TITLE PAGE

Title: A picky predator and its prey: how climate change may impact a ptarmigan specialist.

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MAIN TEXT

Abstract

Species interactions can be altered by climate change but can also mediate its effects. A predator-prey couple reflecting the dynamics of boreal and alpine ecosystems is the gyrfalcon (Falco rusticolus) and the ptarmigan (Lagopus spp.). To determine how climate change may impact the alpine food web, we investigated how ptarmigan abundance and local weather impacts gyrfalcon diet and feeding behaviour, territory occupancy and reproductive success. Using wildlife cameras, we monitored gyrfalcon nests throughout the nesting period to collect data on diet and feeding behaviour. We quantified the gyrfalcon's functional response by describing how ptarmigan kill rates relate to ptarmigan density. The gyrfalcon's numerical demographic and aggregative response were quantified by describing how gyrfalcon reproductive success and territory occupancy, respectively, were related to ptarmigan density, using data from large scale monitoring projects. Ptarmigan were the dominant prey species, occupying 98% of the diet. The proportion of ptarmigan in the gyrfalcon diet, gyrfalcon breeding success, and gyrfalcon territory occupancy increased when spring arrived later, but reproductive success decreased with more snow during the nesting period. Gyrfalcon reproductive success was positively related to ptarmigan density, i.e., a positive numerical demographic response, but gyrfalcon territory occupancy or the ptarmigan kill rate were not related to ptarmigan density. These results indicate that the effect of climate change is not straightforward, and investigating how (a)biotic factors impact both prey and predator is relevant in predicting how a predator will respond to climate change. Following current climate predictions, onset of spring will become earlier, which will change the food web structure through prey availability and diversity, and through interactions with other species. This requires adaptations from gyrfalcons and other predators. We emphasize that the impact of climate change on predators and other species can be more accurately evaluated on a multi-species level, rather than individually.

Keywords: *Falco rusticolus*, *Lagopus spp.*, predator-prey dynamics, functional response, numerical response, climate change.

Introduction

Species interactions are at the foundation of ecosystem functioning, and they can play a role in mediating the impact of climate change on biodiversity (Åkesson et al., 2021; Alexander et al., 2015). Increasing temperature and changes in weather and precipitation patterns due to climate change (IPCC, 2023), pose a threat to biodiversity and functioning of ecosystems (Scheffers et al., 2016; Trew & Maclean, 2021; Zhang et al., 2013). Several studies have reported that environmental change can significantly alter food web dynamics and predator-prey interactions (Bestion et al., 2019; Petchey et al., 1999). Predators may be forced to adjust their diet and switch to alternative prey when a certain prey species declines throughout their distribution (Winfield et al., 2012). A local decline of top-predators can cause a so-called trophic cascade, leading to a shift in food-web dynamics and increased population growth of species in the trophic levels below. Therefore, studies have argued that species interactions should be included in the framework for climate change predictions, rather than solely focusing on the direct effect of climate on a single species (Araújo & Rozenfeld, 2014; Cahill et al., 2013; Gilman et al., 2010). Predator-prey interactions can occur across multiple trophic levels, which makes them highly relevant to study in the context of environmental change (Allesina & Pascual, 2008; Laws, 2017).

Higher trophic levels are affected by climate change disproportionally, since they are also indirectly affected by changes in lower trophic levels (Voigt et al., 2003). Specialist predators face particular vulnerability, because they rely mainly on a single prey species. Their preferred prey species can decline in numbers due to a changing environment, but availability of this prey can also decline, e.g. due to changed habitat structure impacting camouflage or shelter from vegetation (Morin et al., 2021; Zimova et al., 2020). Unlike generalist predators, specialists cannot easily switch to other prey species when availability of their prey species declines. Therefore, assessing the resilience of a specialist predator species to a changing climate involves understanding how their hunting rates and productivity are impacted by fluctuations in the prey population (Peers et al., 2014; Terraube et al., 2015). Evaluating their resilience will also contribute to our ability to anticipate future changes in the food web, given the crucial role predators play in this process.

At higher latitudes or altitudes climate warming is more pronounced (Brunetti et al., 2009; IPCC, 2023), and food webs tend to be relatively simple due to lower species diversity (Gibert, 2019; Paine, 1966). In this study we focus on the bottom-up effect and aim to investigate how diet and demographics of a specialist top predator in an alpine ecosystem are affected by fluctuating prey abundances and climate variables. The focal predator-prey couple is the gyrfalcon (*Falco rusticolus*) and the ptarmigan (*Lagopus spp.*: willow ptarmigan *Lagopus lagopus* or rock ptarmigan *Lagopus muta,* hereafter collectively referred to as ‘ptarmigan’), which live and breed in alpine and sub-alpine areas in central Norway. Both species have a circumpolar breeding distribution, and the entire breeding range of the gyrfalcon overlaps with at least one of the ptarmigan species (Nielsen & Cade, 2017). In several studies, the importance of ptarmigan abundance for gyrfalcon populations has been demonstrated (Barichello & Mossop, 2011; Hagen, 1952a; Nielsen, 1999). Almost all studies on gyrfalcon diet and feeding behaviour show that ptarmigan are the dominant prey species and constitute 50-100% of the diet, suggesting that the gyrfalcon behaves as a specialist predator to a large extent (Booms & Fuller, 2003a; Koskimies & Sulkava, 2011; Robinson et al., 2019), but see Muir and Bird (1984). Though ptarmigan remain the dominant prey throughout the year, the same studies also show that alternative prey, such as migratory birds and small rodents, generally become more evident in the gyrfalcon diet later in the season.

In most strongly linked predator-prey couples, predator behaviour and population dynamics respond to changes in prey abundance and availability. A common method to quantify this relationship is to analyse the functional and numerical response (Solomon, 1949). The functional response describes how prey density affects a predators’ kill rates or consumption rates of a specific prey species (Abrams, 2022), and following Holling (1966), can resemble one of four curve types. The shape of the curve is primarily influenced by kill rate and prey density, with kill rate itself depending on the time spent searching for, handling, and processing prey. For a specialist predator a type II response is typical (Abrams, 1990; O'Donoghue et al., 1998), which describes that kill rate increases with prey density at a decelerating rate, and the predator is limited by its prey processing capacity. The numerical response can be divided into two parts, i.e. the numerical demographic response and the numerical aggregative response. The numerical demographic response describes the relationship between prey density and predator reproductive success, whereas the aggregative response describes the relationship between prey density and territory occupancy of the predator (Bayliss & Choquenot, 2002; Oksanen et al., 2001). For predators that depend on a specific prey species, one would expect a positive relationship in both cases. For species that do not reach their reproductive age in their first year of life, such as the gyrfalcon, the numerical aggregative response may be delayed (Nielsen, 1999).

Compared to other raptors, the breeding density of gyrfalcons in Scandinavia is low, but the population is considered stable (Artsdatabanken, 2021; Franke et al., 2020). Studies show contrasting patterns about the effect of a phenological shift towards warmer springs on ptarmigan and gyrfalcon reproductive success. Some show that advanced snow melt is beneficial, because it leads to earlier availability of nesting sites for both species (Eriksen et al., 2023; Nielsen, 2011; Wann et al., 2016; Wilson & Martin, 2010). More snow-free vegetation is also associated with higher food availability for ptarmigan, and alternative prey for gyrfalcons such as migratory bird species, can arrive to their breeding grounds earlier. But, not all studies agree (Melin et al., 2020) and increased precipitation in spring could also have a negative effect on reproduction in both species (Clarke & Johnson, 1992; Robinson et al., 2017). Such changes in weather can have a direct effect on gyrfalcon reproductive success by affecting nestling survival, but it may also have an indirect effect through changed hunting success and thus feeding behaviour (Kämpfer et al., 2022; Sergio, 2003). Feeding behaviour and feeding rates play a crucial role in determining fledging success and therefore reproductive success (Grames et al., 2023; Olsen et al., 1998).

To this end, we analysed gyrfalcon diet and feeding behaviour during the breeding season and calculated the functional and numerical response of the gyrfalcons in fluctuating ptarmigan abundances. Comparing this to local weather variables should inform us about the potential effect of climate change on this predator-prey couple. Based on previous studies on this matter we formulated the following main predictions:

1. Ptarmigans are the dominant prey species throughout the breeding season, and the proportion of alternative prey will increase towards the end of this period.

2. Gyrfalcons will show a type II functional response, a positive numerical demographic response, and a positive numerical aggregative response with a time lag of 1-3 years.

3. In years with early snow melt, overall amount of prey delivered will be higher, which will result in higher breeding success and territory occupancy.

Materials & methods

The aims and hypotheses for this study were preregistered and are available online at the Open Science Framework (https://osf.io/jwxqz/?view_only=cf09db96bf6044d0aab53b73db49debb).

Study area

The study was conducted in the northeastern part of central Norway. Gyrfalcon territories are found in alpine and sub-alpine mountain regions with a mean elevation of 667 meters above sea level. The habitat is dominated by heathlands and open woodlands covered by scattered patches of mountain birch (*Betula pubescens*), willow (*Salix spp.*), Norway spruce (*Picea abies*), and Scots pine (*Pinus sylvestris*). The patchy vegetation provides food and shelter for herbivores like ptarmigan, hares (*Lepus timidus*) reindeer (*Rangifer tarandus*) and small rodents. In this area, gyrfalcons generally nest in rocky cliffs, almost solely in nests built by common ravens (*Corvus corax*). Variation of the local weather conditions throughout the gyrfalcon breeding seasons during the study period is shown in figure 1.

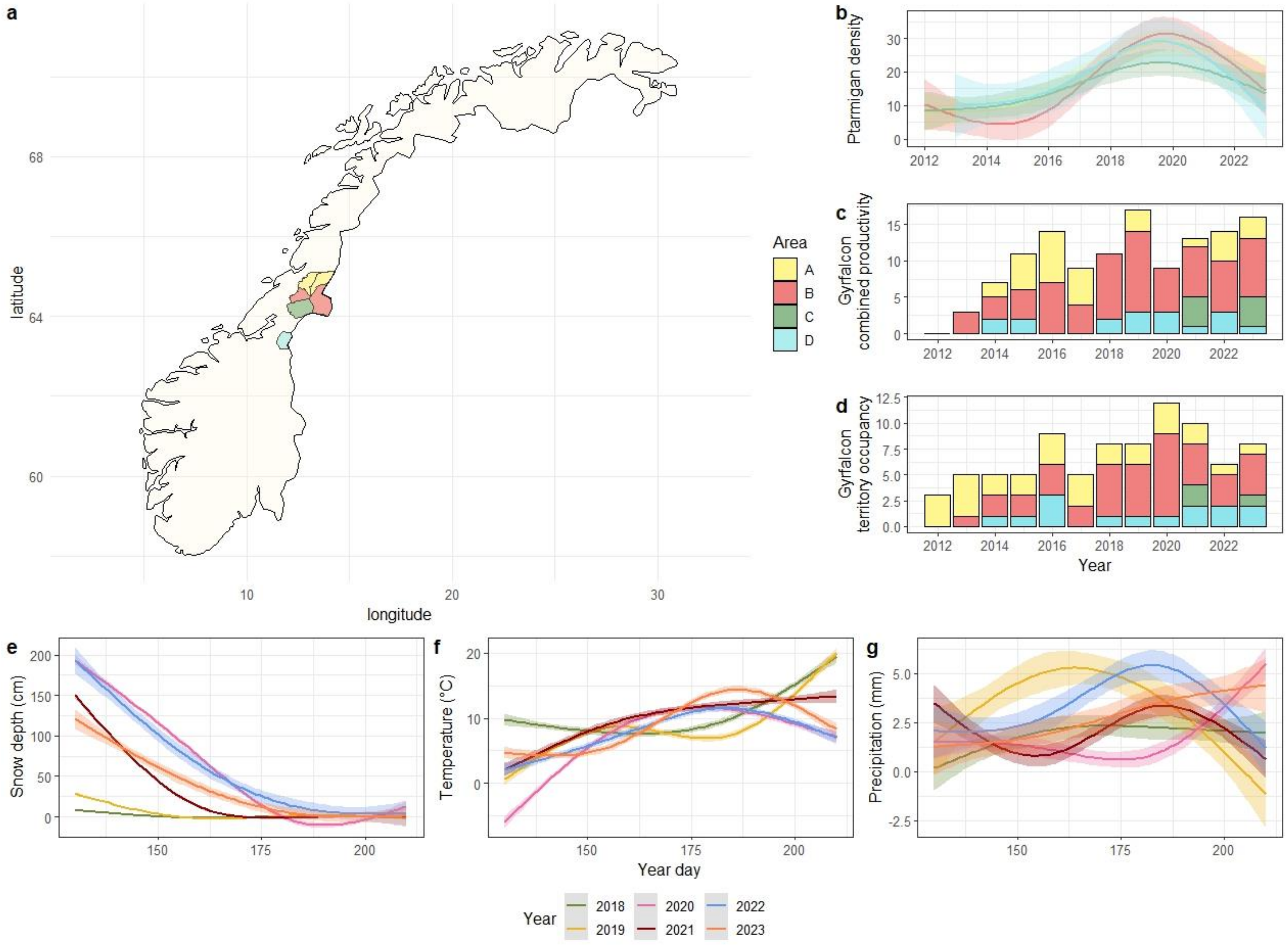

Figure 1. ***(a)*** *The study area and the municipalities included in the study. Northernmost area A consists of municipalities Namsskogan and Røyrvik, B of Grong and Lierne, C is Snåsa, and the southernmost*

*area D is Meråker. (**b**) Estimated ptarmigan densities per area as number of individuals per square kilometre (solid lines), with 95% confidence intervals (shaded ribbons). (**c**) The total number of gyrfalcon nestlings produced per area, i.e. combined productivity, (**d**) The number of occupied gyrfalcon territories per area. (**e**) Estimated relationships between day of the year during the nesting period and predicted snow depth, (**f**) temperature, and (**g**) precipitation. Averages shown in solid lines with 95% confidence intervals (shaded ribbons).*

Data collection procedures

Our analyses were based on four main data sets: i) data from wildlife cameras on gyrfalcon nests, ii) monitoring data of gyrfalcon territory occupancy and reproductive success, iii) ptarmigan abundance data, and iv) gridded weather data, which are each described in more detail below.

Gyrfalcon diet and feeding behaviour

We collected data on diet and feeding behaviour in Lierne municipality from 2018 until 2023. Here, 22 nest sites are monitored for breeding activity annually. We installed two Minox DTC 550 wildlife cameras on a subset of active gyrfalcon nests when the nestlings were between 10 and 20 days old, in late May to early June, and uninstalled them after the nestlings fledged. The cameras recorded activity of the adults and the nestlings from two angles and when the motion sensor was triggered, the cameras were programmed to take pictures with either a 15 or 30 second interval. In 2018 only one camera was installed per nest, set to a 30 second interval. Throughout the study period, we monitored a total of 12 breeding attempts at eight different nests. From the pictures we extracted the following variables about feeding behaviour and diet of the gyrfalcons during the nesting period, every time a prey item was delivered to the nest: i) brood size, i.e. number of nestlings ii) prey species, iii) timing of prey delivery, iv) time spent feeding nestlings v) sex of the parent delivering the prey or feeding the nestlings vi) whether the prey item was a fresh delivery, or a cached item from a previous delivery, which is a common behaviour in gyrfalcons (Booms & Fuller, 2003b). We determined the species of a prey item based on external features, which could be challenging when the prey was plucked and processed before delivery to the nest. Therefore, our dataset contained a significant number of unknown prey items. To address this, we imputed the prey type for missing data cases by estimating the probability that a prey is a ptarmigan for each missing value, using a logistic regression model. The model included sex of the parent delivering the prey, nestling age, precipitation, snow depth and temperature as covariates (see below for a detailed description of the weather variables). Based on these probabilities we drew values from a binomial distribution, 1 for ptarmigan and 0 for alternative prey, to replace missing observations. Throughout the analyses, willow and rock ptarmigan were collectively classified as ptarmigan, as they were virtually impossible to distinguish in the pictures. We assigned an average biomass to each prey species using the AVONET dataset (Tobias et al., 2022) and panTHERIA archives (Jones et al., 2009), for avian and mammalian prey species, respectively. For prey that was classified as a group of species, we used the average biomass of several common species in that category (Table S1). Biomass for unknown prey imputed as ptarmigan was assigned the average biomass for ptarmigan, i.e. rock ptarmigan and willow ptarmigan, and unknown prey imputed as alternative prey was assigned the weighted mean biomass of all alternative prey present in our dataset.

Gyrfalcon population monitoring

We used long term data on gyrfalcon reproductive success and territory occupancy from 2012 until 2023 in four areas (Gjershaug et al., 2008), which consist of six municipalities in total. The areas represent a north-south gradient within the northern part of the county Trøndelag, with A being the northernmost area, and D the southernmost (Fig. 1). In total, 64 nest locations of gyrfalcons are known in all areas combined, which were surveyed nearly every year. The monitoring was done late in the nesting period in June, mostly using helicopters, which is an effective method to survey large areas for raptor activity (Olson et al., 2015). The helicopter flew at a safe distance from nests and could hover, so it was possible to count nestlings with binoculars while disturbance is limited (Grubb et al., 2010). Digital photos of the occupied nests were taken to post-check for errors when counting chicks from the air. Territory occupancy was determined by observing the presence of nestlings in nests or near the nesting site, or by identifying other clear signs of a breeding attempt, such as fresh prey remains, guano stains, and the presence of territorial adults. Gyrfalcon reproductive success was measured as the number of nestlings per nest close to fledging, i.e. nestlings around 42 days old, and territory occupancy was represented by a binary variable being either occupied, or unoccupied.

Ptarmigan abundance

Ptarmigan populations in various regions of Norway are surveyed annually in August using line transects, as part of a monitoring program led by the Norwegian Institute for Nature Research (NINA). Data from the surveys are stored and managed in Hønsefuglportalen, which coordinates grouse line transect surveys across Norway. More detailed information about these surveys can be found in Bowler et al. (2020) and Kvasnes et al. (2018). Data can be accessed through the data portal of Living Norway Ecological Data Network (Nilsen et al., 2022) or via GBIF, and ingested to R using the LivingNorwayR package (Chipperfield et al., 2022). Using the line transect data and the distance sampling method, we estimated abundance and density of ptarmigan in the four areas shown in figure 1. We set up a distance sampling model using the R package Distance (Miller et al., 2019) to estimate annual ptarmigan densities between 2009 and 2023 for each area. In the detection model we used the half-normal key function, a truncation distance of 200 meters and cluster size, i.e. the total number of ptarmigan counted per observation, as a detection covariate. Both rock ptarmigan and willow ptarmigan were included in the ptarmigan density estimates. For all but three municipalities ptarmigan survey data were available for the years between 2009 and 2023. In Grong municipality, ptarmigan line transect surveys were not conducted annually. Lierne is a neighbouring municipality to Grong and since ptarmigan densities tend to be spatially autocorrelated, we used ptarmigan densities from Lierne to extrapolate for area B (Kvasnes et al., 2014). In Meråker the line transect survey data were available from 2013, and for Røyrvik from 2018.

Weather data

Data on weather variables were obtained via the Norwegian Meteorological Institute, using the SeNorge model with the GridTimeSeries API request (Lussana et al., 2018), which provides gridded weather data with a resolution of 1 x 1 kilometre. For each of the nest coordinates in our dataset we extracted daily mean values for temperature (°C), snow depth (cm) and precipitation (mm). For the numerical demographic response analysis, we calculated annual means for each of these variables over the period between 15 May and 1 July, which approximately represents the nestling period. For the numerical aggregative response analysis, we calculated the annual average values for February, as this is approximately when territory establishment occurs in our region (B.C. Moen, pers. comm.). As a proxy for the timing of spring, we used the yearly snow depth on 20 May (SD20), for each of the nest locations. Because the presence of snow is important for the onset of activity of the flora and fauna in spring (Cooper, 2014), we assumed that more snow on the 20 May implies a late onset of spring, and vice versa.

Statistical analyses

All statistical analyses were done using R in R Studio version 2023.09.1, (R Core Team, 2023). An overview of all the models and their structure is shown in Table 1. Rather than pursuing the minimal adequate model, all relevant predictor variables were included in the models following Mundry and Nunn (2009). Interpretation and reporting of the model results were done following Muff et al. (2022), using a combination of p-values and 'language of evidence'. Model assumptions were evaluated through visual inspection of plots from the DHARMa package (Hartig, 2022), to check over- or under dispersion, uniform distribution of the residuals, limit heteroscedasticity and outliers in the model simulations for the linear mixed models, and normally distributed random effects for the generalized linear mixed models. We did not detect multicollinearity in any of the models, which was checked by calculating variance inflation factors (VIF) using the *car* package (Fox & Weissberg, 2019) in R for each of the response variables, with a threshold value of 5.

Diet and feeding behaviour

We analysed diet and feeding behaviour of gyrfalcons based on the nest picture data using linear mixed models and generalized linear mixed models. We set up five models with different response variables that each included the same predictor variables. In our modelling approach AIC selection was used for determining which of two closely related measures for time gave a better model fit, i.e. comparing ‘nestling age’ with ‘Julian day’. An overview of the models and descriptions of each of the response variables used for this part of the analysis are shown as models 1-5 in Table 1. In each of the models, nestID is included as a random effect. This variable indicates the nest location and the year of the breeding attempt, for example ‘A_23’ for nest location A in 2023, so including this as random effect ensures we consider the variation between individual breeding attempts. In model 1 and 2 deliveries of cached prey are excluded from the analysis. For model 2 the modelling assumptions were not met, and this could not be improved by changing model structure. We detected deviations from uniformity of residuals, presence of influential outliers in model predictions and heteroscedasticity. Therefore, interpretation of results based on this model should be approached with caution, as estimates and confidence intervals may be biased and may not fully reflect underlying relationships in the data.

Table 1. Overview of all the models used throughout the analysis. Models are divided up into the different components of the statistical analysis. In two cases the response variable was transformed to adhere to the modelling assumptions. Model numbers are used for reference in the main text. Random factor Nest ID is a combination of the nest location and the year of the breeding attempt.

Model number	Response variable	Transformed	Distribution	Description	Predictor variable(s)	Sample size	Random effect
Diet & Feeding behaviour							
1	Proportion ptarmigan in the diet	No	Binomial	Indicates whether prey brought into the nest is ptarmigan or alternative prey	Julian day, sex, snow depth, temperature, precipitation, SD20 *, nestling age	1062	Nest ID
2	Prey biomass	No †	Gaussian	Biomass of prey items brought into the nest	Julian day, sex, snow depth, temperature, precipitation, SD20, nestling age	1062	Nest ID
3	Total time spent feeding	Square root	Gaussian	Sum of the length of all feeding events per day, per nest, per parent	Nestling age, sex, snow depth, temperature, precipitation, SD20, , nestling age, brood size	321	Nest ID
4	Mean length of feeding	Square root	Gaussian	Mean length of a single feeding event per day, per nest, per parent	Nestling age, sex, snow depth, temperature, precipitation, SD20, , nestling age, brood size	321	Nest ID
5	Prey delivery rate	No	Poisson	Sum of prey delivery events per day, per nest, per parent	Nestling age, sex, snow depth, temperature, precipitation, SD20, , nestling age, brood size	470	Nest ID
Functional response							
6	Weekly kill rate	No	Gaussian	The mean number of ptarmigan killed per week, per nest	Ptarmigan density	42	Year
Numerical demographic response							
7	Combined annual productivity	No	Poisson	The number of chicks produced per area, per year	Ptarmigan density, snow depth, temperature, precipitation, SD20	44	Area
8	Individual reproductive success	No	Poisson	The number of chicks produced per nest, per year	Ptarmigan density, snow depth, temperature, precipitation, SD20	221	Area
Numerical aggregative response							
9	Territory occupancy	No	Binomial	Binary variable indicating whether a nest site is occupied or not	Ptarmigan density autumn, snow depth, temperature, precipitation, SD20	312	Area
10	Territory occupancy	No	Binomial	Binary variable indicating whether a nest site is occupied or not	Ptarmigan density preceding autumn, snow depth, temperature, precipitation, SD20	305	Area
11	Territory occupancy	No	Binomial	Binary variable indicating whether a nest site is occupied or not	Ptarmigan density autumn 2 years ago, snow depth, temperature, precipitation, SD20	300	Area
12	Territory occupancy	No	Binomial	Binary variable indicating whether a nest site is occupied or not	Ptarmigan density autumn 3 years ago, snow depth, temperature, precipitation, SD20	297	Area

* SD20 = Snowdepth on the 20th of May

† Due to very little variation in the data the model assumptions for this model relating to the distribution and normality of the residuals could not be met. Transformations of the data did not improve fit of the model.

Functional response

The functional response was analysed by fitting the data to a type II, a type I and an intercept only model. The model for the type II functional response curve was based on Hollings disc equation (Holling, 1959), but the interpretation of the parameters followed the methods described by Nilsen et al. (2009). The formula is as follows:

$$y = \frac{ax}{h + x}$$

Y is the kill rate as a function of prey density *x*, *a* is the asymptotic kill rate (i.e. the maximum kill rate) and *h* is the half saturation density (i.e. the ptarmigan density where 0.5*a* is reached). We calculated kill rate as the number of ptarmigan brought into each individual nest, sensu Nyström et al. (2005), for each week in the dataset (n=55). Deliveries of prey remains that were cached after the initial prey delivery were excluded in this part of the analysis. For incomplete weeks that only consisted of one to six days, we removed those that spanned fewer than five days (n=14), and weeks with at least five days were adjusted by extrapolating the missing days to obtain a weekly kill rate (n=12). We assigned the corresponding yearly ptarmigan density in Lierne to each of the weeks in our dataset and estimated the nonlinear least-square estimates for a and h. To test for a type I functional response, i.e. a linear relationship in the data, we fitted a linear mixed model with weekly kill rate as response variable, ptarmigan density as the predictor variable and year as random variable (model 8, Table 1). We calculated AIC and R^2 for both models and for an intercept only model to assess their fit to our data. Due to the relatively low sample size and therefore lack of variation in the data we did not have sufficient statistical power to estimate the effects of weather on the functional response or kill rate.

Numerical response

The numerical response was divided into two distinct components: the numerical demographic response relating to breeding success, and the numerical aggregative response relating to territory occupancy, both calculated for the period between 2012 and 2023. For the numerical demographic response, we considered two generalized linear mixed models with the same structure but a different response variable. The first is termed combined productivity, which is the sum of nestlings produced in each area (see Fig. 1) per year, i.e. the combined effect of territory occupancy and reproductive success for each area. When combined productivity is higher, this means the total number of nestlings is higher, which is related to more occupied nests in this area. The second is individual reproductive success, as the number of nestlings produced per nest. We related these two response variables to ptarmigan density and weather, as shown in model 7 and 8 (Table 1). Observations were only included when we were confident about the number of nestlings that was produced at a nest (n=221). For the numerical aggregative response, we included all observations where territory occupancy was assessed (n=319). To account for a potential time lag in the response of the gyrfalcons in territory occupancy, we calculated a 'time-lagged' ptarmigan density for each observation for the same location the year before (t-1), two years before (t-2) and three years before (t-3). Since ptarmigan transect data was not available before 2013 for Meråker, and before 2018 for Røyrvik, a time lag could not be considered for these years and locations. We set up four generalized linear mixed models where territory occupancy is always the response variable, and ptarmigan density with 1-3 year time lags are response variables, together with weather variables for the month February, see models 9 to 12 (Table 1). To correct for temporal autocorrelation in territory occupancy, we incorporated an autoregressive correlation structure into these models using the ar1 function from the glmmTMB package (Brooks et al., 2017).

Results

Diet

By monitoring 12 gyrfalcon nests during the nestling period from 2018 to 2023, we documented 1075 prey deliveries (when excluding 51 cached deliveries, Table S2). After imputation of all unknown prey, including deliveries of cached prey, 1103 prey items were identified as ptarmigan (97,8 %). A complete overview of the model results related to diet and feeding behaviour can be found in Table S3. The proportion of ptarmigan in the diet decreased later in the season (odds ratio (OR) = 0.92, CI: 0.87-0.99, p=0.017). When spring arrived later, indexed by SD20, the proportion of ptarmigan in the diet was greater (OR = 1.05, CI: 1.01-1.09, p=0.010, Fig. 2b). There was no relationship between the proportion ptarmigan in the diet and daily snow depth (p=0.196), temperature (p=0.334) or precipitation (p=0.212). We found weak evidence that males brought in a lower proportion of ptarmigan than females (OR=0.33, CI: 0.01-1.12, p=0.074). The model describing prey biomass did not meet assumptions for valid inference, so the following results should be interpreted with caution. We found evidence for a decrease in prey biomass as the breeding season progresses (β=-0.50, CI: -0.91-0.09, p=0.016), and for an increase in prey biomass when spring arrived later (β=0.25, CI: 0.11-0.39, p=0.001). We found weak evidence that prey biomass decreases with daily snow depth (β=-0.20, CI: -0.31-0.002, p=0.054), but no evidence for a relationship with temperature (p=0.121) or precipitation (p=0.259). Furthermore, there was no difference in prey biomass between prey delivered by males or females (p=0.105).

Feeding behaviour

We recorded a total of 318 feeding events, with a mean feeding time of 40.6 (SE: ± 1.84) minutes per nest per day. When the nestlings became older, the parents spent less time feeding them per day (β=-0.21, CI: -0.25 - -0.18, p<0.001), the average length of a feeding event decreased (β=-0.07, CI: -0.09 - -

0.06, p<0.001), and the number of prey deliveries decreased (IRR=0.98, CI: 0.97-0.99, p<0.001). Males spent less time feeding nestlings per day than females (β=-2.56, CI: -3.05 - -2.07, p<0.001), and brought prey to the nest less frequently (IRR=0.51, CI: 0.42-0.61, p<0.001). We found weak evidence that the mean length of the males' feeding event is shorter than those of females (β=-0.26, CI: -0.51-0.00, p=0.054). The rate of prey delivery increased when brood size was bigger (IRR=1.12, CI: 1.01-1.26, p=0.033), and the time spent feeding per day increased with brood size (β=0.97, CI: 0.49-1.45, p<0.001). Brood size did not affect the mean length of a feeding event (p=0.183). We did not find evidence for a relationship between weather variables and time spent feeding per day (snow depth: p=0.608, temperature: p=0.461, precipitation: p=0.860, SD20: p=0.973), mean feeding time and weather variables (snow depth: p=0.839, temperature: p=0.060, precipitation: p=0.810, SD20: p=0.602) or the prey delivery rate and weather variables (snow depth: p=0.096, temperature: p=0.290, precipitation: p=0.271, SD20: p=0.286).

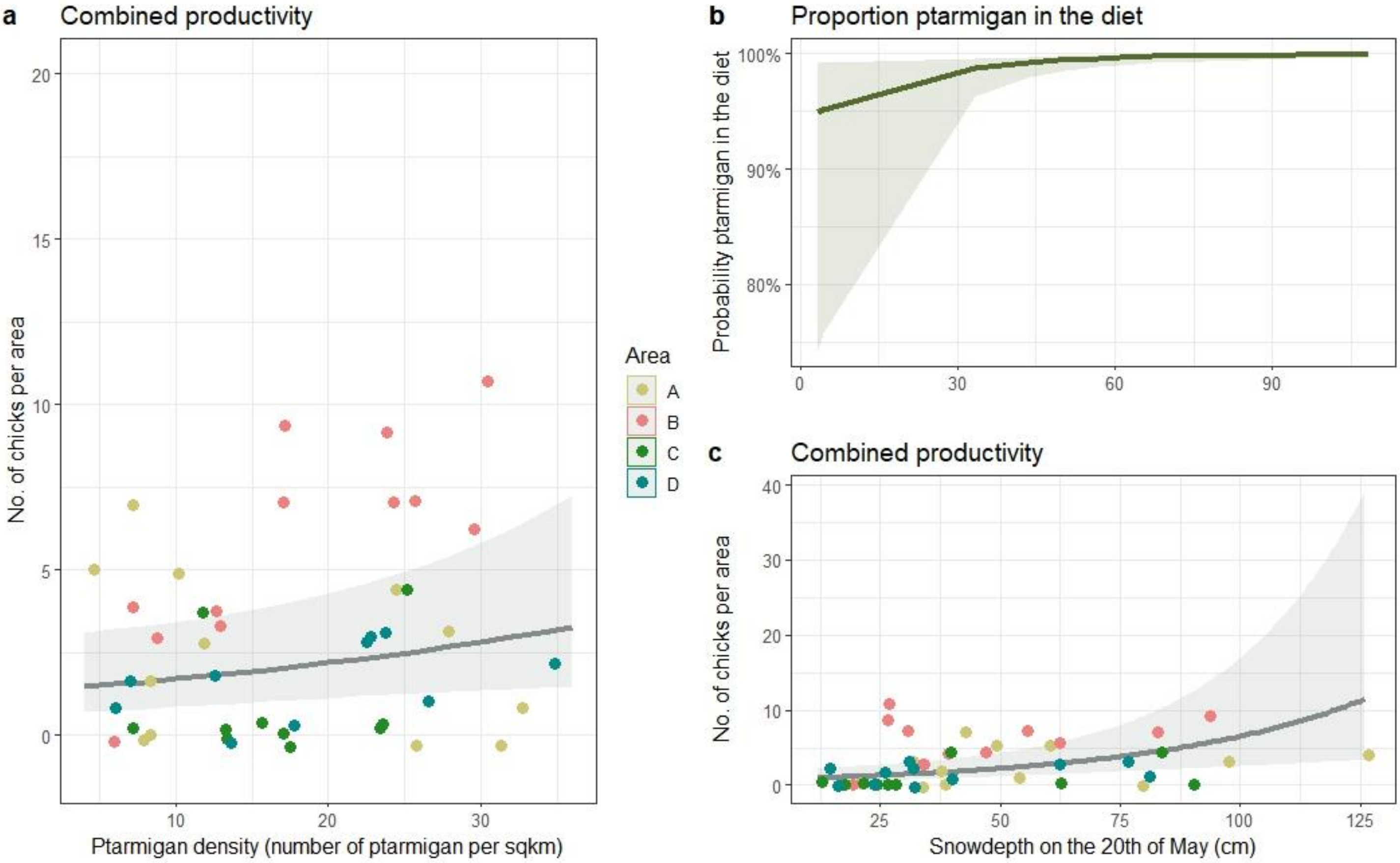

Figure 2. *Model predictions (solid line) and their 95% confidence intervals (shaded ribbons). Left: the relationship between ptarmigan density and reproductive success measured as number of nestlings produced per area, i.e. combined productivity (**a**). Right: the relationship between spring timing, measured as snow depth on the 20th of May, and the proportion ptarmigan in the diet (**b**) and the number of nestlings produced per area (**c**). For combined productivity, raw data points are shown in different colours for the areas A, B, C and D, which is the random factor in these models.*

Functional response

Mean weekly kill rate of ptarmigan fluctuated between 11.0 and 37.0 individuals per nest, with an overall mean of 22.53 (SE: ± 0.95). However, across the range of ptarmigan densities observed in our study [range: 17.1 to 30.4 ptarmigan per km^2], we did not find any clear evidence that the kill rates increased with increasing ptarmigan density, as the intercept-only model (AIC: 274.50) was equally supported by the data as both a type I (AIC: 274.76) and type II functional response (AIC: 274.64). The estimated parameters for the type II functional response were 31.31 (SE: ± 9.31) and 9.47 (SE: ± 10.12) for a and h, respectively. For the type I functional response the slope was estimated at $\beta=0.30$ (CI: -0.26-0.86, p=0.38).

Numerical response

Between 2012 and 2023, we recorded 55 successful gyrfalcon nesting attempts. We found moderate evidence that the combined productivity, i.e. total reproductive success per area, was positively related to ptarmigan density (IRR=1.03, CI: 1.00-1.05, p=0.043, Fig. 2a) and strong evidence that there was a positive correlation with snow depth in mid-May, i.e. SD20 (IRR=1.02, CI: 1.00-1.04, p=0.002, Fig. 2c). We found moderate evidence that combined productivity was negatively related to average snow depth during the breeding period (IRR=0.99, CI: 0.98-1.00, p=0.015). Annual reproductive success per nest showed a positive relationship with SD20 (IRR=1.02, CI: 1.01-1.03, p=0.001), and a negative relationship with average snow depth during the breeding period (IRR=0.99, CI: 0.98-1.00, p=0.003). There was little to no evidence for a positive relationship between ptarmigan density and reproductive success per nest, per year (IRR=1.02, CI: 0.99-1.04, p=0.156).

Of the 319 nest sites surveyed between 2012 and 2023, 84 nest sites were occupied. Our findings did not reveal any correlation between the occupancy of territories and ptarmigan density, regardless of whether we considered a time lag of one-to-three-years (same year: p=0.904, t-1: p=0.722, t-2: p=0.748, t-3: p=0.953, Table S4). Territory occupancy was not influenced by temperature and precipitation (p>0.1, Table S4), but for each considered time lag there was weak evidence for a positive relationship between territory occupancy and snow depth (all: $\beta=0.004$ same year: p=0.073, t-1: p=0.087, t-2: p=0.091, t-3: p=0.090)

Discussion

Gyrfalcons as ptarmigan specialists

In accordance with previous studies on gyrfalcon diet in central (Hagen, 1952a; Langvatn & Moksnes, 1979) and northern Scandinavia (Dementiev & Gortchakovskaya, 1945; Huhtala et al., 1996; Koskimies & Sulkava, 2011; Lindberg, 1984; Nyström et al., 2006), we found that ptarmigan is the main prey species of gyrfalcons in central Norway in the breeding season. During the breeding period, migratory bird species increase in abundance in gyrfalcon territories, and rodents become more readily available. Accordingly, some studies have shown an increase in alternative prey in the diet later in the breeding season (Potapov, 2011; Robinson et al., 2019). Despite a substantial increase in prey diversity (Mellard et al., 2019), we only observed a minor increase of alternative prey in the diet as the breeding season progressed, indicating that adult gyrfalcons in central Norway specialize on ptarmigan throughout the breeding season.

We also investigated gyrfalcon feeding behaviour, and our findings align well with results from previous studies. Female birds invest more time in feeding their nestlings and delivery and feeding rates increase with increasing brood size (Booms & Fuller, 2003b; Sonerud et al., 2014). A decline in feeding rates as nestlings get older may be explained by a reduced energetic need, as they have already passed their peak in energetic requirements before our monitoring period (Konarzewski et al., 1998). We observed no impact of weather variables on feeding behaviour, which suggests that weather primarily influences reproductive success by affecting prey availability or hunting success, rather than through feeding behaviour.

For specialist predators a type II functional response is expected (Holling, 1966). Nyström et al. (2005) revealed a type II functional response of gyrfalcons to ptarmigan density in Sweden, and Nielsen (1999) found evidence for both a type I and type II functional response in Iceland. In our study we found no clear evidence that our data fit a type I or type II functional response. Since kill rates are challenging to calculate for wild populations, sample sizes are often low for such studies (Dale et al., 1994; Nilsen et al., 2009). It is likely that ptarmigan densities differ slightly between gyrfalcon territories, depending on the landscape and vegetation. But, in our analysis we calculated the same yearly ptarmigan densities for all nests within an area, as the line transect data did not allow for more specific density estimates. Besides, the fluctuations in ptarmigan density in our dataset were relatively moderate. A lack of variation in ptarmigan densities may explain why we did not observe a functional response.

Corresponding to our expectations and previous studies (Barichello & Mossop, 2011; Falkdalen et al., 2011; Hörnell-Willebrand, 2008; Nyström et al., 2005), we found a positive numerical demographic response. This relationship is most pronounced when examining combined productivity per area but becomes much weaker, to non-existent, when considering individual nesting success. The numerical aggregative response has not reached consensus in prior studies (Hörnell-Willebrand, 2008; Nielsen, 1999; Nyström et al., 2005; Selas & Kalas, 2007). Our findings could potentially provide clarity to this unresolved issue. 'Combined productivity' is a measure that combines territory occupancy and individual reproductive success. It appears that territory occupancy and reproductive success individually do not show sufficient variation to respond to fluctuating ptarmigan density. However, when combined they do show a correlation with ptarmigan density (Fig. 2a), suggesting that bottom-up control can be an important factor in gyrfalcon population dynamics.

Late springs benefit gyrfalcon reproductive success

In accordance with a study from Iceland (Nielsen, 2011), we found evidence that average snow depth during the breeding period is negatively correlated to both combined productivity and individual reproductive success. This may be attributed to increased nestling survival rates in mild weather and reduced hunting success during poor weather conditions (Fairhurst & Bechard, 2005; Fisher et al., 2015), which is further supported by the indication we found for a negative relationship between prey biomass and daily snow depth. In contrast to these findings, our study revealed that gyrfalcon breeding is more successful the more spring is delayed (i.e. more snow in early spring), that both prey biomass and the proportion of ptarmigan in their diet is higher in later springs, and that territory occupancy seems positively related to snow depth during territory establishment in February. These findings can be complemented by another study from our study area that revealed that ptarmigan mortality is higher in late springs (Eriksen et al., 2024). We propose a few potential interpretations for these findings. Firstly, we speculate that the camouflage mismatch theory could play a role when the transition from white to brown plumage of ptarmigan does not align with the timing of snow melt (Otte et al., 2024; Zimova et al., 2020). This makes ptarmigan more conspicuous and an easy target for predators such as the gyrfalcon, but the same could also happen in very early springs. Secondly, in late springs ptarmigan may be forced to feed on the few snow-free patches where the vegetation is accessible, but they are more exposed to predation. Additionally, due to higher energetic requirements during nesting but lower diet quality with much snow cover (García-González et al., 2016), ptarmigan may also need to spend more time feeding on these few patches when further snow melt is delayed. Finally, in years with late springs, alternative prey species such as migratory birds and rodents are expected to become available later in gyrfalcon territories. With fewer alternative prey available, gyrfalcons are forced to rely even more heavily on ptarmigan, resulting in higher ptarmigan proportions in the gyrfalcon diet and higher mortality rates for ptarmigan. This is likely related to increased gyrfalcon breeding success and territory occupancy, since ptarmigan seem to be their favoured and optimal prey species (Nielsen & Cade, 1990).

Predators in a changing world

In many areas onset of spring is advancing due to the warming climate (Inouye, 2022; Parmesan & Yohe, 2003). Across natural ecosystems mismatches in food availability can have significant consequences, especially at high latitudes. Migratory raptors are forced to advance their arrival to their breeding grounds to synchronize reproduction with the peak of food availability. Successful adaptation has been associated with higher breeding success, while an unsuccessful advancement may result in a phenological mismatch, reducing breeding success (Martinez-Ruiz et al., 2023). The same applies to range shifts in mammalian predators such as the lynx (van Hassel & Bovenkerk, 2023) and wolverine (McKelvey et al., 2011) that need to adapt to maximize the potential for successfully hunting prey. Our study demonstrates that delayed springs are associated with increased gyrfalcon breeding performance, which probably relies on the changing availability of ptarmigan in varying snow conditions. In this context, 'availability' can simply mean abundance, but also visibility and other factors relating to the gyrfalcon's hunting success, which also vary with environmental conditions. Since this change in prey availability due to shifting phenology will result in decreased breeding success under the current climate predictions, this will require adaptations from the gyrfalcon in the future.

Short term effects of climate warming can benefit small herbivores such as ptarmigan, which are important prey of several top predators in high-latitude food webs. In early springs, food and nest availability is higher, there is more shelter from vegetation cover and offspring survival is higher in milder temperatures (Eriksen et al., 2023; Findlay-Robinson et al., 2023; Ingvaldsen et al., 2024; Layton-Matthews et al., 2020; Morrissette et al., 2010). Conversely, there are also long-term processes that could impact small herbivores negatively in the future (Fuglei et al., 2020; Ims & Fuglei, 2005). An example of such a process is the northward or upslope shift of generalist predators such as the red fox (*Vulpes vulpes*) due to ameliorating conditions in higher altitudes and latitudes (Selås & Vik, 2006). This can alter food web structure by increasing predation pressure on small herbivores and competition with local (specialist) predators. In addition, interconnected population cycling of mammalian populations is more prevalent in higher latitudes (Kendall et al., 2002), and has been observed for the ptarmigan and gyrfalcon populations in Iceland (Barraquand & Nielsen, 2018). The food web in Scandinavia is more complex and previous research has shown that ptarmigan population cycles are also closely linked to the rodent cycle (Hagen, 1952b). The alternative prey hypothesis states that in years of high rodent abundance predation pressure is relieved for the ptarmigan. It has been suggested that the attenuation of rodent cycles has led to an increase in predation pressure on ptarmigan, causing a decrease in their population size (Fuglei et al., 2020; Hjeljord & Loe, 2022). This mechanism is also relevant for non-cyclic prey, where the presence or absence of alternative prey can alleviate or enhance predation pressure for certain species, respectively (Kjellander & Nordström, 2003).

These examples illustrate that the impact of climate change is not always straightforward, and simply examining a single species is insufficient (Bowler et al., 2020; Gilman et al., 2010). Even specialist predators such as the gyrfalcon are not only directly connected to their main prey species, but also indirectly to other species, since the ptarmigan is a key player in the dynamics of many other species in the food web as well. This study provides the insight that climate change will likely require adaptations from gyrfalcons and predators alike in alpine areas. Indirect effects of climate change that act through the species predators interact with, are of high importance in assessing their resilience to a changing environment. Contrasting impacts of climate change in the short- and long-term can further complicate these predictions. However, they demonstrate that the influence of climate change almost invariably depends on the local food web context.

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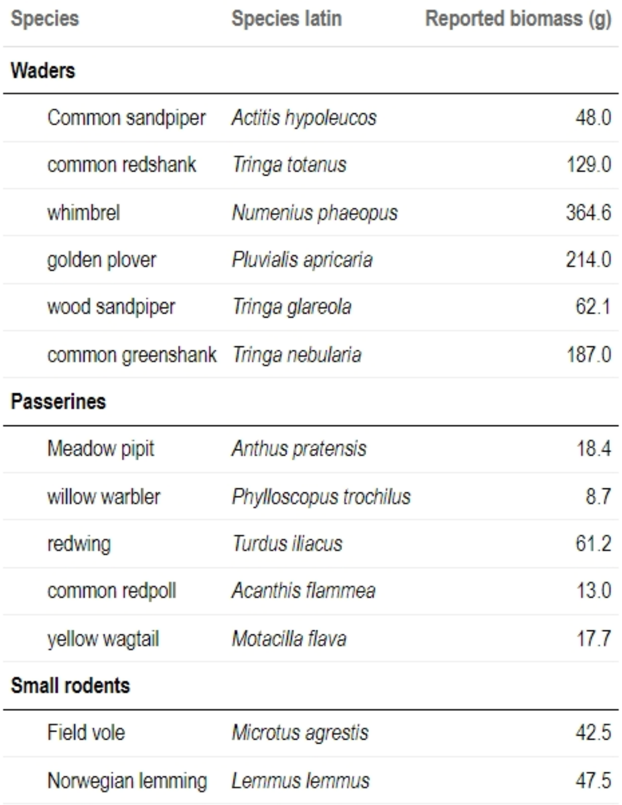
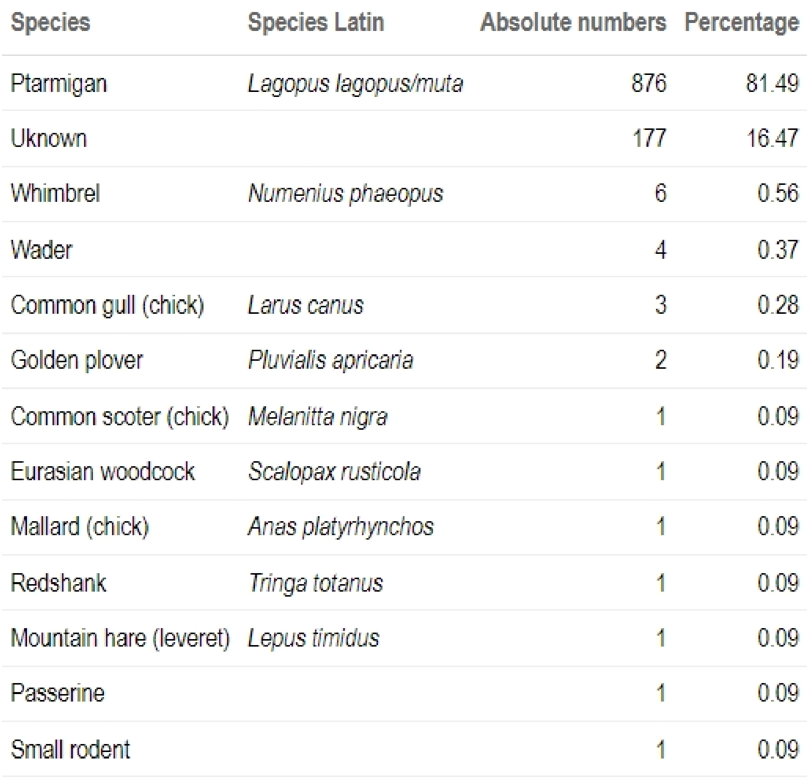
SUPPLEMENTARY MATERIAL

Table S1: Reported biomass of species used to calculate prey biomass classified as a grouped type of prey. Bird biomass is extracted from the AVONET dataset (Tobias et al., 2022) and mammal biomass from the panTHERIA archives (Jones et al., 2009)



Species	Species latin	Reported biomass (g)
Waders		
Common sandpiper	*Actitis hypoleucos*	48.0
common redshank	*Tringa totanus*	129.0
whimbrel	*Numenius phaeopus*	364.6
golden plover	*Pluvialis apricaria*	214.0
wood sandpiper	*Tringa glareola*	62.1
common greenshank	*Tringa nebularia*	187.0
Passerines		
Meadow pipit	*Anthus pratensis*	18.4
willow warbler	*Phylloscopus trochilus*	8.7
redwing	*Turdus iliacus*	61.2
common redpoll	*Acanthis flammea*	13.0
yellow wagtail	*Motacilla flava*	17.7
Small rodents		
Field vole	*Microtus agrestis*	42.5
Norwegian lemming	*Lemmus lemmus*	47.5

Table S2: Prey items delivered to the nest in Lierne municipality between 2018 and 2023 in all nests combined.



Species	Species Latin	Absolute numbers	Percentage
Ptarmigan	*Lagopus lagopus/muta*	876	81.49
Uknown		177	16.47
Whimbrel	*Numenius phaeopus*	6	0.56
Wader		4	0.37
Common gull (chick)	*Larus canus*	3	0.28
Golden plover	*Pluvialis apricaria*	2	0.19
Common scoter (chick)	*Melanitta nigra*	1	0.09
Eurasian woodcock	*Scalopax rusticola*	1	0.09
Mallard (chick)	*Anas platyrhynchos*	1	0.09
Redshank	*Tringa totanus*	1	0.09
Mountain hare (leveret)	*Lepus timidus*	1	0.09
Passerine		1	0.09
Small rodent		1	0.09

Table S3: Results from (generalized) linear (mixed) models describing gyrfalcon diet and feeding behaviour in Lierne municipality between 2018 and 2023. Depending on the type of family, odds ratio, estimates or incidence rate ratios are provided, together with corresponding confidence intervals and p-values. P-values in bold are below the 0.05 threshold.

	Proportion ptarmigan in diet			**Prey biomass (log)**			**Time spent feeding per day (minutes)**			**Mean length of feeding event (minutes)**			**Daily prey delivery rate**		
Predictors	*Odds Ratios*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
Intercept	4157476.055	87.630 – 197246042423.695	**0.006**	628.997	561.397 – 696.596	**<0.001**	10.105	7.718 – 12.492	**<0.001**	5.365	4.307 – 6.422	**<0.001**	4.092	2.487 – 6.734	**<0.001**
Julian day	0.924	0.866 – 0.986	**0.017**	-0.501	-0.907 – -0.094	**0.016**									
Sex, male	0.329	0.097 – 1.116	0.074	-7.678	-16.975 – 1.618	0.105	-2.558	-3.051 – -2.065	**<0.001**	-0.253	-0.509 – 0.004	0.054	0.510	0.424 – 0.612	**<0.001**
Sex, unknown	0.532	0.162 – 1.743	0.297	-7.989	-17.180 – 1.202	0.088	-2.067	-3.096 – -1.037	**<0.001**	-0.397	-0.933 – 0.139	0.146	0.778	0.646 – 0.936	**0.008**
Snowdepth (cm)	0.976	0.940 – 1.013	0.196	-0.155	-0.313 – 0.002	0.054	-0.004	-0.018 – 0.010	0.608	-0.001	-0.008 – 0.006	0.839	1.003	0.999 – 1.007	0.096
Temperature (°C)	1.072	0.928 – 1.237	0.344	0.575	-0.152 – 1.302	0.121	-0.019	-0.071 – 0.032	0.461	0.026	-0.001 – 0.052	0.060	0.992	0.977 – 1.007	0.290
Precipitation (mm)	1.163	0.917 – 1.474	0.212	0.252	-0.186 – 0.691	0.259	-0.003	-0.034 – 0.029	0.860	0.002	-0.014 – 0.018	0.810	1.005	0.996 – 1.014	0.271
Snowdepth on the 20th of May (cm)	1.049	1.012 – 1.087	**0.010**	0.250	0.109 – 0.391	**0.001**	0.000	-0.027 – 0.028	0.973	-0.003	-0.014 – 0.008	0.602	0.998	0.993 – 1.002	0.286
Nestling age (days)							-0.211	-0.245 – -0.177	**<0.001**	-0.074	-0.091 – -0.057	**<0.001**	0.983	0.974 – 0.991	**<0.001**
Brood size							0.969	0.487 – 1.451	**<0.001**	0.154	-0.073 – 0.382	0.183	1.129	1.010 – 1.263	**0.033**
Random Effects															
σ^2	3.29			2405.63			2.76			0.75			0.34		
τ_{00}	0.03 $_{\text{nestID}}$			0.79 $_{\text{nestID}}$			1.64 $_{\text{nestID}}$			0.23 $_{\text{nestID}}$			0.03 $_{\text{nestID}}$		
ICC	0.01			0.00			0.37			0.23			0.07		
N	12 $_{\text{nestID}}$			12 $_{\text{nestID}}$			12 $_{\text{nestID}}$			12 $_{\text{nestID}}$			12 $_{\text{nestID}}$		
Marginal R^2 / Conditional R^2	0.464 / 0.468			0.031 / 0.031			0.509 / 0.692			0.279 / 0.448			0.287 / 0.337		

Table S4: Results from generalized linear mixed models describing the numerical aggregative response of gyrfalcons in six municipalities in central Norway between 2012 and 2023. Odds ratios are provided with corresponding confidence intervals and p-values.

	Numerical response same year			**Numerical response 1-year time lag**			**Numerical response 2-year time lag**			**Numerical response 3-year time lag**		
Predictors	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*
Intercept	0.164	0.040 – 0.667	**0.012**	0.181	0.042 – 0.789	**0.023**	0.152	0.035 – 0.670	**0.013**	0.164	0.033 – 0.816	**0.027**
Ptarmigan density same year	0.997	0.954 – 1.043	0.903									
Temperature (°C)	1.012	0.875 – 1.171	0.874	1.003	0.874 – 1.150	0.969	1.009	0.874 – 1.164	0.904	1.003	0.870 – 1.156	0.968
Precipitation (mm)	0.984	0.879 – 1.102	0.777	0.991	0.881 – 1.115	0.885	0.982	0.876 – 1.100	0.750	0.983	0.878 – 1.102	0.773
Snowdepth (cm)	1.005	1.000 – 1.010	0.074	1.005	0.999 – 1.010	0.087	1.005	0.999 – 1.010	0.091	1.005	0.999 – 1.010	0.090
Ptarmigan density preceding year				0.992	0.951 – 1.035	0.722						
Ptarmigan density 2 years ago							1.007	0.967 – 1.048	0.748			
Ptarmigan density 3 years ago										0.999	0.960 – 1.040	0.953
ICC	0.00			0.00			0.00			0.00		
N	4_{area}			4_{area}			4_{area}			4_{area}		
Marginal R^2 / Conditional R^2	0.023 / 0.023			0.021 / 0.021			0.023 / 0.023			0.021 / 0.021		

Figure S1: The type II functional response curve, describing how kill rate is related to prey density, fitted to data from Lierne municipality from the breeding season covering the years 2018 to 2023. Each open circle represents a weekly kill rate, whereas filled circles represent the mean kill rate per year. Kill rate represents the number of ptarmigan brought into the nest, excluding potential cached prey. Prey density is mean ptarmigan density as number of individuals per square kilometre across the municipality. The fitted curve follows a simplified version of Hollings disc equation, with the formula y = (31.3*x)/(9.4+x), with best fitting estimates filled in.