The effect of treeline proximity on predation pressure: an experiment with artificial nests along elevational gradients in the European Alps

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ABSTRACT
Capsule: Predation rates of artificial nests along elevational gradients were higher closer to the treeline in the European Alps.

Aims: Alpine grassland birds tend to show an avoidance of mature trees, possibly due to an edge effect, such as higher predation pressure close to the treeline. This study aimed to estimate potential predation pressure in relation to the distance from the treeline and other environmental variables by using artificial nests positioned along elevational transects in the Italian Alps.

Methods: A total of 119 artificial nests were positioned and monitored during the breeding season. For each nest, habitat data at small and large scales were collected. Daily nest survival was estimated using MARK.

Results: The most informative model included date, distance from the treeline and a micro-habitat structure variable. In particular, the model showed a positive relationship between nest survival and the distance from the treeline.

Conclusions: This study suggests that if treelines advance due to climate change, the functional habitat loss may be greater than physical habitat loss, since the optimal breeding area would be further away from the forest edge. The conservation of high-elevation grasslands in relation to environmental changes may therefore be addressed through management strategies to maintain open habitats.

Climate and human activity have shaped the landscape and diversity of the European Alps for centuries, but both of these factors are currently undergoing rapid changes. The Alps have experienced a 2°C increase in annual minimum temperatures during the 20th century, with a marked rise since the early 1980s (Beniston et al. 1997). In recent decades, elevational range shifts of vegetation communities have occurred (Grabherr et al. 1994, Pauli et al. 2001), community composition has changed at high alpine sites (Keller et al. 2011), and treeline species have responded to climate warming by colonizing the alpine zone or increasing growth rates (Gindl 1999, Paulsen et al. 2000, Motta & Nola 2001). Moreover, the European Alps have a long history of human presence and exploitation. Pastoral activities have been practised for at least 6000 years (Lichtenberger 1994), thereby shaping the alpine environment and causing a lowering of the treeline ecotone, thus influencing the community composition of plants and animals (Theurillat et al. 2003, Laiolo et al. 2004, Chemini & Rizzoli 2014). At high elevations, the rapidly declining utilization of alpine pastures for livestock grazing is causing an upward shift of the treeline (Dirnböck et al. 2003). These shifts in vegetation, through both climate change and abandonment of pastoral practices, may lead to major habitat changes that will increase fragmentation and cause loss of open habitats at higher elevation (Peñuelas & Boada 2003, Gonzalez & Neilson 2010). High-elevation alpine ecosystems are also affected by human impacts such as tourism and related recreational activities and infrastructures (Laiolo et al. 2004, Rolando et al. 2007, Negro et al. 2010, Caprio et al. 2011). Several previous studies have shown how bird distributions might be affected by changes in climate and land-use (Laiolo et al. 2004, Chamberlain et al. 2013, Melendez & Laiolo 2014). The models developed by Chamberlain et al. (2013) suggested a loss of high-elevation grasslands, which may have severe consequences for breeding alpine birds in the...
future. Loss of open habitats is then likely to become one
the major conservation issues in the Alps, and, even
though currently of no conservation concern, several
mountain bird species could be threatened in the
future.

The factors dictating the distributions of alpine birds
are still not completely clear for most species, but
reproductive success is one of the main factors
influencing bird populations, so it might be
hypothesized that habitat characteristics could have an
influence on distribution via effects on productivity.
Previous studies based on point counts have shown that,
within our study area, several ground-nesting grassland species have much lower occurrence rates
(e.g. Sky Lark _Alauda arvensis_, Wheatear _Oenanthe oenanthe_), or never occur (Water Pipit _Anthus spinoletta_), in the proximity of mature trees (Chamberlain _et al._ 2013 and unpubl. data). This
avoidance may be due to an edge effect (Gates & Gysel
1978), possibly because forest is a reservoir for nest
predators. Evidence for such effects, whereby nest
survival and/or species occurrence is lower in ground-
nesting species close to forest or woodland, exists for
several species (Wilson _et al._ 1997, Chamberlain &
Gregory 1999, Winter _et al._ 2000, Schneider _et al._
2012). Whilst predation on grouse species in alpine
forests has been studied in relation to edge effects and
forest fragmentation (Storch 1991, Svodoboda _et al._
2004), we are unaware of any similar studies that have
been carried out in high-elevation open habitats, but
we hypothesize that an edge effect mediated via nest
predation reduces the habitat quality of grasslands
adjacent to the treeline in alpine grassland birds. In
such a case, there might not be a coincidence between
the habitat with physical characteristics (open
grasslands) suitable for breeding and the functional
habitat, a concept that links biological and physical
characterization (Buffagni _et al._ 2000). In other words,
there may be physically suitable grassland adjacent to
the treeline, which is effectively unusable by ground-
nesting birds due to predation pressure, even though
the structure of the habitat is correct.

The aim of the present study is to reach a better
understanding of the relationship between alpine birds
and their nesting habitat, to identify which habitat
characteristics influence nest predation along the
elevational gradient and to what extent, and possibly
to assess the presence of an edge effect between
the forests of the montane belt and the grasslands of
the alpine belt. The results obtained in this study
could be important in informing conservation
strategies for bird species breeding in high-elevation
grasslands.

**Materials and methods**

**Study area**

The fieldwork for this study was carried out in Val
Troncea Regional Park (44°57′28″N 6°56′28″E;
Figure 1), which is part of the Cottian Alps Protected
Area (Piedmont Region, northwest Italy), during the
months of June and July 2014. The study area covered
an elevational range of between 2184 and 2792 m
above sea level (asl). The area is dominated by Larch
_Larix decidua_ at lower elevations, with some Scots Pine
_Pinus sylvestris_ and Swiss Pine _Pinus cembra_. Shrub
species above the treeline (which occurs at about
2200 m asl) are typically Juniper _Juniperus communis_
and Alpenrose _Rhododendron ferrugineum_. Grasslands
occur throughout the area, consisting of seasonal
pastures (including some below the treeline) and
higher elevation alpine grassland. Scree and rocky areas
are common, especially at higher elevations, and are
dominant above approximately 2700 m asl. A range of
potential nest predators occur on the study area,
including mammals such as Stoat _Mustela erminea_,
Beech Marten _Martes foina_, Red Fox _Vulpes vulpes_ and
Wolf _Canis lupus_, birds such as raptors and corvids
(Raven _Corvus corax_, Carrion Crow _Corvus corone_,
Eurasian Jay _Garrulus glandarius_, Alpine Chough
_Pyrhocorax graculus_ and Red-billed Chough
_Pyrhocorax pyrrhocorax_) and Adder _Vipera berus_.

**Artificial nests**

Artificial nests were used to assess predation rate along
the elevational gradient. In some previous studies,
artificial nests composed of Common Quail _Coturnix coturnix_ or modelling clay (plasticine) eggs, placed in
real nests and positioned to mimic the studied species,
have often been used (Chamberlain _et al._ 1995, Kurucz
_et al._ 2012), in particular to study edge effects (Bátary
& Báldi 2004). An alternative method is to use the
‘hypothetical species’ approach (Jokimäki & Huhta
2000, Seibold _et al._ 2013). This is underpinned by the
assumption that it is in fact almost impossible to build
a nest resembling exactly that of a real ground-nesting
species. The approach adopted was therefore not to
estimate predation rates for any particular species,
rather it was to assess likely predation pressure along
the gradient using nests of a ‘hypothetical species’ (see
Jokimäki & Huhta 2000, Seibold _et al._ 2013). Under
this approach, the random placement of nests is not
likely (nor does it try) to mimic actual nest site choice,
but it allows for variation in vegetation and other
habitat variables, for which the effects on the
The probability of predation can be estimated during data analysis. Similarly to Jokimäki & Huhta (2000) and Seibold et al. (2013), it is therefore assumed that the outcomes of this study are then relevant in terms of measuring nest predation pressure in ground-nesting birds.

For the present study, it was decided to simply place a group of eggs directly on to the ground (which for convenience we hereafter refer to as a 'nest', as in Seibold et al. 2013). The positioned nests (\(n = 119\) nests) were composed alternatively of three Quail eggs (\(n = 61\) nests) or of one Quail egg and two plasticine eggs (\(n = 58\) nests), the latter in order to try and identify nest predators by marks left in the plasticine. The plasticine eggs were coated using Plastidip®, an odourless rubber paint used to eliminate the plasticine smell (Haskell 1995, Purger et al. 2012). Fishing line was sewn into the artificial eggs, so they could be attached to the ground using tent pegs, making the removal of the eggs harder for the predator. The completed eggs with the fishing line and the tent pegs were left on cut vegetation (collected locally) in the open for at least two weeks before the start of the experiment and thereafter were always handled using fabric gloves that had been similarly exposed to the elements, which is a standard technique used under the methodology in order to minimize human and other odours (Whelan et al. 1994).

The nests were placed along eight elevational transects starting from the treeline, for a total of 60 points (Figure 2). Two transects were placed in each of four small valleys, each transect being separated by a minimum of 200 m. The locations of transect routes were pre-selected based on accessibility (i.e. where it was possible to have a more-or-less straight transect that was accessible from the treeline to an elevation of at least 2500 m asl). The points along each transect were at least either 200 m horizontal distance apart or
separated by 100 m in elevation (whichever was first), estimated using a handheld global positioning systems (GPS) device. Once either the required distance or elevation had been reached along a transect, a precise nest location was selected by throwing a stone behind the researcher’s back in a random direction, and the ‘nest’ was placed on the ground at the point where the stone landed. Nests were then checked after a minimum period of days had elapsed (some nests were also subject to intermediate visits). A nest was considered successful if it had survived for a minimum of 14 days of exposure without any predation attempt on any egg. The goal was to make the final nest visit between 14 and 21 days after placement (i.e. an exposure period of 2–3 weeks). Due to bad weather, it was not always possible to visit within this timeframe, so there were some cases where the final visit was made after longer periods, up to a maximum of 25 days. For 59 points, a second attempt was made by replacing the nest after a predation event, or after the final visit if successful, for a total of 119 placed nests; many bird species make a new nest following predation, or have a second clutch following a successful attempt. Replacement nests were positioned 10 m from the first attempt, in a randomly selected direction, to simulate a second attempt within the same territory.

Parameters, such as the clutch size, the number of exposure days (simulating incubation days in a real bird) and the number of attempts, were not chosen to mimic a specific bird species but were consistent with the habits of a suite of alpine grassland species (e.g. Sky Lark, Water Pipit and Wheatear). Nest positioning was not chosen to mimic a specific bird’s behaviour, but was chosen randomly, as above. Location data (using a GPS), nest code and treatment (three Quail eggs, or a Quail egg and model eggs) were recorded. We used different treatments to assess whether the use of PlastiDip®-coated plasticine eggs influenced estimates of predation rates relative to nests containing only real eggs (Purger et al. 2012). Several vegetation and landscape variables were also estimated at each nest. Previous studies have shown that nest survival can be affected by factors such as date, nest height and concealment/vegetation density, as well as larger-scale landscape characteristics (Holm 1973, Johnson 1979, Martin & Roper 1988), therefore habitat characteristics included the percentage of ground cover of different habitat categories in a 0.5 m and in a 100 m radius (Table 1; percentages estimated by eye), and grass and shrub height (H, the mean value of 5 measurements per plot, one in the centre of each nest and four at cardinal points 0.5 m distant from the nest). Distance from the treeline was estimated using land cover data extracted with geographic information systems (GIS) software package, ArcGIS 10.3 (ESRI 2011) from the Piani Forestali Territoriali land cover database available for the whole province (www.regione.piemonte.it/foreste/cms/foreste/pianificazione). Elevation (m) at each point was recorded by the GPS in the field to an accuracy of at least ±10 m (but usually within ±5 m).

Table 1. Covariates used to model nest survival in MARK.

| Covariate | Measurement |
|-----------|-------------|
| sday      | Start date  |
| eday      | End date    |
| tre       | Treatment   |
| val       | Valley      |
| tl        | Treeline distance (m) |
| ss05      | Small shrubs: % cover in 0.5 m radius |
| gr05      | Grass: % cover in 0.5 m radius |
| mi05      | Mosses and lichens: % cover in 0.5 m radius |
| ea05      | Earth: % cover in 0.5 m radius |
| sh100     | Shrub: % cover in 100 m radius |
| nv100     | No vegetation: % cover in 100 m radius |
| H         | Vegetation height (cm) |

Statistical analysis

The variation in habitat attributes along the elevational gradient was analysed for each habitat variable in turn. For variables that were approximately normally distributed, a regression was fitted to the data including both linear and quadratic terms. The latter were dropped and the model re-run with only linear effects if not significant. For data that did not conform to a normal distribution (usually due to a large number of zero values), the data were analysed using Spearman’s rank correlation coefficient.

Nest survival analysis was performed using programme MARK (White & Burnham 1999) which uses a modified form of the Mayfield method (1961, 1975) to estimate daily survival rate (DSR), the probability that the nest will survive from one day to the next. This comprehensive approach to nest survival permits a set of covariates to be incorporated in the analysis (Dinsmore et al. 2002, Dinsmore & Dinsmore 2007), allowing DSR to be a function of the age of the nest, the date and habitat variables. All variables were standardized to a mean of zero prior to modelling. In order to minimize effects of collinearity between continuous explanatory variables, variance inflation factors (VIFs) were calculated using the ‘corvif’ function (package ‘AED’, Zuur et al. 2009). Variables with high VIFs (>3) were sequentially removed until all variables had a value below this threshold. Survival of a nest at each visit was then treated as a binomial variable that depended on the 11 covariates remaining.
after reduction according to VIF listed in Table 1, in addition to treatment as a categorical variable.

The null model, termed S(.) in MARK, in which only a single daily nest survival rate was estimated and no covariates are included, was analogous to the null model described by Dinsmore et al. (2002). Prior to modelling the covariates listed in Table 1, scatter plots were examined to assess likely non-linear trends. Date, measured as either start date (sday, the day in which the nest was positioned) or end date (eday, the day in which the nest was found predated or in which the attempt ended) was the only variable to show non-linear trends, so both linear and quadratic terms were included. As both date variables were closely correlated, it was decided to include only one in the modelling procedure. Full models were compared using either eday or sday in combination with all other variables. Model fit according to Akaike’s Information Criterion, adjusted for sample size (AICc), was much better for eday (ΔAICc = 11.43), so only that variable was considered in subsequent analyses.

Starting from the ‘full’ model that included eday, eday², treatment, valley (a four-level categorical variable representing the four locations used in the study) and the other eight continuous habitat variables listed in Table 1, models were built using a stepwise backward selection procedure, whereby a final model was derived by sequentially eliminating the least important term as determined by the minimum absolute value of the beta estimate divided by the standard error of the covariate. This process was continued until the elimination of a covariate resulted in the increase of the AICc value (Pagano & Arnold 2009, Arnold 2010). The best model set, defined as those with ΔAICc ≤ 2, was then used to estimate DSR. Estimated overall nest success was obtained by raising the DSR estimate to the power of the length in days of the incubation period (i.e. exposure days of successful nests). The study design did not consider a real species, so it was decided to use 16 days (the median number of exposure days for successful nests) as a constant for the purpose of estimating overall nest success over the incubation period.

Results

Habitat variation along the elevational gradient

Several of the variables considered showed marked variation in relation to elevation (see online supplementary material 1 for details of test statistics). For normally distributed variables (Figure 3), there was a significant linear increase in bare earth at 100 m radius and rock cover at both 0.5 and 100 m radius, and in the distance to the treeline, small shrub cover and herb and grass cover (both 100 m radius) showed a non-linear trend with elevation. There was no trend in either grass cover or bare earth cover at 0.5 m radius in relation to elevation. For non-normally distributed data, most variables showed a significant negative relationship with elevation (Figure 4): canopy cover (both scales), medium shrub cover (0.5 m), cover of litter (0.5 m), shrub cover (100 m) and vegetation height. For measures of canopy and shrub cover, there were apparent thresholds at approximately 2300 and 2400 m asl respectively (Figure 4).

Artificial nest predation

Predation occurred in 35.3% (42/119 nests) of the artificial nests, and the predation rate among treatments was almost the same: 35% for the control nests (21/60) and 35.6% for the nests with coated eggs (21/59). In most predation events, the entire nest contents were removed, including the plasticine eggs, and it was not possible to reliably identify the predator in any case. There was no effect of the different treatments on the frequency of predation ($\chi^2 = 0.271, P = 0.602$).

Artificial nest survival

Following stepwise backward model selection, we obtained three models in the best model set with ΔAICc < 2. These were clearly superior to the null model (ΔAICc = 12.42 from the lowest ranked ‘best’ model). Each of these models included a quadratic effect of end date (eday), a positive linear effect of distance from the treeline (tl) and a negative linear effect of the percentage of moss/lichen cover in a 0.5 m radius from the nest (Table 2). Models 2 and 3 included a positive linear effect of vegetation height (H). A positive linear effect of the percentage of shrubs in the 100 m radius from the nest (sh100) was included only in Model 3. (Details of all models are given in online supplementary material 2). There was a clear outlier in the moss/lichen cover data (Figure 4 (d)). To assess its possible effect on the model selection procedure, the MARK analysis was re-run omitting this nest. The results obtained with this second data set were very similar to those obtained with the original data set (details are given in online supplementary material 3), hence the outlier had little effect on the model outcomes.

The mean DSR estimate obtained from MARK, over all models, was 0.986 (se = 0.004, lower confidence
limit = 0.976, upper confidence limit = 0.993). Estimated overall nest survival over a 16-day period was therefore \(0.986^{16} = 0.804\). Graphical representations of the effects of covariates from Model 1 slope estimates are presented in Figure 5, showing the influence of the end date, distance from the treeline and moss/lichen cover in a 0.5 m radius from the nest on DSR. (Results from Models 2 and 3, in particular in terms of treeline distance, were similar and are presented in online supplementary materials 4 and 5). To provide a better understanding of the influence of the treeline on nest survival during the nesting season, DSR and overall survival were calculated for the minimum, the mean and the maximum end dates (Table 3), holding other
variables constant (at mean values) in the models. For the three dates, DSR and overall survival increased further away from the treeline. In the early season, overall survival was very low at all treeline distances. Differences between overall survival at the treeline and at a distance of 1.2 km from the treeline were 0.006 in the early season, 0.129 in mid-season and 0.227 in the late season (Table 3).

Table 2. Intercept and slope estimates from the three models with ΔAICc < 2 in programme MARK for the predicted DSR. The standard error (SE), lower 95% confidence limit (LCL) and upper 95% confidence limit (UCL) are also reported. Covariate labels are given in Table 1.

| Model | Label | Estimate | SE  | LCL  | UCL  |
|-------|-------|----------|-----|------|------|
| 1) Intercept estimate | 4.279 | 0.300    | 3.697 | 4.860 |
| | Covariate slope estimates | eday | 0.039 | 0.017 | 0.005 | 0.073 |
| | | eday² | −0.009 | 0.003 | −0.014 | −0.004 |
| | | tl | 0.001 | 0.000 | 0.000 | 0.001 |
| | | m05 | −0.037 | 0.019 | −0.079 | −0.004 |
| 2) Intercept estimate | 4.256 | 0.297    | 3.674 | 4.838 |
| | Covariate slope estimates | eday | 0.036 | 0.017 | 0.002 | 0.070 |
| | | eday² | −0.009 | 0.003 | −0.014 | −0.003 |
| | | tl | 0.001 | 0.000 | 0.000 | 0.002 |
| | | m05 | −0.036 | 0.019 | −0.074 | −0.001 |
| | | H | 0.014 | 0.011 | −0.008 | 0.036 |
| 3) Intercept estimate | 4.259 | 0.297    | 3.676 | 4.841 |
| | Covariate slope estimates | eday | 0.036 | 0.017 | 0.002 | 0.071 |
| | | eday² | −0.008 | 0.003 | −0.014 | −0.003 |
| | | tl | 0.001 | 0.000 | 0.000 | 0.002 |
| | | m05 | −0.036 | 0.019 | −0.074 | −0.001 |
| | | sh100 | 0.012 | 0.011 | −0.010 | 0.034 |
| | | H | 0.019 | 0.026 | −0.031 | 0.070 |

Discussion

The experimental fieldwork conducted in this study aimed to assess how habitat characteristics may influence nest predation in alpine birds along an elevational gradient, and to assess the occurrence of an edge effect between forest and grassland along the treeline ecotone. The results obtained supported the hypothesis that alpine grassland bird distributions may be influenced by the distance from the treeline, but also by other habitat factors and seasonal effects.

The method

The artificial egg methodology is often used in experimental studies to understand predation rates (Chamberlain et al. 1995, Jokimäki & Huhta 2000, Kurucz et al. 2012, Purger et al. 2012, Seibold et al. 2013). The difference in predation rate between control and coated plasticine eggs was almost the same as that found in a previous study (Purger et al. 2012), suggesting that, at least in theory, use of plasticine eggs to identify predators should not bias the results in relation to ‘control’ artificial nests. Unfortunately, this aspect of the experiment did not work – no predators could be identified and in the majority of cases, the entire nest contents were removed. This method of predator identification has worked in different habitats with a different suite of predators (Chamberlain et al. 1995), but clearly alternative methods to identify nest predators are needed in alpine environments.

It is unlikely that this study can infer much about real predation rates, but relative predation rates of the nests at the egg stage (i.e. when adult activity is low) are likely to be reflected in the results. In particular, we feel that the method provides a good measure of relative predation pressure in terms of the shape of the relationship with the distance from the treeline. Therefore, it is possible to draw inferences about predation and habitat, although experiments that more closely simulate actual, rather than relative, predation rates are likely to be more useful when developing...
conservation strategies. However, it is impossible to mimic certain characteristics of a real nest in such experiments. For example, predators can detect a nest due to the activity of parents around the nest, or of chicks in the nest, and losses due to bad weather or brood parasitism are not included in studies such as ours. Cuckoo density in the area was high, in particular close to the treeline, and they locate nests by observing host adult activity from vantage points. Little is known about which hosts cuckoos use at high elevations, but in some lowland species of open habitats, the proximity of trees (or other vertical structures) has been shown to increase the chances of brood parasitism (Alvarez 1993, Øien et al. 1996, Welbergen & Davies 2009), hence this could also be a potential cost of nesting close to the treeline for alpine grassland birds. Further intensive research monitoring real nests along elevational gradients at the elevations considered, over multiple years to encompass the natural range of inter-annual variation, is needed to confirm the findings here, although there are very few species (with the exception of Water Pipit, e.g. Rauter et al. 2002), which have so far been studied in terms of predation rates in this environment.

**Model predictions**

The overall DSR estimated from programme MARK was 0.986, which corresponds to a failure rate of around 20% for a median exposure time. Whilst it is not possible to make a direct comparison with observed failure rates (given that the output of the model takes into account a number of factors such as exposure time, and that deriving an overall failure rate based on DSR necessitates the use of constant habitat and exposure times), the estimate is nevertheless quite low in comparison to the observed failure rate of 35%. Using the maximum 25 exposure days, rather than the median of 16 days, resulted in a modelled failure rate of 30%, far closer to the observed value. This suggests that the model is overestimating mean survival probability. This could be due to some important (unmeasured) predictors of predation rate not being included in the model. As long as these unknown effects were constant across all artificial nests, then the model can still be considered as showing relative probabilities of predation across the elevational gradient. The extent to which this is likely, and the identification of other possible key predictors, could be assessed through further intensive research.

The effect of the distance from the treeline means that closer a nest is to the forest, the lower is the expected survival due to the higher predation rate, suggesting an edge effect. The overall variation in DSR was small, but such variation may be significant in terms of overall survival. For example, in the middle of the breeding season (i.e. the date set at 18 July, corresponding to a value of eday = 28), DSR varied from 0.981 at the treeline (tl = 0 m) to 0.988 at tl = 1200 m. However, survival over the whole nest period, which in this case was estimated at a constant 16 days, varied from 0.734 to 0.863, a difference of more than 10%. Moreover, at the end of the breeding season, the effects of the distance from the treeline were stronger (Table 3).

DSR increased during the breeding season reaching its maximum and then decreased again. Many previous studies found that DSR varies during the breeding season (Dinsmore et al. 2002; Jehle et al. 2004). The beginning of the breeding season corresponds to the beginning of vegetation growth, and vegetation cover is probably not adequate to conceal the nests at this time, as found in Water Pipits in Russia (Cramp 1988). The decrease at the end of the season could be caused by many factors, but it may be related to predator activity. Predators may have higher demands to feed their young later in the season, or young predators may be dispersing more. The lower survival may also have been influenced by some predators developing a ‘search image’ for detecting cryptic prey, which improves with experience and hence time over the course of the season (Davies et al. 2012).

The cover of mosses and lichens within a 0.5 m radius of the nest (ml05) had a negative effect on nest survival. The presence of this kind of vegetation is probably indicative of very open habitats without forbs and grasses to conceal the nest, facilitating detection by predators. Similarly, the positive effects of vegetation height (models 2 and 3) and shrub cover (model 3) on

| eday | End date | DSR | OS | DSR | OS | DSR | OS | DSR | OS |
|------|----------|-----|----|-----|----|-----|----|-----|----|
| 10   | 30 Jun   | 0.562 | 0.000 | 0.622 | 0.001 | 0.679 | 0.002 | 0.730 | 0.007 |
| 28   | 18 Jul   | 0.981 | 0.734 | 0.985 | 0.785 | 0.988 | 0.828 | 0.991 | 0.863 |
| 41   | 31 Jul   | 0.953 | 0.465 | 0.963 | 0.548 | 0.971 | 0.625 | 0.977 | 0.692 |

**Table 3.** DSR and overall survival (OS) calculated at distance from the treeline (tl) equal to 0, 400, 800 and 1200 m, for three end dates: the minimum (30 June), the mean (18 July) and the maximum (31 July) end dates. Ml05 was set to a constant value of 2.462 (the mean value of the covariate).
DSR are likely to be linked to the probability of detection of a nest by a predator. Vegetation cover was measured only a single time at the initial placement of the nest. Whilst vegetation development at high elevations is slow, some of the longer surviving nests may have experienced an increase in vegetation cover, and therefore a decrease in potential predation, over time. Multiple measures of vegetation cover that took into account seasonal changes may have led to greater effects on vegetation cover in the models.

Studies based on elevational gradients have a number of advantages, in that a range of conditions usually experienced over a wide geographic area can be considered within a relatively small area, hence controlling for large-scale biogeographic influences (Rahbek 2005), and such studies also provide a space-for-time substitution when considering directional changes in habitat and/or climate such as elevational distribution shifts (Hodkinson 2005). However, the strong trends in habitat (Figures 3 and 4) and climate in relation to elevation also mean that there is often a high degree of intercorrelation, and it can be difficult to tease apart the relative importance of different variables along the gradient. An obvious correlate of distance from the treeline is elevation (Figure 3(h)), which was considered in the analysis, but was eliminated before the modelling procedure due to a high VIF. The variables identified as being of likely importance in our analyses were all underpinned by biologically plausible effects (see above), so we feel that the models are likely to represent potentially important ecological mechanisms. Nevertheless, we acknowledge that other unmeasured variables, correlated with elevation, could also be driving the observed trends – only further detailed research is likely to determine the extent to which the detected effects can be concluded as causal.

**Conservation implications**

This study found evidence of an edge effect on predation rates of artificial nests, suggesting that the optimal breeding area for alpine grassland birds is further away from the forest edge. The functional habitat loss caused by changes in climate and land-use may therefore be proportionally greater than physical habitat loss. The observed rates of treeline shifts for the European Alps range from 0.28 m per year (Paulsen et al. 2000) to 3.16 m per year (Gehrig-Fasel et al. 2007). As the edge effect will advance along with the forest, it will cause a significant loss of the available nesting habitats not predicted by current climate change models; this process is illustrated in Figure 6. Moreover, in high mountains, a contraction in the area of grasslands due to advancing treelines at lower elevations, and due to processes preventing development of vegetation at higher elevations (Cannone et al. 2007), may cause further contraction of suitable nesting habitats. In lower mountains, advancing treelines could completely reforest mountain tops, or leave only small isolated patches of grasslands. Such a situation could effectively exclude any ground-nesting birds in the remaining open areas. Without active management constraining the advancing forest and shrubs, alpine grassland birds could lose most of their breeding habitats.

![Figure 6](image-url)

**Figure 6.** A graphical model showing a hypothetical Alpine massif in lateral view (top figures) and top-down view (bottom figures), and how treeline shifts in conjunction with edge effects may drastically reduce the area of suitable habitat for a grassland bird. Forest is represented by dark grey, grassland subject to an edge effect as light grey and grassland without an edge effect as white. In (a) there is sufficient area to allow the existence of two main areas of grassland, which are connected by a corridor with no edge effect. In (b) the same area is represented after an elevational shift in the treeline, there is less grassland overall, which has been fragmented, and a greater proportion of that grassland is unsuitable due to the edge effect.
It should be taken into account that forest advance could lead to an increase in bird diversity in a given area, as species richness tends to be relatively low in high-elevation grasslands. However, not all species have the same conservation value. Most forest species that are colonizing abandoned pastures need no special protection, as only 4% have unfavourable status (Laiolo et al. 2004). Chamberlain et al. (2013) showed that habitat loss will be mostly due to a marked increase in forest extent under the majority of future climate scenarios, potentially threatening several grassland species. Wheatear and Sky Lark, both open habitat species, are listed as of conservation concern in Europe (BirdLife International, 2004), and others, such as the Water Pipit, are likely to be of conservation concern in the future (Chamberlain et al. 2013). Overall, areas above the tree line are of a higher conservation priority than forest (Nagy et al. 2003, Dirnböck et al. 2011, Viterbi et al. 2013). Therefore, bird conservation, and biological diversity in general, will benefit from appropriate management (e.g. through grazing of domestic livestock) intended to halt the ongoing loss of alpine grasslands.

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