

# Differential responses of coexisting owls to annual small mammal population fluctuations in temperate mixed forest

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Montane temperate forests in central and southern Europe host diverse small mammal assemblages, but the fluctuations in these assemblages in correlation with owl predators are still poorly explored. The key questions of our study were how coexisting owls responded to different prey fluctuations and whether any particular small mammal species governed predator–prey co-dynamics. We conducted a long-term study (2004–2020) in low-elevation (300–1100 m above sea level) mixed Beech and Silver Fir forest in the northern Dinaric Alps (central Slovenia). Monitoring data on the main small mammal groups – mice Muridae, voles Cricetidae, dormice Gliridae and shrews Soricidae – and three owl species – the Ural Owl *Strix uralensis*, Tawny Owl *Strix aluco* and Boreal Owl *Aegolius funereus* – were collected annually. To find relationships between prey and predator populations, we used two types of supervised machine learning approaches and addressed three predictive modelling tasks of multi-target regression. The dominant species in the small mammal assemblage, the Yellow-necked Mouse *Apodemus flavicollis*, had a key role in determining predator populations and their breeding performance. We noted higher sensitivity to small mammal fluctuations in boreal zone owl species (Boreal Owl and Ural Owl), which reach their southern distribution limit in the Dinaric Alps, whereas the temperate zone species (Tawny Owl) seemed to be less affected. In years of prey shortage, the Boreal Owl was found to presumably abandon its territories, the Ural Owl suppressed breeding and the Tawny Owl sustained breeding activity by shifting prey selection. Low-elevation forests appeared to be suboptimal habitat for the competitive subordinate Boreal Owl, which may exploit occasional outbreaks of small mammal populations in these habitats even in the presence of larger competitors. Whether low-elevation forests can play a role in maintaining threatened and cold-adapted Boreal Owl populations in central and southern Europe in the face of recent ecosystem changes due to climate and environmental changes remains an open scientific question.

**Keywords:** Boreal Owl, dormice, food web, machine learning, mice, population dynamics, predation, Tawny Owl, Ural Owl, voles.

## INTRODUCTION

Trophic interactions are key determinants of ecosystem function, structure and dynamics, and interacting species, which act as consumers and

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resources, are interconnected within complex food webs (de Ruiter *et al.* 2005). Stable food webs enhance coexistence between predators and prey (Tokeshi 1999) but might lead to species extinctions when predator–prey dynamics are changed, for example through apparent competition effects (Bonsall & Hassell 1997). Therefore, understanding food web dynamics has become crucial in providing solutions for environmental and biodiversity changes due to anthropogenic impacts (de Ruiter *et al.* 2005). The population co-dynamics, which are driven by intrinsic and extrinsic factors, between predators and their prey has been extensively studied in the past, especially in carnivores and raptorial birds (Sundell *et al.* 2004, Samelius *et al.* 2011, Therrien *et al.* 2014). Long-lived predators usually adapt their foraging strategy according to prey availability in the environment (Korpimäki *et al.* 1990, Jedrzejewski *et al.* 1996, Solonen & Karhunen 2002, Malo *et al.* 2004, Lourenço *et al.* 2015, Resano-Mayor *et al.* 2016), and predator–prey links are continuously reconstructed in dynamic adaptive food webs (Kondoh 2005). In temperate forest ecosystems, small mammals are usually the main prey of many coexisting predators (Sidorovich *et al.* 2008). Small mammal assemblages consist of a wide range of species with different traits, including herbivorous voles Cricetidae, insectivorous shrews Soricidae, and omnivorous mice Muridae and dormice Gliridae (Kryštufek & Griffiths 1999), and individual species abundances fluctuate with high amplitudes (Zárybnická *et al.* 2015). To persist, small-mammal-eating predators have had to evolve certain adaptive foraging strategies based on their life-history traits. These might be changes in hunting strategy, breeding performance or breeding dispersal (Poulin *et al.* 2001, Brommer *et al.* 2002, Korpimäki & Hakkarainen 2012).

Vole populations in northern latitudes are known to fluctuate at regular periods of 3–5 years with highly variable amplitudes (Hörnfeldt 1994, Brommer *et al.* 2002, Sundell *et al.* 2004). The periodicity of peak vole years is gradually disappearing southwards (Korpimäki & Krebs 1996, Zárybnická *et al.* 2013), and recently these cycles have been fading out at all latitudes (Hörnfeldt 1994, Cornulier *et al.* 2013, but see Brommer *et al.* 2010). Vole cycles are thought to be an outcome of food availability, climate variables, diseases and competitive interactions (Hörnfeldt 1994, Brommer *et al.* 2010, Selva *et al.* 2012, Ecke

*et al.* 2017) and only partially a result of predator–prey interactions (Sundell *et al.* 2004, Hoset *et al.* 2009). Mast of deciduous trees is an important factor in vole and mouse population increases in temperate Europe, but there remains no widely accepted explanation for small mammal population crashes (Lambin *et al.* 2006, Selva *et al.* 2012). Additionally, Selva *et al.* (2012) also hypothesized a competitive effect of dominant mice over subdominant voles in small mammal assemblages in temperate broad-leaved forests. The Yellow-necked Mouse *Apodemus flavicollis* monopolizes seeds and forces the Bank Vole *Clethrionomys glareolus* to rely on other resources in regular years, although the latter can effectively use exceptional seed production during mast events to drastically increase in abundance. Therefore, vole populations exhibit much higher population bursts in favourable environmental conditions than mice. The life-strategy of dormice, on the other hand, is different, as dormice are long-lived rodents, especially the Edible Dormouse *Glis glis* (Kryštufek *et al.* 2005). Kryštufek and Zavodnik (2003) found 2- to 5-year cycles, but not in a regular pattern. Dormice are hibernating rodents that can suppress their activity and reproduction in mast-poor years, along with aestivation; as a result, these cycles might reflect their activity and not true abundance (Kryštufek 2010). Shrew populations fluctuate irregularly as well and are thought to depend on food supply fluctuations and predation pressure (Henttonen *et al.* 1989, Churchfield *et al.* 1995). Different fluctuations of coexisting small mammals (Ecke *et al.* 2017) may lead to contrasting numerical and functional responses of predators (Sasvári *et al.* 2000, Zárybnická *et al.* 2013).

Among small-mammal-eating predators in forests, the owl guild is an ideal study group for assessing prey–predator co-dynamics, because small mammals represent a major part of the diet in all of the species (Mikkola 1983). In the temperate montane forests of central and southern Europe, the dominant owl species are the Boreal Owl *Aegolius funereus*, Tawny Owl *Strix aluco* and Ural Owl *Strix uralensis* (Vrezec 2003, Brambilla *et al.* 2020). A positive relationship between the proportion of the main prey in the owl diet and its abundance in the field has been documented several times (Korpimäki & Sulkava 1987, Korpimäki 1988, Zárybnická *et al.* 2011, Luka & Riegert 2018). A high proportion of voles in the breeding

diet in northern parts of Europe and the increasing importance of mice toward the south has been observed in all three species (Jäderholm 1987, Korpimäki 1988, Zawadzka & Zawadzki 2007, Zárbybnická *et al.* 2015, Yatsiuk & Filatova 2017, Luka & Riegert 2018, Tumieli & Mirski 2018, Vrezec *et al.* 2018). The Boreal Owl is a small mammal specialist; its diet consists of more than 90% mammalian prey in most parts of its range (Korpimäki & Hakkarainen 2012). Its main prey are voles and mice. When these become scarce, the Boreal Owl can switch to shrews and birds (Jäderholm 1987, Korpimäki 1988, Kämpfer-Lauenstein & Lederer 2010, Zárbybnická *et al.* 2013, Tumieli & Mirski 2018). The Ural Owl is considered a food generalist (Korpimäki & Sulkava 1987), although mammalian prey predominates in its diet (Vrezec *et al.* 2018). Mammals comprise over 90% of the Ural Owl breeding diet in peak vole years (Korpimäki & Sulkava 1987, Sidorovich *et al.* 2003, Andreychev & Lapshin 2017), because voles are its main prey across its European range (Vrezec *et al.* 2018). In low vole years, the Ural Owl can prey upon other mammals, birds and amphibians (Lundberg 1981, Korpimäki & Sulkava 1987, Sidorovich *et al.* 2003). The Tawny Owl is the most opportunistic species in the studied forest owl guild (Mikkola 1983). It preys upon small mammal species available in the highest abundances but may shift its main prey to other non-mammalian species if they are locally abundant (see the review in Obuch 2011). When small mammal populations decrease, the Tawny Owl can efficiently compensate for mammalian prey shortage with birds (Yatsiuk & Filatova 2017, Luka & Riegert 2018).

Forest owl population dynamics can be viewed in different respects, i.e. as a fluctuation in the number of territories or as a fluctuation in breeding performance (Karell *et al.* 2009, Saurola & Francis 2018, Vrezec & Bertoneclj 2018). Owls fluctuate in response to the cycles of voles, their main prey in northern Europe (Lundberg 1981, Korpimäki 1986, Brommer *et al.* 2002, Karell *et al.* 2009), or mice in central Europe (Kämpfer-Lauenstein & Lederer 2010, Zárbybnická *et al.* 2015, Luka & Riegert 2018). However, owls exhibit different responses to food supply (Newton 2002): resident species respond functionally (with a diet shift) or numerically (by adjusting their breeding productivity), while nomadic species, which are prey specialists, search for prey-rich

areas within their breeding range and might not breed every year in the same areas, i.e. they functionally respond with higher breeding dispersal rather than by a diet shift. In Finland, breeding dispersal has been reported to be quite different between the Boreal, Tawny and Ural Owls. About 90% of males and females of the Tawny Owl and Ural Owl breed within a radius of 3 km from year to year, while only 50% of Boreal Owl males and 29% of females stay, and nearly one-quarter of females move more than 100 km from the previous nest-site (Valkama *et al.* 2014). Female Boreal Owl breeding dispersal distances are known to be up to 630 km in northern Europe and 200 km in central Europe (Korpimäki & Hakkarainen 2012). In resident Tawny and Ural Owls, young females can delay reproduction in low vole years and enter the breeding population at older ages (Saurola 1992, Millon *et al.* 2010). A crash in small mammal populations can lead to high mortality of territorial birds (Brommer *et al.* 2002) but also to a high number of breeding pairs when prey populations increase again (Brommer *et al.* 1998, Karell *et al.* 2009). Breeding attempts and breeding success in all owls seem to be positively related to prey abundance in the preceding autumn at all latitudes (Brommer *et al.* 2002, Sidorovich *et al.* 2003, Lehikoinen *et al.* 2011, Zárbybnická *et al.* 2013).

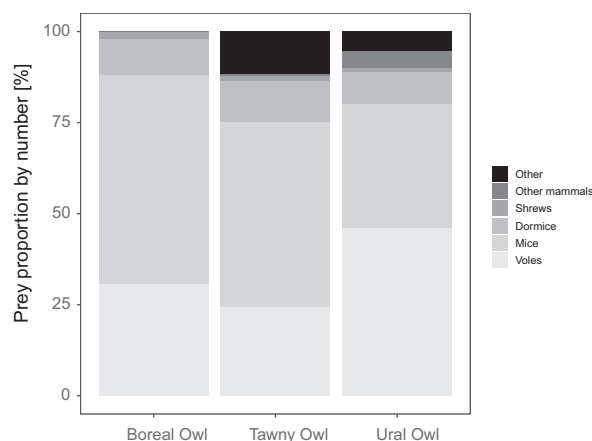
In contrast to other studies, our study guild is located in montane temperate forests, with Boreal and Ural Owls at the southern edge of their distribution, i.e. as glacial relicts (Korpimäki & Hakkarainen 2012, Vrezec *et al.* 2018). The majority of their populations in Europe are confined to the boreal zone (Pietiäinen & Saurola 1997, Huntley *et al.* 2007), whereas in Tawny Owls the main distribution in Europe is in the temperate zone (Petty & Saurola 1997). The coldest monthly mean temperature of  $-10^{\circ}\text{C}$  clearly demarcates Tawny Owl, as a temperate zone species, from Boreal and Ural Owls, as boreal zone species, because this represents the limit for Tawny Owl distribution and the mean range for both boreal zone and cold-adapted owls (Huntley *et al.* 2007, Brambilla *et al.* 2020). This is also reflected in their altitudinal distribution in southern Europe, where only 5–25% of the Boreal Owl and Ural Owl breeding populations are found below 600 m above sea level (asl), whereas up to 70% of the Tawny Owl breeding population is found below 600 m asl (data from Slovenia; Vrezec 2003, 2019a, 2019b, 2019c). We

hypothesize that, given the contrasting traits between all three coexisting owl species, the overall response of predators in the guild is expected to be different in southern European temperate forests. The objective of our study was to use machine learning approaches to build predictive models from collected long-term data to make predictions about the fluctuations of different small mammal populations that affect the territory occupancy and breeding activity of coexisting owl species with different traits. According to current knowledge, we hypothesize that (1) there is a key species in the small mammal forest assemblage that triggers differential owl responses in general; (2) prey decline always leads to a numerical response in owl species, but at different stages, i.e. territory vs. nest occupancy vs. productivity, and magnitudes; and (3) in temperate mixed forests, boreal zone owl species will exhibit higher sensitivity to prey fluctuations than temperate zone owl species.

## METHODS

### Study species and area

The study was conducted at Mount Krim in the northern Dinaric Alps (central Slovenia: 45°58'N, 14°25'E). The area extends over 140 km<sup>2</sup> at an altitudinal range from 290 to 1108 m asl, and most of the area (77%) is covered with temperate mixed forests with Beech *Fagus sylvatica* and Silver Fir *Abies alba* as the dominant tree species (Vrezec *et al.* 2018). Most of this managed forest is in the old growth phase, with trees of more than 30 cm in diameter at breast height, providing enough suitable natural tree holes for owls to breed (Vrezec 2003). About 20% of the study area is open habitats and the remainder consists of urban areas, which are situated mainly in the lowlands (Vrezec & Tome 2004a). The dominant owl species in the area are the Boreal, Tawny and Ural Owls, with the smallest Boreal Owl (female body-weight 275 g) being confined to higher altitudes, the mid-sized Tawny Owl (female body-weight 515–690 g) being confined to lower altitudes and the largest Ural Owl (female body-weight 840–1180 g) having no elevational preferences (Vrezec 2003). According to the available breeding diet data extracted from the nestboxes for all three owl species from the study area (Sotenšek 2012, Vrezec *et al.* 2018, unpubl. data for Boreal Owl),



**Figure 1.** Summary of the available data on the breeding diet composition (proportion of prey item groups by number (%)) of the coexisting forest owls, i.e. the Boreal, Tawny and Ural Owls, in the Dinaric forests of Mount Krim, Slovenia.

mammalian prey dominates with the highest proportions being mice and voles (Fig. 1). Mice, comprising almost exclusively the Yellow-necked Mouse, account for more than half of the Boreal and Tawny Owl prey, while voles, comprising mostly the Bank Vole, predominate in the Ural Owl diet. The Yellow-necked Mouse and the Bank Vole make up the bulk of the diet for all three owls. The third most abundant prey are the dormice. Specifically, the Ural Owl preys upon the Edible Dormouse the most. However, the large Edible Dormouse is completely absent from the Boreal Owl diet and is replaced with smaller dormouse species, i.e. the Hazel Dormouse *Muscardinus avellanarius* and Forest Dormouse *Dryomys nitedula*. Shrews, comprising mostly the Common Shrew *Sorex araneus*, are the least important small mammal prey, contributing only 2.0% or less to the diet of all three owl species. There is an important distinction between the proportion of non-mammalian prey in the diets, which is significant in the Tawny Owl (11.6%), but very low in the Boreal and Ural Owls (0.0% and 4.6%, respectively; Fig. 1).

### Fieldwork

Annually collected monitoring data on the number of owl territories, breeding performance and small mammal abundance from the period 2004–2020 were included in the analysis. The number of owl territories was assessed using playback method

surveys with a conservative survey protocol allowing the recording of spontaneously calling owls as well as responses to playback broadcast – for a detailed description of the survey method see Vrezec (2003), and Vrezec and Bertoneclj (2018). We considered a territory as unoccupied when there was no reply to the playback after two (Tawny Owl) or three (Ural Owl and Boreal Owl) survey visits. The surveys were conducted annually at 25 survey points distributed over the whole altitudinal range. Relative abundances were calculated as a ratio of the number of survey points with detected owl territory to the number of all inspected survey points. Breeding performance was assessed by nest-box monitoring (Vrezec & Bertoneclj 2018). The proportion of occupied nestboxes was considered as a measure of breeding attempts per year. The average clutch size per year was calculated from all breeding attempts with known clutch size (95% of all breeding attempts). In years when no breeding attempts were recorded, the average clutch size in the analysis was defined as 0. Nestboxes on Mount Krim were first set up before 2004 with more added over time, with the last set up in 2019. From 2004 to 2020, between 21 and 66 large nestboxes (dimensions 70 × 35 × 35 cm; suitable for nesting of all three owl species), and up to 14 small nestboxes (dimensions: 50 × 25 × 25 cm; suitable for nesting of the Boreal Owl only), were checked several times from April to June each year. The fieldwork was conducted under licences 35601-75/2012-8 and no. 3561-40/2017-4 issued by the Slovenian Environment Agency.

Small mammals were monitored using different methods focusing on four main dominant species in the assemblage, namely the Yellow-necked Mouse, the Bank Vole, the Edible Dormouse and the Common Shrew. All four species are considered as principal small mammal species in temperate mixed forests in the Dinaric Alps (Skok & Kryštufek 2012). Mice and voles were sampled annually with snap-traps baited with a mixture of canned sardines and rolled oats. Snap-traps were set at two sampling locations, one at lower altitude and one at higher altitude, in the forest at the end of the owl breeding season in June comprising on average  $122 \pm 43$  trap-nights each year. The snap-traps were not assumed to be reflective of the relative abundance of shrews (Whitman 2009); therefore, we used pitfall traps, in which they were caught much more frequently than in the snap-

traps. A transect of 10 pitfall traps per location was left active for 5–13 days. In the pitfall trap samples, the Common Shrew predominated over the Alpine Shrew *Sorex alpinus*, but in the analysis we pooled the abundance data of both species. Three sampling locations distributed over the altitudinal range were monitored in June each year. Dormouse abundance was assessed by counting vocalizing dormice during the night: 5 min of counting vocalizing individuals at 20 survey points distributed over the altitudinal range. Three counts were repeated in July and at the beginning of August each year, when the density of dormice and their activity in the environment reach their annual maxima (Kryštufek & Zavodnik 2003). The annual maximum count per point was taken into the final dataset. Relative abundances were given as the number of caught individuals per 10 trap-nights for voles, mice and shrews and as the number of vocalizing individuals per survey point for dormice. The sampling methods for small mammals were used consistently over the whole study period, which enabled between-year comparisons within each small mammal group.

### Machine learning analysis

We were interested in strong positive relationships between the abundance of small mammals on the one hand and owl territory occupancy, breeding attempts and clutch size on the other. We follow the generally accepted rule of thumb (Akoglu 2018) that correlation is strong if Pearson's coefficient has a value of at least 0.7. To find such relationships, we use advanced supervised machine learning methods.

We have used machine learning methods that can be categorized into two different classes of methods. The first machine learning method, predictive clustering trees (PCTs) for multi-target regression (Struyf & Džeroski 2006), belongs to the class of methods that learn a predictive model. PCTs are hierarchical models that predict the values of several continuous dependent variables simultaneously. The second method belongs to the class of feature importance estimation methods, which determine the relevance of features (independent variables) with regard to the target attributes (dependent variables). The method (Petković *et al.* 2017) uses ensembles of PCTs (Kocev *et al.* 2013), i.e. random forests, in combination with the Genie3 importance score.

We used the two methods to analyse the data in three predictive modelling scenarios, addressing three different multi-target regression tasks. In each scenario, we predicted one property of interest (owl territory occupancy, breeding attempt rates and clutch sizes), simultaneously for all owl species for which it was observed. In this way, we built three PCTs for multi-target regression, predicting (1) owl territory occupancy in the Boreal, Tawny and Ural Owls, i.e. three target attributes; (2) breeding attempt rates in the Tawny and Ural Owls, i.e. two target attributes; and (3) clutch sizes in the Tawny and Ural Owls, i.e. two target attributes. We also computed three feature rankings (importance estimations) – one for each predictive modelling scenario.

For the eight dependent variables, we could learn eight individual single-target models. This would make sense if we were interested in each of the owl species separately and independently from the other owl species. However, as we were interested in the coexistence of the species, we built three multi-target models that predicted the variables of interest for all species simultaneously. Models that predict several targets implicitly capture the dependencies among the targets.

In this study, the above-mentioned machine learning algorithms used the relative abundances of small mammal groups of the current year as descriptive (independent) variables, often referred to as *features*. Since the previous year may also be of crucial importance for owl territory occupancy and breeding performance (Brommer *et al.* 2002), we added the small mammal abundances from the preceding year to the set of independent variables. In the first predictive modelling scenario, the targets (dependent variables) were the relative abundances (territory occupancies) of all three owl species. In the second predictive modelling scenario, the dependent variables were the nestbox occupancies of the Tawny and Ural Owls. In the third predictive modelling scenario, the dependent variables were the mean clutch sizes of the Tawny and Ural Owls. We viewed and addressed all three predictive modelling scenarios as multi-target regression tasks, because all scenarios considered multiple real-valued targets.

We analysed our data in the following manner. First, we built (trained) multi-target regression trees (Struyf & Džeroski 2006), such as those shown in Figures 4, 5 and 6. To this end, we used the CLUS software package that employs the

paradigm of predictive clustering (Blockeel & De Raedt 1998) for structured output prediction (including multi-target regression). We then measured the performance of the PCTs on the training data and estimated their performance on unseen data. We finally calculated the feature rankings for each of the three multi-target regression tasks, using the tree-ensemble-based approach of Petković *et al.* (2017). The CLUS software package supports the learning of individual PCTs, PCT ensembles and feature rankings based on PCT ensembles. It is publicly available at <http://source.ijs.si/ktclus/clus-public>.

#### *PCTs for multi-target regression*

PCTs are hierarchical predictive models, which consist of internal nodes (shown as circles in Figs 4, 5 and 6) and leaves (shown as rectangles). The internal nodes contain tests, comparing independent variables (features, descriptive attributes) to threshold values, tree-branches correspond to test outcomes, and leaves contain predictions for the target (dependent variables).

The PCTs can be used for making predictions. A prediction for an example (a data instance) is made by traversing the tree according to the example's attribute (feature) values and tests in the tree. When a leaf node is reached, a prediction for each target attribute is obtained. A PCT can also be seen as a clustering, i.e. a hierarchy of clusters, represented by the tree's structure. Each node in the tree represents a cluster, which can be described by the tests that appear in the internal tree nodes. Each node holds a test, and if we combine all the tests from the root node to the selected node, we get the description of the cluster at the selected node.

#### *Learning PCTs for multi-target regression*

The PCTs were built by CLUS, which took the collected data (regarding small mammal populations and the three owl species) as input and produced the PCTs as output. In the process of building trees, CLUS considers many alternative trees and, roughly speaking, selects a tree that fits the input data well and is as small as possible.

The trees are built in a step-wise fashion by using the standard heuristic algorithm for top-down induction of decision trees, extended to the multi-target setting. The algorithm starts with all the data points at the root of the tree, where the different data points can have different values of

targets (high variance). At each node (including the root), this algorithm selects a condition (test on an attribute, comparing it to a value) according to which the data are split into subsets, where the targets have lower variance. When all data points have values of the target attributes that are similar to each other (i.e. have low variance), the data are no longer split, but rather a leaf is created, which gives as a prediction the average value of the targets.

At each node of the tree, the algorithm considers all different attributes (independent variables) and all possible values of the respective attributes (that appear in the data) as potential thresholds. It chooses the test that most reduces the variance of the target variables between the node and its children. This means that the condition/test  $c$  is chosen that corresponds to

$$\operatorname{argmax}_c \operatorname{Variance}(S) - \operatorname{Variance}_c(S1) - \operatorname{Variance}_c(S2),$$

where  $S$  is the set of data in the current node and  $S1/S2$  are the subsets for which  $c$  is true/false.

When a split of the data  $S$  is made into subsets, the described top-down induction of decision trees procedure is repeated for each of the two subsets,  $S1$  and  $S2$ . The data are split into subsets until there are too few data points, the variance in the data is very low (the values of the targets for all remaining data points are very similar to each other) or the variance can no longer be reduced, i.e. the independent attributes do not carry any additional discriminative information with regard to the observed target(s). We required at least five examples from the training set to reach each leaf node (to prevent overfitting).

#### Evaluating the quality of PCTs for multi-target regression

Two metrics were used, namely the Pearson's coefficient and relative root mean squared error (RRMSE). These compare the predicted and true values of the target variables over all examples. The mean squared error (MSE) is given by

$$\operatorname{MSE} = \frac{1}{n} \sum_{i=1}^n (Y_i - \hat{Y}_i)^2,$$

where  $n$  is the number of data points,  $Y_i$  are observed values and  $\hat{Y}_i$  are predicted values of a target variable. RMSE (root MSE) is the square root of MSE. Finally, RRMSE normalizes the

RMSE of a model of interest (our trained models) by the RMSE of a simple model that always predicts the average value (calculated on the training data) for each of the target variables. An RRMSE close to 0.0 is desirable, whereas an RRMSE around or more than 1.0 indicates a model with poor performance. The RMSE is derived from the MSE, which is calculated as the average of squared differences between predicted and true values over all examples.

The values of the two chosen metrics are calculated for two different sets of data. First, they are calculated for the data that were used to train the model. We refer to the scores of these metrics as being descriptive (often also called *training errors*). Models exhibiting a training correlation higher than 0.7 are considered to be adequate, as mentioned above.

We also estimated the predictive performance (error) of the PCTs on new/unseen data using leave-one-out cross-validation. This approach divides the dataset into a training part and a testing part, where only one data instance is in the testing part. The number of such dataset divisions exactly matches the number of instances. In our study, this corresponded to leaving out 1 year for the testing part and training on the remaining 16 years (we have 17 data instances). This was repeated 17 times. Within each iteration, the model is trained on the training part and evaluated on the testing part, i.e. the models are evaluated on the data that were not used for training the models. We refer to the scores of these metrics as being predictive (often also called testing errors).

#### Calculating feature rankings

We finally calculated the importance scores of the independent variables/features for predicting the dependent variables/targets collectively and separately. For this, we used multi-target regression feature ranking methods (Petković *et al.* 2017), based on ensembles of multi-target regression trees (Kocev *et al.* 2013). In particular, we calculated the Genie3 importance score, based on random forests of 100 trees for multi-target regression. The importance scores and corresponding rankings reveal the relative importance of each attribute for predicting all targets, jointly and separately. Highly ranked attributes contain the most discriminative information with respect to the target(s) of choice.

## RESULTS

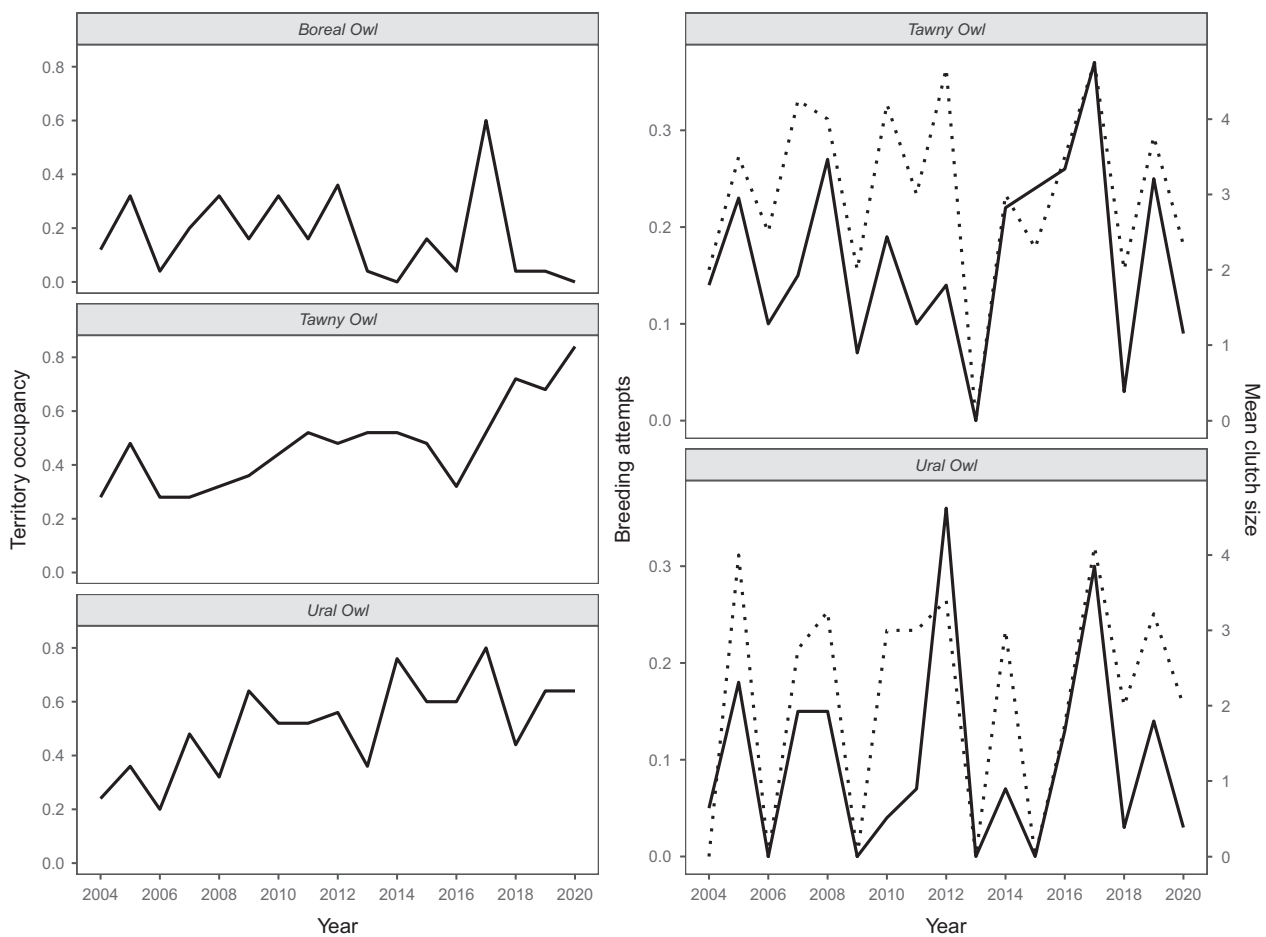
### Studied owl guild characteristics

In the period 2004–2020 at Mount Krim (central Slovenia), we recorded 73 territories of the Boreal Owl, 201 territories of the Tawny Owl and 217 territories of the Ural Owl. In the nestboxes, we recorded two breeding attempts of the Boreal Owl, 90 breeding attempts of the Tawny Owl and 53 breeding attempts of the Ural Owl. Thus, the Boreal Owl was found in the nestbox in 0.2% of 1015 annual nestbox controls, the Tawny Owl in 17.0% of 530 annual nestbox controls and the Ural Owl in 10.0% of 530 annual nestbox controls. As the Boreal Owl was found to be a rare breeder in the nestboxes in our study area, we did not

include Boreal Owl breeding attempts and clutch size data in our further analysis.

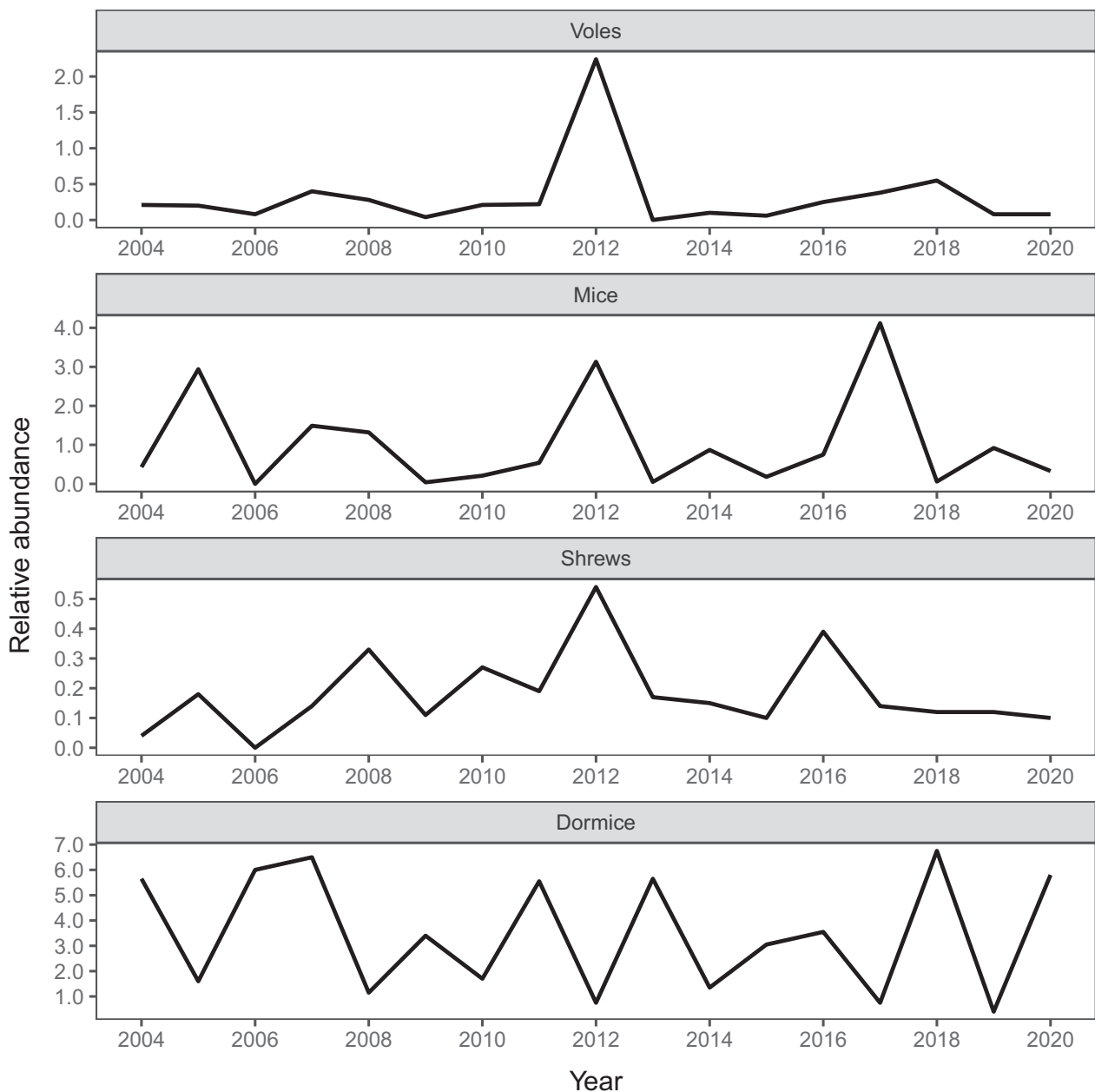
### Owl population, breeding productivity and prey population fluctuations

In the period 2004–2020, relative owl territory densities fluctuated between 0.0 and 0.6 active territories per survey point for the Boreal Owl, between 0.3 and 0.8 for the Tawny Owl, and between 0.2 and 0.8 for the Ural Owl (Fig. 2; Table S1). The proportion of breeding attempts per nestbox fluctuated between 0.0 and 0.4 in the Tawny Owl and Ural Owl, and clutch size per breeding attempt fluctuated between 0.0 and 4.8 eggs in the Tawny Owl, and between 0.0 and 4.1 eggs in the Ural Owl (Fig. 2; Table S1).



**Figure 2.** Population dynamics of owls on Mount Krim in the period from 2004 to 2020. Relative abundances of owls are given as the number of active territories per survey point (territory occupancy) and as the proportion of occupied nestboxes (breeding attempts). The dotted line represents between-year changes in mean clutch size.





**Figure 3.** Population dynamics of small mammals on Mount Krim in the period from 2004 to 2020. Relative abundances of voles, mice and shrews are given as the number of trapped individuals per 10 trap-nights, and the relative abundance of dormice as the number of vocalizing individuals per survey point (see Methods for details).

The relative small mammal population densities in the period 2004–2020 fluctuated as follows: mice between 0.0 and 4.1, voles between 0.0 and 2.2, and shrews between 0.0 and 0.5 of trapped individuals per 10 trap-nights. Dormouse populations in this period fluctuated between 0.4 and 6.7 of vocalizing individuals per survey point. Mice and voles reached a significant population peak in

2012. Several additional population peaks were recorded for the mouse population, which were less clear in voles and shrews (Fig. 3). The Edible Dormouse fluctuation pattern differed from the other small mammal groups, usually reaching peaks when the abundance of the other small mammals was low. In all small mammal families, except shrews, densities from low (< 700 m asl)

**Table 1.** RRMSE and Pearson's coefficients for the PCT shown in Figure 4, which predicts territory occupancy of Boreal, Tawny and Ural Owls.

Territory occupancy	RRMSE		Pearson's coefficient	
	Predictive	Descriptive	Predictive	Descriptive
Boreal Owl	0.9762	0.6179	0.3589	0.7863
Tawny Owl	1.2350	0.9619	-0.6465	0.2734
Ural Owl	1.0758	0.8105	-0.1716	0.5857

Descriptive performance measures were calculated on the training data and predictive ones were estimated with leave-one-out cross-validation.

and high (> 700 m asl) elevations were significantly correlated (Fig. S1).

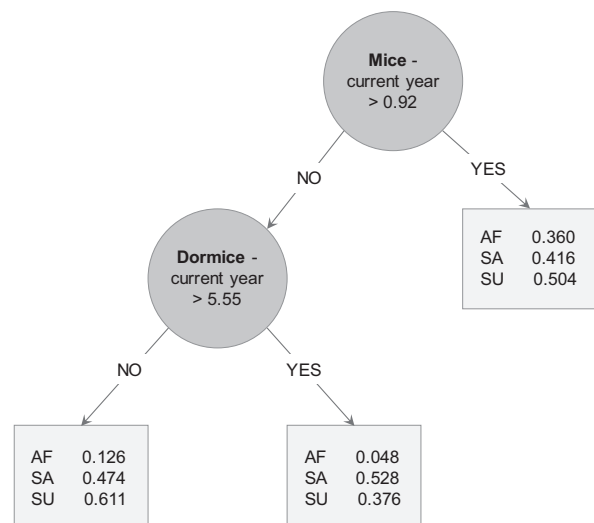
### Owl territory occupancy vs. small mammal abundances

For the model predicting territory occupancy rates in all three owls, there was a strong positive correlation of the Boreal Owl territory occupancy and small mammal relative abundances (Pearson's coefficient: 0.79; Table 1). The correlation coefficient was too low (below 0.7) and the RRMSE too high (close to 1.0) for the model to successfully predict or describe the Tawny and Ural Owl territory occupancy (Table 1). In sum, annual abundances of small mammals positively affected the predicted territory occupancy only for the Boreal Owl, but no statistically detectable correlations were evident for the two *Strix* owls.

The most important small mammal group for determining owl territory occupancy was the mouse group (Table S2). When the relative abundance of mice in the current year was around average or higher (above 0.92), territory occupancy rates were high in all owls (Fig. 4). On the other hand, when the relative abundance of mice in the current year was below average, the territory occupancy rate of the Boreal Owl was low regardless of the relative abundance of dormice in the current year. The relationships with small mammal populations at the level of territory occupancy found for the Tawny and Ural Owls were not substantially different (Fig. 4).

### Owl breeding attempts vs. small mammal fluctuations

The learned PCT for predicting the breeding attempts of the Tawny and Ural Owls (Fig. 5) had high predictive power (Table 2). It demonstrated a



**Figure 4.** A PCT predicting territory occupancy rates for the three forest owl species (AF, Boreal Owl; SA, Tawny Owl; SU, Ural Owl) from the abundances of small mammals in the current and previous years.

strong positive relationship between small mammal relative abundances and breeding attempts of Tawny and Ural Owls (Pearson's coefficients: 0.81 and 0.89, respectively; Table 2). When used for prediction, the model exhibited a correlation that was moderately positive for both owls (0.58 for the Tawny Owl and 0.60 for the Ural Owl).

The abundances of mice in the current and preceding year were the most important attributes influencing the breeding attempts in both *Strix* species (Table S3). The Ural Owl depended on these populations more heavily than the Tawny Owl, considering the importance scores. In poor mouse years, when the relative abundance in the current year was < 0.54, there were almost no breeding attempts by the Ural Owl (Fig. 5). The breeding attempts of the Tawny Owl were moderately affected by low mouse years. A significant drop in breeding attempts was apparent only after preceding average or peak mouse years (> 0.87). In moderate mouse years (> 0.54), the breeding attempt rate of Tawny Owls was high, regardless of the situation in the preceding years, but it was moderately affected and lowered in the Ural Owl after extremely low mouse years (Fig. 5).

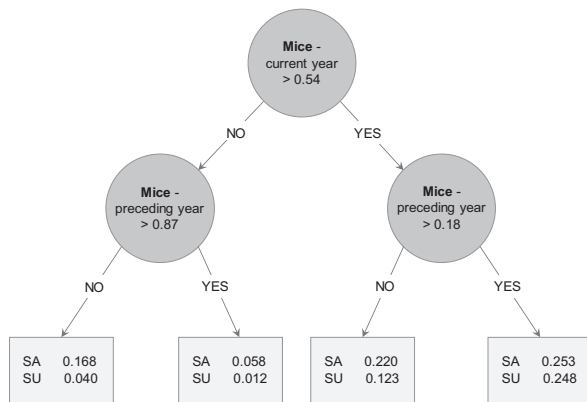
### Owl clutch size vs. small mammal fluctuations

The learned PCT for predicting the clutch size of the Tawny and Ural Owls (Fig. 6) had high

**Table 2.** RRMSE and Pearson's coefficients for the PCT shown in Figure 5, which predicts breeding attempt rates in the Tawny Owl and Ural Owl.

Breeding attempts	RRMSE		Pearson's coefficient	
	Predictive	Descriptive	Predictive	Descriptive
Tawny Owl	0.8378	0.5882	0.5793	0.8087
Ural Owl	0.8289	0.4546	0.6030	0.8907

Descriptive performance measures were calculated on the training data and predictive ones were estimated with leave-one-out cross-validation.



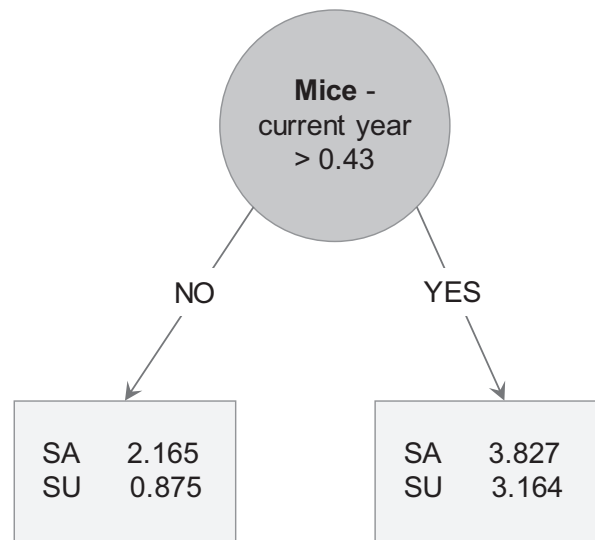
**Figure 5.** A PCT predicting the breeding attempt rate of Tawny Owl (SA) and Ural Owl (SU).

descriptive power but low predictive power (Table 3). It demonstrated a stronger positive relationship of small mammal relative abundances with average clutch size per breeding attempt in the Ural Owl (Pearson's coefficient: 0.78) than in the Tawny Owl (Pearson's coefficient: 0.70; Table 3).

The key predictive attribute was abundance of mice in the current year, whereas the importance of the abundances of the other small mammal groups was low (Table S4). The clutch size of the Ural Owl was substantially lower in low mouse years (< 0.43), but the decrease in mouse abundance affected the Tawny Owl's clutch size to a much lower extent (Fig. 6).

**DISCUSSION**

Our study confirmed that populations of coexisting owl species respond to changes in small mammal abundances at different stages and with different magnitudes, as a consequence of species-specific



**Figure 6.** A PCT predicting the clutch size of Tawny Owl (SA) and Ural Owl (SU).

**Table 3.** RRMSE and Pearson's coefficients for the PCT shown in Figure 6, which predicts clutch size in the Tawny Owl and Ural Owl.

Clutch size	RRMSE		Pearson's coefficient	
	Predictive	Descriptive	Predictive	Descriptive
Tawny Owl	1.0319	0.7177	0.2916	0.6964
Ural Owl	1.0215	0.6319	0.3478	0.7750

Descriptive performance measures were calculated on the training data and predictive ones were estimated with leave-one-out cross-validation.

life histories and survival strategies. The responses of owl predators were highly differentiated in years with low small mammal abundances. The survival strategy in low years was to leave territories in search of prey-rich areas (Boreal Owl), to suppress breeding and wait in the territory for better years (Ural Owl) or to decrease the breeding activity slightly and sustain it by shifting prey selection (Tawny Owl). Our results indicated that the dominant species in the small mammal assemblage, the Yellow-necked Mouse, had the key role in determining predator responses. The role of other small mammal species in the assemblage was secondary for owl predators, allowing them to compensate for food requirements in periods of low population of the dominant prey species. However, the efficiency of utilization of secondary prey in low years was

very different between different owls, leading to marked drops in territory occupancy (Boreal Owl) or breeding attempt rates and clutch size (Ural Owl), but with less significant drops in species that are more flexible in their prey selection (Tawny Owl).

### **Mice control the temperate mixed forest owl guild in southern European mountains**

We found that populations of mice, voles and shrews increase in abundance irregularly, every 2–5 years, which has already been suggested regarding central European temperate forests (Zárybnická *et al.* 2015). In accordance with Kryštufek and Zavodnik (2003), the abundance of dormouse peaks more regularly, every 2–3 years. Nevertheless, our results showed that the key species determining fluctuations of owl predators was the Yellow-necked Mouse. In temperate mixed forests, mice and voles predominate over shrews and dormice (Skok & Kryštufek 2012). We suggest that the Yellow-necked Mouse governs the fluctuations of predators as the most abundant small mammal in the assemblage. Voles can burst only in exceptional years, such as in 2012 in our study area, so have no power in controlling owl predator between-year fluctuations.

### **Boreal zone predators in temperate forest**

The boreal species, i.e. the Boreal and Ural Owls, were found to be more sensitive to small mammal fluctuations than the temperate zone species, i.e. the Tawny Owl, in the temperate mixed forest of southern European mountains. This was reflected in more detrimental numerical responses, which differed between species.

In temperate forests, mice and voles are the main prey for the Boreal Owl (Zárybnická *et al.* 2013, this study). Zárybnická *et al.* (2013) found that the proportion of voles or mice in the Boreal Owl's diet in central Europe is not positively correlated with the rodents' abundance in the field and that the Boreal Owls do not respond to vole or mouse abundance numerically. In contrast, our results show that low small mammal abundances triggered territory abandonment in the Boreal Owl at least in low-elevation temperate montane forests (Fig. 4). In boreal forests, the species is

semi-nomadic, with males being mostly resident and females being migratory with high breeding dispersal (Korpimäki *et al.* 1987, Hakkarainen *et al.* 2002). Female breeding dispersal depends on food fluctuations; they disperse more often and for longer distances when prey populations decline (Sonerud *et al.* 1988). When the abundance of small mammals is low, most males cannot breed because females are scarce in the area (Hakkarainen & Korpimäki 1998). However, our results suggest that at the southern limit of the species distribution, nomadism is perhaps even more pronounced and expands also to males. In low small mammal years, there were hardly any territorial males. As the study from Finland shows, territorial Boreal Owl males are vocally very active in spring and also respond to playback, both breeding and bachelor males (Korpimäki & Hakkarainen 2012). In our study, we conducted playback surveys in three survey visits and spontaneously calling males were recorded additionally in up to five survey visits aiming to survey *Strix* owls. Therefore, we concluded that it is highly unlikely that territorial males went unnoticed in low small mammal years, because calling activity is high in spring and the call of the Boreal Owl can be heard up to 2 km away (Korpimäki & Hakkarainen 2012). We argue that the absence of Boreal Owls in some years was a consequence of species nomadism and not a methodological artefact. Furthermore, the bulk of the Boreal Owl breeding population in Slovenia is found in boreal-type coniferous forests between 1000 and 1400 m asl, and only 30% of the breeding population can be found at lower elevations (Vrezec 2019a). The periodicity of territorial male occurrence and low nestbox occupancy rates indicated that temperate mixed forests at our study site are a suboptimal habitat for the Boreal Owl, which might be typical for forests below 1000 m asl. These habitats are dominated by larger predatory *Strix* owls that can prey upon and competitively exclude the Boreal Owl (Vrezec & Tome 2004a, Korpimäki & Hakkarainen 2012). The almost complete absence of Boreal Owl territorial males in low prey years can be explained by avoidance of intraguild predation, which increases when the main prey decreases (Lourenço *et al.* 2011). Therefore, in low-elevation forests the species occurs in higher abundances only in peak mouse years. There is, however, no available dispersal distance data from the region so the breeding dispersal patterns and nomadism of the Boreal Owl at

the southern limit of its distribution in Europe still await study.

The Ural Owl is the largest and competitively dominant species in the guild (Vrezec & Tome 2004a), and, unlike the Boreal Owl, is a resident species (Valkama *et al.* 2014). Despite being flexible in its diet, it was recently found that voles are the main prey of the Ural Owl in boreal, hemiboreal and temperate forests, although in temperate forests mice are almost equally important (Vrezec *et al.* 2018). Our results indicated that mouse (and not vole) fluctuations govern Ural Owl population responses in temperate forests. However, in contrast to the Boreal Owl, in long-lived and sedentary Ural Owls (Saurola 1992), the numerical response was not reflected in occupied territory fluctuations, but in breeding suppression or a significant clutch size decrease in low mouse years. It seems that, in temperate mixed forests, the Ural Owl cannot find sufficient alternative prey to compensate for a shortage in the main prey (voles and mice). In boreal and hemi-boreal forests, Ural Owls can take a larger proportion of birds in low vole years, but this is not the case in temperate forests, not even in the non-breeding period (Vrezec 2016, Vrezec *et al.* 2018). We suggest that in temperate forests, Ural Owls are more specialized on mice and voles, with dormice as an alternative prey being large, easy to catch and profitable (Vrezec *et al.* 2018). The proportion of dormice biomass in its diet is almost equal to that of mice and voles (Vrezec *et al.* 2018). As the species is dormant, it usually appears in the environment later in the season, in May to October (Kryštufek 2010), and cannot act as alternative prey throughout the year. When preying upon dormice, owl predators have to switch their foraging activity from hunting ground-dwelling prey to

arboreal prey because dormice are almost exclusively active in trees (Skok & Kryštufek 2012), which might lower hunting efficiency.

### Tawny Owl – the temperate zone species

The Tawny Owl was found to be the most adapted species with respect to small mammal fluctuations in temperate mixed forests. The numbers of Tawny Owl territories in temperate regions are known to be relatively stable between years (Hirons 1985, Sunde & Bolstad 2004), so we did not expect high correlation with small mammal abundances. The Tawny Owl's generalistic and flexible foraging (Obuch 2011) enables it to sustain established territories and breeding activity even in low small mammal years (Solonen 2011), as confirmed also by our results. Nevertheless, we have found that its breeding attempt rate as well as clutch size per breeding attempt were slightly decreased in low mouse years, which is in accordance with studies from other parts of the temperate and boreal region (Karell *et al.* 2009, Luka & Riegert 2018). In the forest owl guild, the Tawny Owl is an adaptable mesopredator that is less sensitive to rapid changes in prey availability. Its population fluctuations might be governed by other environmental factors, for example the competitive dominance of larger predators (Vrezec & Tome 2004b) or harsh winter conditions (Francis & Saurola 2004), but this requires further investigation.

### CONCLUSIONS

We have found that sensitivity and responses to prey fluctuations are distinctly different between

**Table 4.** Comparison of estimates of owl responses to annual fluctuations in their food supply between Newton (2002) and this study.

Owl species Data source	Territory occupancy		Breeding attempts		Clutch size	
	Newton 2002	This study	Newton 2002	This study	Newton 2002	This study
Boreal Owl	Strong	Moderate	Slight	NA	Slight	NA
Ural Owl	Moderate	No	Moderate	Strong	Moderate	Strong
Tawny Owl	Slight	No	Strong	Moderate	Moderate	Slight

Responses were scored from minimum and maximum modelled predicted values after Newton (2002): 'no' – no response; 'slight' – < 2-fold change; 'moderate' – 2- to 10-fold change in territory occupancy/breeding attempts or 2- to 3-fold change in clutch size; 'strong' – > 10-fold change in territory occupancy/breeding attempts or > 3-fold change in clutch size; 'NA' – no data.

coexisting owls in temperate mixed forests. Most of the studies on owl–prey co-dynamics have been conducted in boreal forests, where we can expect different responses from those in southern forests. Newton (2002) has summarized the sensitivity of the studied owls to annual fluctuations in their food supply based mainly on boreal studies (Table 4). There are marked differences between our estimates of the responses of all owl species. A broader continental-scale approach is needed in future studies to reveal more general patterns in the ecology of owl predators in relation to their prey and to overcome regionally specific deviations. In the light of recent ecosystem alterations driven by climate and environmental changes, it is of crucial importance to be able to predict species vulnerability on the one hand and ecosystem function on the other. Compared with boreal forests, montane temperate forests are extremely heterogeneous in habitats due to diverse relief and wide range of altitudes. This situation enables the survival of cold-adapted and boreal zone species in fragmented refugial habitats in the southern temperate climate zone. Our study focused on temperate forest between 300 and 1100 m asl, which represents the largest part of the forests in the southern European Dinaric Alps and the Alps and may therefore reflect the most common patterns of small mammal fluctuations and owl responses in the region. However, at higher elevations, responses might be different, giving ecological advantage to the boreal zone species (Boreal and Ural Owls) over temperate zone species (Tawny Owl) because of different prey availability, the presence of competitors and harsher winter conditions. The extreme responses found in the Boreal Owl with presumably high levels of nomadism (even in males) should be viewed at a larger scale than that of this study, because of dispersal within the naturally fragmented spatial network of forest areas in central and southern European mountains. These forest area networks, which share the same nomadic population, are becoming increasingly important in the light of future climate changes. Climate models predict drastic Boreal Owl range constrictions in the Alpine region on the one hand and the expansion of both *Strix* species to higher elevations on the other (Brambilla *et al.* 2020), which could influence Boreal Owl distribution (Vrezec & Tome 2004b, Korpimäki & Hakkarainen

2012). According to our study, the competitively subordinate Boreal Owl, even in the presence of larger predators, can exploit occasional bursts of small mammal populations in temperate forests at low elevations. Whether low-elevation forests can play a role in the conservation of the Boreal Owl population in central and southern Europe is an open scientific question that needs to be resolved given that urgent conservation action is needed for this threatened owl species (Korpimäki & Hakkarainen 2012).

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## AUTHOR CONTRIBUTION

**Urška Ratajc:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Validation (equal); Visualization (lead); Writing-original draft (equal); Writing-review & editing (lead). **Martin Breskvar:** Methodology (equal); Resources (supporting); Validation (equal); Visualization (equal); Writing-review & editing (equal). **Sašo Džeroski:** Formal analysis (lead); Funding acquisition (equal); Methodology (equal); Resources (equal); Supervision (equal); Validation (equal); Writing-review & editing (equal). **Al Vrezec:** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (equal); Resources (equal); Supervision (lead); Validation (equal); Writing-original draft (equal); Writing-review & editing (equal).

## 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 at the end of the article.

**Figure S1.** Correlation of small mammal population densities (dormice, Gliridae; mice, Muridae, voles, Cricetidae; shrews, Soricidae) at low (< 700 m asl) and high altitudes (> 700 m asl) on Mt Krim (*R*, Pearson's coefficient).

**Table S1.** Summary statistics (Min, minimum; Q1, lower quartile; Mean; Q3, upper quartile and Max, maximum) of population dynamics measures for the small mammal groups and Boreal, Tawny and Ural Owl.

**Table S2.** Attribute/feature rankings in terms of their importance for owl territory occupancy in the Boreal, Tawny and Ural Owl.

**Table S3.** Attribute rankings in terms of their importance for breeding attempts rates in the Tawny and Ural Owl.

**Table S4.** Attribute rankings in terms of their importance for clutch sizes in the Tawny and Ural Owl.