

## **Nestling diet and parental food provisioning in a declining mountain passerine reveal high sensitivity to climate change**

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## ABSTRACT

Mountain ecosystems naturally experience strong seasonal weather variations leading to a brief peak in food availability that constrains bird reproduction. Climate change accentuates both the intra- and interannual weather variability, which in turn can reduce the predictability of food resources and hence impact population demography. Yet, relatively little is known about the influence of environmental factors on the breeding ecology of mountain birds. Here, we quantified the nestling diet and provisioning behaviour of the Alpine Ring Ouzel (*Turdus torquatus alpestris*), an emblematic and declining thrush species typical of central European treeline ecotones, and relate these parameters to local weather conditions. Nests were monitored with camcorders to assess prey provisioning frequency and identify items delivered by parents to nestlings, as well as to estimate prey biomass. Our results indicate the prominence of earthworms (Lumbricidae) in the nestling diet, both in terms of abundance (80%) and biomass (90%). Elevated ambient temperatures negatively impacted both prey provisioning rates and biomass delivered to chicks by parents, while rainfall had a positive effect on the delivered biomass. The mean prey item biomass decreased throughout the breeding season, as did the proportion of earthworms in nestlings' diet. These findings highlight the key role played by local weather in parental provisioning behaviour, probably reflecting the low availability of the staple food source, earthworms, in warm and dry weather contexts. In particular, they underpin how climate alterations, notably increasing ambient temperatures and changing precipitation regimes, could impact mountain birds. Although effects on reproductive performance and population dynamics still ought to be studied, these results further our understanding of the ecological mechanisms potentially at play in the decline of wildlife inhabiting high-elevation, climate-sensitive ecosystems.

**Keywords:** earthworms, nest monitoring, Ring Ouzel, temperature, treeline, weather conditions

## INTRODUCTION

In highly seasonal environments such as mountain ecosystems, the reproductive period of animals is short because of the particularly narrow time window with suitable climatic conditions and subsequent brief peak in food availability (Pearce-Higgins 2010; McKinnon *et al.* 2012; Boyle, Sandercock & Martin 2016). Invertivorous mountain species also face rapid fluctuations in prey availability triggered by sudden weather variation (Martin *et al.* 2017), which often result in fairly unpredictable food resources in space and time (Rauter, Brodmann & Reyer 2000). High-elevation species have therefore evolved sophisticated behavioural and eco-physiological adaptations to cope with these highly stochastic environmental conditions (Martin & Wiebe 2004; Arlettaz *et al.* 2015) and to match their reproductive effort with peaks in food supplies. Yet, the advancing spring phenology and increasing frequency of extreme weather events, particularly acute in alpine regions (Gobiet *et al.* 2014), represent an additional challenge for high-elevation wildlife (Martin *et al.* 2017; Scridel *et al.* 2018; de Zwaan *et al.* 2020).

For birds, the relationships between weather conditions and prey availability, which is prey abundance modified by its accessibility (Schaub *et al.* 2010; Douglas & Pearce-Higgins 2014), have been extensively documented. For example, movements of belowground invertebrates are ruled by weather-dependent soil conditions that are of prime importance for ground-foraging invertivorous species (Edwards & Bohlen 1996; Peach *et al.* 2004; Martay & Pearce-Higgins 2020). Similarly, rainfall and low ambient temperatures reduce the activity of many aboveground insects, resulting in temporarily low prey availability (Siikamäki 1996; Winkler, Luo & Rakhimberdiev 2013; Perez *et al.* 2016; Schöll & Hille 2020). As a crucial driver of breeding success, seasonal prey availability is key for population persistence of short-lived species (Siikamäki 1996; Naef-Daenzer, Naef-Daenzer & Nager 2000; Pearce-Higgins *et al.* 2010), so that weather conditions generally have a strong influence on bird population dynamics (Sæther, Sutherland & Engen 2004). In effect, weather-mediated food availability can impact nestling growth rates, fledging success, and also post-fledging survival (Geiser, Arlettaz & Schaub 2008; McKinnon *et al.* 2012; Martin *et al.* 2017; de Zwaan *et al.* 2019; Schöll & Hille 2020). The combination of background climate alterations and increased occurrences of extreme weather events may thus profoundly affect passerines breeding at high elevations (Pearce-Higgins 2010; Martin *et al.* 2017). This risk may even be more acute for migratory species, given the increased probability of a temporal mismatch between reproduction and the peak in food supplies (Visser, Both & Lambrechts 2004). Altogether, this

calls for fine-grained mechanistic appraisals of the factors influencing optimal foraging strategies and reproductive tactics of mountain bird species (Chamberlain *et al.* 2012).

The Ring Ouzel (*Turdus torquatus*) is a migratory thrush species living in the mountain massifs of central and eastern Europe, the UK and Fennoscandia (Glutz von Blotzheim & Bauer 1988). Although demographically stable in various areas of its range (Lehikoinen *et al.* 2019), the species has undergone a recent but steady decline in Switzerland, where ca. 15% of the European population breeds (Knaus *et al.* 2018), and in the UK (Wotton *et al.* 2016). Climate change is considered as the most likely driver of the observed decline in Swiss populations occurring at low elevations, which resulted in an apparent upward range shift (Maggini *et al.* 2011; Knaus *et al.* 2018). In the UK, one of the underlying mechanisms is believed to be warmer summers that reduce prey availability after the breeding season (Beale *et al.* 2006). In effect, Ring Ouzels rely on specific habitat characteristics for efficient foraging that are highly seasonal and temporally limited, showing a preference for relatively high soil moisture and a short grass sward interspersed with bare and litter-covered ground (Sim *et al.* 2013; Barras *et al.* 2020). The earlier onset of vegetation growth and reduction in soil moisture induced by warmer ambient temperatures, as well as more frequent droughts, may indeed drastically reduce the availability of belowground invertebrates (Peach *et al.* 2004; Pearce-Higgins 2010). This might induce food shortage, affecting both fledging success and post-fledging survival (Sim *et al.* 2015) and in turn negatively impacting demographic trajectories (Sim *et al.* 2011). Yet, quantitative evidence about the mechanisms at play is still lacking for the Ring Ouzel, as for many other mountain bird species.

Based on nest video monitoring in the Alps, we assessed, first, the diet composition of Ring Ouzel nestlings to identify key food resources during reproduction. Second, we quantified parental food provisioning activity, delivered prey biomass and female nestling attendance throughout the nestling period. Third, we related these measures to local weather factors, namely ambient temperature, precipitation, sunshine duration, and wind. Fourth, we explored how brood characteristics such as age and number of nestlings influence food provisioning. Finally, we assessed the seasonal variation in the mean dry weight and proportion of prey in the nestling diet.

## MATERIALS AND METHODS

### *Study area and study species*

The study area is situated in the Swiss Bernese Alps, in the canton of Valais (46.33 N, 7.43 E), spanning an altitudinal gradient between 1800 and 2200 m above sea level. The area covers around 200 ha and consists of a wooded summer pasture, characterized by a semi-open landscape where grasslands are interspersed with coniferous tree stands (European larch *Larix decidua* and Norway spruce *Picea abies*), a typical breeding habitat for the Alpine Ring Ouzel *T. t. alpestris* (Glutz von Blotzheim & Bauer 1988). From standardized monitoring surveys of the whole area over the period 2015–2020 (three spring visits at dawn following a predefined walk transect), we estimated on average 40.7 territories/100 ha, i.e. a very high density for the Alps (Knaus *et al.* 2018).

Ring Ouzels are single-brooded in the study area, as assessed reliably with radiotracking during two breeding seasons (2015 and 2017), and we assume that this is the most common reproductive strategy in the Alps. Nests are built in trees, mostly in larches close to the trunk, at a height from 1.5 to 18 m. Females take care of nest building and brooding, with very few exceptions of male assistance in these tasks. Most birds leave the study area immediately after reproduction, before the end of June, partly spending the post-breeding period at higher elevations (Glutz von Blotzheim & Bauer 1988). Migration to overwintering grounds in southern Spain and North Africa occurs mostly in September and October (Glutz von Blotzheim & Bauer 1988).

### *Data collection*

Between April and June 2019, nests were located either during monitoring surveys (described above) or during specific weekly nest-searching sessions over the whole study area. Most nests were found by observing individuals carrying nest material, alarm displays or when incubating females were incidentally flushed. We checked nests regularly (every second or third day) from the ground, using a video camera mounted on a perch, in order to identify date of hatching and to record nestling age. Video monitoring was conducted on a subset of the nests ( $n = 12$ ); those that were not readily accessible were discarded to minimize potential disturbances. Suitable nests had to be reachable with an 8-m ladder and offering the possibility to fix the video system nearby. The video set was attached to a tree 1–3 m from the nest and covered with a camouflage net (see picture in the Supplementary Materials, Fig. S1). It consisted of a Panasonic HC-V180 camcorder coupled with a 20,000 mAh power bank to film continuously.

Because the nestlings are not able to thermoregulate in their early days after hatching, no video monitoring took place until they were at least three days old. Fledging occurs usually at the age of 12–14 days. We aimed to film each nest twice, once during the first week (days 3–8) and once during the second week (days 9–14), in order to capture potential changes in the provisioning activity throughout the nestling period. However, due to logistic constraints or late nest discovery, only 8 out of 12 nests were filmed twice. A day of filming lasted approximately from 6 am to 9 pm. The video system was always installed at least one day before monitoring to ensure that birds get accustomed to its presence and would adopt a normal behaviour. In addition, we always discarded the first hour of video footage to avoid any bias in the estimates of provisioning rates due to potential disturbances when initiating the system at dawn.

On days of video monitoring, we recorded several weather variables. Ambient temperature was measured on an hourly basis using two iButtons (DS1921G-F5; Thermochron, Baulkham Hills, Australia) placed in a constantly shaded place at 0.5 m above ground in the centre of the study area. Hourly precipitation (mm/h) information was retrieved from the nearest weather station (Anzère: 46.305 N, 7.408 E, 3.2 km distance; MeteoSwiss) while information on sunshine duration (min/h) and wind speed (m/s) came from another nearby meteorological station (Montana: 46.299 N, 7.461 E, 4.1 km distance; MeteoSwiss), because these data were not available from the closer station. Since the range of hourly rainfall during video monitoring sessions was rather small (0.0–3.9 mm/h) and we did not expect a linear relationship with provisioning activity over this small range, we transformed this variable into a binary factor of precipitation occurrence.

## *Analysis*

### *Diet composition*

To assess diet composition, prey items were identified to order or family level, with the number of items delivered in each prey load quantified as accurately as possible, which was possible for all video monitored nests except one due to low image quality ( $n = 11$ ). Earthworms (Lumbricidae) were visually assigned to a body size category: small, medium or large, estimated relative to bill length (small: shorter than the bill length, medium: less than twice the bill length, large: more than twice the bill length). To estimate biomass, we relied on estimates of the mean dry weight for each prey category (Supplementary Materials, Table S1). The dry

biomass of Arachnida, Coleoptera adults and larvae, Lepidoptera larvae and adults, Hymenoptera, Diptera and Tipulidae larvae was retrieved from samples collected in a parallel study on the White-winged Snowfinch (*Montifringilla nivalis*) carried out in high-elevation habitats in the same region (Resano-Mayor *et al.* 2019). The mean dry biomass of earthworms was estimated from individuals sampled directly in the study area (10–20 individuals per size category). To increase sample size for nestling diet, we also considered pictures of provisioning parents taken between May 30<sup>th</sup> and June 13<sup>th</sup>, 2017, in the same study area from four nests ( $n_{2017+2019} = 15$ ). Those pictures had been taken from a hide on the ground with a digital camera equipped with a 600 mm telephoto lens.

### *Provisioning rates*

All analyses were performed in the software R 3.6.2 (R Development Core Team 2019). We first considered hourly provisioning rates, i.e. the number of provisioning events per hour. We distinguished rates either while pooling the data of two parents together (hereafter called ‘sex-independent’) or from data on males and females separately (hereafter ‘sex-specific’). Sex-specific provisioning rates were readily estimated as parents are easy to distinguish from plumage colouration. Data was available for 12 different broods, including one where only the female was provisioning. We analysed the impact of ambient temperature, rainfall, sunshine duration and wind on both sex-independent and sex-specific parental provisioning rates. Prior to the analysis, Pearson’s correlation coefficients ( $r$ ) within any pair of explanatory variables were checked for collinearity but no  $|r|$  was  $\geq 0.7$  (Dormann *et al.* 2013). All continuous explanatory variables were standardized (mean = 0 and standard deviation (sd) = 1) to enable comparison of effect sizes from model estimates.

In order to identify the best model explaining variation in provisioning rates (either sex-independent or sex-specific), we followed a two-stage selection approach, where a full model was first fitted (Supplementary Materials, Table S2), followed by a ranking of all possible nested models. The full model was specified as a mixed-effects model with all four weather variables as fixed factors, as well as time of day (linear and quadratic terms) since bird provisioning activity typically follows a daily unimodal pattern (Low *et al.* 2008). In addition, sex (factor coding for male or female) and interaction terms between sex and temperature, and sex and precipitation, were included as fixed effects in the sex-specific model. The non-independence of repeated measurements at the same nest and on the same day was accounted for with nested random intercepts (‘nest’ within ‘day’). In order to select the most appropriate

error distribution and to check for model assumptions fulfilment, we performed a visual assessment of the QQ-plots and scatter plots of the residuals. Based on that, we opted for a normal linear mixed-effects model (LMM) for sex-independent provisioning rates, and for a generalized LMM with Poisson error distribution for sex-specific rates. The latter Poisson LMM was also checked for overdispersion. We verified that there was no pattern of temporal autocorrelation in the model residuals with autocorrelation function plots, using the *acf\_resid* function from the R-package ‘itsadug’ (van Rij, Martijn & Baayen 2017). Models were fitted using the *lmer* and *glmer* functions in the ‘lme4’ package (Bates *et al.* 2015).

Once the appropriate structure for the full model was defined, we proceeded with the second step, ranking candidate models (i.e. models with all possible combinations of explanatory variables from the full model) based on the Akaike Information Criterion adjusted for small sample size (AICc). Candidate models were ranked by AICc in ascending order using the *dredge* function from the ‘MuMIn’ package (Bartoń 2019). We reported all models within  $\Delta\text{AICc} < 2$  from the first-ranked one (i.e. competitive models), after the exclusion of models with uninformative parameters, i.e. more complex versions of better-ranked models resulting in higher AICc values (Arnold 2010). We also calculated marginal and conditional  $R^2$  values of competitive models following Nakagawa and Schielzeth (2013), to evaluate the proportion of explained variance.

### *Biomass*

From the number of identified prey items and their reference dry weight, we could also estimate the taxon-specific and total provisioned dry biomass. However, all prey items could not be identified, due to unfavourable light conditions or a partially hidden prey load in some provisioning events. Therefore, we used the mean biomass per provisioning event over an hour (hereafter mean biomass) rather than the sum of provisioned biomass. We discarded hours with incomplete data, i.e. in which prey items were quantified in less than 75% of the provisioning events, which concerned 46/240 (19.2%) hours in the sex-independent analysis and 109/468 (23.3%) hours in the sex-specific. One of the 12 nests was discarded as light conditions were too poor to allow prey identification. We followed the exact same two-stage selection approach as for the provisioning rates to identify top models explaining variation in the mean prey biomass per provisioning event. In this case, both sex-independent and sex-specific models were fitted as LMMs with a normal error distribution. No pattern of temporal autocorrelation

was evidenced. As several models on the biomass suffered from singularity, we removed the random effect ‘day of year’ in the candidate models.

After identifying the top models explaining biomass variation of all prey categories considered together, we also aimed to describe how important weather variables influenced the biomass proportion of the main food source in the diet, namely earthworms. We thus fitted univariate normal LMMs for rainfall and temperature with earthworm biomass proportion (logit-transformed) as a response variable, considering only sex-independent data.

### *Nestling attendance*

We measured nestling attendance as the time each female individual of a nest spent brooding in min/h (males never brooded). Again, we followed a similar approach to model variation in female nestling attendance as for the provisioning rates and delivered biomass. Data was available from 12 different nests. Yet, no acceptable model fit was obtained, due to the high frequency of hours with no attendance at all, especially in the second week. In addition, visual inspections of temporal autocorrelation plots revealed potential issues for several days and nests. For this part of the analysis, we thus only present descriptive statistics (mean  $\pm$  sd) in relation to weather variables and season rather than model estimates.

### *Brood age and size*

As information about the age and number of nestlings was not included in previous models, we wanted to describe potential relationships of the brood characteristics with parental provisioning rates, delivered biomass and female nestling attendance. We fitted univariate models for each of the three response variables and two explanatory variables, resulting in six models, without using any model selection approach. For this purpose, each of the response variables was averaged at the day level to avoid pseudoreplication and we again used normal LMMs with ‘nest’ as a random factor.

### *Seasonal patterns*

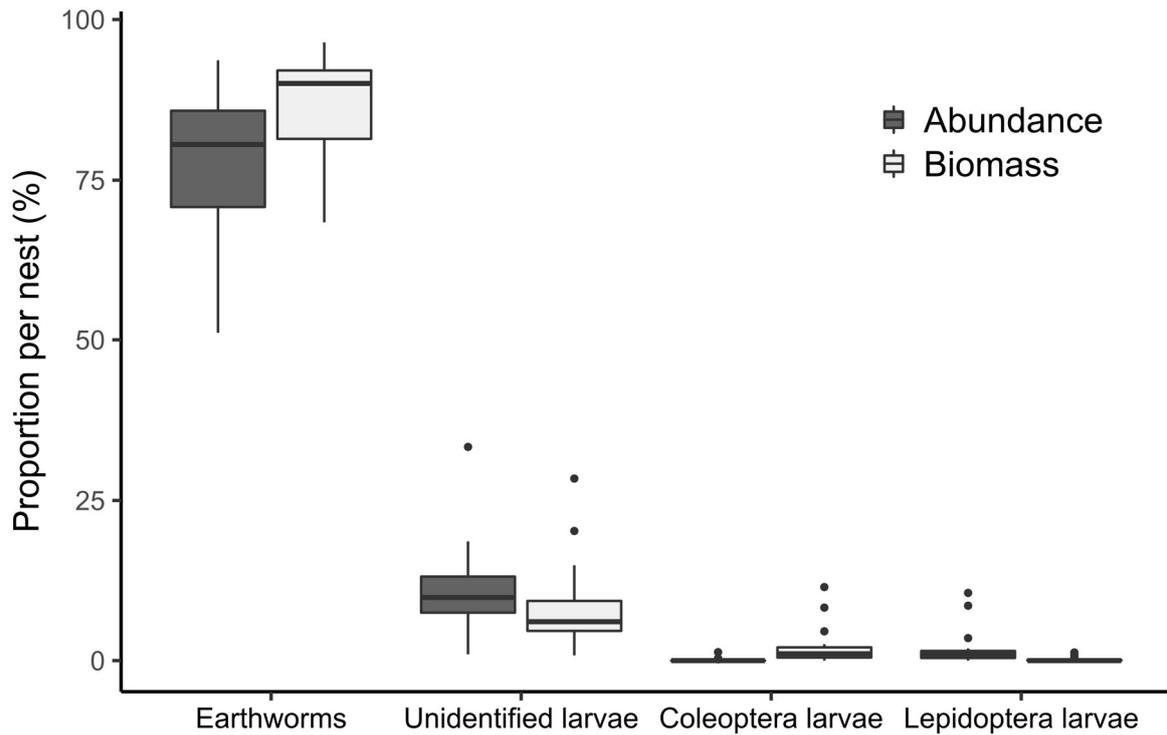
Finally, we explored the seasonal trends in two parameters, namely prey weight and biomass proportion of earthworms. Prey weight was defined as the mean dry weight per delivered prey item (mg/item) over an hour. The biomass proportion of earthworms was again logit-transformed prior to model fitting. For each of these two variables, we used a normal LMM with linear and quadratic terms of date as fixed factors and nest identity as a random effect.

## **RESULTS**

In 2019, the Ring Ouzel breeding season was slightly delayed compared to previous study years due to late and heavy snowfalls. We have indications that some of the earliest nesting attempts failed due to these adverse weather conditions, but those were not concerned by our video monitoring. Altogether, we found 28 nests with a confirmed reproduction attempt. At least 18 broods (64.3%) fledged, while two nests were depredated, one at egg stage and another one at an early nestling stage. The fate of the remaining nests is unknown. In two out of the twelve nests that were video monitored, we observed the loss of the smallest nestling between the first and the second video session. There were, on average, 3.4 nestlings (range 1–5) that fledged per successful nest monitored in 2019, with hatching spanning from May 27<sup>th</sup> to June 13<sup>th</sup>.

### ***Diet composition***

We identified 3998 prey items ( $n_{2017} = 450$ ,  $n_{2019} = 3548$ ) from 15 different nests ( $n_{2017} = 4$ ,  $n_{2019} = 11$ ) (Supplementary Materials, Table S1). In both years, earthworms constituted the bulk of the nestling diet, with a median ( $\pm$  median absolute deviation) per nest of  $80.5 \pm 13.5\%$  of the items provisioned by parents and  $90.1 \pm 9.3\%$  in terms of biomass (Fig. 1). Insect larvae were the second most important group in the nestling diet, but most items could not be identified to order level due to insufficient picture resolution. Identified larvae were either Lepidoptera, Coleoptera or Diptera (Tipulidae) (Fig. 1; Supplementary Materials, Table S1). Prey items that could not be identified made up  $4.7 \pm 3.1\%$  of the total. Other invertebrate groups contributed less than 1% to the median biomass and abundance delivered to the nestlings at each nest.



**Figure 1** Proportion of the main invertebrate categories entering the diet of Ring Ouzel chicks in terms of abundance and biomass per nest. Prey categories with a median contribution < 1% for both prey abundance and biomass are not shown. Box plots represent the median (horizontal bar) as well as lower and upper quartiles (lower and upper hinges, respectively).

### ***Provisioning rates***

Our final dataset contained 1916 provisioning events from 12 different broods while nestlings were 3–13 days old. The mean hourly provisioning frequency ( $\pm$  sd) of the two adults together was  $8.0 \pm 3.4$  (range 0–20). For the sex-independent analysis, we obtained a set of three best-supported models ( $\Delta$  AICc < 2) from the selection procedure (Supplementary Materials, Table S2). Ambient temperature was retained in all models and had a strong negative effect on provisioning rates (Table 1a; Fig. 2a). Wind speed was as well retained in the top model with a negative effect (Table 1a). The marginal  $R^2$  of the first-ranked model, i.e. variance explained only by fixed effects, was quite low (0.10) compared to conditional  $R^2$  (0.27), indicating substantial variation within and between nests. Model selection for the sex-specific provisioning rates yielded two best-supported models, with again a top model showing negative effects of ambient temperature and wind speed (Table 1b), while sex of the provisioning parent was not retained in any models.

## ***Biomass***

The mean delivered biomass ( $\pm$  sd) per provisioning event and nest was  $86.4 \pm 23.6$  mg (range 31.9–163.3 mg). Three best-supported models were obtained from the sex-independent analysis (Supplementary Materials, Table S2). Ambient temperature, as well as time of the day (linear and quadratic terms, unimodal relationship), were retained in all models. Temperature showed a strong negative effect on the provisioned biomass (Table 1c; Fig. 2b), whereas rainfall had a weak positive effect and was retained only in the first model. Again, marginal (0.11) and conditional  $R^2$  (0.37) indicated that random effects explained a larger part of the variance. For the analysis of sex-specific provisioned biomass, three final competitive models were highlighted (Supplementary Materials, Table S2). In contrast to provisioning rates where no sex difference was evidenced, these models showed that males fed on average more biomass to the nestlings than females (Fig. 3). In the first-ranked model, the positive effect of rainfall on the provisioned biomass (Table 1d) was more pronounced than when considering both parents together (Table 1c), yet CI overlapped zero. This effect was replaced by a negative effect of sunshine duration in the second model, while the third model contained only the sex effect (Supplementary Materials, Table S2).

With respect to rainfall and temperature effects on the biomass proportion of earthworms, we showed a negative effect of high ambient temperature ( $\beta = -0.23$ , 95% CI: -0.52–0.07) and a positive effect of precipitation occurrence ( $\beta = 0.32$ , 95% CI: -0.57–1.21), although uncertainties around estimates were high.

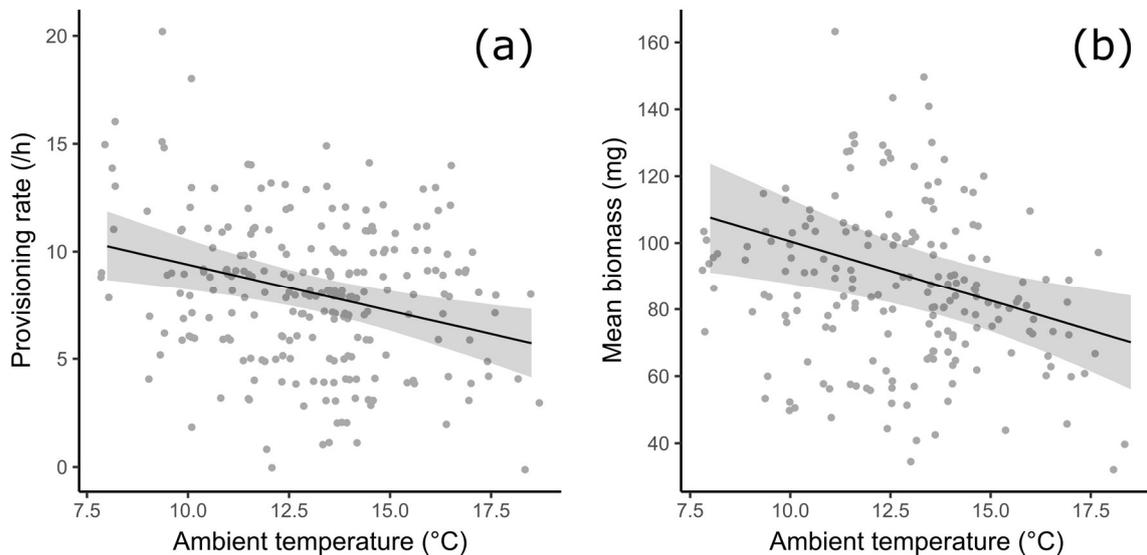
## ***Nestling attendance***

Females spent on average ( $\pm$  sd)  $7.1 \pm 11.5$  min/h to brood nestlings during the day (range 0–50 min/h). On average, nestling attendance was higher during precipitation ( $26.0 \pm 12.1$  min/h) compared to dry weather ( $6.1 \pm 10.5$  min/h), and in the first nestling week ( $12.8 \pm 13.4$  min/h) compared to the second week ( $1.5 \pm 4.5$  min/h). In the first week, nestling attendance was higher at low ( $15.2 \pm 13.0$  min/h) compared to high ambient temperatures ( $7.7 \pm 13.0$  min/h), considering the median temperature (13.5 °C) as a cutoff value.

**Table 1** Coefficients estimates and 95% confidence intervals (CI) of the best-ranked model from the analyses of (a, b) provisioning rates and (c, d) delivered prey biomass in relation to weather variables and time of the day. (a, c) refer to sex-independent models while (b, d) are estimates based on individual, sex-specific models.

Variable	Coefficient estimate	Confidence interval	
		2.5%	97.5%
<i>a. Provisioning rates, sex-independent</i>			
<b>Ambient temperature</b>	-1.00	-1.63	-0.40
Wind	-0.46	-0.93	0.00
<i>b. Provisioning rates, sex-specific</i>			
<b>Ambient temperature</b>	-0.13	-0.21	-0.05
<b>Wind</b>	-0.06	-0.12	-0.00
<i>c. Delivered mean prey biomass, sex-independent</i>			
<b>Ambient temperature</b>	-8.16	-13.48	-2.84
<b>Time of day</b>	4.06	0.53	7.59
<b>Time of day<sup>2</sup></b>	-4.97	-9.19	-0.75
Rain occurrence (yes)	9.44	-2.80	21.69
<i>d. Delivered mean prey biomass, sex-specific</i>			
Rain occurrence (yes)	12.57	-0.43	25.58
<b>Sex (male)</b>	16.64	10.55	22.71

Variables names are displayed in bold if CI do not overlap zero



**Figure 2** Relationships between (a) hourly provisioning rates and (b) hourly mean delivered prey biomass per feeding event vs. ambient temperature. Regression lines and 95% Bayesian credible intervals stem from the first-ranked model in the respective sex-independent analyses.

### **Brood age and size**

The number of nestlings positively affected daily provisioning rates while their age had no clear effect (Table 2). On the contrary, the age of nestlings had a strong negative effect on attendance by the female, whereas we could not show any effect of brood size. Finally, neither the age nor the number of nestlings had detectable effects on the daily delivered biomass (Table 2).

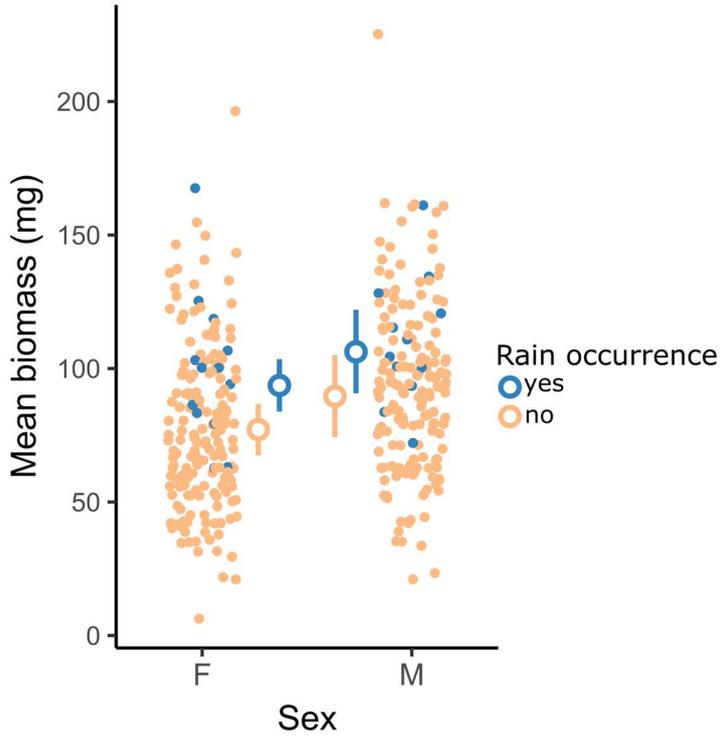
### **Seasonal patterns**

The mean dry weight of prey ( $\pm$  sd) was  $41.5 \pm 12.3$  mg/item (range 14.2–83.3 mg, excluding an outlier at 112.6 mg). It showed a unimodal relationship with date (linear:  $\beta = 0.49$ , 95% CI: -2.05–3.02; quadratic:  $\beta = -2.19$ , 95% CI: -3.96–0.42), with a temporal decrease towards the end of the breeding season (Fig. 4a). The same seasonal decrease was evidenced for the biomass proportion of earthworms in the diet (Fig. 4b; linear:  $\beta = 0.16$ , 95% CI: -0.14–0.49; quadratic:  $\beta = -0.30$ , 95% CI: -0.51–0.09).

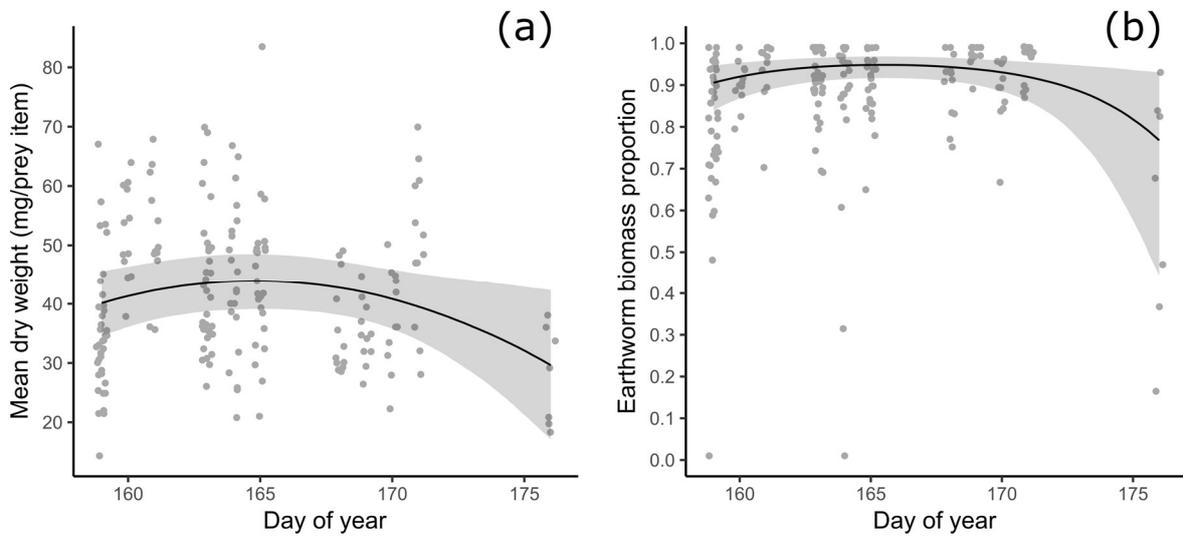
**Table 2** Coefficient estimates  $\pm$  95% CI for brood characteristics (age and brood size) in relation to the daily average in hourly provisioning rates, hourly mean of delivered prey biomass (per provisioning event) and hourly female nestling attendance, as drawn from univariate linear mixed-effects models.

Variable	Coefficient estimate	Confidence interval	
		2.5%	97.5%
<i>Provisioning rates</i>			
Age of nestlings	0.23	-0.47	0.89
<b>Number of nestlings</b>	0.78	0.09	1.48
<i>Delivered mean prey biomass</i>			
Age of nestlings	-5.75	-13.22	1.90
Number of nestlings	2.34	-5.48	10.13
<i>Nestling attendance</i>			
<b>Age of nestlings</b>	-6.90	-10.01	-3.80
Number of nestlings	0.86	-3.63	5.21

Variables names are displayed in bold if CI do not overlap zero.



**Figure 3** Effects of sex and precipitation occurrence on the hourly mean delivered prey biomass per feeding event. Empty circles depict model estimates and bars 95% Bayesian credible intervals from the first-ranked model.



**Figure 4** Seasonal variation in (a) the mean dry weight of delivered prey items per hour and (b) the biomass proportion of earthworms per provisioning event. Day 160 represents June 9<sup>th</sup> and shaded areas are 95% Bayesian credible intervals.

## DISCUSSION

Mountain regions across the world are suffering from rapid and pronounced environmental change, impacting high-elevation biodiversity (La Sorte & Jetz 2010). The mechanisms at play in species' negative demographic trends remain poorly understood, however, as detailed knowledge of even basic species-specific ecological requirements is lacking. This study provides detailed insights into the nestling diet and patterns of parental food provisioning in a declining and emblematic alpine passerine, indicating how climate alterations and weather variations can mechanistically affect its trophic and breeding ecology. Indeed, the clear relationships between the provisioning efficiency of Ring Ouzel parents and weather circumstances highlight the challenges the species is facing. Parents forage most efficiently under cool ambient temperatures and during rainfall, which both boost the availability of the earthworms that constitute the bulk of nestlings' diet. Our findings further evidence a decrease in the mean dry biomass of prey items with the advancement of the reproductive season, suggesting a marked peak in staple food availability that temporally constrains breeding. Given the rapid increase in ambient temperatures and frequency of droughts forecasted for the Alps (Gobiet *et al.* 2014; CH2018 2018), Ring Ouzels thus appear particularly vulnerable to climate change.

The proportion of earthworms in the diet of Alpine Ring Ouzel nestlings was extremely high, both in terms of frequency (80%) and biomass (90%), in line with former faecal studies in the UK (70% of dry biomass from 60 nests; Burfield 2002) and previous qualitative appraisals from the Alps (Glutz von Blotzheim & Bauer 1988). Invertebrate larvae, in particular Coleoptera and Diptera (Tipulidae), also entered chick's diet but representing a minor fraction, as previously reported from British faecal analyses (Burfield 2002). Yet, discrepancies in diet composition might arise from different assessment methods: while faecal analyses often underestimate the presence of soft-bodied invertebrates in the diet (Moreby & Stoate 2000; Pearce-Higgins 2010), small prey items may be overlooked on pictures and videos (Douglas, Evans & Redpath 2008), in particular for multiple-prey loaders like the Ring Ouzel. The similarities in nestlings' diet composition in the two breeding populations is remarkable, especially considering the differences between the breeding habitat in the UK (heather moorland) and in the Alps (semi-open pastures), which host probably rather distinct invertebrate communities. Note, however, that a study using neck-collars in the Carpathians (in 39 nests) showed that Lepidoptera larvae were more important than earthworms in terms of biomass proportion (Korodi Gál 1970). This pattern was driven by a single species, *Hadena*

*monoglypha*, and suggests that the Ring Ouzel can opportunistically adapt its diet to temporally or locally abundant and profitable invertebrate prey.

We suspect that the importance of earthworms is mostly driven by either high prey size and weight or their high digestibility for nestlings (Moreby & Stoate 2000), if not a combination of both. A predominance of large soft-bodied invertebrates in the composition of chicks' diet has been reported for numerous bird species, including at high elevations (e.g. Brodmann & Reyer 1999; Pearce-Higgins 2010; Resano-Mayor *et al.* 2019). Ring Ouzels are generally single-brooded in the Alps, where they reproduce particularly early compared to other sympatric mountain bird species and during the brief time window between the snowmelt onset and the growth of dense ground vegetation (Barras *et al.* 2020). In contrast to soil invertebrates, grass-dwelling insects (e.g. Lepidoptera larvae and Orthoptera) are typically scarce so early in the season. Moreover, the Ring Ouzel, as many thrush species, is typically specialised in foraging on invertebrate prey present just below the soil surface. All our findings hence corroborate that earthworms represent a staple commodity for Ring Ouzels in Alpine treeline ecosystems.

The frequency and biomass of prey provisioning to chicks were negatively affected by ambient temperature, which was a better predictor than time of the day in all models. In altricial bird species, relationships between parental provisioning rates and ambient temperature are rather complex (e.g. Rauter, Brodmann & Reyer 2000; Geiser, Arlettaz & Schaub 2008). Prey provisioning is usually more frequent under high temperatures, due to increased invertebrate availability or activity (Geiser, Arlettaz & Schaub 2008; Low *et al.* 2008; Arlettaz *et al.* 2010; Winkler, Luo & Rakhimberdiev 2013) and because brooding requirements for thermoregulation of the chicks are reduced (Geiser, Arlettaz & Schaub 2008; Perez *et al.* 2016). Alternatively, however, provisioning is higher at low ambient temperatures as a parental response to fulfil the increased energy expenditure of actively thermoregulating nestlings (Rauter, Brodmann & Reyer 2000) or if prey availability is negatively affected by high ambient temperatures. As a matter of fact, earthworms respond to changes in ambient temperature and soil moisture by moving deeper into the soil under warm and dry weather conditions (Edwards & Bohlen 1996; Martay & Pearce-Higgins 2018; Onrust *et al.* 2019). This may underpin our observation of a slight but non-significant decrease in their biomass proportion in the diet with increasing ambient temperatures. Since earthworms are considered as climate-sensitive invertebrates (Pearce-Higgins 2010), mountain bird species that rely on them as a food source appear especially vulnerable in the face of climate change.

The weak positive effects of rainfall and overcast on the biomass delivered to the nestlings also suggest that earthworm availability was driving the patterns of parental provisioning activity. Nonetheless, we could not detect any increase in the proportion of earthworm biomass delivered under rainy conditions. Among insectivorous birds, rainfall usually exerts a negative effect on prey provisioning, and consequently breeding success, because it reduces the activity of flying insects and the accessibility of ground-dwelling invertebrates (Siikamäki 1996; Geiser, Arlettaz & Schaub 2008; Arlettaz *et al.* 2010; Perez *et al.* 2016; Schöll & Hille 2020). Ring Ouzels seem to stand out from other passerine bird species in this respect, obviously due to a trophic niche specialised on earthworms. Indeed, earthworms are more active in the upper ground layers and hence more accessible when the soil is humid and soft (Edwards & Bohlen 1996; Onrust *et al.* 2019), notably during or shortly after rainfall (Martay & Pearce-Higgins 2018) or during the snowmelt period. It is noteworthy that the larger prey biomass provisioned under such weather circumstances was mostly ascribable to exceptionally high amounts of food provided by the male, because then females were often found brooding nestlings to protect them from rainfall. The positive effect that wet and penetrable soils have on the availability of earthworms and other invertebrates (e.g. Tipulidae larvae) is thus key not only for birds in lowland agricultural landscapes (Peach *et al.* 2004; Smart *et al.* 2006; Onrust *et al.* 2019), but also in alpine ecosystems (Pearce-Higgins *et al.* 2010; Resano-Mayor *et al.* 2019; Barras *et al.* 2020).

Our results further evidence a decrease in the mean dry weight of delivered prey items with the advancement of the breeding season. The parallel decrease in the earthworm fraction in prey biomass indicates that this reduction in prey weight was caused mostly by a diet shift towards smaller invertebrates. As we could not show any strong relationships between nestlings' age and daily provisioned biomass or provisioning frequency, this pattern likely results from a general drop in earthworm availability towards the end of the breeding season. This is in line with an established decrease in foraging habitat suitability with the advancement of the season due to progressive soil desiccation and ground vegetation densification (Barras *et al.* 2020), with the aforementioned consequences on earthworm accessibility. This pattern will be further exacerbated in years with high summer ambient temperatures and prolonged droughts, negatively impacting the breeding success and first-year survival probability, such as reported for Ring Ouzels (Beale *et al.* 2006; Sim *et al.* 2011) and the European Golden Plovers (*Pluvialis apricaria*) in the UK (Pearce-Higgins *et al.* 2010), or Snowfinches in Italy (Strinella *et al.* 2020). In fact, the brood reduction that was observed on two occasions in our

study (loss of the smallest nestling) suggests that food resources might actually be limiting (Magrath 1989; Siikamäki 1996). Single brooding and rapid movements to higher elevations just after fledging also point towards a short window of breeding opportunities (Barras *et al.* 2020), as typically observed in alpine bird species (Boyle, Sandercock & Martin 2016). At this stage, however, this one-year study and the limited number of nests surveyed limit our ability to link demographic parameters such as productivity and juvenile survival rate to weather conditions. Finally, one ought to mention that a large fraction of the variation in provisioning rates and delivered biomass remained unexplained in our models, suggesting additional, unknown factors at play. Generally, we need more studies on the mechanical interlinks between climate, food supply and availability, and the demography of mountain birds (Chamberlain *et al.* 2012).

In conclusion, this study demonstrates that local weather considerably impacts the foraging ecology of an alpine bird during the reproductive period, with potential far-reaching consequences for population survival. Subject to a pace of warming double that recorded in the lowlands (Pepin *et al.* 2015), mountain birds face new challenges in meeting the food requirements of their offspring, notwithstanding the additional impacts of concomitant land-use change (Chamberlain *et al.* 2016). An earlier and accelerated spring snowmelt (Klein *et al.* 2016) can only accentuate the risk of a phenological mismatch for migratory species like Ring Ouzels, with potentially detrimental consequences for population dynamics (Visser, Both & Lambrechts 2004; McKinnon *et al.* 2012). While the breeding phenology of sedentary alpine specialists seems to be quite plastic (Martin *et al.* 2017), the question for non-resident species is whether they will gradually be able to anticipate their spring arrival on the breeding grounds. Last but not least, increasing frequency and magnitude of extreme weather events (Gobiet *et al.* 2014; CH2018 2018), such as prolonged drought periods (Beale *et al.* 2006) or late cold storms (Martin *et al.* 2017), may pose an additional challenge for mountain bird reproduction. Although we showed that provisioning activity peaked in wet and fresh weather conditions, cold storms characterized by abundant snowfall or frost in the core of the breeding season might lead to complete nesting failure (Martin *et al.* 2017), as observed in our study population at the beginning of the breeding season.

From a conservation perspective, measures aiming at directly boosting food availability in treeline ecotones would be beneficial for the Ring Ouzel, albeit challenging to implement. One could take advantage of current management practices of alpine grasslands in the Alps; extensively managed summer pastures, for instance, contribute to maintain a high density and

biomass of earthworms (Steinwandter *et al.* 2017; Jernej *et al.* 2019) while keeping the grass sward short enough for efficient foraging. Moreover, some shading of the ground as well as a thicker litter layer generated by the tree canopy may buffer against excessive soil warming and desiccation compared to open areas above the treeline (Körner 2012; Müller *et al.* 2016). For this reason, supporting extensive, traditional summer pasturing in treeline ecosystems might contribute to maintain suitable foraging grounds under a changing climate. Further studies focusing on the response of other mountain birds and their invertebrate prey communities to environmental change and various management options (e.g. grazing intensity; see Douglas & Pearce-Higgins 2014) are yet needed to guide comprehensive conservation strategies for the mountain avifauna.

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## SUPPLEMENTARY MATERIALS

**Table S1** Reference values for mean dry weight per prey item, as well as overall abundance and proportion of the different taxonomic groups exploited by Ring Ouzel parents to provision nestlings (n = 15 nests).

Invertebrate category	Mean dry weight (mg/item)	Abundance	Proportion (%)
Lumbricidae (small)	21.1	1789	44.7
Lumbricidae (medium)	62.7	999	25.0
Lumbricidae (large)	112.6	427	10.7
Unidentified larvae	28.3	375	9.4
Unidentified	12.6	245	6.1
Coleoptera larvae	52.6	70	1.8
Tipulidae larvae	17.6	51	1.3
Lepidoptera larvae	14.6	15	0.4
Diptera adult	5.0	9	0.2
Hymenoptera adult	0.8	7	0.2
Coleoptera adult	3.2	6	0.2
Lepidoptera adult	2.1	4	0.1
Arachnida	4.4	1	0.0
Total	–	3998	–

**Table S2** Set of best models, defined as within  $\Delta AIC < 2$  from the first-ranked model and obtained after the selection process for each of the different analyses.

Models	df	AICc	$\Delta AICc$	weight	marg. $R^2$	cond. $R^2$
<i>a. Provisioning rates, sex-independent</i>						
<i>Full model</i>						
Temp + wind + time of day <sup>2</sup> + sunshine + rain						
<i>Top models</i>						
Temp + wind	6	1237.1	0.00	0.41	0.10	0.27
Temp + time of day	6	1237.1	0.03	0.41	0.09	0.26
Temp	5	1238.8	1.72	0.18	0.09	0.26
<i>b. Provisioning rates, sex-specific</i>						
<i>Full model</i>						
Temp + wind + time of day <sup>2</sup> + sunshine + rain + sex + sex x rain + sex x temp						
<i>Top models</i>						
Temperature + wind	5	1980.9	0.00	0.61	0.06	0.23
Temperature + time of day	5	1981.8	0.92	0.39	0.06	0.23
<i>c. Delivered prey biomass, sex-independent</i>						
<i>Full model</i>						
Temp + wind + time of day <sup>2</sup> + sunshine + rain						
<i>Top models</i>						
Temperature + time of day <sup>2</sup> + rain	7	1735.5	0.00	0.34	0.11	0.37
Temperature + time of day <sup>2</sup> + sunshine	7	1735.6	0.03	0.34	0.11	0.36
Temperature + time of day <sup>2</sup>	6	1735.7	0.14	0.32	0.10	0.37
<i>d. Delivered prey biomass, sex-specific</i>						
<i>Full model</i>						
Temp + wind + time of day <sup>2</sup> + sunshine + rain + sex + sex x rain + sex x temp						
<i>Top models</i>						
Rain + sex	5	3462.3	0.00	0.50	0.07	0.25
Sunshine + sex	5	3463.4	1.18	0.27	0.07	0.24
Sex	4	3463.8	1.53	0.23	0.06	0.26

‘df’ stands for degrees of freedom and ‘marg.’ and ‘cond.  $R^2$ ’ stand for marginal and conditional  $R^2$  values (i.e. the proportion of explained variance by fixed effects only, and by both random and fixed effects, respectively). Models in (a) and (b) include nested random factors ‘nest’ and ‘day of year’. Random factor ‘day of year’ was removed in models in (c) and (d) as leading to convergence issues. ‘Temp’ stands for temperature, ‘x’ for interactions and ‘2’ as superscript indicates that both linear and quadratic terms were included.



**Figure S1** Picture of the video monitoring system (in red circle) installed to record provisioning activity at a Ring Ouzel *Turdus torquatus alpestris* nest (in red square). Photo credits: A. G. Barras