



# Climate change and perishable food hoards of an avian predator: Is the freezer still working?

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## Abstract

Changing climate can modify predator–prey interactions and induce declines or local extinctions of species due to reductions in food availability. Species hoarding perishable food for overwinter survival, like predators, are predicted to be particularly susceptible to increasing temperatures. We analysed the influence of autumn and winter weather, and abundance of main prey (voles), on the food-hoarding behaviour of a generalist predator, the Eurasian pygmy owl (*Glaucidium passerinum*), across 16 years in Finland. Fewer freeze–thaw events in early autumn delayed the initiation of food hoarding. Pygmy owls consumed more hoarded food with more frequent freeze–thaw events and deeper snow cover in autumn and in winter, and lower precipitation in winter. In autumn, the rotting of food hoards increased with precipitation. Hoards already present in early autumn were much more likely to rot than the ones initiated in late autumn. Rotten food hoards were used more in years of low food abundance than in years of high food abundance. Having rotten food hoards in autumn resulted in a lower future recapture probability of female owls. These results indicate that pygmy owls might be partly able to adapt to climate change by delaying food hoarding, but changes in the snow cover, precipitation and frequency of freeze–thaw events might impair their foraging and ultimately decrease local overwinter survival. Long-term trends and future predictions, therefore, suggest that impacts of climate change on wintering food-hoarding species could be substantial, because their ‘freezers’ may no longer work properly. Altered usability and poorer quality of hoarded food may further modify the foraging needs of food-hoarding predators and thus their overall predation pressure on prey species. This raises concerns about the impacts of climate change on boreal food webs, in which ecological interactions have evolved under cold winter conditions.

## KEYWORDS

boreal forest, food hoarding, freeze–thaw events, predator–prey interactions, pygmy owl, starvation risk

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## 1 | INTRODUCTION

Animal populations have always been influenced by changes in climatic conditions (Dempster, 1975). Weather can affect numbers of individuals via changes in survival, breeding success and geographic range, but also by influencing their habitat or food availability (Dempster, 1975; Newton, 2013). In recent years, large-scale climatic changes, largely of anthropogenic origin, have been causing disruptions in numerous species, by affecting distribution patterns, population abundance, phenological processes and behaviours, ultimately determining population declines and local extinctions (Dunn & Møller, 2019; Møller, Fielder, & Berthold, 2010; Pearce-Higgins & Green, 2014). Temperature has been rising in many places at a rapid pace, but the warming has not occurred evenly in the planet or through the year. Increases in temperature have been larger at northern latitudes during winter and spring (Houghton et al., 2001; IPCC, 2014). Furthermore, precipitation has also been increasing both due to the temperature changes and to the altered air circulation patterns induced by these changes. Global climatic trends during the past decades are expected to accelerate during the coming years (IPCC, 2014), likely affecting the behaviour and phenology of many animal species.

Foraging is a fundamental behaviour of individuals throughout their whole life and is strongly affected by climatic conditions and resource availability. By affecting survival and reproductive success, it can determine if a population will thrive, decline or even become extinct (Stephens, Brown, & Ydenberg, 2007). Most studies analysing how weather changes can affect foraging behaviour focus on the breeding season (reviewed in Both, 2010). Climate change can influence the timing of breeding and mismatches can rise if the phenology of predators and prey are differentially affected (e.g. tits and caterpillars; Dunn, 2004; Durant, Hjermmann, Ottersen, & Stenseth, 2007). Despite the great importance of winter foraging, both for overwinter survival and preparation for breeding season, the effects of climate on foraging during the non-breeding season are understudied (but see e.g. Halonen, Mappes, Meri, & Suhonen, 2007; Sechley, Strickland, & Norris, 2015; Sutton et al., 2019; Terraube, Villers, Poudré, Varjonen, & Korpimäki, 2017).

Animals that hoard perishable food to cope with harsh wintering conditions are predicted to be especially susceptible to climate change (Sutton, Strickland, & Norris, 2016). Species susceptibility also increases according to the amount of time the food is hoarded for (from a low susceptibility of a few hours or days to a high susceptibility if hoarded for months). Food-hoarding predators that collect prey in the autumn to be used throughout the winter might therefore be particularly vulnerable to variation in climate. Due to the difficulty of collecting data on food hoards and on hoarding individuals, previous studies were not able to quantify the effects of climate on the main aspects of the food-hoarding behaviour of a predator.

To understand how weather conditions can affect food-hoarding behaviour, we analysed 16 years of data on the food hoarding of Eurasian pygmy owls (*Glaucidium passerinum*; hereafter 'pygmy owl'). This small avian predator hoards large quantities of highly perishable food (i.e. small mammals and birds) to facilitate overwinter

survival. Pygmy owls have been shown to be susceptible to weather variations. In particular, the beginning of the food-hoarding season appears to be linked to temperature; when daily temperatures drop below 0°C in autumn, pygmy owls seem to start collecting food hoards (Schulenburg & Wiesner, 1986; Solheim, 1984). Furthermore, during the food-hoarding season, an increase in the frequency of days with precipitation during autumn reduced total prey biomass in food hoards and body condition of female pygmy owls (Terraube et al., 2017). An increase in snow cover has also been associated with decreased hoarding of small mammals (Halonen et al., 2007). Previous studies have shown that food-hoarding behaviour of pygmy owls varies in relation to the availability of main prey species (i.e. abundance voles of the genera *Myodes* and *Microtus*) and age and sex of the individual (Masoero, Laaksonen, Morosinotto, & Korpimäki, 2020; Masoero, Morosinotto, Laaksonen, & Korpimäki, 2018), with increasing food hoards in years of vole abundance, in yearling individuals and in females. However, it has not been yet examined how weather conditions, together with main prey abundance and individual traits, can affect the phenology of hoarding or the accumulation, consumption and perishability of the food items.

Our aim was to examine how changing climate in winter can affect species hoarding highly perishable food, which is essential for surviving the season. We did so by analysing how weather factors and food abundance can determine the initiation of hoarding, the accumulation, consumption and rotting of the hoards, and whether there are sex- or age-specific differences in the weather responses. Based on previous knowledge, we expected that (i) the initiation of the food hoarding would be mainly determined by temperature in early autumn; (ii) an increasing number of days with precipitation and deeper snow cover would reduce the accumulation of new prey items and (iii) lead to an increase in the consumption of the prey items already in the food hoard; (iv) hoards that were initiated early would be more likely to rot than hoards that initiated later and higher temperatures would increase the rotting of the food hoards. In addition, we also expected (v) later initiation of the hoarding, faster accumulation of food items and overall lower consumption in years of high vole abundance than in years of vole scarcity. We predicted that (vi) females and yearlings begin food hoarding earlier, to accumulate hoards faster and to consume them more than males and adult owls respectively. With regard to time-trends, we expected (vii) that in more recent years, food-hoarding season would begin later and that more food hoards would rot during autumn due to the rising temperatures in the study area. Finally, we predicted that rotten food hoards may (viii) decrease the local overwinter survival of individual owls.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

Our study area is located in the vicinity of Kauhava, western Finland (63°N, 23°E), where ca. 300 pairs of nest boxes (two

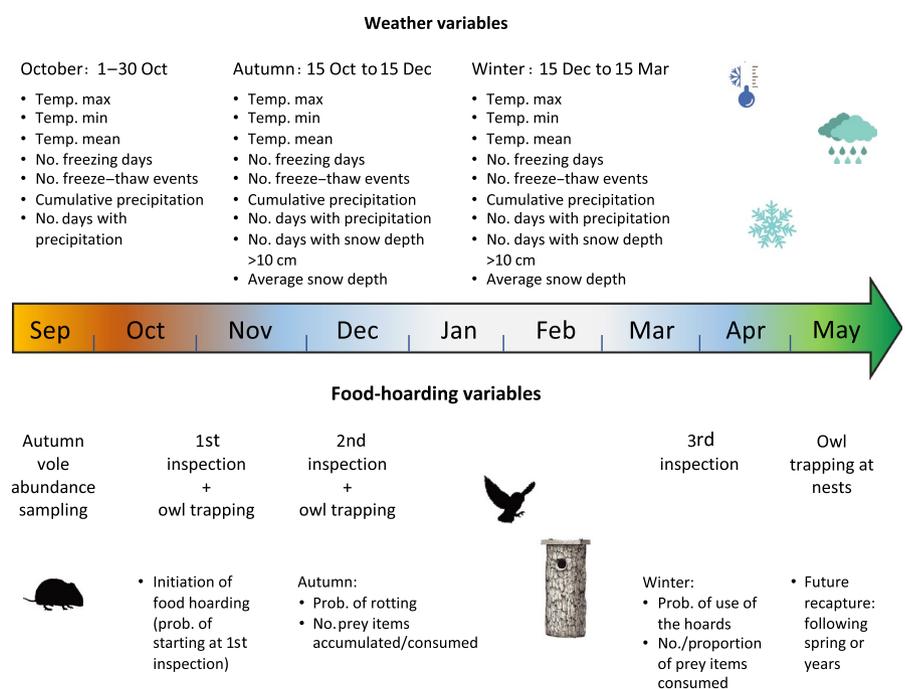
boxes 50–100 m apart per each ‘forest site’) were provided for pygmy owls as food-hoarding and breeding sites (see details in Masoero et al., 2018; Morosinotto, Villers, Thomson, Varjonen, & Korpimäki, 2017). Two nest boxes per forest site allow pygmy owls to have at least one box available throughout the year, since Siberian flying squirrels (*Pteromys volans*) also occupy these boxes throughout the year (Morosinotto et al., 2017; Turkia, Korpimäki, Villers, & Selonen, 2018). The entrance hole of the nest boxes had a diameter of 45 mm, which prevents other owl and diurnal raptor species from entering the boxes (Morosinotto et al., 2017; Solheim, 1984). The study area covers 1,000 km<sup>2</sup> and is a mosaic of managed forest including clear-cut and sapling areas and different-aged forests and agricultural land (Hakkarainen et al., 2003; Morosinotto et al., 2017).

In the study area, detailed data on the food-hoarding season and on the hoarding individuals were collected from 2003 until 2018. Boxes were inspected twice during each autumn—a first inspection between the last week of October and first week of November and a second inspection between the last week of November and first half of December (Figure 1). Prey items were counted and marked, and the food hoard was assessed both by look and smell as either fresh or rotten (smelly and appearance degrading) during both autumn inspections. The spring inspection was carried out between late March and early April before the start of the egg-laying period. Due to the fact that most hoards were completely rotten by spring and prey items were difficult to identify, only data such as prey species and number were collected at this stage.

Individuals collecting the food hoards were identified at the hoarding boxes during the autumn inspection either by direct capture (individuals marked with aluminium rings) or indirect identification (RFID method; Gibbons & Andrews, 2004). Captured individuals were marked with aluminium ring and provided with an RFID tag, a microchip with a unique code inserted under the skin

over the muscle of the upper back. The majority of the owls (81%) at food hoards were captured with nest-box traps (a model of the box equipped with swing door). Additional data on encounters of individual owls were collected by setting up the antenna of the RFID-reader around the entrance hole of the box with the food hoard in case we did not succeed in capturing the owl with the nest-box trap. Data on the local overwinter survival of owls were also collected during April to May 2003–2019. Female owls were trapped and ringed or re-trapped by hand when brooding small chicks in the nest-box. Male owls were attracted to the vicinity of the nest with a playback recorder and a model pygmy owl, and trapped with a neck-loop attached on the top of a fishing pole. Supplementary data from parent males were collected by setting up the antenna of the RFID-reader around the entrance hole of the nest-box when the trapping of males with loop was not successful.

Pygmy owls are sexually dimorphic, with females larger than males, and sex was determined on the basis of wing length, tail length and body mass (as in Masoero et al., 2018). The age was estimated according to wing moult (Lagerström & Syrjänen, 1990), and individuals were divided in two classes: individuals in their hatching year (hereafter ‘yearlings’) and older individuals (hereafter ‘adults’). We collected data on 702 food hoards with an identified hoarder, for a total of 354 individuals more or less equally divided among age and sex classes. All the necessary data (two autumn inspections, freshness at the second inspection, spring inspection, detailed data on accumulated prey for all inspections) were collected for about 41% of the analysed food hoards, so each analysis was carried out on a subset of the data set that had the most complete data for the used variables (specific sample size is therefore provided for each group of analyses, see Section 2.3). More detailed information on the study area and on the study system can be found in Morosinotto et al. (2017), Terraube et al. (2017) and Masoero et al. (2018, 2020).



**FIGURE 1** Study design of when the weather and food-hoarding variables were collected or measured according to the temporal scale

Abundances of main prey of pygmy owls (bank voles, *Myodes glareolus*, and voles of the genus *Microtus* combined) have been estimated by snap-trappings each year in early May (i.e. breeding season) and in mid-September (before the food hoarding of owls) in two different locations since 1973. The data collected during September from 2003 to 2018 were used for the analyses of this study. Sampling was carried out in the four main habitat types (i.e. cultivated field, abandoned field, spruce forest, pine forest). Fifty baited Finnish metal mouse snap traps were set at 10 m intervals in vole runways on each sample plot and were checked daily for three consecutive days. Thus, the area of a sample plot was 0.5 ha and the pooled trapping effort was 600 trap-nights in both western and central parts of the study area. Previous studies have shown that densities of *Microtus* and bank voles fluctuate in synchrony in the study area and that the regional synchrony of vole population cycles extends up to 80 km, therefore covering the whole study area (Huitu, Norrdahl, & Korpimäki, 2003; Korpimäki, Norrdahl, Huitu, & Klemola, 2005). The number of bank voles and *Microtus* voles captured was standardized to the number of animals caught per 100 trap-nights and pooled together to obtain the vole abundance index in the analyses (for more details on trapping methods and vole cycles in the study area, see Korpimäki et al., 2005; Masoero et al., 2018; Morosinotto et al., 2017; Terraube et al., 2017).

## 2.2 | Weather variables

The climate data were obtained from the Finnish Meteorological Institute (FMI), collected in the middle of our study area (Kauhava airport) during 1973–2018. Each variable was calculated over three different time spans of the year (except for the two snow variables due to the lack of snow in October during 2003–2018, see Figure 1; Supplementary Information S1). For each group of analyses the most appropriate time span was chosen according to when the response variable was measured. The time spans were as follows: just before and during the start of the autumn food-hoarding season (1–30 October), during the hoarding season when the food is most commonly hoarded (15 October–15 December) and during the wintertime when the hoarded food is usually consumed (15 December–15 March). The most important climatic variables influencing the quality of hoarded food are temperature, freeze–thaw events and precipitation (reviewed by Sutton et al., 2016), and we considered the following variables: (a) For precipitation, we used both the number of days with precipitation (total daily precipitation >0.1 mm) and the total sum of precipitation. (b) Temperature variables were the average mean, minimum and maximum daily temperature, the number of freezing days (maximum daily temperature below the average initial freezing point of meat,  $-1.9^{\circ}\text{C}$ ) and the number of freeze–thaw events. Freeze–thaw events were defined as the number of times in which the minimum temperature was below the average initial freezing point of meat ( $-1.9^{\circ}\text{C}$ )

and the maximum temperatures were above it, according to a study by Sutton et al. (2019). (c) Snow cover was evaluated both as average snow depth and the number of days with more than 10 cm of snow.

## 2.3 | Climate and food-hoard analyses

Generalized linear mixed-effect models (GLMMs) were used to examine the relationship between climatic variables and the main characteristics of the food-hoarding behaviour of pygmy owls in the study area. Conditional boxplots, pairwise scatterplots, Pearson correlation coefficients (not included together if  $|r| > .5$ ; see Supplementary Information S1) and Variance Inflation Factors (variable set with  $\text{VIF} < 2$ ) were used to investigate relationships between variables (Zuur, Ieno, & Elphick, 2010). Continuous variables included in the models were standardized ( $\mu = 0$  and  $\sigma^2 = 1$ ; using the *scale* function in R) before model fitting so that the magnitudes of the coefficients were comparable (Schielzeth, 2010).

Our interest was to understand which variables best described the response variable, therefore due to the large number of weather variables we divided each analysis into two parts. First, variables in each of the three weather groups (precipitation, temperature, snow cover) were chosen and models were ranked according to the Akaike information criterion corrected for small sample size ( $\text{AIC}_c$ ). Each model always included year, vole abundance and age and sex of the owl. Second, we constructed a set of nested models starting from a full model that included the weather variables (in total three variables, the ones with the lowest  $\text{AIC}_c$  in each weather group), year, vole abundance index and age and sex of the owl. We therefore hypothesized that owls of different age and sex might vary in their reaction or be differently affected by weather conditions, and tested the interactions of weather variable  $\times$  age and weather variable  $\times$  sex. All nested models always included the variables vole abundance index, age and sex of the owl, because they were identified as important variables during previous studies (Masoero et al., 2018, 2020). If models had a difference in terms of  $\text{AIC}_c$  ( $\Delta\text{AIC}$ ) lower than 2 and a similar weight, the simpler model with a lower number of interactions was retained. Two random effects were used in the models as follows: ‘forest site’, to avoid spatial pseudo-replication, and ‘individual identity’ of the owl. Even if variability among sites and individuals was always very small, they were treated as random effects, to avoid pseudoreplication errors seen when data from different experimental units are used as independent replicates and pooled in the same analysis (Hurlbert, 1984). Model selection tables are reported in Supplementary Information S2. All analyses were performed using R v 3.6.1 (R Core Team, 2019), using ‘lme4’ (Bates, Maechler, Bolker, & Walker, 2015) and ‘glmmadmb’ (Bolker, Skaug, Magnusson, & Nielsen, 2012) packages. ‘Visreg’ (Breheny & Burchett, 2017) was used to visualize regression lines. Estimated marginal means (i.e. least square means) and

post hoc Tukey tests were obtained through the package 'emmeans' (Lenth, 2019). The statistical analyses carried out can be grouped as follows (see Figure 1 for guidance).

1. Food-hoarding trends. All of the following response variables (2–6 below) used for the variation in the food-hoarding characteristics were first checked for a temporal trend during the course of the study. GLMMs were used with year as the only continuous explanatory variable.
2. Initiation of hoarding ( $N = 503$ ). By using all the boxes that were inspected twice and that had a food hoard during autumn, it was possible to examine the probability that the food hoard was initiated already at the first inspection. The response was constructed as a binomial variable stating if the hoard was already present at the first inspection ('1') or only at the second ('0'). The number of days between the first autumn inspection and the autumn equinox was added as an additional variable in all models, to control for variability in the inspection date. The weather variables for October were used in this analysis, as this month includes the days just before and during the first start of the hoarding season.
3. Accumulation of hoarded prey items during autumn ( $N = 275$ ). The accumulation of new prey items included all the food hoards that had new prey items not present at the first inspection. The variable was modelled as for count data, using a zero-truncated negative binomial distribution. Climatic variables calculated for the food-hoarding season (15 October–15 December) were used in the analysis.
4. Consumption of hoarded prey items during autumn ( $N = 205$ ). For this analysis we included only the hoards that had a lower number of prey items in the second inspection than in the first one. The variable was modelled as for count data, using a zero-truncated negative binomial distribution. Climatic variables calculated for the food-hoarding season (15 October–15 December) were used in the analysis.
5. Use of the hoards and consumption of the hoarded prey items during winter. The overall use of the hoards was analysed by first modelling the probability that at least some of the prey items in the hoard were used ( $N = 496$ ). The response for this part was constructed as a binomial variable stating if the hoard was used (at least one prey items was consumed, '1') or not ('0'). Data on hoards with at least one inspection in autumn and an inspection in spring were included in these analyses. Since we were interested in the consumption of prey items, hoards that had more prey items in the spring inspection than in the autumn one were categorized as 'not used' for the purpose of this analysis. For the actual consumption, we modelled both the number and the proportion of used prey items for the food hoards that were used ( $N = 394$ ). The number of prey items was modelled as count data, using a zero-truncated negative binomial distribution. For the second part, the response variable was proportional and it was constructed using the 'cbind' command in R (Crawley, 2012; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) that allows to take into account the actual number of prey items instead of just the proportion. Climatic variables calculated for the winter season (15 December–15 March) were used in the analyses.
6. Rotting of the food hoards during autumn and use of the rotten food hoards. For those cases in which the box was inspected during both inspections and the food hoard was scored as fresh or rotten ( $N = 408$ ), it was possible to analyse the probability that the hoard was still unspoiled ('fresh') or had started to rot ('rotten') by the time of the second autumn inspection. The number of days between the second autumn inspection and the autumn equinox was added as an additional variable in all models to control for variability in inspection date. Climatic variables calculated for the food-hoarding season (15 October–15 December) were used in the analysis. After this, we ran analyses unrelated to the climate analyses, to examine whether the freshness (fresh/rotten) of the food hoard in autumn affected either the probability of using the food hoard ( $N = 385$ ) or the proportion of prey items used ( $N = 304$ ) during the winter. These models included the freshness of the hoard (fresh/rotten) and vole abundance in autumn, and as random effects forest site and individual identity.
7. Effects of the rotten hoards on recapture probability of owl individuals. We tested for the effect of the rotting of the food hoards on the local survival of individuals. We modelled the recapture probability of owl individuals in the next spring or later on as a binomial variable ('0' never encountered, '1' encountered again either as a breeder or food-hoarder within the study area in the following years). The GLMM included the freshness of the hoard (fresh/rotten), vole abundance in autumn, age and sex of the owl (fixed effects) and forest site and individual identity as random effects. We tested the interactions freshness  $\times$  vole abundance, freshness  $\times$  age, freshness  $\times$  sex, to examine whether the effect of having a rotten hoard differed with the abundance of the main prey or for owls of different age and sex.
8. Climate trends were tested both during 1973–2018 (long-term trends) and during the study period (2003–2018; short-term trends). According to the nature of the tested variable, either linear models (continuous response variable, with a normal distribution) or GLMs with a Poisson family link (count variables, e.g. Number of freezing days) were used.

## 3 | RESULTS

### 3.1 | Temporal changes in food hoarding

The analyses for the temporal trends of the response variables during the course of the study (2003–2018) showed no significant trends for the initiation of the food hoarding, the rotting of the food hoards during autumn, the number of prey items accumulated and consumed in autumn and in the number and the proportion of prey items used in the food hoards during winter (Table 1). There was, however, a significant increase in the probability of using the food hoard during the winter (Table 1).

**TABLE 1** Generalized linear models analysing the temporal trends of the response variables for the food-hoarding characteristics considered in this study during 2003–2018. Significant variables ( $p < .05$ ) are shown in bold

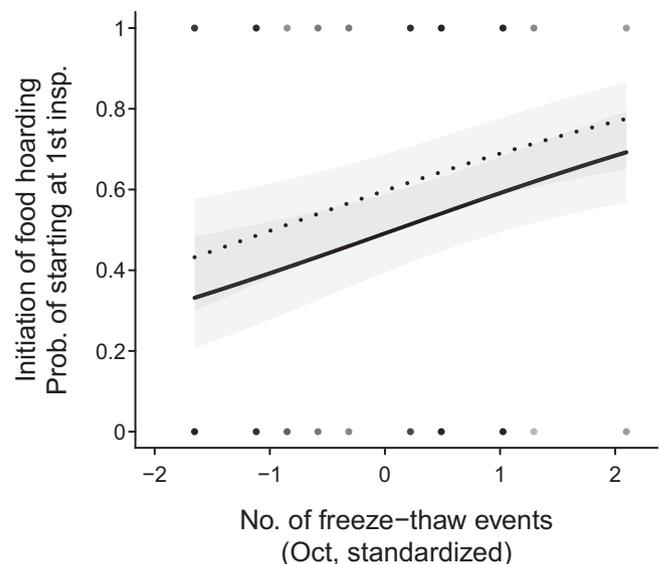
Response	Intercept (estimate $\pm$ SE)	Year (estimate $\pm$ SE)	$\chi^2$	$p$
Initiation of food hoarding (probability of a hoard already in late Oct–early Nov)	0.152 $\pm$ 0.103	-0.128 $\pm$ 0.102	1.59	.2078
No. of prey items accumulated in autumn	2.817 $\pm$ 0.059	0.045 $\pm$ 0.050	0.81	.3682
No. of prey items consumed in autumn	1.059 $\pm$ 0.112	-0.005 $\pm$ 0.087	0.00	.9572
Probability of use in winter	1.415 $\pm$ 0.158	-0.288 $\pm$ 0.122	5.54	<b>.0185</b>
Proportion of prey items consumed in winter	1.453 $\pm$ 0.258	-0.106 $\pm$ 0.182	0.34	.5594
No. of prey items consumed in winter	2.207 $\pm$ 0.094	-0.093 $\pm$ 0.048	3.82	.0507
Rotting in autumn	-0.298 $\pm$ 0.135	0.131 $\pm$ 0.131	1.00	.3162

**TABLE 2** Generalized linear mixed-effect model analysing the variation in the probability of initiating the food hoard already in late October to early November in relation to the number of freeze–thaw events in October, pygmy owl sex (M = estimate of males) and age (Yr = estimate of yearlings) and autumn vole abundance (vole index) during 2003–2018. The variable ‘inspection date’ (standardized number of days between the first inspection of the boxes and the autumn equinox) was included in the model to control for variability in the inspection date. For categorical variables, parameter estimates are given relative to a reference category indicated among brackets. Significant variables ( $p < .05$ ) are shown in bold.  $N = 503$  food hoards

Explanatory	Estimate $\pm$ SE	$\chi^2$	$p$
(Intercept)	-0.042 $\pm$ 0.194		
No. of freeze–thaw events–Oct	0.403 $\pm$ 0.122	10.89	<b>.0010</b>
Year	-0.221 $\pm$ 0.114	3.74	.0532
Age (Yr)	0.428 $\pm$ 0.216	3.92	<b>.0477</b>
Sex (M)	-0.072 $\pm$ 0.208	0.12	.7307
Vole index	-0.222 $\pm$ 0.110	4.05	<b>.0442</b>
Inspection date	0.374 $\pm$ 0.109	11.69	<b>.0006</b>
Random effects	N	Variance	
Forest site	208	0.332	
Individual ID	278	0.221	

### 3.2 | Initiation of hoarding

On average, half (54%) of the hoards over all years were found already during the first inspection at the end of October to early November, but there was large variation between years (range 33%–89%). The probability that the food hoard was already initiated at the end of October to early November increased strongly with increasing numbers of freeze–thaw events in October (Table 2; Figure 2; Model selection tables are reported in the Supplementary Information S2). It was also higher in years of vole scarcity than of vole abundance (Figure 3a), and yearling owls

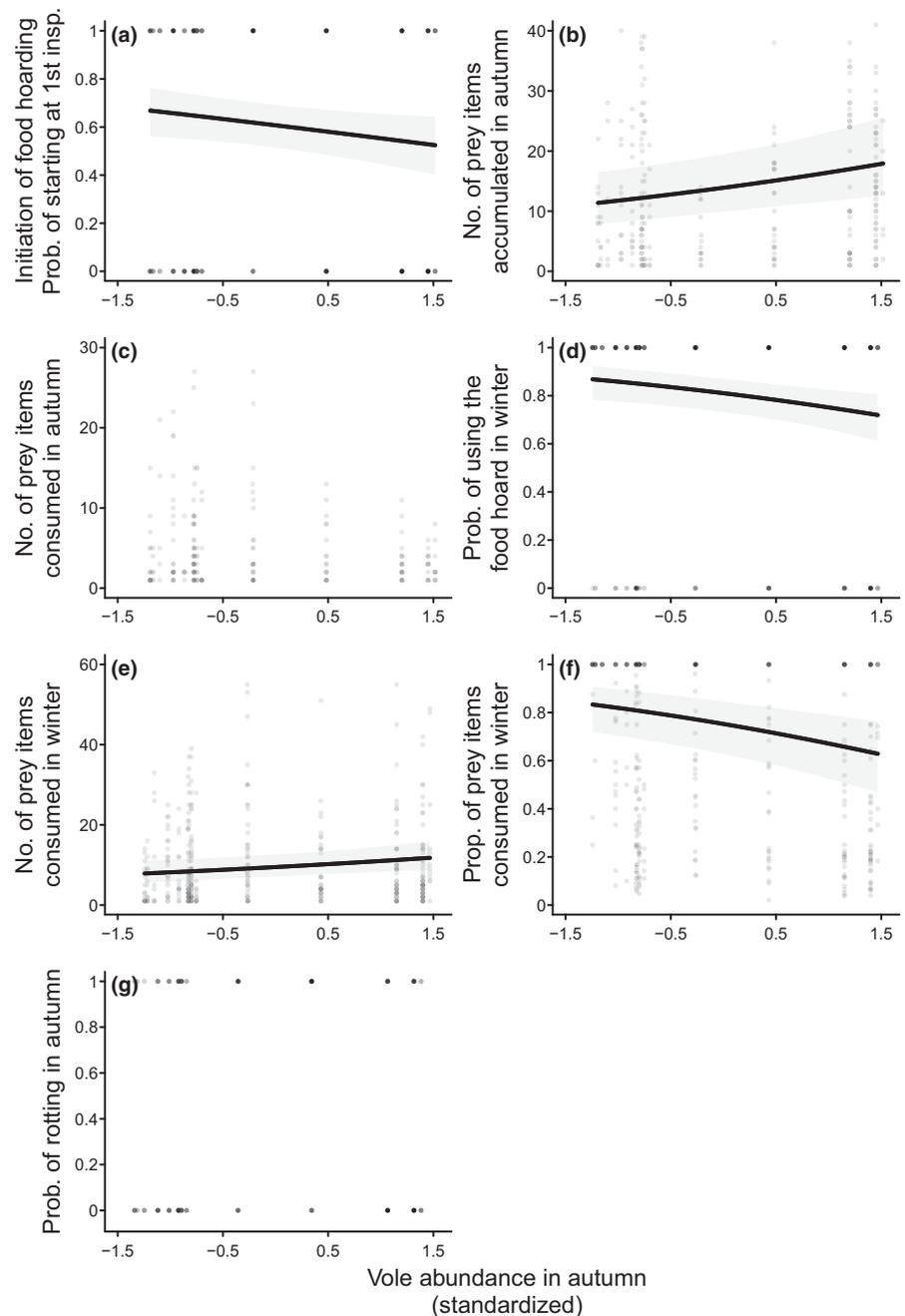
**FIGURE 2** Probability (and 95% CI) of initiating the food hoard already at the first autumn inspection (late Oct to early Nov) in relation to the number of freeze–thaw events in October for adult (continuous line) and yearling (dotted line) pygmy owls. Predicted values are calculated on average values of the other continuous variables. Observed values are represented with dots; darker colours represent a larger number of observations

had a higher probability to start hoarding food already before the first inspection (estimated marginal means, EMMs  $\pm$  SE: yearlings  $0.58 \pm 0.03$ , adults  $0.48 \pm 0.04$ ). Food hoarding tended to begin later in more recent years when accounting for the other variables (Table 2).

### 3.3 | Accumulation and consumption of hoarded prey items in autumn

During late October to early December, the accumulation of prey animals in food hoards (Table 3 model a) showed no significant relationship with the number of days with  $>10$  cm snow cover, despite

**FIGURE 3** Food-hoarding characteristics of pygmy owls during 2003–2018, in autumn (a–c,g) and winter (d–f), in relation to the vole abundance index in autumn. Predicted values are calculated using average values of the other continuous variables. Continuous lines indicate a significant relationship ( $p < .05$ ), whereas the absence of the line indicates a non-significant relationship. Observed values are represented with dots, with darker colours meaning a larger number of observations



this variable being present in the best model (Supplementary Information S2). More prey items were accumulated with a higher vole abundance in autumn (Figure 3b). Males collected fewer prey items than females (EMMs  $\pm$  SE:  $7.52 \pm 0.93$  prey items per hoard for males vs.  $14.68 \pm 1.78$  prey items per hoard for females). The number of prey items consumed (Table 3 model b) increased with the number of days with snow cover (Figure 4a) and with the number of freeze–thaw events (Figure 4b), and tended to be lower at higher vole abundance (Figure 3c). Year was not included in the top model predicting either the number of prey items consumed or the accumulation of prey animals in food hoards, suggesting that there were no temporal trends.

### 3.4 | Consumption of the hoarded prey items in winter

The yearly percentage of used food hoards (at least one prey item consumed) during the course of the winter averaged 89% ( $\pm 1.8$  SE). The best model in terms of AIC<sub>c</sub> value included the number of freeze–thaw events and vole abundance in autumn (Table 4 model a; see Supplementary Information S2). The probability to use the hoard increased with the number of freeze–thaw events (Figure 5a) and decreased with abundance of voles before the food-hoarding season (Figure 3d). There were no significant differences according to age and sex of the owl.

Response	Explanatory	Estimate $\pm$ SE	$\chi^2$	<i>p</i>
(a) No. of prey items accumulated in autumn ( <i>N</i> = 275)				
	(Intercept)	2.926 $\pm$ 0.090		
	No. of days with snow depth >10 cm—Oct to Dec	-0.095 $\pm$ 0.060	2.52	.1123
	Age (Yr)	-0.027 $\pm$ 0.098	0.07	.7865
	Sex (M)	-0.327 $\pm$ 0.095	11.96	<b>.0005</b>
	Vole index	0.168 $\pm$ 0.054	9.69	<b>.0019</b>
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	159	0.000	
	Individual ID	183	0.000	
(b) No. of prey items consumed in autumn ( <i>N</i> = 208)				
	(Intercept)	0.827 $\pm$ 0.180		
	No. of freeze-thaw events—Oct to Dec	0.180 $\pm$ 0.080	5.05	<b>.0246</b>
	No. of days with snow depth >10 cm—Oct to Dec	0.352 $\pm$ 0.110	16.38	<b>.0001</b>
	No. of days with snow depth >10 cm—Oct to Dec $\times$ Age (Yr)	-0.330 $\pm$ 0.158	4.37	<b>.0366</b>
	Age (Yr)	0.130 $\pm$ 0.097	1.81	.1791
	Sex (M)	0.298 $\pm$ 0.166	3.31	.0689
	Vole index	-0.050 $\pm$ 0.183	0.08	.7832
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	130	0.605	
	Individual ID	145	0.465	

**TABLE 3** Generalized linear mixed-effect models analysing the variation in the number of prey items accumulated (a) and consumed (b) in pygmy owl food hoards in relation to climatic variables (15 October–15 December), pygmy owl sex (M = estimate of males) and age (Yr = estimate of yearlings) and autumn vole abundance (vole index) during 2003–2018. Interactions between terms are indicated with 'x', and significant variables (*p* < .05) are shown in bold. For categorical variables, parameter estimates are given relative to a reference category indicated among brackets

If the food hoard was used, on an average 65% ( $\pm 1.8$  SE) of the prey items were consumed during the winter (mean number  $\pm$  SE: 10.04  $\pm$  0.54, range: 1–55). For the number of consumed prey items, the best model included a negative effect of the number of days with snow cover deeper than 10 cm (Table 4 model b, see Supplementary Information S2). Pygmy owls consumed fewer prey items when there was a longer amount of time with a deep snow cover (Figure 5b). The best model explaining the proportion of prey items used during the winter included cumulative precipitation sum, the number of days with freezing days and its interaction with the age of the owl, the average depth of snow cover and its interaction with sex, year and vole abundance in autumn (Table 4 model b). A high number of freezing days appeared to slightly decrease the proportion of prey items used by adults, whereas it had a strong positive effect on the proportion consumed by yearlings (Figure 6a). Pygmy owls consumed a higher proportion of the hoarded prey items with increasing average snow cover (Figure 6b) and decreasing cumulative precipitation (Figure 6c). There was a decreasing temporal trend for both the number and the proportion of prey items consumed during 2003–2018. A low proportion, but a high number of prey items were consumed with abundance of voles (Figure 3e,f).

### 3.5 | Rotting of the food hoards in autumn

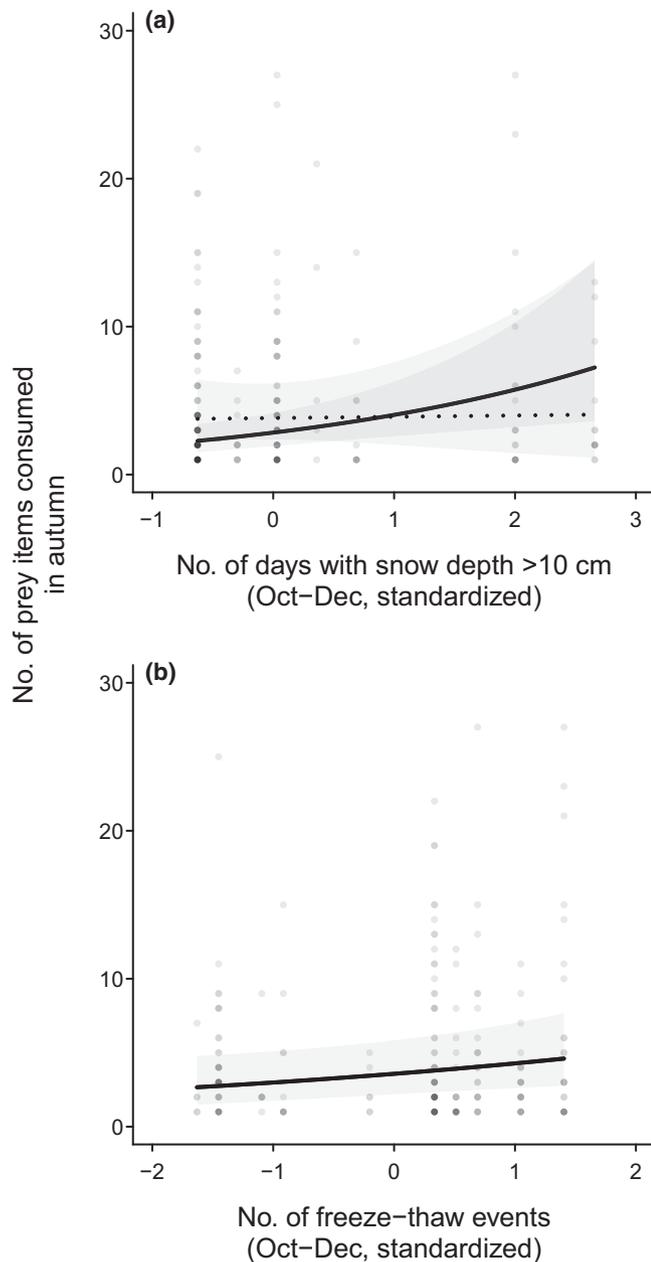
During the course of the study, 43.9% of the hoards were found rotten during the second autumn inspection (late November to early December).

The best model indicates that the probability that the hoard would rot from late October to early December increased if the hoard was already present at the first inspection and with increasing number of days with precipitation during the food-hoarding season (Table 5; Figure 7; Model selection tables are reported in Supplementary Information S2). No significant effects of vole abundance or age and sex of the owl were detected on the rotting probability of the food hoards (Table 5).

The probability of food hoard use and the proportion of prey items consumed in food hoards during the winter were positively related to the freshness of the whole food hoard in late November to early December, and were also negatively related to vole abundance (Table 6; Figure 8). No relationship was found for the number of prey items consumed.

### 3.6 | Rotten food hoards and recapture probability of hoarders

There was a difference between the sexes in how the freshness of the food hoard in late November and early December was associated with recapture probability (Table 7; Figure 9). The recapture probability was lower for females with a rotten food hoard than for those with a fresh food hoard (post hoc Tukey test:  $z = 2.062$ ,  $p = .0391$ ), while no such difference was found for males ( $z = -0.785$ ,  $p = .4322$ ). There were no associations of recapture probability of hoarding owls with either vole



**FIGURE 4** Predicted values (and 95% CI) of number of prey items consumed in food hoards of pygmy owls in relation to snow cover (a) and freeze-thaw events (b) during the food-hoarding season (15 October–15 December). Adults are represented with a continuous line and yearlings with a dotted line. Predicted values are calculated using average values of the other continuous variables. Observed values are represented with dots, with darker colours meaning a larger number of observations

abundance in the current autumn, owl age or their interactions with the freshness of the food hoard (Table 7).

### 3.7 | Climate trends

The climate variables showed some clear trends in the study area during 1973–2018, whereas less clear changes were found during the 16 year study period (2003–2018). Estimates for the main trends are provided

here; see Supplementary Information S1 for all the trends and statistics. During 1973–2018, temperatures both in autumn (mean temperature, slope  $\pm$  SE:  $0.08 \pm 0.02$ ) and winter ( $0.06 \pm 0.03$ ), and precipitation in winter (cumulative precipitation, slope  $\pm$  SE:  $0.60 \pm 0.27$ ) increased, but trends for these variables were not significant during 2003–2018. The number of freezing days and the number of freeze–thaw events in October declined during 1973–2018, but not during 2003–2018. During the two food-hoarding months (15 October–15 December) in autumn, more marked trends emerged during 1973–2018, but again not in the short-term period. For these food-hoarding months there was in the long term not only a decline in the number of freezing days, but also an increase in the mean, average minimum and average maximum temperatures, and both in the long and short term a decline of the number of days with >10 cm of snow. The average snow depth also tended to decline, albeit non-significantly. Since 1973, the cumulative precipitation and minimum temperature during the winter months (15 December–15 March) increased and the number of freezing days and the number of freeze–thaw events declined both during 1973–2018 and 2003–2018.

## 4 | DISCUSSION

Our study revealed strong effects of weather on an important aspect of the biology of boreal animals in winter, a rarely studied time of their annual cycle. Variation in food hoarding of pygmy owls was a result of a complex combination of climatic variables, main prey abundance and interactions between age and sex of owls. The number of freeze–thaw events, precipitation and snow cover during the hoarding season were the main weather variables that best explained variation in food-hoarding behaviour of pygmy owls. First, we found that pygmy owls started hoarding food early in the autumn when there was a high number of freeze–thaw events before the food-hoarding season and they also tended to start later in recent years. Pygmy owls consumed more hoarded food already in autumn with increasing number of freeze–thaw events and depth of snow layer. During the winter, the probability of using the hoard increased with more frequent freeze–thaw events. The proportion of prey items that was used increased with lower precipitation, deeper snow cover and, for yearling owls, with more frequent freezing days. More food hoards were found rotten with more frequent precipitation days during the autumn. Food hoards were found decayed more often in late November to early December, if they were already present 1 month earlier. Rotten food hoards were used more in years of vole scarcity. Having rotten food hoards was linked with a lower future recapture probability in female owls, indicating that they either died or permanently emigrated from the area. The long-term trends in the weather-related variables that had influence on the food hoarding of pygmy owls indicate that this behaviour will change with changing climate, which may have important consequences in the boreal food webs.

### 4.1 | Initiation of food hoarding

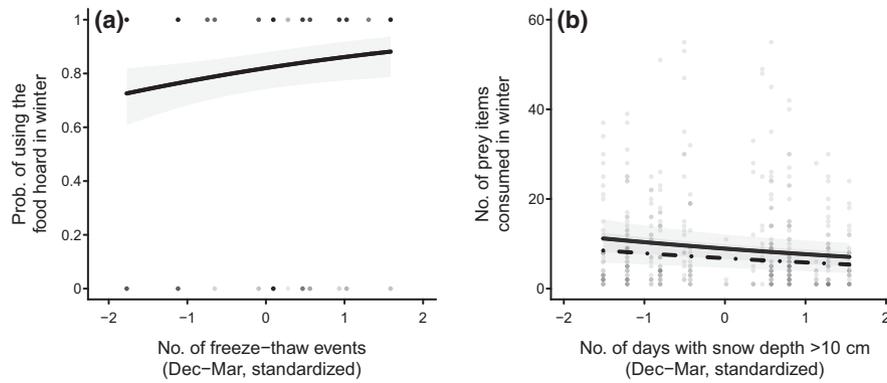
In accordance with our expectation (i), a low number of the freeze–thaw events delayed the beginning of the hoarding by pygmy owls.

Response	Explanatory	Estimate $\pm$ SE	$\chi^2$	<i>p</i>
<b>(a) Probability of use in winter (N = 496)</b>				
	(Intercept)	1.510 $\pm$ 0.259		
	No. of freeze–thaw events–Dec to Mar	0.307 $\pm$ 0.130	5.58	<b>.0181</b>
	Age (Yr)	–0.086 $\pm$ 0.250	0.12	.7317
	Sex (M)	–0.003 $\pm$ 0.238	0.00	.9892
	Vole index	–0.348 $\pm$ 0.121	8.29	<b>.0040</b>
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	211	0.000	
	Individual ID	301	0.157	
<b>(b) No. of prey items consumed in winter (N = 394)</b>				
	(Intercept)	2.251 $\pm$ 0.100		
	No. of days with snow depth >10 cm–Dec to Mar	–0.150 $\pm$ 0.054	7.74	<b>.0054</b>
	Year	–0.150 $\pm$ 0.048	9.62	<b>.0019</b>
	Age (Yr)	0.029 $\pm$ 0.101	0.08	.7731
	Sex (M)	–0.273 $\pm$ 0.098	7.71	<b>.0055</b>
	Vole index	0.149 $\pm$ 0.057	6.87	<b>.0088</b>
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	193	0.049	
	Individual ID	258	0.162	
<b>(c) Proportion of prey items consumed in winter (N = 394)</b>				
	(Intercept)	1.069 $\pm$ 0.321		
	No. of freezing days–Dec to Mar	–0.132 $\pm$ 0.228	3.18	.0747
	No. of freezing days–Dec to Mar $\times$ Age (Yr)	0.821 $\pm$ 0.272	9.12	<b>.0025</b>
	Average snow depth–Dec to Mar	0.043 $\pm$ 0.202	1.80	.1799
	Average snow depth–Dec to Mar $\times$ Sex (M)	0.403 $\pm$ 0.227	3.13	.0767
	Cumulative precipitation–Dec to Mar	–0.376 $\pm$ 0.184	4.17	<b>.0413</b>
	Year	–0.398 $\pm$ 0.190	4.39	<b>.0362</b>
	Age (Yr)	0.057 $\pm$ 0.226	0.43	.5124
	Sex (M)	0.731 $\pm$ 0.385	3.37	.0665
	Vole index	–0.399 $\pm$ 0.115	12.01	<b>.0005</b>
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	193	2.994	
	Individual ID	258	5.860	

**TABLE 4** Generalized linear mixed-effect models analysing the probability of use of a pygmy owl's food hoard (a) and, if used, the number (b) and proportion (c) of prey items consumed during the winter in relation to climatic variables (15 December–15 March), pygmy owl sex (M = estimate of males) and age (Yr = estimate of yearlings) and autumn vole abundance (vole index) during 2003–2018. Interactions between terms are indicated with 'x', and significant variables ( $p < .05$ ) are shown in bold. For categorical variables, parameter estimates are given relative to a reference category indicated among brackets

Also as expected (iv, v), the food hoarding started later at high vole abundance, and yearlings started earlier than adults. We also found that the initiation of food hoarding tended to become later over the 16 years of the study. In our study area, the temperatures in October were generally above zero, so a decrease in the number of freeze–thaw events is caused by an increase in the minimum temperature. Our result therefore provides support for the earlier notion that pygmy owls initiate to collect food hoards

when daily temperature drops below 0°C in autumn (Schulenburg & Wiesner, 1986; Solheim, 1984). The novelty of our result is that the decrease in temperature, indicated by freeze–thaw events, might provide a better cue for food-hoarding individuals than other temperature variables. High abundance of voles in the environment might, however, induce owls to slightly delay food hoarding due to the high availability of every-day hunting opportunities; in a low vole abundance year it might take longer to accumulate a



**FIGURE 5** Probability of using the food hoard (a) and no. of hoarded prey items consumed (b, and 95% CI) by pygmy owl in relation climatic variables during the winter (15 December–15 March). If present, different line marks represent sex differences (continuous line for females and dot-dashed line for males). Predicted lines are calculated using average values of the other continuous variables. Observed values are represented with dots, with darker colours meaning larger number of observations

sufficient food hoard. The high variability in the initiation of the food hoarding and the relationship with climate and food availability support the idea that photoperiod might not be a main determinant of food-hoarding behaviour, as also found by a previous study on a food-hoarding passerine (the black-capped chickadee *Poecile atricapillus*; Karpouzos, Hernandez, MacDougall-Shackleton, & MacDougall-Shackleton, 2005). Overall, the delaying trend in the beginning of the food-hoarding season during the course of the study indicates a likely effect of global warming on the phenology of this behaviour.

#### 4.2 | Accumulation and consumption of the hoarded prey in relation to climate

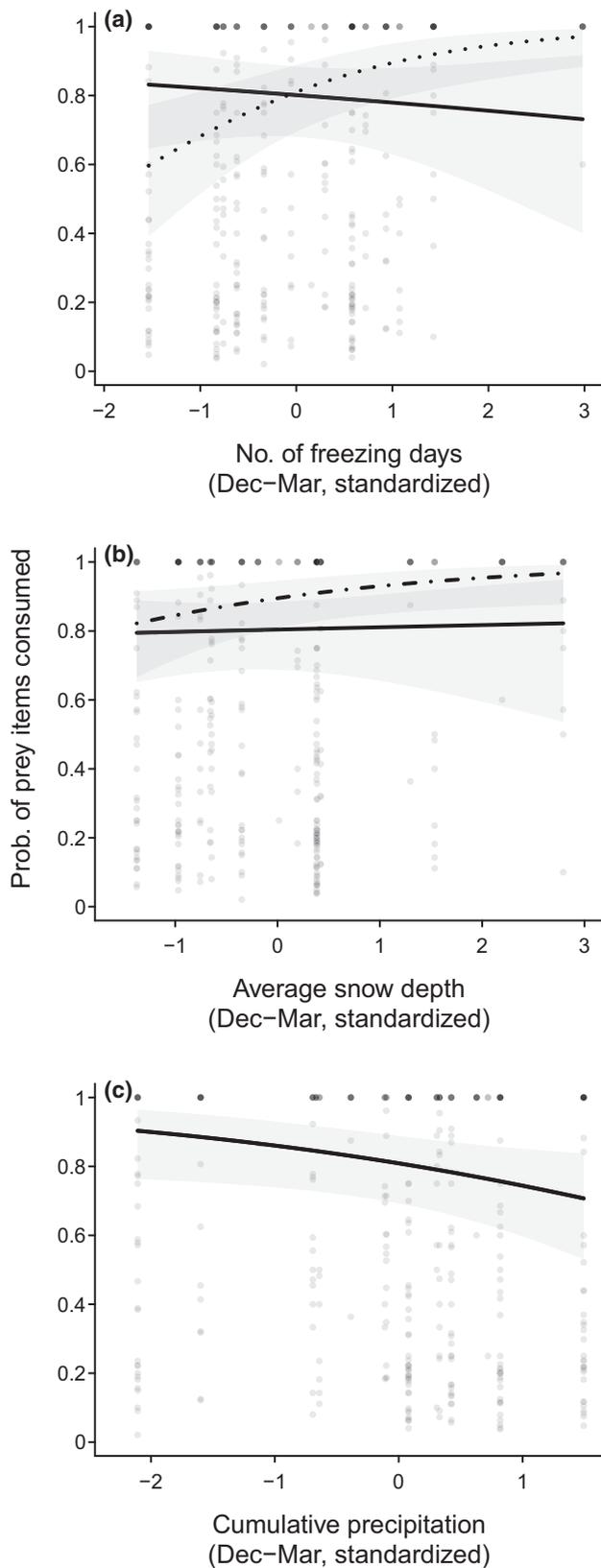
We were not able to confirm the prediction on the negative effect of deep snow cover on the accumulation of new prey items during autumn (ii), despite being in the best model, there was no significant effect of snow cover. Nonetheless a higher vole abundance led to a larger number of prey items accumulated during the autumn (prediction v). Although it did not affect accumulation of prey, snow cover affected the consumption of hoarded food. Indeed, the consumption of new prey items during autumn increased with a high number of days with a snow cover >10 cm (in accordance with what we expected [iii]), but only in adults, while yearlings kept a more constant consumption. Also during winter, a deep snow cover for both age classes of owls were associated with a high proportion of hoarded prey items being consumed by pygmy owls. A long period with a deep snow cover can reduce availability of small mammals to hunting pygmy owls (Korpimäki, 1986; Sonerud, 1986; Szép, Bocz, & Purger, 2018), therefore leading to the consumption of hoarded food. This result is consistent with earlier studies on the accumulation and consumption of prey items in relation to the date of permanent snow cover (Halonen et al., 2007). In addition, we also found that a high number of freeze–thaw events in autumn and of freezing days in winter was linked with an increase in consumption, which could be explained by an increase in the metabolic needs of owls due

to the high fluctuation in temperature (Prinzinger, 1982). As found previously (Masoero et al., 2018), females hoarded more prey items than males, but in contrast with our expectations (vi) no age differences were found in the accumulation of prey items.

The overall percentage (65%) of hoarded prey items that were consumed during the winter was similar with a previous study (61%, Halonen et al., 2007). Harsh wintering conditions and colder weather and precipitation may impair everyday hunting and likely lead to an increase in the use of the hoarded food, especially for inexperienced yearlings. As explained for the increase in the consumption in autumn, also through the winter small mammals may be less available due to the deeper average snow cover (Sonerud, 1986; Szép et al., 2018). A high number of freeze–thaw events indicates a mild winter; a larger number of owl individuals might be able to overwinter and survive in the study area in such conditions and also the hoarded food items might be actually easier to eat because they are not completely frozen.

#### 4.3 | Effect of rotten hoards on owls

As expected (iv), food hoards that were already present at the first inspection showed a much higher decaying status compared to more recent hoards in the end of the hoarding season (late November–early December). They also showed higher rotting with more frequent days with precipitation during the food-hoarding season. Contrary to our expectations (iv, vii), there seemed to be no immediate link between rotting and temperature in autumn and no temporal trend in the rotting of the prey items. As shown by Sutton et al. (2016), humidity brought by heavy rain and snow precipitation can increase microbial growth and proliferation, and contribute to the degradation of perishable food. Throughout the winter, the rotting of the hoarded prey could be furthermore facilitated by higher precipitation and temperatures and larger number of freeze–thaw events of the more recent winters, but unfortunately the data in our possession did not allow to inspect the status of the hoards and the rotting throughout the winter.



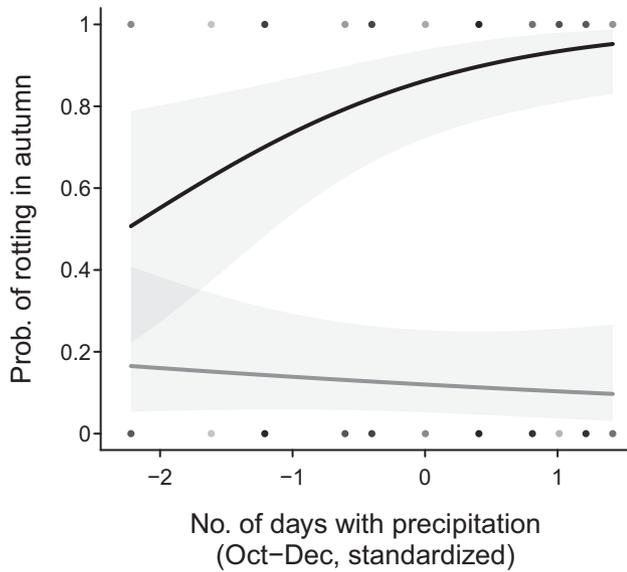
The probability of using the food hoard and the proportion of prey items used during the winter was higher from fresh food hoards than from hoards that were rotten at the last autumn inspection. This difference was, however, only apparent in years

**FIGURE 6** Proportion (and 95% CI) of hoarded prey items consumed by pygmy owl in relation to number of freezing days (a), snow cover (b) and precipitation (c) during the winter (15 December–15 March). If present, different line marks represent age (continuous line for adults and dotted line for yearlings) or sex (continuous line for females and dot-dashed line for males) differences. Predicted lines are calculated using average values of the other continuous variables. Observed values are represented with dots, with darker colours meaning larger number of observations

**TABLE 5** Generalized linear mixed-effect model analysing the probability of rotting of prey items during the food-hoarding season of pygmy owls in relation to the number of days with precipitation (15 October–15 December), if the hoard was already present at the first inspection (Yes or No), pygmy owl sex (M = estimate of males) and age (Yr = estimate of yearlings) and autumn vole abundance (vole index) during 2003–2018. The variable ‘inspection date’ (standardized number of days between the second inspection of the boxes and the autumn equinox) was included in the model to control for variability in the inspection date. Interactions between terms are indicated with ‘x’, and significant variables ( $p < .05$ ) are shown in bold. For categorical variables, parameter estimates are given relative to a reference category indicated among brackets.  $N = 408$  food hoards

Explanatory	Estimate $\pm$ SE	$\chi^2$	$p$
(Intercept)	$-2.145 \pm 0.476$		
No. of days with precipitation–Oct to Dec	$-0.168 \pm 0.239$	1.39	.2381
No. of days with precipitation–Oct to Dec $\times$ Hoard at 1st inspection (Yes)	$0.982 \pm 0.381$	6.66	<b>.0099</b>
Hoard at 1st inspection (Yes)	$3.829 \pm 0.623$	31.13	<b>&lt;.0001</b>
Age (Yr)	$0.107 \pm 0.387$	0.08	.7821
Sex (M)	$-0.021 \pm 0.393$	0.00	.9566
Vole index	$-0.128 \pm 0.187$	0.47	.4931
Inspection date	$0.743 \pm 0.203$	13.33	<b>.0003</b>
<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
Forest site	199	0.000	
Individual ID	246	2.640	

of high main food abundance, while in years of low food abundance, the use of rotten food increased to similar level to that of fresh food. The use of partially rotten prey items by owls has been shown before (Roulin, 2004), but we are not aware of any previous study on the possible detrimental effects that eating rotten food could have on avian and mammalian predators. Pygmy owls have been shown to clean old nest material from the boxes before the breeding season (Baroni, Korpimäki, Selonen, & Laaksonen, 2020). It is therefore possible that rotten prey items are not consumed but thrown away, but this was never observed during



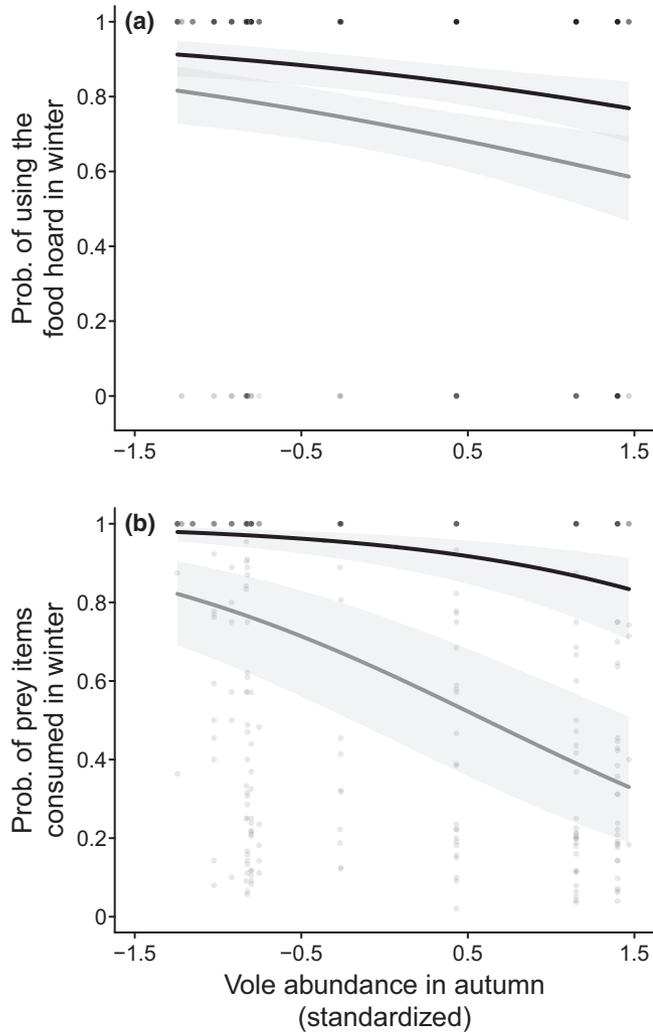
**FIGURE 7** Probability (and 95% CI) of rotting of the prey items during the food-hoarding season of pygmy owls if the hoard was present already at the first inspection (late Oct to early Nov; black line) or started later (late Nov to early Dec; grey line), in relation to the number of days with precipitation during the food-hoarding season (15 October–15 December). Predicted values are calculated using average values of the other continuous variables. Observed values are represented with dots, with darker colours meaning a larger number of observations

**TABLE 6** Generalized linear mixed-effect models analysing the probability of use of a pygmy owl's food hoard during winter (a) and, if used, the proportion (b) and number (c) of prey items consumed during the winter in relation to its freshness (fresh/rotten) and autumn vole abundance (vole index) during 2003–2018. Significant variables ( $p < .05$ ) are shown in bold. For categorical variables, parameter estimates are given relative to a reference category indicated among brackets

Response	Explanatory	Estimate $\pm$ SE	$\chi^2$	$p$
(a) Probability of use in winter ( $N = 385$ )				
	(Intercept)	1.820 $\pm$ 0.197		
	Freshness (rotten)	-0.854 $\pm$ 0.259	10.83	<b>.0016</b>
	Vole index	-0.421 $\pm$ 0.133	9.99	<b>.0010</b>
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	195	0.000	
	Individual ID	243	0.000	
(b) Proportion of prey items consumed in winter ( $N = 304$ )				
	(Intercept)	2.822 $\pm$ 0.360		
	Freshness (rotten)	-2.321 $\pm$ 0.300	59.89	<b>&lt;.0001</b>
	Vole index	-0.825 $\pm$ 0.120	47.87	<b>&lt;.0001</b>
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	174	4.145	
	Individual ID	205	8.239	
(c) No. of prey items consumed in winter ( $N = 304$ )				
	(Intercept)	2.124 $\pm$ 0.100		
	Freshness (rotten)	-0.016 $\pm$ 0.105	0.02	<b>.8801</b>
	Vole index	-0.098 $\pm$ 0.051	3.63	<b>.0566</b>
	<b>Random effects</b>	<b>N</b>	<b>Variance</b>	
	Forest site	174	0.052	
	Individual ID	205	0.133	

inspection of food hoards in early spring in the surroundings of the hoard.

As predicted (viii), female owls with rotten food hoard in autumn had lowered recapture probability. This result indicates that the local survival of females is reduced because of the spoilage of the hoarded food, which could be due to either increased mortality or increased dispersal of females from the study area. Larger female owls accumulate more voles in the food hoards during winter than do smaller males that might be better able to capture birds and therefore hunt on a day-to-day basis (Masoero et al., 2020). Even if food hoards did not rot, previous studies have shown that cached food has lower quality than fresh food (Careau, Giroux, Gauthier, & Berteaux, 2008; Sutton et al., 2016), and this loss in quality is faster with higher temperatures (Sechley et al., 2015). Therefore, food limitation in female owls can be induced both by the use of poor-quality or rotten food, or by the effort of hoarding a large amount of food that cannot be used. This spoilage-induced food limitation could be highly detrimental especially for female owls since they should be in good body condition because of their parental investment in the future breeding season. This is supported by the fact that increasing frequency of days with precipitation in the autumn reduced the body condition of female pygmy owls via declined total prey biomass in food hoards (Terraube et al., 2017). In Canada jays, warming temperatures have been connected to the decline of the population (Waite & Strickland, 2006), and the



**FIGURE 8** Probability of using the food hoard (a), and proportion (b, and 95% CI) of hoarded prey items consumed by pygmy owl if the hoard was categorized as fresh (black) or rotten (grey), in relation to the vole abundance index in autumn. Observed values are represented with dots, with darker colours meaning larger number of observations

number of freeze–thaw events in the autumn decreased the reproductive success, brood size and nestling condition in the following spring (Sutton et al., 2019).

In a climate change scenario, postponing the initiation of the food-hoarding season with the warming temperatures, might help to reduce the likelihood that the food hoard deteriorates during the autumn, and therefore increase the overwinter survival of owls. Our work provides a first evidence in this direction. The strategies to limit hoard degradation are several (handling techniques, exploitation of chemical properties in the environment and exploitation of certain climatic factors to decrease food perishability; review in Sutton et al., 2016), but, as far as we know, there is no earlier evidence of adaptation of food-hoarders by postponing the start of the food-hoarding season. Opposing effects of weather conditions (e.g. early snow accumulation or altered precipitation) might determine a start of the food-hoarding season that is not optimal with respect to

**TABLE 7** Generalized linear mixed-effect models analysing the probability of recapturing of food-hoarding pygmy owls in the future (following spring or years) in relation to the freshness (fresh/rotten) of the food hoard, autumn vole abundance (vole index) and sex (M = estimate of males) and age (Yr = estimate of yearlings) of the individual, during 2003–2018. Interactions between terms are indicated with ‘x’, and significant variables ( $p < .05$ ) are shown in bold. For categorical variables, parameter estimates are given relative to a reference category indicated among brackets

Explanatory	Estimate $\pm$ SE	$\chi^2$	<i>p</i>
(Intercept)	-0.711 $\pm$ 0.312		
Freshness (rotten)	-0.820 $\pm$ 0.430	0.37	.5413
Freshness (rotten) $\times$ Sex (M)	1.109 $\pm$ 0.559	3.92	<b>.0475</b>
Age (Yr)	-0.134 $\pm$ 0.271	0.24	.6219
Sex (M)	0.756 $\pm$ 0.326	15.63	<b>&lt;.0001</b>
Vole index	0.216 $\pm$ 1.133	2.64	.1040
Removed terms			
Freshness (rotten) $\times$ Age (Yr)	-0.202 $\pm$ 0.565	0.12	.7203
Freshness (rotten) $\times$ Vole index	-0.048 $\pm$ 0.311	0.02	.8768
Random effects	N	Variance	
Forest site	195	0.000	
Individual ID	243	0.000	



**FIGURE 9** Probability of recapture (black line) and 95% CI (in grey) of food-hoarding pygmy owls in the following spring or later on in relation to sex of the individual (f, females; m, males) and freshness (fresh/rotten) of the food hoard at the time of the second inspection (late Nov to early Dec)

the temperature. Nonetheless, several are the questions that remain unanswered—for example, will owls adapt and stop hoarding food or will they keep on wasting energy in hoarding prey that will get spoiled and might lower their survival in the long term?

#### 4.4 | Climate change and food-hoarding predators

In high latitude ecosystems, including our study area, autumns have already become warmer, and winters have become milder with increasing precipitation. Temperature changes were not strong during the short-term study period, but show clear trends in the long term and are predicted to continue along this path (Collins et al., 2013). Thermal seasons are predicted to change in the northern European countries, with a strong decrease in the length of the thermal winter (Ruosteenoja, Markkanen, & Räisänen, 2020; Ruosteenoja, Räisänen, & Pirinen, 2011).

Freeze–thaw events, precipitation and snow cover, all of which are weather characteristics that are highly susceptible to climate change, determine variations in the main traits of the food hoarding of pygmy owls. Increased precipitation together with the increase in temperature will lead to wetter autumns and winters, likely with a decrease in the snow cover and an increase in rainfall. On one hand, mild winters and a shallow snow cover mean unfavourable conditions for the hoarded food, but could favour overwinter survival and everyday foraging throughout the winter (Mysterud, 2016). On the other hand, the increase in temperature and in the number freeze–thaw events leads to the formation of ice layers in the snow cover (Marsh & Woo, 1984), which makes it more difficult for aerial predators to hunt by penetrating through the snow cover. An increase in precipitation in winter could furthermore impair flying and prey capture, since a high number of days with precipitation in the autumn reduced food-hoard biomass in pygmy owls (Terraube et al., 2017). Increasingly unpredictable and extreme weather patterns may further contribute negatively on the foraging and food hoarding of overwintering predators, but this question remains unstudied. Future studies are also needed to better quantify the effect of changes in climate and food-hoarding conditions on the winter survival and reproduction of pygmy owls and other food-hoarding predators.

## 5 | CONCLUSIONS

This work is an important first step in understanding how climate change can impact predator–prey interactions during winter (the non-breeding season). Previous studies on the effect of climate change on predator–prey interactions mainly focus on the match–mismatch processes in insectivorous birds (e.g. Both, van Asch, Bijlsma, van den Burg, & Visser, 2009; Burgess et al., 2018) and birds of prey and voles (review in Bretagnolle & Terraube, 2019) during the breeding season. In addition, black bear (*Ursus americanus*) predation on caribou (*Rangifer tarandus*) has been shown to be facilitated by time-lagged higher summer growing degree days, whereas coyote (*Canis latrans*) predation increases with current precipitation and winter temperature (Bastille-Rousseau et al., 2018).

We conclude that by increasing the frequency of freeze–thaw events and precipitation, as well as by modifying the structure of the snow cover, global warming and increasing precipitation can lower overwinter survival of pygmy owls, because their ‘freezers’ may no longer work properly in boreal regions. Unexpectedly, we found that

pygmy owls may partly be able to adapt to climate change by delaying the initiation of food-hoard collection and that they also quite often consumed rotten prey, which may, however, be poor-quality food. During winter, altered usability and overall quality of the hoarded food may further modify the overall predation pressure by pygmy owls on prey species, because they may have to hunt more small birds to compensate for the rotten food items in hoards. These mismatches, trophic cascades and regime changes can have negative impacts both at the population (predator or prey abundances) and at the community level (e.g. Mills et al., 2013; Post, Peterson, Stenseth, & McLaren, 1999). Our findings together with the global future predictions thus suggest that climate change has the potential to strongly impair the foraging behaviour and food intake of wintering predators, likely impacting the whole boreal food web.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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