ORIGINAL ARTICLE

Changes in over-winter prey availability, rather than winter climate, are associated with a long-term decline in a northern Tawny Owl population

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Abstract

Although the associations between climate, food conditions and reproduction in the wild has been the focus of numerous studies in recent years, we still know little about population level responses to climate and fluctuating food conditions in long-lived species and during longer periods of time. Here, we assessed the relative importance of the abundance of the main prey in winter (small mammals), and winter climate on population size and productivity in a Tawny Owl (*Strix aluco*) population in southern Finland during a 40-year period. We studied how population trends changed over time and in relation to winter weather and small mammal abundance on three levels: total estimated population size, proportion of breeders and population productivity. We identified declining trends in each population parameter over time, as well as directional changes in climate variables and prey abundance. Overall, small mammal abundance was the foremost predictor in explaining the variation in the number of active territorial pairs (population size). Moreover, both prey abundance and winter temperature significantly affected the proportion of territorial pairs that attempted to breed and thereby total offspring production, which reveals the relevance of winter weather conditions for population productivity. These results provide additional support to the view that changes in climate can modify predator–prey interactions leading to functional changes in the food web.

Keywords Climate change · Birds of prey · Vole cycle · Predator–prey interaction · Boreal environments · Population trend

Zusammenfassung.

Langfristige Abnahmen einer nördlichen Waldkauzpopulation stehen eher mit Veränderungen der Beuteverfügbarkeit im Winter im Zusammenhang als mit dem winterlichen Klima

Obwohl die Beziehungen zwischen Klima, Nahrungsbedingungen und Reproduktion im Freiland in den letzten Jahren im Fokus zahlreicher Studien standen, wissen wir auf Populationsebene immer noch wenig über die Reaktionen auf das Klima und auf schwankende Nahrungsbedingungen bei langlebigen Arten und über längere Zeiträume hinweg. Wir

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betrachten hier die relative Bedeutung der Häufigkeit der primären Winterbeute (Kleinsäuger) sowie des Klimas im Winter auf Populationsgröße und Produktivität einer Waldkauzpopulation (*Strix aluco*) in Südfinnland während eines 40-Jahres-Zeitraumes. Auf drei Ebenen – der geschätzten Gesamtpopulationsgröße, dem Anteil an Brutvögeln und der Populationsproduktivität – untersuchten wir, wie sich Populationstrends mit der Zeit und im Verhältnis zu Winterwetter und der Kleinsäugerhäufigkeit veränderten. Für jeden Populationsparameter fanden wir über die Zeit abnehmende Trends sowie gerichtete Veränderungen der Klimavariablen und der Häufigkeit der Beutetiere. Allgemein trug die Häufigkeit von Kleinsäugern am meisten zur Erklärung der Variation der Anzahl aktiver Revierpaare (Populationsgröße) bei. Außerdem beeinflussten sowohl Beutehäufigkeit als auch die Temperatur im Winter signifikant den Anteil von Revierpaaren, die einen Brutversuch unternahmen und somit die gesamte Produktion an Nachkommen, was die Relevanz der winterlichen Wetterbedingungen für die Produktivität einer Population demonstriert. Unsere Ergebnisse unterstützen die Ansicht, dass Klimaveränderungen Räuber-Beute-Beziehungen modifizieren und dadurch zu funktionalen Veränderungen im Nahrungsnetz führen können.

Introduction

Understanding the factors driving changes in population viability on a long-term period scale is a central question in population ecology and conservation. A careful monitoring of animal populations in relation to natural and human-induced pressures is crucial to identify their response to environmental change as well as proper conservation actions to recover declining populations. This is fundamental to maintain stability in ecological communities, since declines in natural populations can hinder the regular functioning of ecosystems.

An increasing body of research has highlighted how climate change can impact bird population dynamics (Sillett et al. 2000; Jenouvrier et al. 2003; Saether et al. 2004; Jenouvrier 2013) by altering resource requirements and interspecific interactions through phenological mismatches, including asynchronies between species breeding period and the peak of food availability (Durant et al. 2007; Burger et al. 2012; Parejo 2016; Burgess et al. 2018). Particularly crucial for the functioning of ecosystems are predator–prey interactions and studies concerning avian predators have showed that these relationships can be influenced by climatic fluctuations (Jenouvrier et al. 2003; Bond and Lavers 2014; Bretagnolle and Terraube 2019).

In boreal environments climate change can modify predator–prey interactions by altering the behavior and population cycles of small mammals, which are the main food source for many birds of prey (Jäderholm 1987; Tornberg and Reif 2007). In Fennoscandia, voles often constitute the largest fraction in the diet of avian predators. This is likely because voles can be particularly abundant due to their cyclic population dynamics, with huge fluctuations between years (low, intermediate and peak phases). Yet climate change has induced a dampening and irregularities of these cycles, which shifted from the typical 3-year cycles (Sundell et al. 2004) to almost annual fluctuations (Hörnfeldt et al. 2005; Brommer et al. 2010). These dampened cycles have profound repercussions on vole-eating predators, impairing their reproductive success and fitness overall (Brommer et al. 2002; Hörnfeldt et al. 2005; Karell et al. 2009), since they adjust their reproductive strategies to these prey fluctuations (Lehikoinen et al. 2011). In years with a low abundance of voles, the population productivity is markedly lower since vole-dependent raptors often skip breeding (Karell et al. 2009).

To date, only few studies have attempted to differentiate the relative importance and weight of climatic conditions and fluctuating prey abundance on population size and productivity of avian predators on a large temporal scale (Lehikoinen et al. 2011, 2013; Solonen 2014). Furthermore, because monitoring studies of birds of prey often rely on the number of breeding pairs without taking into account the total size of the population including non-breeding individuals, very little is known about how the total pool of potential breeders in the population is affected by the joint effects of climate and prey fluctuations. In addition, the extent to which the proportion of actual breeders within this pool of potential breeders is affected by climate in territorial birds of prey is largely unknown and insights on this matter could lead to more accurate evaluations of population trends. In particular, territorial species are likely to be largely affected by fluctuations in environmental factors since they are mostly sedentary and not inclined to abandon their territories.

Here, we aim to investigate the respective role and impact of climate (winter temperature and snow cover) and prey availability (small mammal abundance) in modulating a predator population in a boreal environment. To do so, we focused on three different population level estimates: (1) Population size: an estimate of the total number of active territorial pairs within the population (both breeding and non-breeding pairs); (2) Proportion of breeding pairs: the

fraction of breeding pairs out of the total number of territorial pairs; and (3) Population productivity: annual mean and the total number of fledglings produced by the breeding pairs within the population.

We considered all these variables to gain a more accurate view of the population trend over time. Relying solely on the mere number of territorial pairs may lead to a simplified evaluation of the population trend, since it overlooks the reproductive performance. To assess whether a population is really growing it is vital to see if territorial pairs reproduce or if they simply occupy a territory without breeding. A high number of territories is not necessarily enough to confirm if a population is stable if the fraction of established territorial pairs that are breeding depends on environmental fluctuations. We estimated both mean and total number of fledglings produced as a measure of population productivity since we were interested in addressing if there were trends in reproductive output (mean brood size) and/or if population productivity was mainly a product of the number of territorial/breeding pairs.

To answer these questions, we used the Tawny Owl as model species. Tawny Owls are mainly woodland raptors breeding across most of Europe, including Fennoscandia (Cramp and Simmons 1985). As a year-round resident species (Southern 1970), the Tawny Owl has to cope with local environmental variation. This species can prey upon a great variety of prey across its distributional range but locally common small mammal species constitute its main prey (Kekkonen et al. 2008; Karell et al. 2021; Ratajc et al. 2022). For this reason, the breeding performance of Tawny Owls has been shown to be highly connected to small mammal fluctuations, where it skips breeding in unfavorable small mammal years, and recruitment of new breeders to the population requires high small mammal abundance (Southern 1970; Jędrzejewski et al. 1996; Karell et al. 2009). Southern Finland, which is the northern limit of the range distribution of the Tawny Owl, has been subject to large changes in winter conditions due to the ongoing global warming (Tietäväinen et al. 2010; Mikkonen et al. 2015). Increasing temperatures in southern Finland have also been demonstrated to affect survival in this species (Karell et al. 2011). Therefore, the Tawny Owl represents a good study system to study variation in population size and productivity in relation to both climate and small mammal abundance. Here, we analyze the numerical response to climate and prey of a Finnish population of nest-box breeding Tawny Owls monitored over 40 years. We predict that: (1) Population size is relatively stable to climate and prey availability. Tawny Owl adult survival is not markedly affected by the vole cycle (Karell et al. 2009). Therefore, we do not expect a strong effect of small mammal abundance on population size (Southern 1970). Instead, we expect winter conditions (winter temperature and/or snow days) to have an effect

on population size since it influences Tawny Owl survival (Francis and Saurola 2004; Karell et al. 2011). For example, deep snow cover predicts low survival in Tawny Owls (Francis and Saurola 2004; Karell et al. 2011). For this reason, we expect the number of active territories to be negatively associated with winter days with deep snow cover. (2) Proportion of breeding pairs fluctuates depending on both prey availability and winter climate. We expect the proportion of breeding pairs to be positively associated with small mammal abundance (Southern 1970; Karell et al. 2009). Similarly, we further expect the proportion of breeders in the population to increase with milder winters. (3) Population productivity assessed as annual mean and the total number of fledglings is expected to be dictated by prey availability and winter climate. In Tawny Owls population, productivity is directly related to breeding activity (proportion of breeding pairs), but also to the reproductive output among the breeding pairs. In years with low small mammal availability, Tawny Owl broods are generally smaller (Millon et al. 2014) and we also expect that harsh winter conditions (both winter temperature and snow cover) make it more difficult for the Tawny Owls to allocate their resources in reproduction and hence that the overall productivity is lower.

Materials and methods

Study area

Tawny Owls were surveyed in an area of c. 250 km² in southern Finland (60° 15´ N, 24° 15´ E), including mixed forests as well as rural landscapes. Here, almost 125 nest boxes were installed between 1975 and 1980 and Tawny Owl pairs used them successfully. Over the years, from 1975 to 2021, KA, TK, PK, KK, JEB, CM and AP systematically controlled the nest boxes and ringed the owls.

Field survey protocol

Since the Tawny Owl is highly responsive to conspecific calls due to its territorial behavior (Southern 1970), playback surveys are broadly used to survey its presence/absence in the territory, similarly to what is done with several other territorial bird species (Zuberogoitia and Martínez 2000; Worthington-Hill and Conway 2017; Vrezec and Bertoncelj 2018). Playback surveys were carried out in early spring (March–April) each year in constant locations along roads transecting the study area. We conducted at least two visits at each location. All surveys always started after sunset and lasted c. three hours. They were conducted in rainless and windless nights (Zuberogoitia et al. 2019), also avoiding extremely cold temperatures (Takats and Holroyd 1997). Playback calls were stopped as soon as an individual

responded (or after 15–20 min if there was no response). Here, we assume a territory to be actively occupied if there was an owl responding to playback. From late April, all nest boxes (including those in territories where the owls did not reply to playback) and additional possible breeding sites in natural cavities were checked carefully. This was done to check for potential 'silent' territories where owls might have been present but did not respond to our broadcasted calls during the survey. Although we acknowledge that the playback method could have limitations in identifying the individuals that can reply to the playback without actually holding a territory, this has been minimized in our study, thanks to multiple playback visits at the same locations and the checks at the nest boxes, which confirmed the presence/absence of the owls.

We considered as 'breeding pairs' all the pairs that attempted to breed and laid at least one egg in a given nest box (territory), regardless of the final output of the reproduction. Upon hatching, the reproductive output was then measured and parental owls were identified and/or ringed in the nest boxes when the offspring were 1–2 weeks old. When the oldest chick was c. 25–28 days old, all offspring in the brood were ringed for identification. The census and handling of owls were conducted by KA, TK, PK and KK. For further details regarding the census protocol, see Karell et al. (2009).

Small mammal abundance and climate

To identify the factors influencing territory occupancy and productivity, we considered in our analyses small mammal abundance, mean winter temperature and snow days. Estimates of prey abundance were obtained as described in Karell et al. (2009). In short, snap trapping of small mammals was conducted in late autumn each October from 1982 onwards. The trapping was carried out in two sites ca. 25 km apart within the study area. Both sites consist of an open and a wooded habitat where snap traps were placed. Traps were set as transects of 16 trapping spots (10 m between them) with three traps in each spot. In total, 48 traps were set for each habitat, which were activated for 2 consecutive nights, giving a total of 384 trap nights (see Karell et al. 2009). The most abundant small mammals trapped were represented by field voles (*Microtus agrestis*) and bank voles (*Clethrionomys glareolus*). Wood mice (*Apodemus flavicollis*) and shrews (*Sorex* spp.) constituted a smaller proportion. We here consider a more general index for small mammal abundance, which includes not only voles, but also mice and shrews. The index we used for small mammal abundance was computed by dividing the total number of caught individuals per the total of trap nights. Since Tawny Owl capability to establish territories and reproduce depends on the possibility to gain resources, i.e., the availability of prey in

the previous autumn (Brommer et al. 2002; Kekkonen et al. 2008; Karell et al. 2009), we considered the small mammal abundance of the autumn prior to the monitoring of the owl population. For instance, for owls monitored in spring 1983 we considered small mammal abundance in autumn 1982.

Winter climate variation was analyzed in terms of mean winter temperatures and the number of snow days. The former was calculated for each year by computing the average of the monthly mean temperatures between the winter months (December, January, February), always starting from December of the previous year. The latter was determined by computing the number of snow days occurred in each year with a snow depth > 5 cm. The number of snow days was considered all-year-around since days with snow depth > 5 cm occurred frequently also in non-winter months (e.g., March, April and November). Climate data of the long-term period 1982–2021 were obtained from the National Finnish Meteorological Institute for the meteorological station located in Helsinki, Kaisaniemi (ca. 50 km east to the center of the study area).

Statistical analyses

The statistical analyses were carried out using R Software 3.6.3 (R Development Core Team 2021). First, we used simple linear models to inspect the temporal variation of snow days, mean winter temperature and small mammal abundance over the long-term period 1982–2021 in our study area. For small mammal abundance, a quadratic effect was also tested.

Second, we fitted multiple linear models to analyze the effects of snow days, mean winter temperature and small mammal index on the owl population at three different levels: total population size, proportion of breeding owls, mean- and total population productivity in 1982–2021. Population size (normally distributed) was expressed as the total number of actively defended territories detected via playback surveys in the study area. The variation in the proportion of breeding owls among all active territories was analyzed by fitting a GLM with binomial distribution of errors. The total number of offspring produced in the population, i.e., population productivity, was analyzed by fitting a negative binomial GLM due to the presence of overdispersion with the Poisson family (residual deviance/degrees of freedom > 2). For GLMs, we calculated the R-squared values (R^2) using the formula: $1 -$ residual deviance/null deviance (Faraway 2016). Small mammal abundance, year, snow days and mean winter temperature were specified as continuous explanatory variables in all models. All variables were centered around a mean of zero and scaled by the standard deviation to improve the interpretability of regression coefficients (Schielzeth 2010).
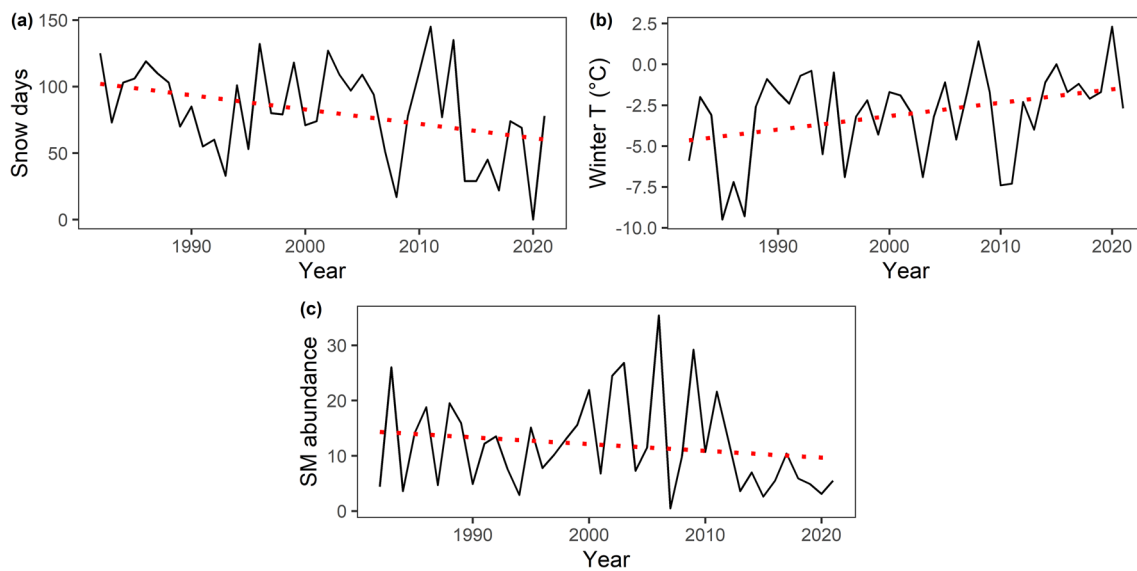
Fig. 1 Trend of snow days, i.e., the number of days in which the depth of snow cover was > 5 cm (**a**), mean winter temperature (**b**) and small mammal (SM) abundance (**c**) over the years. Presented data refer to the period 1982–2021

We adopted a multi-model inference approach aimed at identifying which model(s) could best explain the variation in population size, proportion of breeders and population productivity. Thus, for each of these, we built a first full model including all covariates (small mammal abundance, mean winter temperature, snow days and year). Before proceeding with the model comparisons, the VIF (Variance Inflation Factor) implemented in the car package (Fox and Weisberg 2019) was used to check for potential correlation between the variables, where a value exceeding 5 would indicate problems of collinearity (James et al. 2014). No collinearity was found (VIF < 3 overall). Besides checking the presence of overdispersion in the negative binomial GLM, all models were graphically inspected to ensure the model assumptions were met (i.e., independence of data, normality of residuals, variance homogeneity, no influential observations).

From the saturated model, we built a set of candidate models containing all possible combinations of explanatory variables. Overall, we obtained 16 candidate models, the same for each response variable, from which we selected the best model(s) (i.e., top models) using Akaike's information criterion corrected for small sample size (AICc), considering as support to our choice a difference less than two units ΔAICc relative to the best ranked model (Burnham and Anderson 2002). Then, for each model, we calculated the Akaike weight as well as the relative importance, i.e., the weight (*w*), of each covariate (Burnham and Anderson 2002). The latter was calculated as the sum of Akaike weights from the candidate models that contained the given variable (Burnham and Anderson 2002).

Both linear models and GLMs were fitted with the stats package, while the multi-model inference approach was performed with the MuMIn package (Barton 2020).

Results

Temporal variation in environmental variables

Our analyses revealed that in the period 1982–2021, the average number of snow days decreased by c. 42 days ($\beta \pm \mathrm{SE} = -1.07 \pm 0.46$ days/year, $t = -2.34$, $p = 0.02$; $R^2 = 0.13$) and the mean winter temperature increased by c. 3 °C ($\beta \pm \mathrm{SE} = 0.08 \pm 0.04$ °C/year, $t = 2.31$, $p = 0.03$; $R^2 = 0.12$), documenting a general shift towards milder and less snowy winters. The temporal trends for both winter temperature and snow days were linear (Fig. 1a, b), whereas there was a non-linear negative temporal trend in small mammal abundance (low–high–low small mammals) over time (Year: $\beta \pm \mathrm{SE} = -1.43 \pm 1.29$, $t = -1.11$, $p = 0.27$; Year^2: $\beta \pm \mathrm{SE} = -2.91 \pm 1.46$, $t = -1.99$, $p = 0.05$; $R^2 = 0.12$; Fig. 1c).

Population size

Model selection identified two best-fit models ($\Delta \mathrm{AICc} < 2$) out of the 16 candidate models explaining the variation in Tawny Owl territory number (Supplementary Table S1a). Small mammal abundance emerged as the variable with the overall highest relative importance (Supplementary Table S2) and had a strong positive and significant effect on population size (Fig. 2a), i.e., when food is abundant there
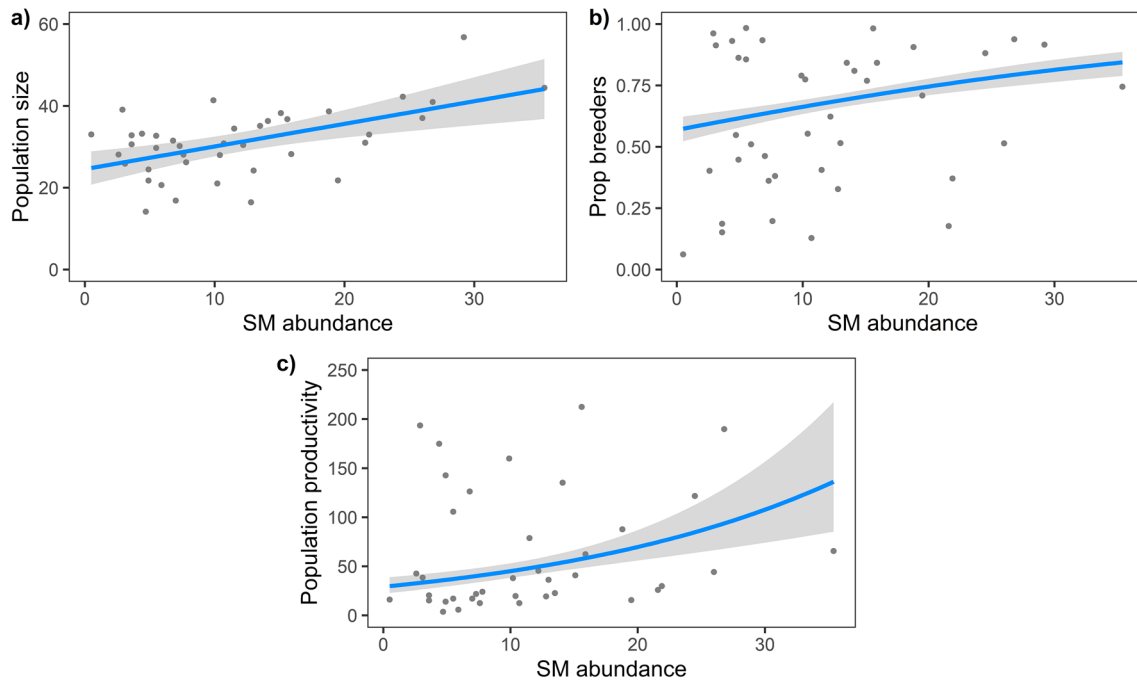
Fig. 2 Effect of small mammal (SM) abundance on Tawny Owl population size (**a**), proportion (Prop) of breeders (**b**) and population productivity (**c**). The depicted blue lines are based on the outcome of the first top model out of all possible candidate models

are more active Tawny Owl territories. Both snow days and winter temperature had a lower weight than small mammal abundance (Supplementary Table S2), but they were separately included in the two top candidate models. According to the first top model, territory number declined over the years ($\beta \pm \mathrm{SE} = -2.86 \pm 1.25$, $z = -2.28$, $p = 0.03$; Table 1a; Fig. 3a) and there were more active territories in years of high small mammal abundance ($\beta \pm \mathrm{SE} = 4.63 \pm 1.21$, $z = 3.82$, $p = 0.001$; Table 1a; Fig. 2a) and in years with fewer snow days with a snow cover > 5 cm ($\beta \pm \mathrm{SE} = -3.01 \pm 1.28$, $z = -2.35$, $p = 0.02$; Table 1a; Fig. 4a).

Proportion of breeding owls and population productivity

Model selection identified the model containing small mammal abundance, mean winter temperature and year as the best one in explaining the proportion of breeding owls among the active territories (Figs. 2b, 3b and 4b, Supplementary Table S1b). According to this model, the proportion of breeding owls declined over the years (Fig. 3a) and there was a positive effect of small mammal abundance and mean winter temperature (Table 1b), meaning that years with high food abundance and milder winters had larger proportion of breeders. The number of snow days was less relevant and was not included in the top model (Supplementary Table S1b, Supplementary Table S2).

Table 1 Coefficients and R-squared values (R^2) of top candidate models for Tawny Owl population size (a), proportion of breeders (b) and population productivity (c)

Population size	β	SE	t	p
(a)				
(Intercept)	30.925	1.152	26.837	< 0.001
Year	− 2.856	1.253	− 2.279	0.03
Snow days	− 3.005	1.279	− 2.349	0.02
Small mammal abundance	4.631	1.214	3.815	0.001
$R^2 = 0.38$				
(b)				
(Intercept)	0.691	0.062	11.135	< 0.001
Year	− 0.292	0.069	− 4.209	< 0.001
Mean winter temperature	0.215	0.068	3.174	0.002
Small mammal abundance	0.334	0.062	5.357	< 0.001
$R^2 = 0.34$				
(c)				
(Intercept)	3.829	0.078	49.150	< 0.001
Year	− 0.344	0.085	− 4.053	< 0.001
Mean winter temperature	0.221	0.085	2.605	0.009
Small mammal abundance	0.364	0.079	4.573	< 0.001
$R^2 = 0.48$				

Data collection refers to the period 1982–2021 ($n = 40$). The column headings indicate the variable estimate (β), the standard error (SE), the t-value (t) or z-value (z) and p-value (p)
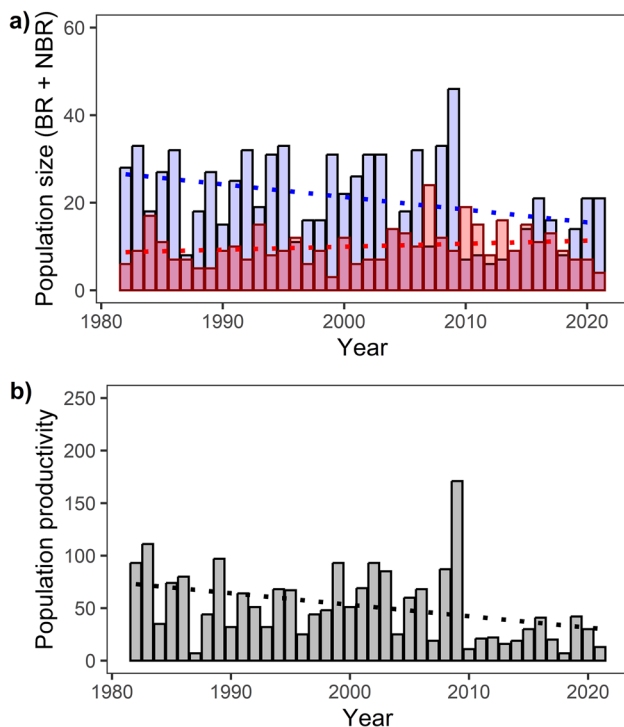
Fig. 3 Bar plots illustrating Tawny Owl population trends over time, from 1982 to 2021. In panel (**a**), the blue bars indicate the number of breeding pairs (BR) within the population per each year, while the red bars the number of non-breeding pairs (NBR). Their sum provides the population size per each year. The blue dotted line shows the trend of breeding pairs while the red dotted line shows the trend in non-breeding pairs that have been observed across the years. In panel (**b**), the bars indicate the total number of fledglings produced by the breeding pairs each year and the dotted line shows the declining trend that has been observed

Mean brood size was larger in years with high small mammal abundance and after snow-rich and warmer winters (Table S3), but there was no temporal trend in mean brood size in the population (Table S3, Year).

The population productivity, measured as the total number of fledglings produced in the population, was positively associated with both small mammal abundance (Table 1c, Fig. 2c) and mean winter temperature prior to breeding (Table 1c, Fig. 4c). There was a significant decline in productivity over time (Table 1c, Fig. 3b). The relative importance and weight of snow cover were low, indicating that it did not affect population productivity (Supplementary Table S1c, Supplementary Table S2).

Discussion

In our study, we found strong irregularities in small mammal abundance, with dampened fluctuations in recent years, and visible directional changes in the winter climate: the number

of days with snow cover has decreased and the mean winter temperature has increased in the same time period. In concert with these environmental trends, we found support for a clear negative trend over 40 years in total population size, in the proportion of active breeding pairs and in population productivity within the nest-box breeding population of Tawny Owls in southern Finland. We show that over time, population size was largely dictated by the abundance of small mammals, the main prey available in winter; whereas, both the proportion of breeders and productivity were associated with small mammal abundance combined with the positive impact of milder winters. In addition to the effect of small mammal abundance and winter climate, we show an overall negative temporal trend in Tawny Owl population.

Effect of prey and climate on population size

Using a multi-model inference approach, we found that small mammal abundance was the most influential variable affecting the total number of defended Tawny Owl territories (population size). This result confirms the previously documented effect of small mammals on Tawny Owl population size in the North (Francis and Saurola 2004; Karell et al. 2009; Saurola and Francis 2018). Small mammals account for most of the diet of several predators, including Tawny Owls (Southern 1970; Jędrzejewski et al. 1996; Kekkonen et al. 2008), especially in the autumn–winter seasons at higher latitudes, when most alternative prey have migrated (birds), or are inactive or unavailable (amphibians and reptiles) (Petty 1999). Thus, it is difficult for the year-round territorial Tawny Owls to compensate the shortage of small mammals with other resources. In our data, we find that the in more recent years, the small mammal abundance remains consistently low and shows dampened annual variation, in concordance with a decline in Tawny Owl population size. In contrast to our prediction, we observed a greater variability with higher changes in the number of active territories and breeding pairs between years associated with small mammal abundance. Indeed Tawny Owl population size in our study area is less stable compared to European populations at lower latitudes, which are more stable even in years with low small mammal abundance (Southern 1970; Jędrzejewski et al. 1996; Sunde and Bølstad 2004; Sunde 2011; Gryz et al. 2019). It is likely that in temperate environments prey availability, both small mammals and other alternative prey, is generally higher and more stable, thus allowing lower fluctuations in population size compared to our population, which is at the northern margin of the species distributional range.

Our data indicate that also winter weather condition plays a role in regulating Tawny Owl population size and this finds agreement with previous studies showing that winter conditions affect Tawny Owl survival (Francis and Saurola
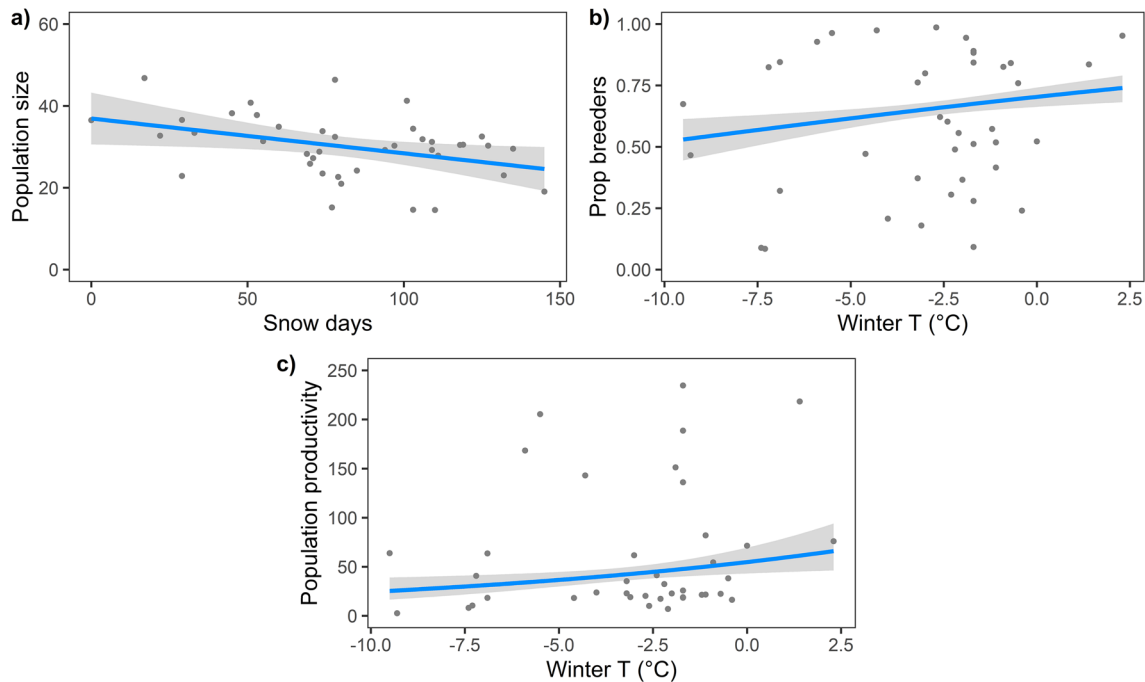
Fig. 4 Effect of climate (snow days or mean winter temperature) on Tawny Owl population size (**a**), proportion (Prop) of breeders (**b**) and population productivity (**c**). The depicted blue lines are based on the outcome of the first top model out of all possible candidate models

2004; Karell et al. 2011). We obtained two equivalent models with 'winter condition' as top models (ΔAICc < 2), thus indicating that winter conditions are relevant for population size and the AICc increases markedly if either of the winter condition variable (temperature or snow) is dropped (Supplementary Table S2). However, we could not statistically determine which winter condition variable (snow days or winter temperature) was the most relevant in affecting population size. Still, small mammal abundance had the highest weight among all covariates. This is also in line with Millon et al. (2014), who found a greater relative importance of prey abundance over climate in driving Tawny Owl population dynamics in a UK population. This suggests that, rather than winter temperature, population size is mainly governed by small mammals and the declining trend might be associated with the decrease of small mammal abundance over time, which was not compensated by a higher accessibility to alternative prey despite the warmer winters. Most potential alternative prey are not active (e.g., water voles, amphibians, etc.) or migrate south (e.g., passerines) during winter. Tawny Owls at lower latitudes can instead rely more easily on other prey (birds and insectivores) in winter (Żmihorsk and Osojca 2006), which can contribute to sustain populations in case of shortage of rodents. Our results, therefore, confirm that for opportunistic small mammal-eating predators, the foremost important requirement to establish territories and maintain them in the long-term

period is a consistent availability of prey rather than benign winter weather conditions.

Effects of prey and climate on the proportion of active breeders and population productivity

In our study, we were able to quantify the proportion of the actively defended territories where reproduction took place, i.e., the proportion of breeders, which allowed us to inspect if this variable was differently associated with climate and small mammal abundance compared to the total population size. As predicted, our findings indicate that the proportion of active breeders in the population was significantly higher in years with higher small mammal abundance and milder winter temperatures. Harsher winter temperatures increase the energy requirements needed to survive (Karell et al. 2011) and to gain resources required for reproduction (Lehikoinen et al. 2011). Large or medium-sized birds of prey like the Tawny Owl have to gain and store an adequate amount of energy resources in order to breed (Jönsson 1997; Hirons 1985; Lehikoinen et al. 2011), which can be challenging after cold winters if food conditions are poor. Our best statistical model attributed the highest weight to prey abundance, though both predictors explained the variation in the proportion of breeders with a similar effect. Likewise, both mean and total offspring produced within the population was positively associated with both small mammal abundance and mean winter temperature, and also here the effect of

small mammal abundance was more important than mean winter temperature. Indeed, in our Tawny Owl population, small mammal abundance and winter temperature are also predictors of offspring recruitment because local recruitment is higher in years with abundant voles and warmer winters during the juvenile stage (Morosinotto et al. 2020).

All our models point to the direction that small mammal abundance is a more important direct predictor of Tawny Owl population maintenance than winter climate. Our results suggest that the most deleterious effects of changing winter conditions on boreal small mammal-eating predators are likely to be indirect, expressed by changes in the abundance and availability of the main prey. Consequently, significant cascading effects in the trophic web are more likely to increase, with the potential to dampen predator–prey interactions and ecosystem stability.

Our results are obtained through a multi-model inference approach, which may lead to an overreliance on certain models. However, these results are strongly supportive of previous results. Indeed in this species, we previously observed that Tawny Owl survival is strongly linked to winter temperature and snow condition (Karell et al. 2011) while reproduction is regulated by vole abundance (Karell et al. 2009). Also, offspring recruitment to the population is affected by the combined impact of small mammal abundance and temperature in the autumn and winter post-fledgling (Morosinotto et al. 2020) and winter temperature also affects natal dispersal in this species (Passarotto et al. 2022). Thus, our findings of the overall population dynamical patterns build on these previous results and provide valuable additional support to the view that predator population dynamics are associated with prey abundance and climatic conditions.

In addition to the effects of winter climate and small mammals on population size, we also find an additional temporal trend with a steady decline in all population estimates: population size, proportion of breeders and productivity. On the contrary, we do not find temporal trends in mean brood size, which highlights that the temporal trend observed here is directed to changes in the number of territorial pairs and not to the reproductive performance of these pairs. Whether these declines in population parameters are related to degradations in habitat quality, forest structures or other changes in the environment can only be speculated upon, but certainly calls for explicit studies to evaluate the causes of this trend.

Conclusions

We conclude that in boreal environments small mammal abundance appears to drive fluctuations in the number of territories, while climatic conditions are, together with small mammal abundance, mainly associated with fluctuations in the proportion of breeders and population productivity. The recurring milder winters in the boreal zone may cause changes in the population dynamics of small mammals, leading to deleterious cascading effects on predators and biotic interactions.

Availability of data and materials The dataset generated and analyzed for this study will be uploaded in a data repository upon acceptance. Before that, the dataset is available from the corresponding author upon request. Researchers interested in access to the dataset may contact the corresponding author at giuseppeorlando96@gmail.com.

Code availability The R code will be uploaded in a data repository upon acceptance and may be also requested by contacting the corresponding author at giuseppeorlando96@gmail.com.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Ethics approval All applicable national, international and institutional guidelines regarding the care and use of wild animals were followed carefully. Tawny Owls were captured, handled, and ringed with an appropriate ringing license.

Consent to participate Not applicable.

Consent for publication Not applicable.

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