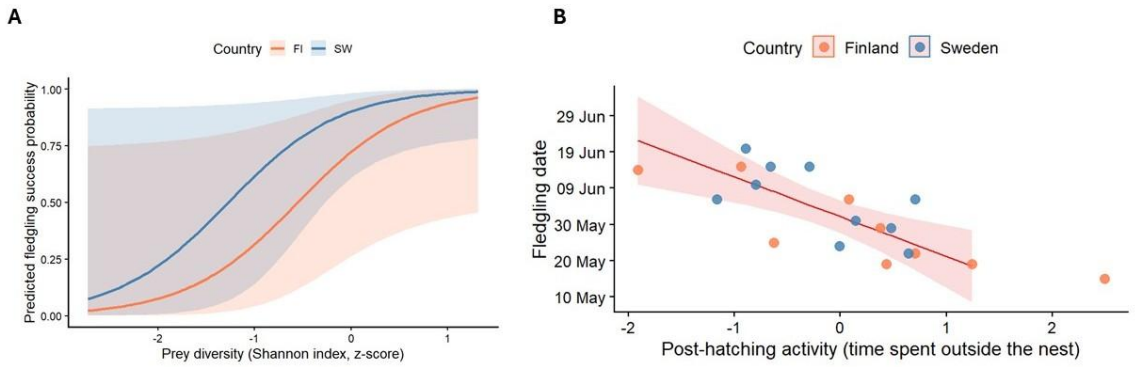
Fig.4 Principal component analysis (PCA) biplot of behavioural, dietary and habitat variables across nests in FI and SW.

Reproductive performance

Fledgling success was significantly positively associated with diet diversity (Shannon index; GLM: $\chi^2 = 5.87$, df = 1, p = 0.015; Fig.5 A). Post-hatching activity showed a positive but non-significant association with fledgling success. No significant effects were detected for pre-hatching activity, total prey biomass, habitat composition, country or year.

Fledging date (DOY) was significantly associated with post-hatching activity (linear model: $F_{1,8} = 15.67$, p = 0.004; Fig.5 B), with higher provisioning rates associated with earlier fledging. No

338 significant effects were found for pre-hatching activity, diet diversity, prey biomass, habitat
339 composition, year, or country, although nests in SW showed a non-significant tendency
340 towards later fledgling.



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342

343 **Fig.5** Effects of parental investment and diet diversity on reproductive performance. (A)
344 Relationship between prey diversity (Shannon index) and fledgling success probability. (B)
345 Relationship between post-hatching activity (time spent outside the nest) and fledgling date
346 (DOY). Points represent individual nests. Lines represent model predictions with shaded areas
347 indicating 95% confidence intervals.

348

349 **Table 3** Results of the linear model testing the effects of parental behaviour, diet, habitat,
350 country, and year on fledging date (DOY). Estimates are shown as β ± SE. Statistically significant
351 effects ($p < 0.05$) are shown in bold.

Resp. variables	Ind. variables	β ± SE	t	p
Fledgling date (DOY)	Pre-hatching activity	-0.98 ± 2.51	-0.39	0.705
	Post-hatching activity	−10.96 ± 2.77	−3.96	**0.004**
	Prey biomass	0.19 ± 3.00	0.06	0.951
	Prey diversity (Shannon)	1.17 ± 2.29	0.51	0.624
	Coniferous forest	−1.78 ± 3.31	−0.54	0.606

Deciduous forest	−3.94 ± 2.77	−1.42	0.194
Mixed forest	1.24 ± 3.17	0.39	0.707
Country (SW)	13.79 ± 6.96	1.98	0.083
Year	4.25 ± 5.57	0.76	0.467

352

353 **Discussion**

354 This study provides an integrative view of how parental behaviour, diet composition and
355 activity rhythms shape together the reproductive strategies in tawny owls across two
356 populations. By combining behavioural observations, diet analyses and temporal activity
357 patterns, we show that while overall parental strategies are conserved across geographic
358 contexts, variation emerges in how parental behaviour and resources are expressed and
359 delivered, with important consequences for reproductive performance.

360 Parental time allocation changed predictably across breeding phases, reflecting changing
361 reproductive demands. Time spent inside the nest was highest before hatching and declined
362 as chicks developed. This changes from incubation and brooding to active provisioning is a
363 fundamental pattern widely reported in birds and aligns with life-history predictions on
364 parental investment (e.g., Martin 1987; Clutton-Brock 1991). For example, in Mute swans
365 (*Cygnus olor*) females modified their daily patterns of resting and nest maintenance between
366 incubation and fledgling phases, while males maintained consistent activity patterns,
367 indicating phase-specific adjustment in parental roles (Włodarczyk 2017). Despite ecological
368 differences between FI and SW, parental time allocation was consistent in our study. The
369 absence of a country effect suggests that the temporal effort of parental care is conserved,
370 likely constrained by shared physiological demands and offspring developmental
371 requirements as shown in other species (Tarwater and Brawn 2010; González-Medina et al.

2016; Martin et al. 2025). Year effect on the time spent inside the nest suggests some sensitivity to annual environmental variation, (e.g. weather or prey fluctuations; Crombie and Arcese 2018; Mwangi et al. 2018; Machín et al. 2018), but did not alter the overall pattern. Similarly, the lack of habitat effects suggests that parental time allocation is relatively robust to landscape variation at this spatial scale.

In contrast to parental time allocation, diet composition differed significantly between populations, despite similar diet diversity and total prey biomass. This indicates that tawny owls exploit different prey communities while maintaining comparable energetic provisioning. Similar patterns have been reported in other raptors and generalist predators, where populations show flexibility in prey use but converge on equivalent energetic intake (Durant et al. 2004; Zárybnická and Vojar 2013; Solonen et al. 2017; Karell et al. 2021). Such decoupling between composition and biomass suggests that dietary flexibility allows individuals to compensate for local prey availability without altering total investment. This flexibility may buffer environmental variability and stabilize reproductive output across populations. At the same time, variation in prey type, rather than quantity, may influence nutritional balance, prey handling time, or delivery frequency, potentially affecting chick development and condition.

Provisioning activity was strongly structured in time, it was not uniform with a pronounced nocturnal bias. However, activity patterns were highly similar between populations, as indicated by strong temporal overlap and the absence of differences in mean delivery timing. This suggests that diel rhythms in tawny owls are tightly constrained, likely by species-specific foraging ecology and prey activity patterns. Comparable constraints have been documented in other nocturnal and crepuscular predators, where activity timing remains stable across

environments despite variation in prey communities (Erkert et al. 2012; Eriksen and Wabakken 2018; Li et al. 2022; Storrie et al. 2022; Wei et al. 2025). Together, these results indicate an important asymmetry in parental strategies: the timing of provisioning ("when") is conserved, whereas resources composition ("what") remains flexible across environments. Prey-specific analyses revealed clear temporal differences among prey types: small mammals were predominantly delivered at night, consistent with their activity patterns, whereas larger prey and some bird categories showed more diurnal tendencies. These patterns likely reflect differences in prey behaviour, detectability and handling constraints, suggesting the idea that temporal variation in provisioning is primarily driven by prey ecology rather than population-level differences.

The integrative approach shows that different components of parental investment influence distinct aspects of reproductive performance. Diet diversity (Shannon index) was positively associated with fledgling success, suggesting that a more diverse diet enhances offspring survival, potentially through improved nutritional balance or reduced dependence on fluctuating prey resources. Similar links between diet diversity and reproductive success have been reported in several bird species, including raptors and seabirds (Jodice et al. 2006; Whitfield et al. 2009; Dawson et al. 2011; Kowalczyk et al. 2014; Shin and Yoo 2016; Westerberg et al. 2019; Carrillo-Hidalgo and González-Dávila 2025). In contrast, provisioning behaviour, specifically post-hatching activity (time spent outside the nest), was more closely linked to fledging timing. Increased activity outside the nest was associated with earlier fledging, indicating that higher provisioning effort may accelerate chick development. However, this behavioural component did not significantly affect fledgling success, suggesting that growth rate and survival are influenced by different aspects of parental investment.

Together, these results highlight that diet diversity and provisioning effort are functional separate. Diet diversity improves offspring survival but does not appear to influence developmental timing, while provisioning effort accelerates development without significantly affecting survival. This indicates that parents do not optimize one single fitness component, but they try to balance multiple outcomes at the same time.

Future research should quantify prey nutritional quality and composition to distinguish between energetic and micronutrient effects. In addition, higher-resolution behavioural data and experimental manipulation of food availability would help disentangle causal relationships between provisioning effort, diet composition, and reproductive outcomes.

Overall, tawny owl reproductive strategies reflect a combination of conserved behavioural patterns and flexible resource use. While parental timing and effort are constrained, diet composition provides a key axis of ecological adaptation. These components influence reproductive outcomes in different ways, highlighting the importance of separating diet diversity, diet composition and provisioning behaviour when investigating reproductive strategies.

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663

664 **Supplement material**

665 **Supplementary Table 1** Average masses of species and other groups used to estimate prey

666 mass (extracted from Karell et al. 2021). Reference 1: Siivonen and Sulkava 2002. 2: Juutilainen

667 1998. 3: Bjärvall and Ullström 2010.

Species	Weight (g)	Reference
Arvicola amphibius (water vole)	177	1

Microtus agrestis (field vole)	25	2
Myodes glareolus (bank vole)	22	1
Sorex spp. (shrews)	7	2
large birds	350	2
thrush-sized birds	90	
finch-sized birds	23	2
small birds	11	2
Apodemus flavicollis (yellow-necked mouse)	26	1
Micromys, Sicista (small mice)	8	1
Rattus norvegicus (rat)	257	2
Pteromys volans (Siberian flying squirrel)	133	1
Lepus spp. (hares) young	150	2
bats	16	3
Mustela nivalis (least weasel)	50	1
Sciurus vulgaris (squirrel)	285	2
Talpa europaea (European mole)	75	2
Rana sp. (frogs)	36	2
Zootoca vivipara (viviparous lizard)	10	2

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669 **Supplementary Table 2** Eigenvalues and percentage of variance explained by each principal
670 component (PC) from the PCA of behavioural (time spent inside and outside the nest), dietary
671 (prey diversity and biomass) and habitat variables. The cumulative percentage of variance is
672 also shown.

Principal component	Eigenvalue	Percentage of variance	Cumulative percentage of variance
PC1	1.951	36.6%	36.6%
PC2	1.095	20.5%	57.1%
PC3	0.959	18.0%	75.1%

PC4	0.497	9.3%	84.4%
PC5	0.414	7.8%	92.2%
PC6	0.368	6.9%	99.1%
PC7	0.047	0.9%	100.0%

673

674 **Supplementary Table 3** Contributions of each variable to the first two principal components
675 (PC1 and PC2) from the PCA. Higher values indicate stronger influence of each variable on the
676 corresponding component.

Variable	Contribution to Dim.1	Contribution to Dim.2
Pre-hatching time spent inside the nest	20.5%	20.8%
Post-hatching time spent outside the nest	0.0%	45.0%
Prey biomass	0.1%	0.1%
Prey diversity	1.9%	0.7%
Coniferous forest	27.5%	18.8%
Deciduous forest	25.4%	9.0%
Mixed forest	24.6%	5.6%

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