



Drivers of nest site selection and breeding success in an Alpine ground-nesting songbird

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Abstract

Birds breeding in high-Alpine habitats must select a suitable breeding site and achieve successful reproduction within a restricted time. During four breeding seasons, we monitored nest sites of the Northern Wheatear (*Oenanthe oenanthe*), a high-Alpine long-distance migrant. We investigated how ecological factors predicted the selection of a site for nesting within the home range, using conditional logistic regression. Birds preferred south-exposed productive pastures on gentle slopes, interspersed with non-vegetated ground and human-made rockpiles. The direct vicinity of conspecific nests was avoided, as were shrubby or north-exposed areas. We investigated if habitat also influenced breeding success. We analysed the impact of environmental factors on breeding success, which was primarily driven by predation. The probability of the brood fledging successfully decreased on north-exposed slopes or on areas with low coverage of non-vegetated ground. The vicinity of conspecific nests did not have a clear effect. Further, we describe how breeding success varied within and between years. Within years, replacement broods had a higher breeding success. The apparent absence of variation in breeding success between years and a delay of the breeding period in the year with late spring onset suggest a high level of tolerance with respect to inter-annual variation of meteorological conditions. Since the preferred habitat is still widely available in the Alps and given the negative population trends in Western Europe, the Alpine range might serve as a refuge for the Northern Wheatear, as long as low-intensity management and heterogeneous habitats are maintained.

Keywords *Oenanthe oenanthe* · Alpine grassland · Conditional logistic regression · Nest site selection · Breeding success · Replacement brood

Zusammenfassung

Entscheidende Faktoren für die Wahl des Neststandorts und für Bruterfolg bei einem bodenbrütenden alpinen Singvogel.

Vögel, die in hochalpinen Lebensräumen brüten, müssen einen geeigneten Neststandort auswählen, an dem sie ihre Brut innerhalb eines begrenzten Zeitraums erfolgreich abschließen können. Während vier Brutsaisons haben wir Neststandorte des Steinschmätzers (*Oenanthe oenanthe*), eines hochalpinen Langstreckenziehers, erhoben. Wir untersuchten mittels konditionaler logistischer Regression, inwieweit ökologische Faktoren die Wahl eines Neststandortes innerhalb des Reviers vorhersagen. Die Vögel bevorzugten südexponierte, produktive Weiden an sanft ansteigenden Hängen, die von

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vegetationsfreien Stellen und von Menschen angelegten Steinhaufen durchsetzt waren. Die unmittelbare Nähe zu Nestern von Artgenossen wurde ebenso gemieden wie bebuschtes oder nordexponiertes Gelände. Weiter untersuchten wir, ob der Lebensraum auch den Bruterfolg beeinflusst. Bruterfolg wurde in erster Linie durch Prädation bestimmt, aber auch der Einfluss weiterer Umweltfaktoren konnte analytisch gezeigt werden. An nordexponierten Hängen oder in Gebieten mit wenig bewachsenem Boden nahm die Wahrscheinlichkeit ab, dass die Brut erfolgreich ausflog. Die Nähe von Nestern von Artgenossen hatte keinen eindeutigen Einfluss. Schließlich beschreiben wir, wie der Bruterfolg innerhalb und zwischen den Jahren variierte. Innerhalb von Jahren hatten Ersatzbruten einen erhöhten Bruterfolg, doch zwischen Jahren beobachteten wir kaum Schwankungen im Bruterfolg. Der interannuell relativ konstante Bruterfolg, sowie eine verspätete Brutzeit im Beobachtungsjahr mit spätem Frühlingsbeginn, deuten darauf hin, dass Steinschmätzer jahresspezifische Schwankungen in den meteorologischen Bedingungen auffangen können. Da der bevorzugte Lebensraum in den Alpen immer noch weit verbreitet ist, könnte das Alpengebiet als Rückzugsgebiet für den Steinschmätzer dienen, der in tieferen Lagen Westeuropas negative Bestandstrends zeigt. Voraussetzung dafür ist jedoch, dass eine Bewirtschaftung mit geringer Intensität und heterogene Lebensräume beibehalten werden.

Introduction

Organisms in seasonal habitats face multiple challenges when breeding within a restricted period with favourable conditions (Lack 1968; Martin and Wiebe 2004; Perrins 1970). In temperate mountain habitats, the availability of suitable habitat and the abundance of food resources change over the breeding season and may vary between years (Martin 2001). In a broader time frame, Alpine habitats are under pressure from climate change and land-use modifications, leading to changes in seasonality and habitat structure and eventually to population declines (La Sorte and Jetz 2010; Chamberlain et al. 2013; Lehikoinen et al. 2014; Scridel et al. 2018).

Breeding ecology is central to understand the underlying mechanisms of population trends. The selection of a suitable nesting site affects breeding success and is usually driven by environmental factors (Hinde 1956; Martin 1993). The factors related to the selection of a nest site are often similar to, but not necessarily the same as, those influencing breeding success per se (Arlt and Pärt 2007; Gilroy et al. 2011). The selection of breeding habitats often depends on the availability of suitable nest locations, but also on the suitability of the surrounding habitat, especially for foraging and feeding the nestlings (Brambilla et al. 2017; Resano-Mayor et al. 2019; Barras et al. 2020). While access to food resources is key to breeding success, other factors such as predation risk may influence the choice of a breeding site (Martin 1993; Low et al. 2010; Schneider et al. 2012). Moreover, for bird species that rely on the same territory during their presence in the breeding region, the suitability of the habitat is also important during the pre- and post-breeding periods (Arlt and Pärt 2008; Müller et al. 2023).

Topographic characteristics such as elevation, slope, and aspect often influence the microhabitat and the microclimate of a nest and hence can influence incubation behaviour and breeding success in high-Alpine bird species (Camfield

and Martin 2009; MacDonald et al. 2016; Niffenegger et al. 2023a, b). Habitat structures in the surroundings of the nest, including perches and shelter for the fledglings, can also explain nest site selection. Vegetation development, which generally follows snowmelt in Alpine environments, drives the abundance of food resources and also their accessibility (Brambilla et al. 2017; Resano-Mayor et al. 2019; Barras et al. 2020; Müller et al. 2023). For ground-foraging birds, shrub and fast-growing grass reduce access to food. On the other hand, short swards and bare ground improve accessibility (Schaub et al. 2010; Tagmann-Ioset et al. 2012; Müller et al. 2023). Social factors, such as intra-specific competition, as well as predation, often influence nest site selection and breeding success (Lack 1968; Martin 1993).

We investigated the influence of environmental predictors on nest site selection and breeding success in an Alpine population of the Northern Wheatear. While the populations of this long-distance migrant have undergone a strong decline in Europe (van Oosten et al. 2015; Keller et al. 2020; López-Ramírez et al. 2024), the Swiss Alps are still a stronghold with positive trends overall (Knaus et al. 2018). This calls for a better understanding of the habitat selection and breeding success of this bird in changing Alpine ecosystems. In this territorial species, adults usually use the same area throughout their presence in the breeding region (Müller et al. 2023; Rime et al. 2023). The availability of nest sites is a limiting factor at lowland breeding grounds (Brooke 1979; van Oosten et al. 2014; Kämpfer and Fartmann 2019), but seems not as limiting in the Alps, where the species nests under stones, in burrows, rockpiles, or walls (Wartmann 1985; Glutz von Blotzheim and Bauer 1988; Maumary et al. 2007; Knaus et al. 2018). If nest sites themselves are sufficiently available, habitat around the cavities is expected to predict the selection of a nest site and to influence breeding success.

We surveyed nests in a high-Alpine valley during four breeding seasons to investigate the influence of surrounding

habitat on the selection of nest sites and the breeding success of Northern Wheatears. We expected nests to be south exposed and preferably located close to suitable foraging habitats, i.e. relatively productive pastures interspersed with rocks and high prevalence of bare ground (Müller et al. 2023; Sander et al. 2023). We predicted the habitat to influence breeding success, which is likely to be mediated by other factors such as predation. We further discuss how breeding success varied within and between years and how breeding phenology was related to inter-annual meteorological variation.

Methods

Study area and study species

Our study area was situated in Val Piora, Swiss Alps (46°33'N, 8°42'E, Fig. 1). It encompassed 6 km² of Alpine grassland interspersed with rocks, screes, rockpiles and low shrub, ranging from 1850 and 2.450 m a.s.l. Most of the relatively productive parts of the area are grazed by milk cows under a low-intensity rotational management in July and August. The area is generally covered by snow between November and April. It harbours > 100 pairs of Northern Wheatears, i.e. > 15 pairs/km², a typical population density in Alpine habitats (Knaus et al. 2018). Wheatears are present between May and September (most of the breeding birds arrive at the end of April or early May) and overwinter in the Sahel (Schmaljohann et al. 2016; Meier et al. 2022; Müller

et al. 2023; Rime et al. 2023). Incubation lasts 14 days, and chicks remain in the cavity for 14 days before fledging (Glutz von Blotzheim and Bauer 1988; Conder 1989). Successive, successful broods regularly occur in lowland populations, generally in less than half of the breeding pairs (Conder 1989; Buchmann et al. 2009; Öberg et al. 2014; van Oosten et al. 2017). In the Alps, wheatears only have one brood, but in case of failure they generally attempt to renest (Wartmann 1985; Müller et al. 2023; Sander et al. 2023). In our study area, observations and unpublished camera trap images suggested that typical predators were mustelids such as stoat *Mustela erminea*, weasel *Mustela nivalis*, and badger *Meles meles*. Fox *Vulpes vulpes* also predated nests, as well as Alpine marmot *Marmota marmota*. This primarily herbivorous rodent seemed to predate nests opportunistically (Y.R., personal observations).

Study design

We monitored nests during four breeding seasons between 2019 and 2022. Breeding success was assessed in 2020, 2021, and 2022. From mid-May to the end of July, we weekly surveyed the entire study area following constant transects (Fig. 1). Nests were searched during the building phase, by following incubating females during their foraging excursions until they returned to the nest, or while both parents were feeding chicks. The coordinates of the nest were recorded in tablets using Qfield (QGIS Development Team 2020). The nest content was monitored using an endoscope (Meier et al. 2022; Müller et al. 2023; Rime et al. 2023).

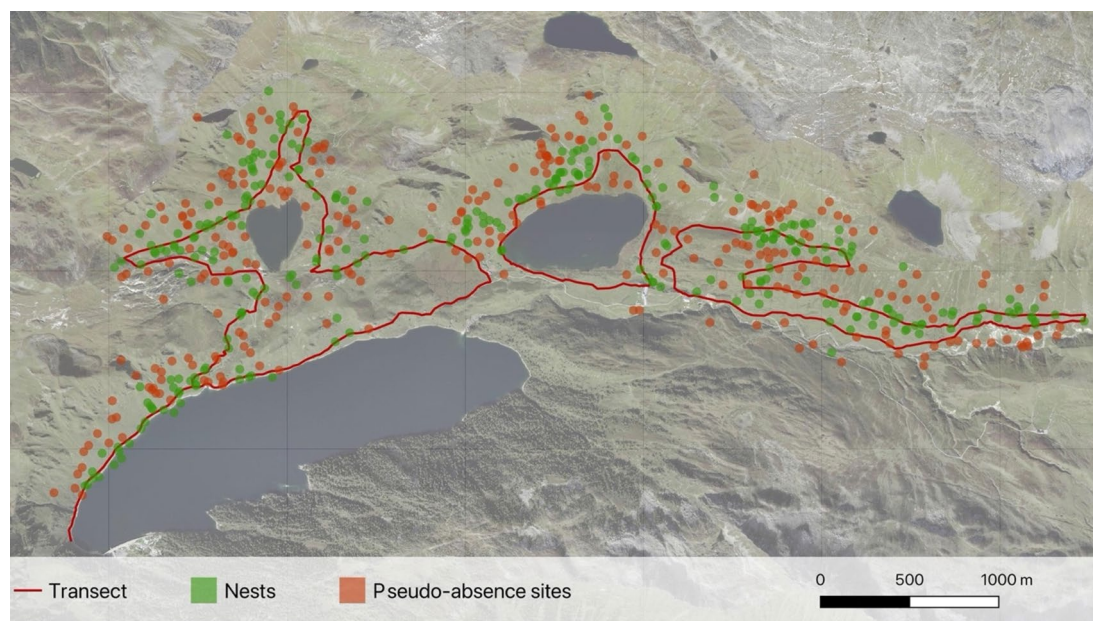


Fig. 1 Map of the study area with the transect (red solid line), nest sites (green dots), and pseudo-absence sites (red dots)

Each nest was revisited weekly until fledging. At each visit, we assessed whether the nest was intact or failed. The start of incubation was calculated based on the age of the chicks. Age was estimated using reference pictures of chicks from known age with a precision of ± 1 day (as described in Öberg et al. 2014). Assessing productivity with a precise count of fledglings was difficult. Predation generally resulted in complete brood loss: hence, we considered a brood successful if at least one chick fledged. In case of predation, clear signs were generally visible, such as nest dug out, a damaged nest cup, presence of eggshells, feathers, or blood. Broods with unknown fate were included in the nest site selection analyses, but excluded from analyses on breeding success. To describe breeding phenology, we summed the clutches laid by 5-day periods in each breeding season. We distinguished between first broods and late broods, i.e. certain replacement broods, based on the gap between them using threshold dates in each year (9 June for 2020, 19 June for 2021, and 9 June for 2022; see Fig. 4 in “Results” for the annual phenology). Data on precipitation, temperature, and hours of sun exposure were obtained for each month of the breeding season from a nearby automated meteorological station at the same elevation (Robiei, 46°26'N, 8°30'E, 1898 m a.s.l., distance to the study site = 16 km).

Habitat variables

For each nest, we extracted remotely sensed habitat variables within a 25-m radius (Table 1). This radius was selected based on previous territory mapping (Müller et al. 2023). To compare the selected sites with the available habitat in the territory, we randomly generated one pseudo-absence location per nest site at a distance of 50–200 m, where we extracted the same variables as we did for the nest sites (Table 1). Actual nest locations in any year of the study were excluded from the potential area for pseudo-absence sites. Given the high density of nests, we used only one pseudo-absence location per nest site.

Average values of the topographic variables (elevation, slope, and aspect) within the 25-m radius were extracted from the digital elevation model SwissAlti3D (Swisstopo 2018) with a resolution of 0.5 m. Aspect was transformed into northness ($\cos(\text{aspect})$) and eastness ($\sin(\text{aspect})$). We calculated an NDVI (normalized difference vegetation index) raster from Sentinel 2 satellite imagery (ESA 2015), with a spatial resolution of 10 m in Google Earth Engine (Gorelick et al. 2017). We applied a cloud filter ($< 50\%$ cloud cover) and selected, for each year, the closest image to mid-May (beginning of snowmelt period and territory settlement) and mid-June (end of the snowmelt period and peak of the breeding period, Müller et al. 2023; Rime et al. 2023). Mean values within the 25-m radius were extracted in R using the *extract* function from the *terra* package (Hijmans

et al. 2022). The proportion of non-vegetated ground, i.e. bare ground and stones, was calculated using a supervised image classification algorithm from the SCE plug-in in QGIS (QGIS Development Team 2020) based on the 2022 *SwissImage* aerial pictures with 10-cm resolution (Swisstopo 2022). Due to limitations of the algorithm in distinguishing between spectral signatures of the different types of vegetations (woody vegetation, grass, and trees), shrubs (*Rhododendron ferrugineum* and *Juniperus communis*) were mapped manually in QGIS (QGIS Development Team 2020) from the *SwissImage* pictures with a 10-cm resolution. We also did so for artificial rockpiles in the study area. We calculated the three-dimensional distance to the nearest nest of a conspecific in the same year for each actual nest site and pseudo-absence site. To do so, we used the Pythagorean theorem based on the horizontal distance and the vertical elevational difference from the SwissAlti3D DEM (Swisstopo 2018).

Nest data

We surveyed 292 nests and retained 281 for the analyses: 55 in 2019, 93 in 2020, 68 in 2021, and 65 in 2022. Eight nests were discarded because they were located on the shore of a temporarily empty lake, which is not representative of a natural habitat in the Alps, and three had insufficient data. Out of 281 nests, we could assess the breeding success for 191 (6/55 in 2019, 68/93 in 2020, 58/68 in 2021, 59/65 in 2022). Only the 185 nests from 2020, 2021, and 2022 were used for modelling the probability of nest success.

Statistical analyses

All analyses were conducted in R, version 4.2.0 (R Core Team 2023). Models were fitted in a Bayesian framework (Gelman et al. 1995; McElreath 2018). We performed two analyses: first, we used a paired design comparing nest sites with pseudo-absence locations to model nest site selection. Second, we investigated the environmental drivers influencing breeding success, comparing successful with failed broods. We selected predictors (Table 1) based on a priori assumed biological importance (Korner-Nievergelt et al. 2015). The same predictors were included as fixed effects in both analyses. Dates of start of incubation were included only for breeding success.

All predictors were standardized (mean = 0, SD = 1). Non-linear effects were accounted for by including the first and second orthogonal polynomials of all variables using the *poly* function in the *stats* package (R Core Team 2023). Model selection was only done for non-linear effects, by comparing the WAIC value with and without the quadratic polynomials of each predictor (Korner-Nievergelt et al.

Table 1 Predictors used to model the nest site selection (presence compared to pseudo-absence) and the breeding success probability, with the category of a variable, the name of the variable, the data source, the description of the variable, the unit, the specification of data transformation, and the mean and range of variables for (1) the actual nest sites, (2) the pseudo-absence sites, and (3) the data subset used to model breeding success

Variables recorded in a 25-m radius around nest sites							
Category	Variable	Data source	Description	Unit	Data transformation	Nest sites ($n=281$) mean; range	Pseudo-absences ($n=281$) mean; range
Topographic variables	Elevation	SwissAlti3D DEM	Mean elevation above sea level in 25-m radius	m	z	2033; 1849 to 2278	2059; 1854 to 2447
	Slope	SwissAlti3D DEM	Mean inclination of the slope in 25-m radius	%	z	23; 0.5 to 63.5	27.6; 4 to 61.2
	Northness	SwissAlti3D DEM	$\cos(\text{aspect}) \cdot \pi / 180$ from the mean aspect value in a 25-m radius		z	"-0.73; -1 to 0.84"	"-0.62; -1 to 0.89"
	Eastness	SwissAlti3D DEM	$\sin(\text{aspect}) \cdot \pi / 180$ from the mean aspect value in a 25-m radius		z	0.09; -1 to 1	0.05; -1 to 1
Remotely sensed variables	NDVI May	Sentinel-2 satellite image	Normalized difference vegetation index for mid-May in the corresponding year	Index	z	0.27; -0.07 to 0.73	0.29; -0.07 to 0.8
	NDVI June	Sentinel-2 satellite image	Normalized difference vegetation index for mid-June in the corresponding year	Index	z	0.63; 0.11 to 0.86	0.62; 0.12 to 0.87
Man-made landscape elements	Non-vegetated ground	Supervised image classification SwissImage 10 cm	Non-vegetated mineral ground (bare soil, stones and rock)	%	z	6.9; 0 to 40.7	4.4; 0 to 40.8
	Shrub	SwissImage 10 cm and on-site mapping	Area of shrub	m ²	z	162; 0 to 1933	372; 0 to 1961
	Rockpiles	SwissImage 10 cm and on-site mapping	Number of rockpiles in a 25-m radius		z	2.7; 0 to 25	0.3; 0 to 11
	Distance3D	SwissAlti3D DEM	Three-dimensional (pythagorean distance from horizontal and vertical distances) to the nearest nest in the same year	m	z	118; 13 to 502	130; 53 to 294
Conspecific interaction							110; 13 to 351

Table 1 (continued)

Variables recorded in a 25-m radius around nest sites

Category	Variable	Data source	Description	Unit	Data transformation	Nest sites ($n=281$) mean; range	Pseudo-absences ($n=281$) mean; range	Breeding success ($n=191$) mean; range
Phenology	Estimated start of incubation	Nest monitoring	Estimated day of the start of the incubation	Day	of the year	z	–	155; 134 to 191

2015). We retained the models with the lower WAIC and eventually excluded non-linear terms in the final models based on this selection. There was no strong collinearity among explanatory variables (all Spearman's correlation coefficients $|r_s| \leq 0.5$).

Nest site selection was modelled with nest sites (1) and the randomly generated pseudo-absence (0) as a binary response variable. To account for non-independence of the observations of a year, year was included as a random factor. We applied a conditional logistic regression using the function *stan_clogit* in the *rstanarm* package (Goodrich et al. 2020). We used uninformative priors (Kass and Wasserman 1996; Berger 2006). Presence and pseudo-absence pairs were defined as strata in the conditional logistic regression, which links the presence and pseudo-absence locations in the model. To interpret the effect of each variable on the nest site selection probability, we plotted predictions from the model relative to a reference, defined as the mean value of each predictor, assuming a 50% presence probability for the reference point. Such an arbitrary value is needed to produce effect plots, since the conditional logistic regression does not estimate an intercept.

We modelled the probability of a nest to be successful in relation to environmental factors following Bolker (2019). We built a generalized linear model with a binomial distribution, using a complementary log–log link function accounting for exposure time (the number of days a nest was active between two visits; ignoring this would lead to biased survival estimates because failed nests are underrepresented, Mayfield 1961). This method allows for intervals between visits that are not equally spaced (for a comparison with RMark, see electronic supplementary material). We modelled the probability of a nest to be intact, i.e. without predation or abandonment, using the function *glm* from the *stats* package in R (R Core Team 2023). The status of the nest at each visit (alive or failed) was used as a response variable, and the observation year was included as a fixed effect factor of three levels in the model (excluding the 6 nests from 2019 due to the limited effort in nest monitoring in this year). We used the function *sim* from the package *arm* (Gelman et al. 2018) to draw from the joint posterior distribution and present plots showing the effect of each predictor on the probability of nesting success, with the other predictors set to their means. For all estimates and effect plots, we present 95% uncertainty intervals using the 2.5% and 97.5% quantile from the posterior distribution (Korner-Nievergelt et al. 2015). Data and code associated with this work are available at <https://doi.org/10.5281/zenodo.10984085> (Rime and Korner 2024).

Table 2 Summary output of the nest site selection model and the breeding success model (Bayesian mixed-effect model)

Variables	Nest site selection					Breeding success		
	Estimate	Mean	SD	2.5%	97.5%	Estimate	2.5%	97.5%
Elevation	−1.747	−1.8	0.4	−2.621	−0.922	0.290	−0.117	0.708
Slope	−0.394	−0.4	0.2	−0.856	0.053	−0.268	−0.657	0.128
Northness	−0.526	−0.5	0.2	−0.940	−0.145	−0.344	−0.622	−0.065
Eastness	0.187	0.2	0.2	−0.202	0.591	−0.017	−0.321	0.299
Rockpiles	1.473	1.5	0.3	0.920	2.178	−0.414	−0.667	−0.155
Shrub	−0.162	−0.2	0.2	−0.475	0.130	0.067	−0.246	0.377
Non-vegetated ground	0.752	0.8	0.2	0.451	1.087	0.436	−0.028	0.893
NDVI May	−0.012	0.0	0.3	−0.624	0.550	0.055	−0.549	0.672
NDVI June	0.945	0.9	0.2	0.472	1.444	−0.055	−0.599	0.475
Distance3D	0.372	0.4	0.2	0.064	0.707	0.245	−0.105	0.597
Start of incubation	—	—	—	—	—	0.133	−0.239	0.483
Year 2021	—	—	—	—	—	−0.488	−1.897	0.874
Year 2022	—	—	—	—	—	−0.455	−1.515	0.610

The probability of the presence of a nest site was modelled comparing actual nest sites and randomly selected pseudo-absence sites using a mixed conditional logistic regression, with presence vs absence pair as strata argument and observation year as random effect. The probability of success was modelled using a Bayesian mixed-effect model using a logistic regression with a logit-link function, including observation year as a random effect. The other variables were included as fixed effects in each model, with the start of incubation being used as predictor only in the breeding success model. For each model, estimates where the 95% credible intervals do not contain 0 are highlighted in bold

Results

Our models suggest that nest site is selected depending on a set of environmental factors (Table 2, Fig. 2). Nests were built preferably at lower elevations (within the elevational gradient at our study site) and on gentle rather than steep slopes, suggesting a preference for gentle slopes over steep slopes. Northness had a negative effect, indicating an avoidance for north-exposed slopes, while eastness had no effect. Artificial rockpiles had a strong positive effect on nest site selection. Shrub did not have any clear effect, whereas a larger proportion of non-vegetated ground increased the probability of a location to be used for nesting. The NDVI in May did not show a clear effect, but the NDVI in June had a positive effect. Finally, we observed a preference for locations away from other nests in the same year, with a positive effect of the three-dimensional distance to the nearest nest.

The overall observed breeding success of 191 nests was 0.62. Failure was almost always due to predation; this cause was attributed for all but five cases out of 73 failures (other causes were brood abandonment or unknown cause). Yearly observed breeding success was similar across years: 0.60 in 2020 ($n=68$), 0.66 in 2021 ($n=58$) and 0.64 in 2022 ($n=59$). The modelled breeding success, which accounts for exposure time of the nests, estimated the reproductive success at 0.61 [0.33; 0.80] for 2020, 0.45 [0.18; 0.70] for 2021, and 0.47 [0.26; 0.64] for 2022, with no statistically

clear difference between years (Table 2, Fig. 3). Data from the six nests from 2019 were excluded from the model.

The logistic regression with a complementary log–log link function accounting for exposure of the nests showed effects of some environmental predictors on breeding success, with fewer variables involved compared to nest site selection (Table 2, Fig. 3). Elevation seemed to have a positive effect on the probability of breeding success, while slope showed a negative effect but had large uncertainty. Northness had a clear negative effect, while eastness apparently did not influence the probability of a successful brood. Broods were less likely to be successful at sites with more rockpiles. Shrub showed no clear effect on breeding success. No clear effect was detected for NDVI in May or in June. Non-vegetated ground had a positive effect on breeding success. The distance to the nearest conspecific nest and the estimated date of start of incubation were positively correlated with the breeding success, but their estimates had high uncertainty.

Breeding success showed no clear weather-related differences (2021 was rainier, colder, and with later snowmelt, while 2020 and 2022 were drier, warmer, and with exceptionally early snowmelt; Fig. 4). We monitored 153 first broods (observed success = 0.61) and 32 replacement or late broods (observed success = 0.75). The mean start of incubation of the first broods was 29 May. In 2020 (early, warm, and dry spring), the mean start of incubation of first broods

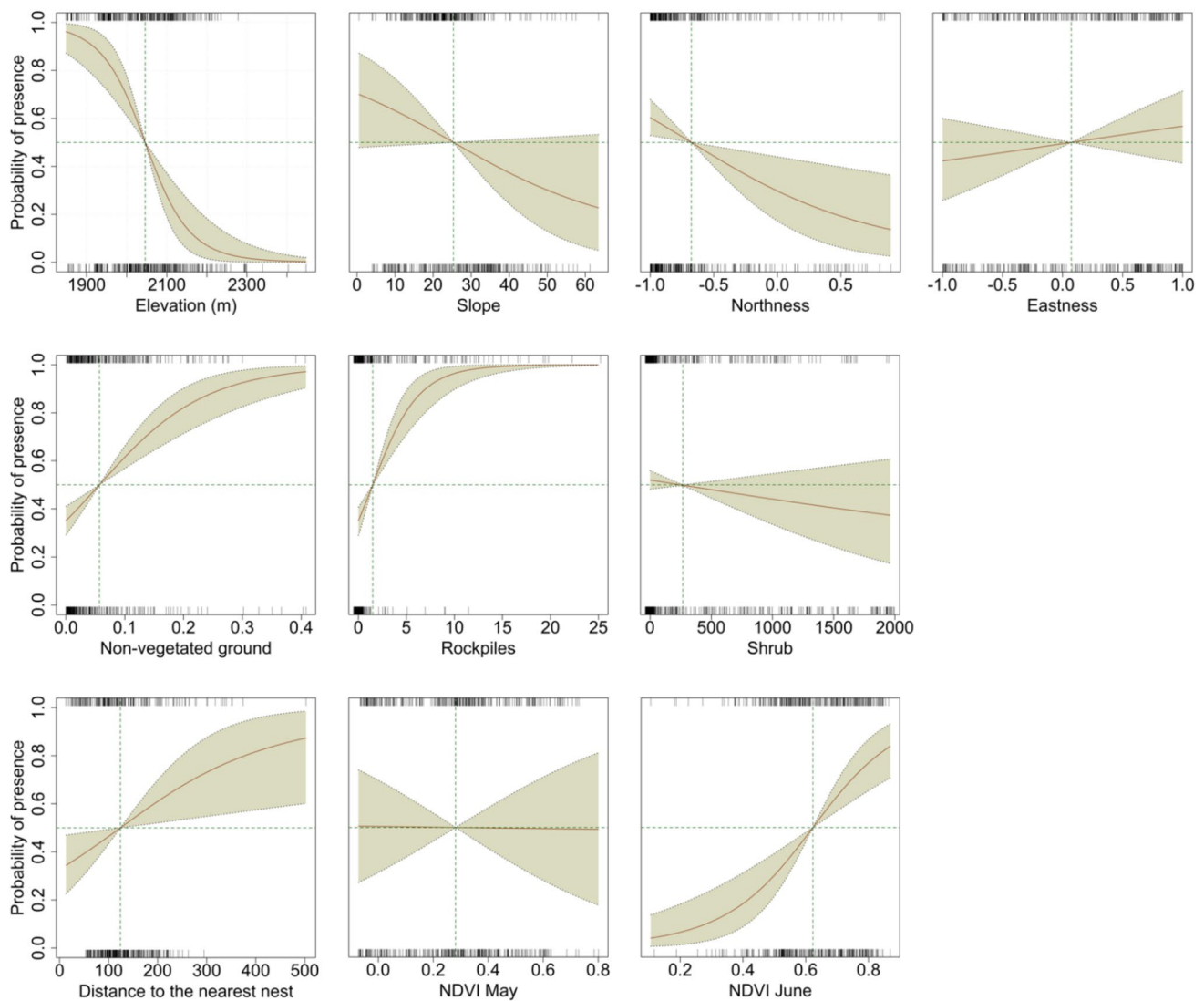


Fig. 2 Predictions from the conditional logistic regression showing the relative probability of the presence of a nest site compared to a reference point, which is defined as the probability of presence for the mean observed value of the plotted predictor. Other predictors

were set to their mean. The coloured areas are 95% credible intervals, and the ticks show the row data (upper side=presence, lower side=pseudo-absence)

was 28 May, in 2021 (late, cold and wet spring) 5 June, and in 2022 (early, warm, and dry spring) 25 May (Fig. 4 and electronic supplementary material Table S1). The earliest incubation started on 14 May (2020), 24 May (2021), and 16 May (2022). The incubation of the latest brood started on 10 July. A mean $\pm$ SD clutch size of 4.97 ± 0.7 eggs (range 3 to 6 eggs) could be assessed for 74 nests. First broods had 5.03 ± 0.66 eggs, and replacement broods had 4.33 ± 0.82 eggs. Due to a larger uncertainty in the ageing of the chicks and the corresponding estimation of hatch date, 2019 data were excluded from the yearly comparison of breeding phenology.

Discussion

The selection of a nest site in Northern Wheatears from an Alpine population was consistently influenced by topography, vegetation productivity, and habitat composition, especially by the direct proximity of suitable foraging habitat. The probability of successful breeding was mainly driven by predation, with indirect effects of topography and habitat composition. A comparison between three breeding seasons suggested a delay in laying dates with late spring onset and cold, rainy weather. However, breeding success seemed overall similar in 2020, 2021, and 2022, indicating a high tolerance to inter-annual variation of meteorological conditions in Alpine habitats.

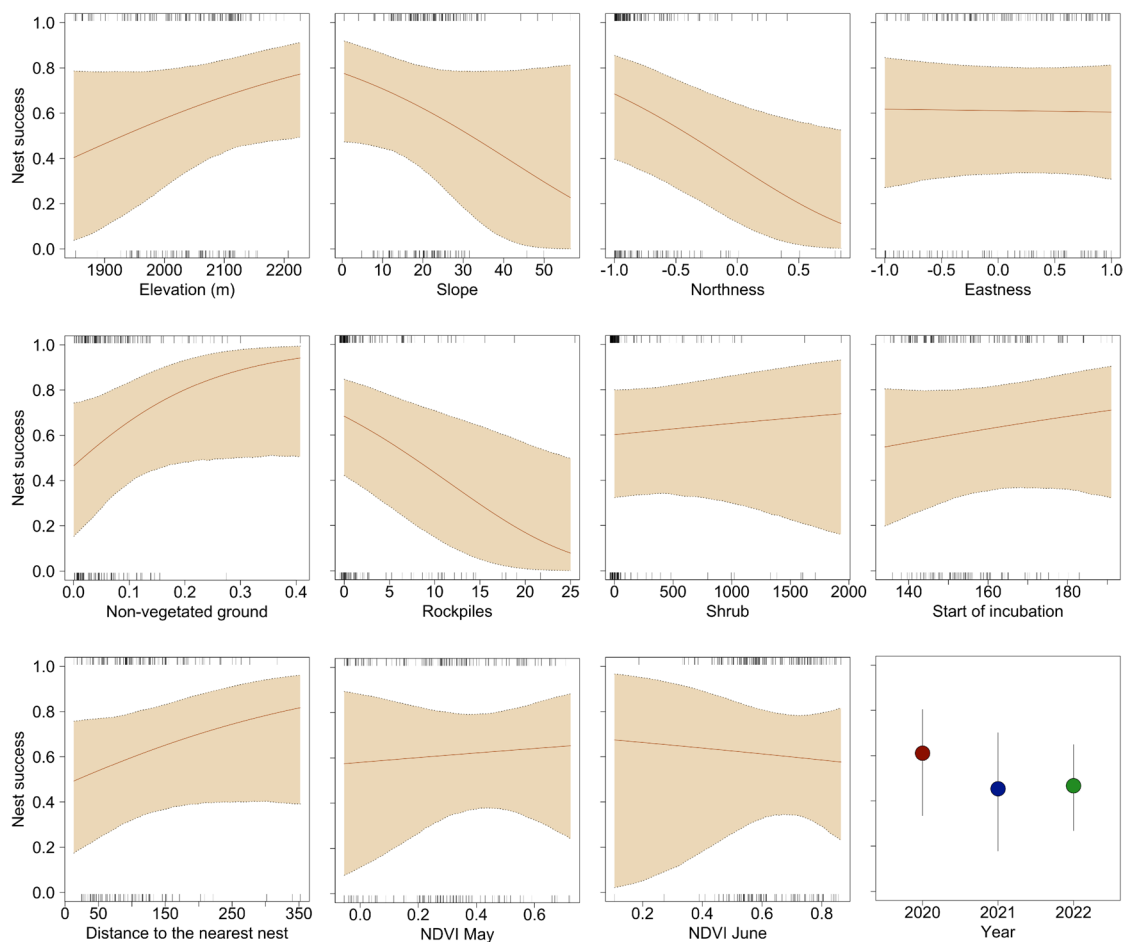


Fig. 3 Predictions from the logistic regression showing the average effect (solid line) of each predictor on breeding success (0=failed broods, 1=successful broods), when other predictors were set to their

mean. The coloured areas are 95% credible intervals, and the ticks show the row data

In Alpine ecosystems, fine-scale habitat characteristics often explain a species' distribution (Jähnig et al. 2020; Müller et al. 2023). While the restricted availability of nest cavities can be limiting for Northern Wheatears in parts of their range (Conder 1989; Currie et al. 2000; Kämpfer and Fartmann 2019), nest cavities are abundant in heterogeneous, well-structured Alpine grasslands such as those in our study area (Wartmann 1985; Sander et al. 2023). Hence, rather than the availability of cavities, the surrounding habitat played a major role in the selection of a nest site. Other Alpine species such as the white-winged snowfinch (*Montifringilla nivalis*) also select a nest based on the surrounding habitat quality, but often move longer distances between the nest and the foraging sites (e.g. Niffenegger et al. 2023a, b). In our study on Northern Wheatears, most of the parameters influencing nest site selection were related to the suitability of the vicinity of the nest (25 m) for foraging. Foraging preferences were described in another study at the same site (Müller et al. 2023). Wheatears use stones as perches, from

which they access ground-dwelling invertebrates in short flights (Wartmann 1985; Sander et al. 2023). Access to these food items is enhanced by low vegetation and bare ground, within areas of relatively high productivity in low-intensity farmed pastures. The preference for gentle south-exposed slopes (Wartmann 1985; Glutz von Blotzheim and Bauer 1988; Knaus et al. 2018) is probably due to the presence of herbaceous vegetation, where food abundance is higher compared to cliffs, debris, or shrub (Müller et al. 2023). Even though we did not detect collinearity between elevation and slope, the avoidance of areas at higher elevation is probably related to the topography of our study area, where sites at higher elevation are steeper and less productive. Our results are restricted to the habitat in direct vicinity of the nest site and do not account for the habitat used at larger distances or in the pre- and post-breeding period (Alba et al. 2023; Müller et al. 2023; Rime et al. 2023).

The probability of a site being selected for nesting increased with the amount of human-made rockpiles in

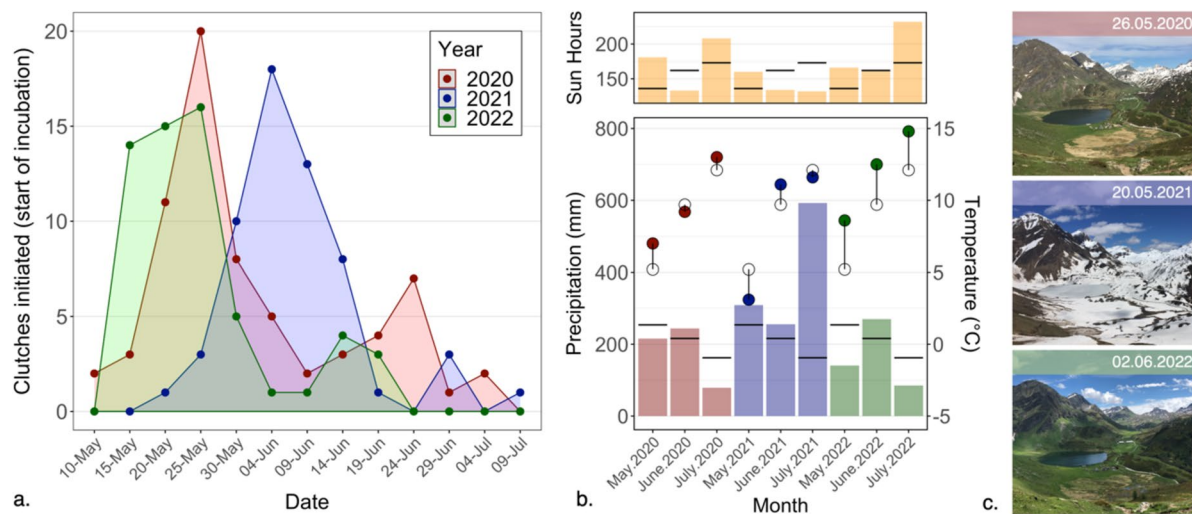


Fig. 4 **a** Distribution of clutches laid per 5-day period in 2020 (red), 2021 (blue), and 2022 (green), showing a clear difference between 2021 (late snowmelt year with cold and rainy meteorological conditions during the breeding season) compared to 2020 and 2022 (early snowmelt years with warm and dry meteorological conditions during the breeding season). **b** Hours of sun per month (in orange, the black

bar shows the average 1991–2020), sum of precipitation per month (coloured bars for each month of the breeding season, the black bar shows the average 1991–2020), and the mean monthly temperature (filled dots) compared to the average 1991–2020 (empty dots). **c** The study area in three contrasting years with large variations in spring onset and snowmelt

the surroundings, highlighting the importance of these typical elements of Alpine pastures under low-intensity traditional management. These rockpiles often hosted nest cavities in our study area, but also offered a place to hide for fledgelings. Moreover, they were located in productive pastures that are favoured for foraging (Müller et al. 2023). As for other insectivorous birds, access to ground-dwelling arthropods (Schaub et al. 2010; Tagmann-Ioset et al. 2012; Rime et al. 2020) most likely explains the preference for sites with more non-vegetated ground on nest site selection (Müller et al. 2023). For the same reason, shrub was usually avoided for foraging (Müller et al. 2023), but not clearly avoided for nesting.

Nest sites were more likely located in areas where the vegetation was productive relatively to the surrounding landscapes during food provisioning, with a positive correlation between selected sites and NDVI in June, i.e. after snowmelt. However, NDVI only informs on the vegetation greenness around the nest site and not on the fine-scale vegetation structure (Müller et al. 2023; Sander et al. 2023). No clear effect was detected for the measure of vegetation greenness in May, when birds arrived from migration and snow was melting (Sander et al. 2021; Rime et al. 2023). According to our observations, vegetation development was faster on steeper slopes that are first free of snow but that were avoided for nesting. The absence of effect of NDVI in May suggests that birds did not select their territory based on the state of the vegetation upon arrival, but used other cues, potentially gathered in the previous year (Pärt et al. 2011).

In addition to these habitat-related predictors, conspecifics played a role in the selection of a nest site. A distance of more than 124 m to the nearest nest was preferred, which is probably explained by a high breeding density of this territorial species and the result of a trade-off between breeding in favourable habitat while keeping a sufficient distance to minimize energy expenditure in defending the surroundings of the nest against competitors (Brooke 1979; Conder 1989; Arlt and Pärt 2007).

As in other parts of the Alps (Wartmann 1985; Sander et al. 2023), the probability of a nest to be successful was mainly driven by predation, one of the main factors influencing reproductive success (Martin 1995; Martin and Briskie 2009). The influence of habitat quality on breeding success hence needs to be interpreted mainly indirectly, i.e. through the influence of topography, habitat composition, or vegetation productivity on the risk of predation.

Topography influenced the breeding success: we found a strong negative correlation, indicating lower breeding success with north-exposed aspect. Predation risk is usually higher at lower temperatures, when provisioning rates must be increased (Moreno 1989; Low et al. 2008; Schneider et al. 2012; Öberg et al. 2015). Habitat composition also influenced breeding success. Non-vegetated ground, favoured for selecting a nest site, had a positive effect on breeding success. Predation risk was found to increase in low-quality foraging habitats in a Swedish lowland population (Pärt 2001). Previous studies on lowland and high-elevation populations of the Northern Wheatear showed enhanced access to ground-dwelling prey in short vegetation and patches of

bare ground: birds breeding in better habitats might need less frequent but more effective provisioning visits to the brood, thus reducing predation risk (Arlt and Pärt 2007; Arlt et al. 2008; Low et al. 2010; Müller et al. 2023; Sander et al. 2023).

The distance to conspecific nests seemed positively correlated with breeding success, but the uncertainty of the model was high. Breeding further away from conspecific may reduce the negative effects of intra-specific competition in this territorial species (Conder 1989; Currie et al. 1998, 2000; Alba et al. 2023). Social factors might also explain why rockpiles in the surroundings, which were favoured for selecting a nest site, negatively affected breeding success. Higher breeding densities in this a priori optimal habitat might lead to more competition (Maurer 1984) and to an increased risk of predation from predators specialized in preying on birds, as they might target areas with high densities of nests (Taylor 1976; Andersson and Wiklund 1978; Larivière and Messier 1998). The overall advantages of breeding in areas with rockpiles, such as a high-quality foraging habitat (Müller et al. 2023), nest cavity availability, perches (Alba et al. 2023), and refuge for fledgelings, are probably more relevant when selecting a nest site than a potentially increased predation risk.

Although the effect in our model was weak, the observed breeding success seemed higher in replacement broods compared to first broods. This confirms similar findings in the Italian Alps (Sander et al. 2021, 2023). Due to a short breeding season, second broods are rare at high elevation (Wartmann 1985; Müller et al. 2023) and mostly consisted of replacement broods after predation in our study. A better success late in the season contrasts with lowland populations, where late breeding is associated with a decrease in fitness (Öberg et al. 2014). Nevertheless, Sander et al. (2023) found a reduced weight of chicks in late breeders, which might therefore face other disadvantages such as delayed moult with carryover effects on survival (Tinbergen and Boerlijst 1990; Magrath 1991; Buchmann et al. 2009; Streby et al. 2014; Sander et al. 2023).

With a time-limited availability of food resources to feed the chicks (Martin and Wiebe 2004; Chamberlain et al. 2023), many bird species are facing a mismatch between breeding timing and the optimal availability of food resources (Both and Visser 2001; Visser et al. 2004; Jones and Cresswell 2010; Saino et al. 2011). Such mismatch was found for Alpine bird species (e.g. Wann et al. 2019; Schano et al. 2021) and was described as a potential cause for variation in breeding success of Northern Wheatears (Sander et al. 2021). We did not measure food availability or food provisioning here, but found no evidence of changes in breeding success in years with varying spring onset and different meteorological conditions. The onset of the breeding season occurred later in spring 2021, which was marked by late snowmelt and rainy, cold weather

conditions. This contrasted with 2020 and 2022, years with early snowmelt and warm weather, indicating that wheatears can adjust lay dates to annual phenology. Overall, breeding success seemed similar between these years, suggesting a limited sensitivity of this species to inter-annual variations in spring onset and weather conditions. Furthermore, the probability of success seemed higher in late broods. This would not be expected if the birds were not able to time the onset of breeding to the availability of food resources (Jones and Cresswell 2010; Saino et al. 2011; Wann et al. 2019). Hence, habitat quality in general might be more relevant for Northern Wheatears than the seasonality of food resources. Nonetheless, the relationships between inter-annual cyclic fluctuations of predators and their alternative prey may also influence the annual breeding success, with potentially more complex interactions with weather conditions (Ibáñez-Álamo et al. 2015; Maag et al. 2024). However, our short-term study does not suggest changes in breeding success between years.

In the context of a decline of the Northern Wheatear in Europe (Gedeon et al. 2015; Keller et al. 2020), the positive situation in the Alps (Knaus et al. 2018) indicates that mountain ranges are currently crucial for the conservation of the species at a continental scale. Our results highlight a preference for south-exposed, relatively productive grasslands with high heterogeneity on a small spatial scale, a habitat still widely available in the Alps. As the species underwent recent upwards distribution range shifts (Knaus et al. 2018; Hallman et al. 2022; López-Ramírez et al. 2024), habitats in pastures directly above the treeline such as our study site might no longer be suitable in the future. Nonetheless, at present, thanks to the tolerance of the Northern Wheatear for changing weather conditions among years, a warmer climate might improve the breeding conditions for the species in the Alps, as long as habitat quality is maintained. A loss of habitat suitability at lower elevations, especially through bush and shrub encroachment (Laiolo et al. 2004; Braunisch et al. 2016), might be buffered by conserving traditional pastoral activities and promoting heterogeneous habitats. The situation in the well-preserved high-elevation valley where this study took place is not entirely representative of other locations in the Alps, particularly to those subject to land abandonment or, conversely, to agricultural intensification.

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Data availability Data and code are available at <https://doi.org/10.5281/zenodo.10984085>.

Declarations

Conflict of interest The authors declare that they have no competing interest.

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