INTRA- AND INTER-TROPHIC INTERACTIONS OF GENERALIST FOREST PREDATOR

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Doctoral Dissertation
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ZNOTRAJ- IN MED-TROFIČNE INTERAKCIJE GOZDNEGA PLENILCA GENERALISTA

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Abstract

We are witnessing major shifts in ecosystems due to intense anthropogenic pressures on the environment in recent decades, including rapid climate change, which is one of the strongest drivers of a global biological response. Raptors, which are at the top of the trophic web, are important indicators of ecosystem health. Tawny Owl (Strix aluco) is one of the most monitored raptor species in Europe, whose population traits may indicate various ecological processes and shifts at the ecosystem level. The goals of this dissertation were to investigate the population ecology traits of the Tawny Owl on a pan-European scale and to explore the species interactions on both inter- and intratrophic level. Our aim was to analyse the response of the Tawny Owl to fluctuations in small mammal populations, to compare it with other owls in the forest guild, and to investigate the long-term dynamics of the Tawny Owl's competition with the Ural Owl. Our literature review on the Tawny Owl population ecology traits revealed that diet is the most extensively studied trait across Europe. Some spatial gaps in the knowledge of the ecology and biology of the species in Europe were identified, as well as gaps in certain population parameters. Based on our results, we proposed a minimal recommended scheme for monitoring population contextual data as one of the first steps towards a pan-European monitoring scheme. Our long-term monitoring data on Tawny Owl population (and other owl and prey species) from montane Dinaric forests in Central Europe enabled us to analyze its role in this ecosystem. To explore Tawny Owl's intertrophic relationships, we used supervised machine learning approaches and addressed several modelling tasks of multi-target regression. Tawny Owl was able to successfully shift to alternative prey and sustain breeding activity even in low years of their main prey populations - the Yellow-necked Mouse (*Apodemus flavicollis*), which was found to have had a key role in determining predator populations. Tawny Owl, as a generalist predator and a temperate zone species, seemed to be less affected by small mammal fluctuations than its competitors, boreal zone owl species, Boreal (*Aegolius funereus*) and Ural Owl (*Strix aluco*). When further exploring Tawny Owl's intratrophic relationship with the Ural owl, we found that due to concurrent population growth and range expansion, their competition for space and nest sites was gradually intensifying, including direct nest displacements of the smaller Tawny Owl by the larger Ural Owl. Breeding Ural Owl females were significantly larger in shared territories with Tawny Owls compared to those in unshared territories. To our knowledge, we have described the first micro-evolutionary example in top predators driven by intensified intraguild interactions enhanced by climate change. The effects of global change are complex and understanding or predicting the consequences demands excellent knowledge of the indicator species role in the ecosystem and the dynamics of its interactions in the community. We have shown that recent climate changes are also inducing rapid changes in top predator assemblages, which is just the tip of the iceberg in terms of our understanding of establishment of new ecosystem dynamics. Besides predictive models, a comprehensive and long-term population-monitoring scheme was demonstrated as an invaluable technology for following trends in ecological traits, interactions of the indicator species and for detecting ecosystem response to stress.

Povzetek

V zadnjih desetletjih smo priča velikim spremembam ekosistemov zaradi intenzivnih antropogenih pritiskov na okolje, vključno s hitrimi podnebnimi spremembami, ki so eden najmočnejših dejavnikov globalnega biološkega odziva. Roparske ptice, ki zavzemajo najvišji trofični nivo, so pomembni pokazatelji stanja ekosistema. Lesna sova (*Strix aluco*) je ena najbolj opazovanih vrst roparskih ptic v Evropi, njene populacijske značilnosti pa lahko kažejo na različne ekološke procese in spremembe na ravni ekosistema. Cilji pričujoče disertacije so bili raziskati ekološke populacijske značilnosti lesne sove v vseevropskem merilu in raziskati njene medvrstne interakcije na med- in znotrajtrofičnem nivoju. Naš cilj je bil analizirati odziv lesne sove na nihanja populacije malih sesalcev, ga primerjati z drugimi sovami v cehu gozdnih sov in raziskati dolgoročno dinamiko kompeticije lesne sove s kozačo (*Strix uralensis*). Pregled literature o ekoloških značilnostih populacij lesne sove je pokazal, da je prehrana njena najbolj raziskana značilnost v Evropi. Ugotovljene so bile nekatere prostorske vrzeli v poznavanju ekologije in biologije vrste v Evropi ter vrzeli v nekaterih populacijskih parametrih. Na podlagi rezultatov smo predlagali minimalno priporočeno shemo monitoringa populacijskih kontekstualnih podatkov, kar je eden prvih korakov k vseevropski shemi monitoringa lesne sove. Naši dolgoročni podatki spremljanja populacije lesne sove (in drugih vrst sov ter plena) iz montanskih dinarskih gozdov v srednji Evropi so nam omogočili analizo njene vloge v tem ekosistemu. Da bi raziskali medtrofične odnose lesne sove, smo uporabili pristope nadzorovanega strojnega učenja in obravnavali več nalog modeliranja z večciljno regresijo. Lesna sova je lahko uspešno izkoriščala alternativni plen in se razmnoževala tudi v letih s šibkimi populacijami njenega glavnega plena - rumenogrle miši (*Apodemus flavicollis*), za katero smo ugotovili, da ključno vpliva na populacije plenilcev. Izkazalo se je, da je lesna sova kot plenilec generalist in izvorno vrsta zmernega pasu manj občutljiva na nihanja populacij malih sesalcev kot njena kompetitorja, ki sta izvorno vrsti borealnega pasu; koconogi čuk (*Aegolius funereus*) in kozača. Pri nadaljnjem raziskovanju znotrajtrofične interakcije lesne sove s kozačo smo ugotovili, da se je zaradi sočasnega povečanja populacije in širjenja območja njuna kompeticija za prostor in gnezdišča postopoma stopnjevala, kar je vključevalo tudi neposredni pregon z gnezda; manjšo vrsto, lesno sovo, je pregnala večja vrsta, kozača. Samice gnezdečih kozač so bile značilno večje na teritorijih, ki so si jih delile z lesno sovo, v primerjavi s samicami na teritorijih, ki si jih vrsti nista delili. S tem smo opisali prvi primer mikroevolucije pri končnih plenilcih, ki jo poganjajo vedno bolj intenzivne znotrajcehovske interakcije, spodbujene s podnebnimi spremembami. Učinki globalnih sprememb so kompleksni in razumevanje ali napovedovanje posledic zahteva odlično poznavanje vloge indikatorske vrste v ekosistemu in dinamike njenih interakcij v združbah. Pokazali smo, da nedavne podnebne spremembe povzročajo tudi hitre spremembe v združbah končnih plenilcev, kar je le vrh ledene gore v smislu našega razumevanja vzpostavljanja nove ekosistemske dinamike. Poleg napovednih modelov smo pokazali pomen celovite in dolgoročne sheme monitoringa populacij kot neprecenljivo orodje za sledenje trendom ekoloških značilnosti in interakcij indikatorskih vrst ter za odkrivanje odziva ekosistema na stres.

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Chapter 1

Introduction

1.1 Background and Problem Description

1.1.1 Global change and indicator species

Due to intense anthropogenic pressures on the environment, such as land use change, overexploitation of natural resources and pollution, major shifts in ecosystems took place in the past decades (Foley et al., 2005; IPCC, 2019; Sala et al., 2000; Tylianakis et al., 2008). Additionally, rapid climate change is one of the strongest drivers of a global biological response and shifts on all ecosystem levels are expected (Bellard et al., 2012; Lurgi et al., 2012; Parmesan, 2006; Quratulann et al., 2021; Tylianakis et al., 2008; Walther et al., 2002). Resulting biotic invasions and local biodiversity loss are potentially even more serious threats to ecosystem functioning than direct effects of abovementioned global change stressors (Hooper et al., 2012; Kuczynski et al., 2018; Pyšek et al., 2020; Thomas et al., 2004). Many studies have shown that the species distributions are shifting toward higher latitudinal and altitudinal ranges in response to global warming (Parmesan, 2006; Pizzolotto et al., 2014; Walther et al., 2002; Wilson et al., 2007). Future forecasts, particularly those based on species distribution models that include climate change effects, predict positive trends of generalist and declining trends of specialist species (Brambilla et al., 2020; Parmesan, 2006). The rise of generalist species has already been documented on different trophic levels (Britton et al., 2009; Clavel et al., 2011; Davey et al., 2012; de Gabriel Hernando et al., 2022; Warren et al., 2001). On the other hand, specialist species are getting more and more vulnerable and in many, the risk of local extinction is increasing (Clavel et al., 2011; Homburg et al., 2014; Jiménez-Alfaro et al., 2016; Warren et al., 2001). However, it seems the main cause of local extinctions is not limited species physiological tolerance to higher temperatures, but rather changed species interactions (Cahill et al., 2013).

Biological indicators have long been used to monitor ecological integrity and the concept has frequently been incorporated into policies and regulations (Carignan & Villard, 2002; Rapport, 1992). Indicator species are measurable characteristics of the structure, composition, or function of ecological systems (Niemi & McDonald, 2004). In the light of the complexity of ecological processes, their use is very cost-effective since the status of a single species (or a group of species) is relatively simple to measure. Additionally, the results can be easily interpreted and presented to policy makers and to the public (Siddig et al., 2016). However, the selection of specific indicator(s) and correct identification of their indicative traits is a challenging task as there are many preliminary conditions for a species to be a good potential indicator (Rapport, 1992; Sergio et al., 2008; Siddig et al., 2016). The most important condition is that the indicator and its trait(s) enable distinguishing anthropogenic change against natural variability (Niemi & McDonald, 2004). To ensure this excellent knowledge about the indicator species is essential. Assessing and predicting the consequences of global change demands that we understand the role of the species in the ecosystem and the dynamics of its interactions in the community. For following trends in ecological traits, interactions of the indicator species and for detecting ecosystem response to stress, a comprehensive and long-term population-monitoring scheme is an invaluable tool.

Raptors are important indicators of ecosystem health because of their trophic position at the top of the food chain (Hardey et al., 2013; Peniche Peyron, 2021; Sergio et al., 2008). Additionally, some of their life-history traits, such as low density, low fecundity, long period of juvenile dependence and longevity, increase their vulnerability to anthropogenic changes of their habitats, making them suitable as sentinel species (Espín et al., 2016; Movalli et al., 2019; Sergio et al., 2008). In comparison to other birds, raptors are far more threatened; about half of raptor species in the world have declining global populations, mostly due to habitat destruction and degradation (McClure et al., 2018). Pollution is another important factor in declining raptor populations, since raptors can bioaccumulate high concentrations of persistent pollutants (Newton, 2017). The decline of the Peregrine Falcon *(Falco peregrinus)* populations in the mid-20th century due to contamination by DDT (González-Rubio et al., 2021; Movalli et al., 2018; Ratcliffe, 1993) is a classic example of using indicators for both environment condition assessment and diagnosis of the cause of change (Niemi & McDonald, 2004).

1.1.2 Intertrophic interactions

As the speed and the extent of global change are creating more and more unpredictable conditions, ecosystem functioning (productivity, nutrient dynamics, decomposition) and community stability are of increasing research importance. Community stability consists of several key elements; resilience/constancy, resistance or robustness/recovery (Begon et al., 2006; de Bello et al., 2021). Overall, community stability can be defined as a tendency to return to (or close to) its original state (Begon et al., 2006). There has been much debate over what are the mechanisms behind stability. In general, biodiversity has been determined as the main factor (Chen et al., 2021; Pennekamp et al., 2018; Singh, 2002; Wang & Loreau, 2016). Community stability thus depends mainly on community complexity; i.e. species richness and complexity of interspecific interactions, such as competition, predation, parasitism, mutualism and detritivory (Begon et al., 2006; Dhondt, 2012). In this subchapter, we will focus on predation in particular.

Predation can be defined as the interaction in which one organism kills (and consumes) another (Abrams, 2000; Begon et al., 2006). It occurs at different levels; it can be inter- or intratrophic and inter- or intraspecific (Abrams, 2000; Holt, 1977; Polis, 1981; Sergio & Hiraldo, 2008). Predators affect prey populations directly (declined prey populations because of the predator killing prey) or indirectly (decreased prey individual fitness because of the fear of predation) (Cresswell, 2010). On the other hand, as predators depend on the availability of prey, co-dynamics of predator-prey populations are common, especially in cases of specialized predators and fluctuating prey populations (Sundell et al., 2004). For example, predator populations such as foxes, mustelids and raptors strongly respond to cyclic population fluctuations of hares and small mammals in North America or lemming and vole population cycles in Europe (Cheveau et al., 2004; Dhondt, 1987; Doyle & Smith, 1994; Fuglei & Ims, 2008; Greenhorn et al., 2021; Lehikoinen et al., 2011; Sundell et al., 2013). Many raptors respond either numerically (e.g. supress breeding) or functionally (e.g. switch to alternative prey) to fluctuations in abundance of small mammals, especially if they are their main prey (Karell et al., 2009; Korpimäki & Norrdahl, 1991; Newton, 1979; Poulin et al., 2001; Sonerud, 1986; Zárybnická et al., 2015). The evolution of prey-predator interaction leads towards prey evolving to avoid predation and the predator to maintain the relationship (Pianka, 2011). Coupled oscillations in predator–prey interactions are thus a result of a series of time-delayed 'numerical responses', when abundance of one species changes in response to the abundance of the other species (Begon et al., 2006).

In northern latitudes in Europe, voles (Cricetidae) usually represent the largest proportion in the diet of raptors specialized to small mammals, such as kestrels, buzzards and owls (Korpimäki & Norrdahl, 1991; Reif et al., 2004; Riegert et al., 2020). Vole populations are known to fluctuate on a large scale at regular periods of 3 – 5 years and with highly variable amplitudes (Hörnfeldt, 1994; Brommer et al., 2002). The periodicity of their mass occurrence is the most prominent in northern latitudes and is gradually disappearing southwards (Korpimäki & Krebs, 1996). Mice (Muridae) too exhibit population fluctuations, but less regular with occassional population bursts (Zárybnická et al., 2013; Zub et al., 2012). In Central and Southern Europe, mice tend to be an equal or even more important food source for raptors (Gryz & Krauze-Gryz, 2019; Luka & Riegert, 2018; Vrezec et al., 2018; Zárybnická et al., 2013). In general, small mammal communities tend to be richer in Southern Europe (Kryštufek & Griffiths, 1999; Torre et al., 2018) and the number of prey species and food niche breadth of raptors tend to increase southwards as well (Korpimäki & Marti, 1995). However, size of mammalian prey increases northwards (Korpimäki & Marti, 1995), which can be an advantage for mammal-eating predators during prey peak years and allow for larger clutches (Newton, 1979). In general, breeding productivity of birds tends to increase with latitude (Hendricks, 1997; Mougeot et al., 2011; Newton, 1979; Overskaug & Bolstad, 1998), most likely due to longer days at northern latitudes in the summer and a dramatic increase in productivity (Carrillo & González-Dávila, 2009; Hendricks, 1997). Lower nest-predation risk at high latitudes could also be an important factor (McKinnon et al., 2010). On the other hand, lack of food in low small mammal years in northern latitudes promotes longer dispersal of raptors in comparison to southern raptor populations (Andersson, 1980; Korpimäki, 1993; Korpimäki et al., 1987; Vasko et al., 2011).

Between-year and between-season fluctuations in small mammal populations are thought to be an outcome of food availability, weather variables, predation, diseases and intraspecific regulation mechanisms (Ecke et al., 2017; Hörnfeldt, 1994; Pedersen & Greives, 2008; Pucek et al., 1993; Sundell, 2003). Small mammal abundances are usually highest in the autumn of the year after peak mast year (Pucek et al., 1993), which are occasional years when there is a large-scale synchronous production of seeds (Begon et al., 2006). Beech seeds are the preferred seeds for small mammals in temperate mixed forests (compared to spruce and fir seeds; Nopp-Mayr et al., 2012) and small mammal populations are able to respond to increased resource availability very rapidly (Jensen, 1982; Pucek et al., 1993). Evidence from several studies suggests that in recent decades mast frequency in European beech, a major forest-forming tree in temperate Europe, has increased (Hacket-Pain & Bogdziewicz, 2021). Masting cycles are regulating seed predator abundances by satiation and starvation, and changes in mast seeding patterns may disrupt this regulation (Bogdziewicz et al., 2020). More frequent masting years may induce increasing densities of small mammal population in the future and, consequently, raptor breeding frequency and productivity (Brommer et al., 2002; Lehikoinen et al., 2011; Luka & Riegert, 2018). Increased breeding frequency could lead to positive long-term trends in raptor population density because it is one of the main variable components in lifetime reproduction (Saurola, 1989; Saurola & Francis, 2018). Additionally, better prey availability can result in smaller territories (Schoener, 1968; Zabel et al., 1995), which allows for increased territory densities and lower near-neighbour distances.

1.1.3 Intratrophic interactions

Intratrophic interactions are species interactions within the same trophic level, e.g. facilitation or competition (Begon et al., 2006). In this sub-chapter, we will focus on an interspecific competition that is usually defined as an interaction in which resource use by one species affects resource availability for the other species (Dhondt, 2012). It is one of the key interactions between ecologically similar species in an assemblage and one of the main forces that shape ecological and evolutionary processes (Pianka, 2011). Resource exploitation (exploitation competition) or direct aggressiveness (interference competition) can decrease fecundity, growth or survival of individuals (Begon et al., 2006). For example, in some raptors exploitation competition is evident in competition for nesting sites, and decreased fledgling survival in vicinity of the dominant predator as a result of intensive interference competition (Hakkarainen et al., 2004). Subordinate competitor is usually forced to adjust its niche and is spatially, temporally (i.e. alter their spatial and temporal activity patterns) or trophically segregated (i.e. shifting their diet to alternative prey) from the dominant predator (Schoener, 1974). For example, Eurasian Sparrowhawks *(Accipiter nisus)* delay their breeding time when dominant predators, the Goshawks *(Accipiter gentilis)*, are nesting close to their territory (Rebollo et al., 2017). Competing predators can thus co-exist if they differentiate their realized niches, but they can also be eliminated or excluded from a habitat by dominant competitor (Begon et al., 2006). For example, nesting failures in the Common Buzzard *(Buteo buteo)* are significantly more common in the vicinity of breeding Goshawks (Hakkarainen et al., 2004; Kostrzewa, 1991). In the Alps, Eagle Owl *(Bubo bubo)* can depress the population of Tawny Owls *(Strix aluco)* significantly (Sergio et al., 2007) and exclusion of Tawny Owl by the dominant Ural Owl *(Strix uralensis)* has been reported from different parts in Europe (Kajtoch et al., 2015; Korpimäki, 1986; Vrezec & Tome, 2004a). In resident hole-nesting owls, besides food and habitat, availability of nest-sites may be a particularly important factor in competitive interactions (Korpimäki, 1986) and can even result in displacements from nests and mixed broods (Saurola, 2023).

Interspecific competition is thus most likely to occur in predators of the same guild (Polis & Holt, 1992), which is a group of sympatric species (regardless of their taxonomic relationships) that exploit environmental resources in a similar fashion (Root, 1967). Raptor guilds can be defined based on their hunting tactics, diet, activity time, or habitat use (e.g. type of nesting sites; Brambilla et al., 2020; Krüger et al., 2002; Poole & Bromley, 1988; Robinson, 1994; Vrezec & Tome, 2004b). When the dominant raptor species acts as both competitor and predator, intraguild predation occurs (Polis, 1981). Intraguild predation is more common when food resources are scarce (Morosinotto et al., 2017). By killing the subordinate predator and reducing resource competition, the dominant predator not only obtains energetic benefits if consuming the intraguild prey, but also increases chances for successful breeding (Sergio & Hiraldo, 2008). The subordinate predator, on the other hand, may suffer the costs of both interspecific competition and risk of intraguild predation, which can lead to reduced breeding productivity (Morosinotto et al., 2017; Sergio & Hiraldo, 2008). On a community level, intraguild predation can thus limit the populations of top predators, which may increase diversity of the predator community (Sergio et al., 2007).

Intraguild predation in raptor communities that include owls is a common phenomenon, and reported for at least 11 intraguild killer species (Sergio et al., 2007; Sergio & Hiraldo, 2008; van Lanen et al., 2011; Zuberogoitia et al., 2005). The largest European owl, the Eagle Owl, is a super-predator, capable of killing any predator of smaller or similar body weight (Lourenço & Rabaça, 2006). In fact, the killer species being larger than its victim seems to be a general rule (Sergio & Hiraldo, 2008). Even slight body size difference is sufficient for interactions aggressive enough to exclude the smaller and weaker predator, as in the case in invading Barred Owls *(Strix varia)* to the Northern Spotted Owl *(Strix occidentalis)* range in North America (Kelly & Forsman, 2004; Long & Wolfe, 2019).

In the light of global change, the risk of competitive exclusion is a particularly important research topic. Climate change can induce species distribution and phenological shifts can change interactions in communities (and vice versa; changed interactions result in species range/phenological shifts) (Antão et al., 2022; Blois et al., 2013; Brambilla et al., 2020; Carter et al., 2018; Pinsky et al., 2020; Schleuning et al., 2020; Tylianakis et al., 2008; Van der Putten et al., 2010). Furthermore, invasive species can cause local extinctions, trigger ecological cascades and decrease ecosystem stability (David et al., 2017; Doody et al., 2017; Dueñas et al., 2021; Frelich et al., 2012; Kimbro et al., 2009; Vagnon et al., 2022). Communities dominated by predation rather than interspecific competition are generally more stable, since more niche overlap and higher species richness are possible (Begon et al., 2006). Consequently, many trophic connections ensure community robustness to species losses (Dunne et al., 2002).

1.1.4 The model study species: the Tawny Owl *(Strix aluco)*

Tawny Owl is the most widespread and common owl species in Europe (König & Weick, 2008). It is considered as primarily a forest species, even though it is a very adaptable species regarding habitat selection and has successfully occupied different rural and urban environments (Gryz & Krauze-Gryz, 2018; Pagaldai et al., 2021; Petty, 1989; Ranazzi et al., 2002; Solonen, 2014). The Tawny Owl is regarded as a mesopredator species, regularly preying upon smaller competitors. For example, Little Owl (*Athene noctua*) (Michel et al., 2016) and Boreal Owl (Vrezec & Tome, 2004b) were found to avoid Tawny Owl due to high predation risk. Tawny Owl's high plasticity in habitat, prey and nest-site selection enables it to co-exist with top predators, such as the Ural Owl (Kajtoch et al., 2015). However, in some habitats and regions it can also act as a top predator or largest raptor, especially in southern Mediterranean forests (Capizzi et al., 1998; Ranazzi et al., 2000).

Tawny Owl territory size depends on habitat quality and is, in general, smaller in dense woodland (Galeotti, 2001). Fragmentation of forest was found to positively correlate to home-range size (Redpath, 1995). On the other hand, open areas or sparse forest patches are an important owl hunting ground (Lundberg, 1980; Southern & Lowe, 1968). It is a nocturnal species, with a sit-and-wait hunting strategy, but can adjust the hunting method to the available prey type (Cramp, 1985). Tawny Owl diet has been extensively studied. It is a food generalist that 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 (Lesiński et al., 2016; Obuch, 2011; Yatsiuk & Filatova, 2017). When small mammal populations decrease, the Tawny Owl can efficiently compensate for mammalian prey shortage with birds (Luka & Riegert, 2018; Yatsiuk & Filatova, 2017).

The selection of Tawny Owl out of the local predator community as a model study species is based on a combination of criteria referring to species traits (Sergio et al., 2008) and properties of our research area (see next paragraph). Tawny Owl is a well studied species, with well known ecology and biology (Cramp, 1985; Galeotti, 2001), it is a charismatic species (Sergio et al., 2005), easy to monitor (Hardey et al., 2013; Vrezec & Bertoncelj, 2018), its main prey has many interactions with other species in the community (Cornulier et al., 2013), and it may be an important trigger of trophic cascades. Additionally, its population traits reflect certain ecological processes and shifts at the ecosystem level, such as weather conditions, anthropogenic habitat alterations, and prey population fluctuations (Fanfani et al., 2015; Lesiński et al., 2009; Santos et al., 2013; Solonen et al., 2015).

Our research area is the area of Mt Krim, central Slovenia, which is a part of the Northern Dinaric Alps. Dinaric Mountains are covered by large adjacent areas of mature uneven-aged temperate forests, which were much less intensively managed than the rest of temperate mixed forests in Europe in the past centuries (Nagel et al., 2017). Such forests are more resilient and stable in an increasingly changing environment (Diaci et al., 2017). Since forest management is one of the key anthropogenic disturbances, Dinaric forests are suitable for studies of historical natural processes (Nagel et al., 2017) and as a part of the "warming band" area (Schönwiese & Janoschitz, 2008), they also provide a suitable area for studying the effects of another increasingly important anthropogenic influence - climate change. Alps and Dinaric Mountains are among the areas in Europe for which a projection of water balance (a measure integrating both changes in precipitation and temperature) under the influence of climate change in Europe predicts the most striking differences in the next few decades (Dezsi et al., 2018). Brambilla et al. (2020) predict that climate change in the Alps and the broader area will cause a disruption in networks of species interactions of an avian forest guild, which includes Tawny Owl and a few closely related owl species. Thus, Mt Krim, as a Dinaric forest covered area, is ideal for studying Tawny Owl's potential for being an indicator species for at least some of the factors listed in the previous paragraph. Tawny Owl population is strong here, the small mammal assemblage in the area is rich, and the competition with a close relative, the Ural Owl, strong (Vrezec, 2003; Vrezec & Tome, 2004a, 2004b; Vrh & Vrezec, 2006). As a mesopredator, Tawny Owl threfore enables studies of both inter- and intratrophic interactions in these high diversity temperate montane forests.

1.2 Objectives and Hypotheses

Tawny Owl is one of the most monitored raptor species in Europe, but long-term monitoring schemes that would track both population density and breeding productivity are scarce (Derlink et al., 2018). The objective of this dissertation is to analyze Tawny Owl's role in the community using population monitoring data (1998 – 2021) from temperate mixed forests of Dinaric Mountains for Tawny Owl and other owl species in the guild (Boreal and Ural Owl) and their main prey groups (voles, mice, dormice and shrews). We investigate Tawny Owl's inter- (prey-predator dynamics) and intraguild interactions (competition with other guild predators), and assess the value of long-term monitoring schemes for Tawny Owl as a supporting tool for ecotoxicological research on the one hand and as a powerful tool for detection of ecosystem response to climate change on the other. Additionally, based on identification of important gaps in the knowledge about Tawny Owl spatial patterns of ecological traits on a panEuropean level, we aimed to propose the first harmonized large-scale population monitoring scheme.

Based on the background presented in the previous sub-chapters, we constructed and investigated the following hypotheses (a short explanation is given after each hypothesis):

H1 Diet is the most studied Tawny Owl's ecological trait across Europe and is highly variable at large scale.

Out of ecological traits listed in Table 1 of the paper in Chapter 2, we hypothesise that the diet would be the most studied, since collecting pellets or nest material is one of the simplest methods for acquiring any ecological information on the species. In general, the diet of raptors can vary considerably on a continental scale (Lourenço et al., 2011a; Roulin, 2015; Vrezec et al., 2018). Since Tawny Owl is a food generalist, able to adapt to local prey availability (Lesiński et al., 2016; Obuch, 2011; Yatsiuk & Filatova, 2017), we can expect high diet variability at large scale.

H2 Tawny Owl dispersal distance and clutch size at a panEuropean level are increasing towards north.

Increasing breeding productivity with latitude has been found in many bird species (Hendricks, 1997; Mougeot et al., 2011; Newton, 1979; Overskaug & Bolstad, 1998) and longer dispersal distances in northern latitudes (in comparison to southern populations) are known in several raptor species (Andersson, 1980; Korpimäki, 1993; Korpimäki et al., 1987; Vasko et al., 2011). This might be evident even in sedentary species with known low dispersal power, i.e. in Tawny Owl.

H3 There is a key small mammal species in the Dinaric forest assemblage that triggers owl breeding responses.

Many raptor populations respond to fluctuations in abundance of small mammals, especially if they are their main prey (Karell et al., 2009; Korpimäki & Norrdahl, 1991; Newton, 1979; Poulin et al., 2001; Sonerud, 1986; Zárybnická et al., 2015). Voles usually represent the largest proportion in the diet of raptors specialized to small mammals in Northern Europe (Korpimäki & Norrdahl, 1991; Reif et al., 2004; Riegert et al., 2020), and mice tend to be an equal or even more important food source for raptors in Central and Southern Europe (Gryz & Krauze-Gryz, 2019; Luka & Riegert, 2018; Vrezec et al., 2018; Zárybnická et al., 2013). Both voles and mice are present in the Dinaric forests, but we expect that only one dominant species plays a key role in owl breeding responses.

H4 Prey decline always leads to a numerical response in forest owl species, but at different breeding stages in different owl species, i.e. territory vs. nest occupancy vs. productivity, and magnitudes.

Studies in Northern and Central Europe have shown that Boreal Owls respond to lack of prey with nomadism, while Ural and Tawny Owl respond with breeding supression (either at the level of breeding attempts or clutch size) (Newton, 2002). Due to different diet preferences and levels of specialization between the owl species of Dinaric forests, we expect different responses with different magnitudes.

H5 In temperate mixed forests of Dinaric Mountains, boreal zone owl species exhibit higher sensitivity to prey fluctuations than temperate zone owl species.

In contrast to similar studies from northern latitudes, in Dinaric Mountains the Boreal and Ural Owl (boreal zone species) are at the southern edge of their distribution, whereas Tawny Owl is at relative centre of its distribution, which is mainly in the temperate zone (Huntley et al., 2007; Galeotti, 2001). Given the contrasting traits between these coexisting owl species, the overall response of predators in the guild is expected to be different in southern European temperate forests compared to boreal forests, and temperate zone species is expected to be the most adapted to conditions in the region.

H6 Tawny Owl population in Dinaric forests is increasing due to expanding its range towards higher elevations.

Tawny Owl is expanding its distribution northwards (at higher latitudes) and towards higher elevations due to climate change effects (warmer winters and reduced snow cover) (Brambilla et al., 2020; Francis & Saurola, 2004). Milder winters are thus expected to enable Tawny Owl to expand towards higher elevations also in Dinaric Mountains.

H7 Tawny Owl intrusion into Ural Owl dominated areas in Dinaric forests increases intraguild interactions, notable in competition for nest-sites.

Since both species are resident hole-nesting owls, an intense competition for available nest-sites may be expected (Korpimäki, 1986; Saurola, 2023). Plausible results of nest-site competition can even be displacements from nests and mixed broods (Saurola, 2023).

H8 Intensified intraguild interactions adversely affect breeding productivity of both species in Dinaric forests.

Competition is an interaction that can decrease fecundity, growth or survival of individuals in both competing species (Begon et al., 2006). The subordinate predator in intraguild competition may suffer not only from the costs of interspecific competition but also from the risk of intraguild predation, which can both lead to reduced breeding productivity (Morosinotto et al., 2017; Sergio & Hiraldo, 2008).

1.3 Original Publications

The dissertation is based on two published peer-reviewed papers and one manucript:

1. Ratajc, U., Lourenço, R., Espín, S., Virosta, P. S., Birrer, S., Studler, D., Wernham, C., & Vrezec, A. (2023). The importance of population contextual data for large-scale biomonitoring using an apex predator: The Tawny Owl (*Strix aluco*). Science of the Total Environment, 860, 160530.
https://doi.org/10.1016/j.scitotenv.2022.160530

2. Ratajc, U., Breskvar, M., Džeroski, S., & Vrezec, A. (2022). Differential responses of coexisting owls to annual small mammal population fluctuations in temperate mixed forest. Ibis, 164(2), 535–551.
https://doi.org/10.1111/ibi.13029

3. Vrezec, A., Ratajc, U. (2023). Climate change is intensifying intraguild interactions between top predators and creating new potential evolutionary pathways. (Manuscript).

The first paper (Chapter 2) covers the first two hypotheses, defined in Chapter 1.2. Next three hypotheses (H3-H5) are investigated in the second paper (Chapter 3), and the last three (H6-H8) in the manuscript (Chapter 4). At the beginning of these chapters, contributions of each research article to the relevant field of science are given and my contribution to the paper is described.

A full list of relevant publications (e.g. conference presentations) is given in the Bibliography section.

1.4 Organization of the Thesis

This dissertation is organized in five chapters. The current chapter is an introduction of the dissertation topic. After the overview of the problem background, it provides aims and hypotheses of the thesis.

The following three chapters are in the form of two published peer-reviewed articles and one manuscript, and are a presentation of methodology, results and discussion of my dissertation. Finally, the main findings and scientific contributions are summed up in the Conclusions chapter, where I also propose some follow-ups for further research.

Chapter 2

Tawny Owl's Ecological Traits and its Indicative Potential

In this chapter, we review several population ecological traits of the Tawny Owl on a panEuropean level and propose a harmonised monitoring scheme feasible across Europe. Tawny Owl carcasses are the most frequently collected raptor carcasses by European natural history museums (Ramello et al., 2022), which makes it an excellent candidate for both active and passive sampling for exotoxicological, disease and ecological studies. Our recommended minimal monitoring scheme is the first attempt to harmonize the monitoring schemes across Europe in order to provide the most essential information about the population on a large scale. This will be useful not only in ecotoxicology but also for overall ecosystem assessments, since data on ecological traits and their trends also indicate the population status.

The work on this topic was published in journal Science of the Total Environment (Ratajc et al. 2023; Supplementary data is given in Appendix A) and is the main part in this chapter. It addresses the first two hypotheses listed in Chapter 1.2:

H1 The diet is the most studied Tawny Owl's ecological trait across Europe and is highly variable at large scale.

H2 Dispersal distance and clutch size at a panEuropean level are increasing towards north.

Both hypotheses were partly confirmed. Diet is by far the most studied ecological trait in Tawny Owl and we found a distinct large-scale gradient of prey species of different trophic levels, where lower trophic level prey, i.e. herbivorous voles, are taken more frequently in the north, whereas higher trophic level prey, i.e. omnivorous mice, are taken more frequently in the south. Nevertheless, the variability on a local level seems to be even more distinct, since Tawny Owl is a food generalist and an opportunistic predator and easily adapts to local prey assemblage and shift in prey availability (Gryz & Krauze-Gryz, 2016; Luka & Riegert, 2018; Obuch, 2011). We confirmed that clutch size changed significantly with longitude. Dispersal distance, however, was found to increase towards the northeast. Nevertheless, Tawny Owl can still be considered as a low-dispersal non-migratory species.

My contributions to this publication are conceptualization of the research (together with her co-authors) and carrying out the majority of the literature review and data collection. I did the analysis, prepared figures and tables, drafted the manuscript and revised it following the feedback from co-authors and the reviewers.

2.1 The Importance of Population Contextual Data for Large-Scale Biomonitoring Using an Apex Predator: The Tawny Owl (*Strix aluco*)

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Review

The importance of population contextual data for large-scale biomonitoring using an apex predator: The Tawny Owl (*Strix aluco*)

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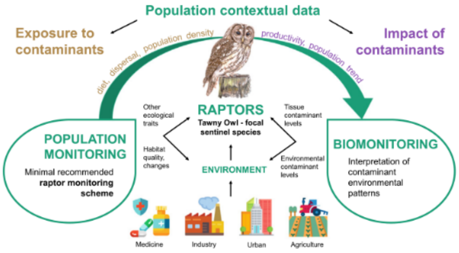
HIGHLIGHTS

- Tawny Owl is focal raptor sentinel species for contaminants in the environment.
- Contextual data is needed for correct interpretation in contaminant assessments.
- Population contextual data indicating contaminant exposure/impact were summarized.
- Review of spatial variation in Tawny Owl's population contextual data
- A minimal recommended raptor monitoring scheme on a pan-European level is proposed.

GRAPHICAL ABSTRACT



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ABSTRACT

Top predators are often used as sentinel species in contaminant monitoring due to their exposure and vulnerability to persistent, bioaccumulative and, in some cases, biomagnificable contaminants. Some of their ecological traits can vary in space and time, and are known to influence the contamination levels and therefore information on ecological traits should be used as contextual data for correct interpretation of large-scale contaminant spatial patterns. These traits can explain spatiotemporal variation in contaminant exposure (traits such as diet and dispersal distances) or contaminant impacts (traits such as population trend and clutch size). The aim of our research was to review the spatial variation in selected contextual parameters in the Tawny Owl (*Strix aluco*), a species identified by the COST Action *European Raptor Biomonitoring Facility* as one of the most suitable candidates for pan-European biomonitoring. A considerable variation in availability of published and unpublished contextual data across Europe was found, with diet being the most extensively studied trait. We demonstrate that the Tawny Owl is a suitable biomonitor at local scale but also that taking spatial variation of other contextual data (e.g. diet) into account is necessary. We found spatial gaps in knowledge about the species ecology and biology in Southern Europe, along with gaps in certain population parameters (e.g. population

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trends) in several countries. Based on our findings, we proposed a minimal recommended scheme for monitoring of population contextual data as one of the first steps towards a pan-European monitoring scheme using the Tawny Owl.

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1. Introduction

Various organisms have been used in ecotoxicological studies in an effort to monitor the potential environmental effects of a vast array of chemicals that are a product of human activities (García-Fernández et al., 2020). Top predators were found to be good sentinel species for environmental pollution because of their position at the top of food chains, which makes them more susceptible to persistent, bioaccumulative and, in some cases, biomagnificable contaminants (Helander et al., 2008; Shore and Taggart, 2019); they can also be a target of direct and indirect poisoning (Helander et al., 2009; Molenaar et al., 2017). Raptors, including birds of prey (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes), are a group of top predators that have been regularly used in ecotoxicological studies (Gómez-Ramírez et al., 2014; Espín et al., 2016) and have long been considered as good candidates for long-term and wide-scale contaminant monitoring schemes (Berg et al., 1966; Seidensticker and Reynolds, 1971; Movalli et al., 2017, 2018, 2019; Shore and Taggart, 2019; Badry et al., 2020).

Towards developing a harmonised continental-wide raptor biomonitoring scheme in Europe, the COST Action European Raptor Biomonitoring Facility (hereafter ERBFacility; https://erbfacility.eu/ and https://www.cost.eu/actions/CA16224/) was established with the aim to design and build key elements of a "Facility" (or framework) for pan-European raptor biomonitoring. This network is gathering existing knowledge and advancing raptor ecotoxicology and ecology in order to step up from local contaminant studies with raptors to a continental-scale biomonitoring scheme with raptors as focal species. ERBFacility's ultimate goals are to improve the evaluation of effectiveness of chemicals regulations and conventions, enhance risk assessment of specific chemicals and provide early warning of emerging contaminant problems. The key elements of ERBFacility are: a European Raptor Sampling Programme, which gathers raptor samples and relates them to contextual data from the field; a distributed European Raptor Specimen Bank, which stores these samples and related data; and a European Raptor Biomonitoring Scheme, which analyses raptor samples for contaminants on an ongoing basis (Movalli et al., 2019; Badry et al., 2020; Espín et al., 2021; Dulsat-Masvidal et al., 2021).

The challenges of implementing a long-term and wide-scale biomonitoring scheme include the selection of the focal species and the focal samples for analysis, but also the capacity to obtain representative and reliable contextual data that allow correct and enhanced interpretation of contaminant levels (Badry et al., 2020; Espín et al., 2021; Dulsat-Masvidal et al., 2021). Spatial and temporal variation in environmental and ecological conditions are key elements in large scale and long-term ecotoxicological studies, and these require comprehensive knowledge of the life-history of the focal species (Shore and Taggart, 2019; Badry et al., 2022).

Ecological traits are known to influence exposure to environmental contaminants, and thus should be considered as contextual data for a correct interpretation of large-scale spatial and temporal patterns of contaminants (Mañosa et al., 2003; Espín et al., 2014; Monclús et al., 2020). Diet is one of the most relevant traits to be considered in the interpretation of contamination levels in raptors, since intraspecific variations in diet composition and trophic pathways are known to influence individual burden (Palma et al., 2005; Lourenço et al., 2011b; Gil-Sánchez et al., 2018; Badry et al., 2019). However, at a continental scale, the diet of raptors can show considerable variation

(Lourenço et al., 2011a; Roulin, 2015; Vrezec et al., 2018), which might lead to differential exposure to contaminants in different regions. The exposure to contaminants in raptors can also be affected by their movement behaviours and space use, most often accounted for as home range size, habitat selection, dispersal and migratory movements (Christensen et al., 2012; Blanco et al., 2018; Badry et al., 2020). Additionally, contextual data are crucial in early-detection of the environmental impacts of contaminants on raptor populations and consequently biodiversity (Thompson et al., 1991; Hörnfeldt and Nyholm, 1996; Newton and Haas, 1988; Shore and Taggart, 2019). In the short-term, contaminant impacts can manifest through several breeding parameters, such as decreasing trends in overall breeding success corresponding to increasing contaminant levels (Newton and Haas, 1988; Nygård and Gjershaug, 2001; Helander et al., 2008; Gil-Sánchez et al., 2018) and consequently in long-term population effects (Newton and Wyllie, 1992; Ratcliffe, 1993; Helander et al., 2008; Shore and Taggart, 2019).

The suitability of raptor species as focal species for large-scale contaminant biomonitoring is determined by a set of ecological and morphological traits related to the focal contaminants (Badry et al., 2020; Monclús et al., 2020). Taking into consideration several key traits, including distribution, habitat, foraging, diet and migration, the Tawny Owl (*Strix aluco*) was found to be among the most suitable sentinel species to monitor mercury, anticoagulant rodenticides, pesticides and medicinal products (Badry et al., 2020). It is a strictly residential species with (considering its body size) relatively small home ranges, with adults usually being specific to an area within 1 km radius from sampling point (Sunde, 2011). As such, the Tawny Owl is a promising biomonitor on a local level. The species has already been used in various long-term studies of environmental contaminants taking into account different matrices from passive or active sampling (Yoccoz et al., 2009; Ahrens et al., 2011; Bustnes et al., 2013; Eriksson et al., 2016; Varela et al., 2016). In the case of passive sampling, Tawny Owl carcasses are the most frequently collected raptor carcasses by European natural history museums (Ramello et al., 2022), giving promising availability of suitable tissue matrices for pan-European ecotoxicological studies. The species population is among the most monitored raptor populations in Europe (Derlink et al., 2018), providing good potential also for active sampling, as well as the availability of extensive background knowledge for assessing contaminant exposure and population impacts at continental scale.

We aimed to review key population contextual data for the Tawny Owl from across Europe, as potential indicators of contaminant exposure and impact. Based on an extensive literature review, we assessed for the first time the geographical differences in key population contextual parameters, which underpin interpretation of ecotoxicological results. We assessed geographical variation in selected parameters across Europe and evaluated their importance for contaminant studies. The lack of available contextual data can lead to uncertain conclusions from contaminant results, therefore our objective was also to identify the gaps in our knowledge about the species contextual data spatial coverage within the species' European range. We proposed a minimal recommended scheme for monitoring of population contextual data for Tawny Owl, which would not only provide crucial data to improve interpretation of biomonitoring results, but also indicate population status and other essential information for overall conservation assessments.

2. Methods

2.1. Study area

The study area was defined to encompass the 39 Member and Cooperating Member countries in the European Cooperation in Science and Technology network (COST https://www.cost.eu/about/members/), including the 27 member states of the European Union and the Near Neighbour and International Partner Countries within Tawny Owl distribution range, excluding Russia (adapted according to Keller et al., 2020).

2.2. Study species

According to recent taxonomy, there are seven subspecies of Tawny Owl, among which only two, *S. a. aluco* and *S. a. sylvatica*, inhabit Europe including Turkey and Israel (Gill et al., 2022). These two subspecies form the bulk of the Tawny Owl population that is confined to Europe (Mikkola, 2013) and were those considered in the current review. The European population has been genetically differentiated into three clades corresponding to three glacial refugia in the Balkans, Italy and Iberia (Brito, 2005). The most distributed clade, the Balkan clade, expands over most of Europe including Northern Europe and Great Britain (Brito, 2005) (Fig. 1). The Balkan and Italian clade are taxonomically defined as *S. a. aluco*, while Iberian clade corresponds to *S. a. sylvatica*. However, the status of *S. a. sylvatica* is questionable since it is not genetically supported (Brito, 2005). In the eastern Turkey possibly the fourth clade occurs corresponding to the Caucasian/Caspian subspecies *S. a. wilkonskii* (Brito, 2005), but this was not included in the study. The Tawny Owl is also a highly colour polymorphic species (Galeotti, 2001), with colour morphs related to different physiological and ecological traits. Grey owls seem more common in colder and drier climates and brown individuals in warmer and wetter climates (Galeotti and Cesaris, 1996) but the fitness of colour morphs is changing due to fluctuating environmental conditions (Roulin et al., 2004; Karell et al., 2021; Solonen, 2021) and disease infections (Galeotti and Sacchi, 2003; Gasparini et al., 2009; Karell et al., 2017). This great inter- and intra-population polymorphism might induce spatial differences in species traits that might affect contaminant exposure and impacts.

The Tawny Owl is an adaptable mesopredator of temperate climate zone that is not sensitive to rapid temporal changes in prey availability (Gryz et al., 2019; Ratajc et al., 2022). Its population size is more governed by other environmental factors, e.g. extreme low or high temperatures and snow cover (Francis and Saurola, 2004; Pavón-Jordán et al., 2013; Comay et al., 2022), competitive dominance or predation by larger predators (Vrezec and Tome, 2004; Sunde, 2005; Sergio et al., 2007) or anthropogenic factors that could increase species mortality or decrease habitat suitability (Silva et al., 2012; Santos et al., 2013; Fröhlich and Ciach, 2018; van der Horst et al., 2019). Reported densities of territories vary greatly between areas and regions, ranging from 0.2 up to 143.0 territories per 10 km^2 (Ranazzi et al., 2001; Vrezec, 2003). The species is sedentary since most breeding adults remain within a few km from their birth site (Cramp, 1985), with home range size of adults ranging from 20 to nearly 300 ha (Coles, 2000; Sunde, 2011; Burgos and Zuberogoitia, 2020). In the post-fledging dependency period, which is easily recognized as persistent begging (Sunde and Naundrup, 2016), the fledged young depend entirely on food provision by the parents within their territory (Coles, 2000; Sunde, 2011; Burgos and Zuberogoitia, 2020). Their independence, usually followed by post-fledging dispersal, is triggered by cessation of parental investment (Southern et al., 1954; Sunde, 2008). Post-fledged young can disperse some hundreds of kilometers away, but the majority disperse <100 km, however, proportion of longer movements is higher in Northern Europe (Cramp, 1985). Mean natal dispersal is usually much lower (e.g. in Finland, it is only 14 km for males and 17 km for females; Valkama et al., 2014).

The Tawny Owl is predominantly a forest species of deciduous and mixed forests (Galeotti, 2001; Vrezec, 2003; Marchesi et al., 2006; Bartolommei et al., 2012), but also of coniferous forest stands in extreme conditions (Sunde et al., 2001; Comay et al., 2022). However, the species is highly adaptable in habitat selection (Rumbutis et al., 2017), frequently occupying fragmented and heterogeneous landscapes and even urban areas (Redpath, 1995; Ranazzi et al., 2000; Solonen and af Ursin, 2008; López-Peinado et al., 2020). As a hole-nesting bird, the Tawny Owl readily uses nest-boxes (Petty et al., 1994; Vrezec and Bertoncelj, 2018), enabling detailed studies on species demography. Annual survival of young (8–48 %) is lower than that of adults (52–87 %) due to high predation risk after fledging, but also very few young birds hatched in highly productive years survive till the next year due to the crash of small mammal populations the following winter (Sunde, 2005; Newton et al., 2016;

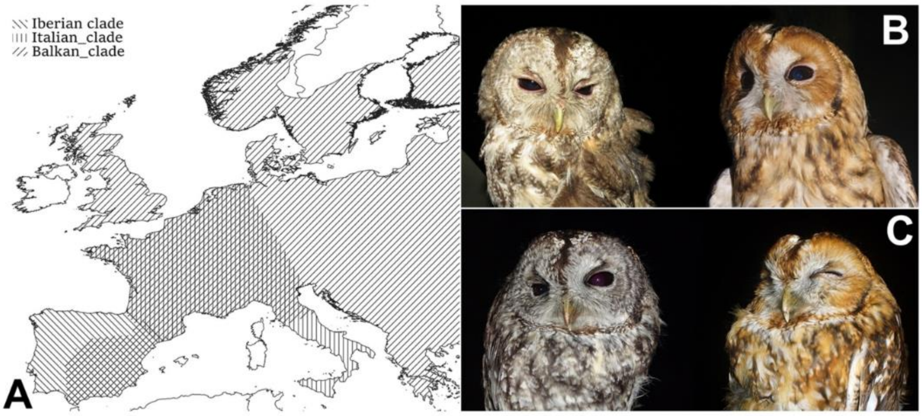

Fig. 1. Distribution areas of the three clades of Tawny Owl in Europe (distribution areas are adapted after Brito, 2005 and are approximate; the area was chequered if the clade represented at least 20 % of the population) (A), and inter- and intrapopulation colour variation of owls in two clades: Balkan clade from Slovenia corresponding to *S. a. aluco* (B) and Iberian clade from Portugal corresponding to *S. a. sylvatica* (C).

Saurola and Francis, 2018). In a latitudinal gradient, Tawny Owl productivity increases towards the north (Overskaug and Bolstad, 1998), but lifetime reproduction seems to be higher in the south (Bucciolini et al., 2022), which might depend on longevity of owls due to natal environmental conditions (Millon et al., 2011), colour morphs (Brommer et al., 2005), nest predation (Sasvári and Hegyi, 2011) or prey cycle phase at their first breeding (Millon et al., 2010). Timing of breeding depends on prey availability and weather conditions, and clutches are laid earlier in good vole years with low snow cover, therefore owls in warmer habitats, i.e. urban areas, breed earlier than owls in forests (Solonen, 2014).

2.3. Population contextual data

We defined the 'population contextual data' as a range of parameters about raptor populations that can indicate the level of exposure to contaminants and/or the level of contaminant impact on the raptor populations, the latter providing early warning of threats to populations (Table 1). In the review, we considered only contextual data relevant to the breeding populations or at the breeding sites.

2.4. Data collection

2.4.1. Initial literature search

We have carried out an extensive literature search to acquire published research papers and other publications (e.g. reports and theses) about the Tawny Owl in Europe (published online before December 2020). Using the Google Scholar search engine, our search formula was: "*Strix aluco*" OR "tawny owl". The search resulted in a database of published papers and other publications, which were checked for population contextual data. This enabled us to select the most extensively studied population contextual data for detailed analysis of their spatial patterns in Europe.

2.4.2. Selection of case population contextual parameters and collecting data

When selecting population contextual parameters to study their large-scale pattern in Europe, we followed two criteria: (1) their relative importance for better interpretation of biomonitoring results, and (2) the data availability across Europe as found in our initial literature search. The objective was to cover at least two key exposure contextual parameters, i.e. parameters that can assess the risk of contaminant exposure of the Tawny Owl, and at least two key impact contextual parameters, i.e. changes as potential indicators of contaminants affecting the population in the region (listed in Table 1). Accordingly, we selected five parameters: in the exposure group, we considered the data on Tawny Owl's diet and dispersal, and in the impact group, population trends and clutch size. Spatial patterns in population density could indicate both exposure to, and impacts of, contaminants.

Furthermore, a detailed literature search has been carried out for selected population contextual data in order to mobilise as much available data as possible from available sources including published sources, grey literature and existing databases. At this step, our search formula was more focused: "*Strix aluco*" OR "tawny owl" AND "diet" OR "breeding" OR "clutch" OR "reproduction". We obtained additional data by direct contact with researchers to acquire information about the existence (or complete lack) of literature on the diet of Tawny Owl from the countries where no or few records were found using the search engines; microstates were not considered in this case because of their small area.

In the diet analysis, we included only articles reporting either numbers or percentages for main prey groups. We included studies with 20 or more prey items in total. The data from each study were separated into different entries in our database if more locations were clearly defined. Since we were interested in differences between percentages of main prey groups (mammals, birds, invertebrates, reptiles and amphibians), we could only include articles with a detailed list of prey species or a summarized list with the same prey groups. To ensure prey proportion comparability in further analysis, we had to exclude entries which reported only mammals or vertebrates (i.e. did not report or quantify some prey groups - most frequently invertebrates). Not all articles provided data which enabled us to calculate both numeric and biomass percentages. Although prey biomass percentages are more important in terms of total contaminant levels (Mañosa et al., 2003; Lourenço et al., 2011b), numeric percentages of prey can also be used to understand the effects of diet composition and prey contamination on the spatial variation of contaminant levels in raptors (Palma et al., 2005). Due to food web bioaccumulation of contaminants, the exposure to contaminants is related to the trophic level of the prey and in predators preying on higher trophic level prey, higher exposure is expected (Newton, 1979; Helander et al., 2008; Lourenço et al., 2011b; Shore et al., 2014). Therefore, we calculated percentages of mammal prey by trophic level categorised to the groups of herbivores (e.g. voles, rabbits), omnivores (rats and mice), insectivores (e.g. shrew, moles and bats) and carnivores (e.g. weasel) in the diet of the Tawny Owl. A detailed list of mammal

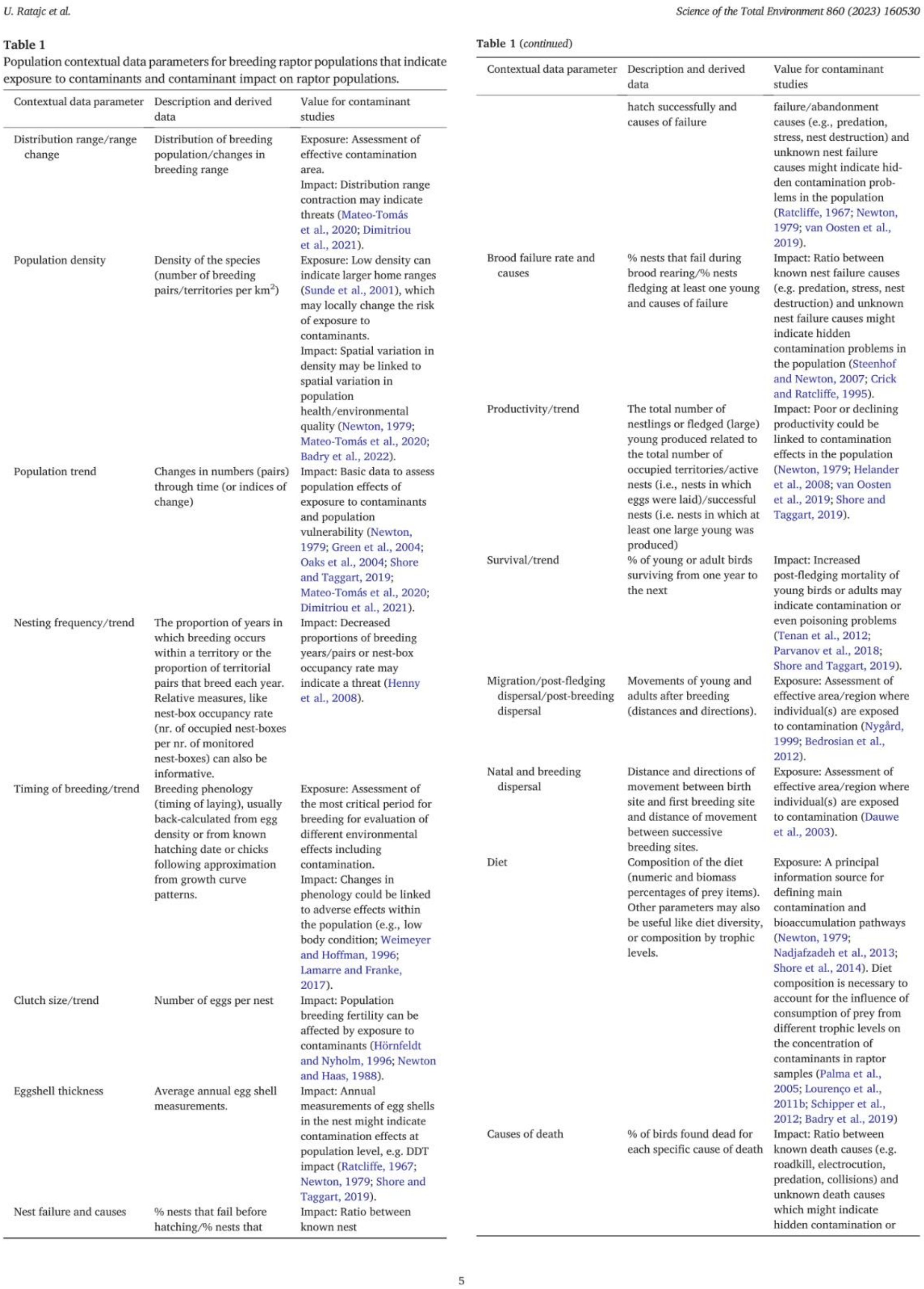

Table 1
Population contextual data parameters for breeding raptor populations that indicate exposure to contaminants and contaminant impact on raptor populations.

Contextual data parameter	Description and derived data	Value for contaminant studies
Distribution range/range change	Distribution of breeding population/changes in breeding range	Exposure: Assessment of effective contamination area. Impact: Distribution range contraction may indicate threats (Mateo-Tomás et al., 2020; Dimitriou et al., 2021).
Population density	Density of the species (number of breeding pairs/territories per km^2)	Exposure: Low density can indicate larger home ranges (Sunde et al., 2001), which may locally change the risk of exposure to contaminants. Impact: Spatial variation in density may be linked to spatial variation in population health/environmental quality (Newton, 1979; Mateo-Tomás et al., 2020; Badry et al., 2022).
Population trend	Changes in numbers (pairs) through time (or indices of change)	Impact: Basic data to assess population effects of exposure to contaminants and population vulnerability (Newton, 1979; Green et al., 2004; Oaks et al., 2004; Shore and Taggart, 2019; Mateo-Tomás et al., 2020; Dimitriou et al., 2021).
Nesting frequency/trend	The proportion of years in which breeding occurs within a territory or the proportion of territorial pairs that breed each year. Relative measures, like nest-box occupancy rate (nr. of occupied nest-boxes per nr. of monitored nest-boxes) can also be informative.	Impact: Decreased proportions of breeding years/pairs or nest-box occupancy rate may indicate a threat (Henny et al., 2008).
Timing of breeding/trend	Breeding phenology (timing of laying), usually back-calculated from egg density or from known hatching date or chicks following approximation from growth curve patterns.	Exposure: Assessment of the most critical period for breeding for evaluation of different environmental effects including contamination. Impact: Changes in phenology could be linked to adverse effects within the population (e.g., low body condition; Weimeyer and Hoffman, 1996; Lamarre and Franke, 2017).
Clutch size/trend	Number of eggs per nest	Impact: Population breeding fertility can be affected by exposure to contaminants (Hörnfeldt and Nyholm, 1996; Newton and Haas, 1988).
Eggshell thickness	Average annual egg shell measurements.	Impact: Annual measurements of egg shells in the nest might indicate contamination effects at population level, e.g. DDT impact (Ratcliffe, 1967; Newton, 1979; Shore and Taggart, 2019).
Nest failure and causes	% nests that fail before hatching/% nests that hatch successfully and causes of failure	Impact: Ratio between known nest failure/abandonment causes (e.g., predation, stress, nest destruction) and unknown nest failure causes might indicate hidden contamination problems in the population (Ratcliffe, 1967; Newton, 1979; van Oosten et al., 2019).
Brood failure rate and causes	% nests that fail during brood rearing/% nests fledging at least one young and causes of failure	Impact: Ratio between known nest failure causes (e.g. predation, stress, nest destruction) and unknown nest failure causes might indicate hidden contamination problems in the population (Steenhof and Newton, 2007; Crick and Ratcliffe, 1995).
Productivity/trend	The total number of nestlings or fledged (large) young produced related to the total number of occupied territories/active nests (i.e., nests in which eggs were laid)/successful nests (i.e. nests in which at least one large young was produced)	Impact: Poor or declining productivity could be linked to contamination effects in the population (Newton, 1979; Helander et al., 2008; van Oosten et al., 2019; Shore and Taggart, 2019).
Survival/trend	% of young or adult birds surviving from one year to the next	Impact: Increased post-fledging mortality of young birds or adults may indicate contamination or even poisoning problems (Tenan et al., 2012; Parvanov et al., 2018; Shore and Taggart, 2019).
Migration/post-fledging dispersal/post-breeding dispersal	Movements of young and adults after breeding (distances and directions).	Exposure: Assessment of effective area/region where individual(s) are exposed to contamination (Nygård, 1999; Bedrosian et al., 2012).
Natal and breeding dispersal	Distance and directions of movement between birth site and first breeding site and distance of movement between successive breeding sites.	Exposure: Assessment of effective area/region where individual(s) are exposed to contamination (Dauwe et al., 2003).
Diet	Composition of the diet (numeric and biomass percentages of prey items). Other parameters may also be useful like diet diversity, or composition by trophic levels.	Exposure: A principal information source for defining main contamination and bioaccumulation pathways (Newton, 1979; Nadjafzadeh et al., 2013; Shore et al., 2014). Diet composition is necessary to account for the influence of consumption of prey from different trophic levels on the concentration of contaminants in raptor samples (Palma et al., 2005; Lourenço et al., 2011b; Schipper et al., 2012; Badry et al., 2019)
Causes of death	% of birds found dead for each specific cause of death	Impact: Ratio between known death causes (e.g. roadkill, electrocution, predation, collisions) and unknown death causes which might indicate hidden contamination or

Table 1 (*continued*)

Contextual data parameter	Description and derived data	Value for contaminant studies
		poisoning problems in the population (González et al., 2007; Isomursu et al., 2018; Alarcón and Lambertucci, 2018).
Threats (including persecution)	Information on the existence of threats to populations on a regional or national scale (qualitative data)	Impact: Important for placing any impacts of contaminants or poisoning on populations into the context of other negative influences in the area (Villafuerte et al., 1998; Whitfield et al., 2003; González et al., 2007).
Morph variability	% of colour morphs in polymorphic species	Exposure and impact: Colour morphs are usually related to different physiological traits (Galeotti and Sacchi, 2003; Gasparini et al., 2009), which might affect the level of contaminant exposure through physiological or behavioral patterns as well as their effects (Karell et al., 2021; Romano et al., 2021; Passarotto et al., 2022).
Genetic variation	Level of genetic heterogeneity in the population	Exposure and impact: Populations with low genetic variability are usually more susceptible to different environmental changes, diseases and contamination (Brown et al., 2009; Mussali-Galante et al., 2014).
Age and sex structure	% of population (breeding/non-breeding) by age class and % of population (breeding/non-breeding) according to the sex	Impact: Basic data that can indicate age- and sex-specific mortality in the population (Solonen and Lodenius, 1990; Naccari et al., 2009).
Diseases	Veterinary control of dead or alive birds for different known diseases and parasites (% of infected individuals)	Exposure: Infection rate in the population might indicate higher susceptibility to contamination as a stress factor (Galeotti and Sacchi, 2003). Impact: Diseases might cause additional mortality and breeding productivity decrease as parallel effect to contaminants (van Velden et al., 2017).
Habitat quality/selection	Habitat type selection (quantitative data)	Exposure: This can help indicate where the species is most exposed to the contaminants. Exposure or habitat use may vary between seasons (Delibes et al., 2001; Badry et al., 2022).
Food availability	Trend of availability of main prey or other food sources (i.e. carrion) in the environment	Exposure: Food availability governs population fluctuations and size in raptors and is thus crucial in interpretation of raptor population dynamics. Can also be a source of contamination (Bustnes et al., 2011; Dimitriou et al., 2021). Changes in diet due to food stress may increase exposure of individuals to certain contaminants.

species and their categorisation by trophic level is provided in the Supplementary material (Table A.1).

We chose clutch size as a measure of Tawny Owl's breeding performance because the mean number of eggs per nest was more frequently reported than brood size or number of fledglings in the reviewed studies (the two are combined under "Productivity" in Fig. 2).

When gathering data on diet and clutch size, georeferencing was carried out based on the research area description if no coordinates were given by the authors. In cases where the data were gathered for a larger area (e.g. a region or country), the central coordinates were used. We used decimal degree geographic coordinates.

Data on Tawny Owl population size and population trend were adapted from the BirdLife International (2017) assessment (and from Shirihai et al., 1996, for population size in Israel). For each country, we calculated the crude density from the estimated average of the population size per distribution area (number of pairs per 100 km^2).

Ringing data (recoveries and recaptures), were acquired from the EURING database (du Feu et al., 2009), to which we added ringing data for Slovenia from the Slovenian Bird Ringing Centre (Slovenian Museum of Natural History) database. The ringing dataset included data from 1910 to 2021. Some data entries had a doubtfully large time difference between ringing and the last retrapping, most likely indicating data errors. Thus, according to the highest reported age of the Tawny Owl in Europe (22 years, 5 months; Fransson et al., 2017), we excluded entries with >22.5 years time difference. Young owls remain in their natal territory for an additional 2.5–3 months after fledging, in which time they still receive parental care (Southern, 1970; Coles and Petty, 1997; Sunde, 2011; Sunde and Naundrup, 2016). To avoid data entries of retrapping fledged young (pulli) before post-fledging dispersal, we excluded entries of birds marked as nestlings/fledglings with <5 months of the time difference between ringing and retrapping (Coles and Petty, 1997; Sunde, 2011). Juveniles were considered as those birds which were ringed as nestlings or fledglings not able to fly, whereas adults were considered as those birds which were ringed as fully grown with age 2 y and more. Only maximum distance from the ringing location per ring ID and the coordinates of

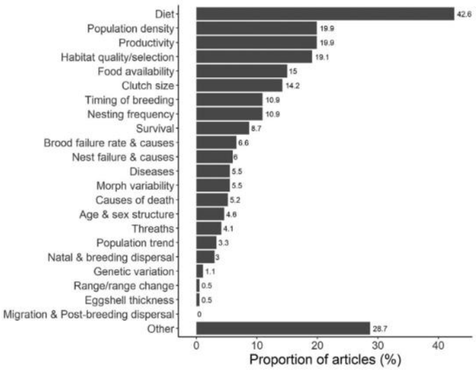

Fig. 2. Frequency of published articles covering the population contextual data of Tawny Owl in Europe ($N = 366$). Some articles offered data on several topics, thus the overall sum totals >100 %.

the ringing location were used in the spatial analysis. In this paper, we used the term juvenile-adult ringing distance in birds ringed as juveniles and recaptured/recovered as full-grown birds, and adult-adult ringing distance in birds ringed as adults. Juveniles can be recaptured or recovered at their post-fledging dispersal and thus the ringing distances do not necessarily reflect the natal dispersal. The adults can be recaptured or recovered within their stable territory and have not dispersed, therefore these distances do not necessarily reflect the breeding dispersal of this sedentary species. However, since most Tawny Owls establish a breeding territory within the first year of life (Southern, 1970), we assumed that the adult-adult ringing distances provide a good proxy for between-year movement distances of adults. We aimed to compare available recovery and recapture data on Tawny Owls in Europe in relation to their spatial differences between regions related to the scale of contaminant exposure. We did not adjust ringing data by considering only recovery data of dead ringed owls (Saurola and Francis, 2004) due to large discrepancies in the number of available data between countries and regions.

2.4.3. Data analysis

To investigate spatial patterns in the traits of the Tawny Owl that are relevant as population contextual data in ecotoxicological studies, we considered 20 dependent variables: 18 variables describing diet composition, 1 variable describing dispersal, and 1 variable describing breeding success. As explanatory variables we focused exclusively on latitude and longitude. Since the dependent variables may not respond linearly to latitude and longitude, we used generalized additive models (GAMs) to relate the dependent and explanatory variables. Smoothing parameters in GAM were chosen via a restricted maximum likelihood method (REML). We fitted five competing models combining the two explanatory variables and the use of smoothing factors for each dependent variable (Table 2). If needed, variables were log transformed to correct distribution, reduce the effect of any outliers and to improve model fit (see Table 2). We then used a multi-model comparison approach (Burnham and Anderson, 2002), and compared the five competing models for each variable, including a null model (intercept only) used as a measure of the explanatory power of the variables. The selection of the best models for each dependent variable was based on Akaike's Information Criterion (AICc), using as threshold a ΔAICc below 2.0 (Burnham and Anderson, 2002). When the null model was included in the set of best models, we considered that the variables latitude and longitude had low explanatory power of the data variability. Models were validated using diagnostic plots.

Kruskal-Wallis rank test was used to compare mean dispersal distances of different regions (regionalization by United Nations geoscheme, but separating the United Kingdom from continental Europe) and a Dunn test with the Bonferroni correction was performed to test for differences in mean dispersal distances between regions.

To obtain a visual output of the continuous variation of the dependent variables across Europe, we transformed the point spatial data for the proportions in the diet, dispersal distance and mean clutch size into raster data using the inverse distance weighted (IDW) interpolation. IDW interpolation is a common method in spatial analysis that predicts values based on the assumption that the influence of each measured point decreases with increasing distance. In the function “idw” (R package “gstat”) the IDW power was set to 3 and the interpolation was calculated over a 0.2° × 0.2° grid. Interpolation maps were delimited by the distribution area of the Tawny Owl.

All statistical analyses and visualisations were carried out using R 4.0.3 statistical software (R Core Team, 2021) in RStudio (RStudio Team, 2021) with packages mgcv (v.1.8-33, Wood, 2017), MuMIn (Bartón, 2020), gstat (v.2.0-6, Pebesma, 2004), tmap (v.3.3, Tennekes, 2018), and ggplot2 (Wickham, 2016).

3. Results

3.1. Review of published population contextual data for Tawny Owl in Europe

We obtained 366 journal articles and other available literature (reports, theses, book chapters, conference proceedings) with the initial literature search (see Methods), which covered various population contextual data (Fig. 2). Diet was the contextual data most frequently found in Tawny

Table 2

A list of dependent variables, their arithmetic mean and range and explanatory variables included in the best models. N - numeric percentage, B - biomass percentage, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon); s(lat)].

Dependent variable	Explanatory variables included in the best models	Arithmetic mean (%) ± SD	Range (%) (min–max)
N of mammals	lat, s(lat)	67.8 ± 21.2	4.4–100.0
N of birds log transformed	lon, s(lon)	12.9 ± 14.4	0.0–90.1
N of invertebrates log transformed	lon, s(lat), s(lon)	12.2 ± 16.6	0.0–95.6
N of amphibians log transformed	lon, s(lat), s(lon)	6.4 ± 10.7	0.0–60.4
N of reptiles log transformed	lon, s(lat), s(lon)	0.4 ± 1.8	0.0–27.2
N of herbivore mammals	s(lat)	33.9 ± 19.7	0.0–94.3
N of omnivore mammals	lat, s(lat), s(lon)	26.6 ± 17.0	0.0–96.7
N of insectivore mammals log transformed	lat, s(lat), s(lon)	10.6 ± 10.5	0.0–63.4
N of carnivore mammals log transformed	lat, s(lat)	0.05 ± 0.1	0.0–1.1
B of mammals	Null model	79.0 ± 17.7	14.0–100.0
B of birds log transformed	Null model	15.4 ± 16.2	0.0–76.0
B of invertebrates log transformed	s(lon)	1.5 ± 3.1	0.0–15.9
B of amphibians log transformed	lat, s(lat), s(lon)	3.2 ± 4.7	0.0–24.1
B of reptiles log transformed	Null model	0.4 ± 1.2	0.0–7.0
B of herbivorous mammals	Null model	38.6 ± 21.4	0.0–95.4
B of omnivorous mammals	lat, s(lat)	36.0 ± 20.8	0.0–98.8
B of insectivorous mammals log transformed	lat, s(lat)	5.4 ± 6.7	0.0–49.4
B of carnivorous mammals log transformed	s(lat)	0.1 ± 0.6	0.0–4.5

Owl literature (n = 156; 42.6 % of articles). The most often presented measure of productivity was the number of nestlings or fledglings per territory or per active or successful nest (under "Productivity", n = 73; 19.9 % of articles), followed by clutch size (n = 52; 14.2 % of articles). A considerable percentage of articles (n = 105, 28.7 %) focused on other topics, such as vocal activity, parasites, toxicology, behaviour, interspecific interactions and physiology. Out of these, a little less than half of the articles did not include data on any of the population contextual data (n = 51; 13.9 % of all articles). Population trend, natal and breeding dispersal, genetic variation, range change, eggshell thickness and post-breeding dispersal are among the most understudied parameters.

3.2. Diet composition

3.2.1. Main prey groups

We used diet data from 192 articles with 403 data entries in total, which were published in the period from 1930 to 2020. From these, 17 % were published before 1980 and 45 % after 2000. There were no available diet data from Bosnia and Herzegovina, Albania, Kosovo and North Macedonia. Only 42 % of articles included both numeric and biomass percentages for either main prey groups or groups of mammals by trophic level. Out of these, 11 % did not calculate the frequency percentage of invertebrates and 28 % did not determine invertebrate biomass. Thus, in the analysis of the main prey groups numeric percentages, 66 % of the collected articles could be included (72 % of data entries), whereas in the analysis of the main prey groups by biomass percentage, 32 % of the collected articles were considered (18 % of data entries).

Mammals were the most frequent prey (67.8 % on average, Table 2) across Europe, with slightly lower numeric percentages in the Mediterranean and increasing northwards. Biomass percentages of mammalian prey were also the highest among the main prey groups (79.0 % on average). Little spatial pattern of changing mammal percentages in the diet with latitude was obvious (Fig. 3), rather the spatial pattern was found significant only in the case of numeric percentages (Tables 2 and A.3 to A.5).

In the case of the numeric percentage, birds and invertebrates had similar importance in Tawny Owl diet (mean 12.9 % and 12.2 %, respectively). Birds, however, represented much larger biomass percentages than invertebrates (mean 15.4 % and 1.5 %, respectively). The map of interpolated bird numeric percentage shows an overall low percentage across Europe with some local exceptions, mostly from urban areas (Fig. 3). The explanatory variables in the selected GAM models were longitude ("lon") with and without the smooth factor "s(lon)", suggesting that the numeric percentage of birds increased with longitude (Tables 2, A.6 and A.7). On the contrary, the map of interpolated invertebrate numeric percentage indicates that the importance of invertebrates in the diet was decreasing towards north, and both latitude and longitude were identified as explanatory variables of the spatial pattern in invertebrate numeric percentage (Tables 2, A.9 and A.10). Invertebrates were present in only 77.8 % of data entries in the analysis of numeric percentages and their biomass percentages were very low across Europe (Fig. 3), but a significant pattern of decreasing biomass percentage towards the east was found (Tables 2, A.11 and A.12). There was no specific spatial pattern in bird biomass percentage (Fig. 3, Tables 2 and A.8).

Amphibians and reptiles were rarely a part of Tawny Owl diet in any significant percentage. Amphibians were present in 73.6 % of data entries and reptiles in 31.8 % of data entries in the numeric percentage analysis, and in 63.9 % and 34.7 % of data entries, respectively, in biomass percentage analysis. There seemed to be subtle spatial variations in the importance of amphibians and reptiles in the diet (Figs. 3 and A.1). The amphibian numeric and biomass percentages slightly increased towards the north and had a bimodal pattern along the longitude, with peaks at around 7° and 21° in numeric percentage, and at 3° and 26° in biomass percentage (Tables 2, A.13 to A.16). The numeric percentages of reptiles slightly decreased with latitude and increased with longitude (Tables 2, A.17 and A.18). There was no significant spatial pattern in reptile biomass percentage (Tables 2 and A.19).

3.2.2. Mammals by trophic level

We could include 94 % of the collected articles in the analysis of numeric percentages (92 % of data entries) and 38 % of articles (24 % of all data entries) in the analysis of biomass percentages of mammal groups by trophic level. Herbivorous and omnivorous mammals were the most important mammalian prey. The mean numeric percentage of herbivorous mammals was 33.9 % and of omnivorous 26.6 % (Table 2). The numeric percentage of herbivorous mammals increased northwards (Fig. 3). On the contrary, the numeric percentage of omnivorous mammals decreased northwards and also changed with longitude. Both spatial patterns were found to be significant (Tables 2, A.21 and A.24). A map of the interpolated biomass percentages revealed an opposite SW-NE gradient between the two groups. However, the spatial pattern of herbivore biomass percentages was not statistically significant (Tables 2 and A.22), and in omnivores, only changes with latitude were found to be significant (Tables 2, A.25 and A.26).

Insectivores and carnivores were less important prey of the Tawny Owl (Fig. A.1). The mean numeric percentage of insectivorous mammals was 10.6 % and of carnivorous mammals only 0.05 % (Table 2). However, insectivores were recorded in 94.0 % of the data entries, whereas carnivores were recorded in only 19.2 %. The numeric percentages increased northwards, along with changes in insectivore numeric percentages with longitude (Tables 2, A.27 and A.28). In the dataset providing biomass percentages, insectivores were reported in 93.8 % of the data entries while carnivores were consumed in 14.4 % of the cases. Mean biomass percentages of both insectivorous and carnivorous mammals were very low (5.4 % and 0.1 %, respectively, Table 2). Both insectivore and carnivore biomass percentages in Tawny Owl diet were found to increase significantly with latitude (Tables 2, A.30 and A.34).

3.3. Population density

The overall mean crude density in the research area was 13.5 pairs/100 km^2 (n = 37 countries, SD = ±9.9). The lowest densities were found in Moldova (0.2 pairs/100 km^2) and Finland (0.7 pairs/100 km^2) (Fig. 4A). In Belgium, Slovenia and Bosnia and Herzegovina the crude densities were found the highest (41.9, 34.8 and 34.1 pairs/100 km^2, respectively). In Western Balkan the crude densities found were the highest in Europe, while populations were less dense at the edges of the distribution range (e.g. Norway, Finland, Spain, Turkey).

3.4. Clutch size

We analysed 73 data entries for Tawny Owl mean clutch size from 49 studies covering 16 countries. The range of mean clutch size across Europe was between 2.4 and 4.5 (median = 3.35, mean = 3.3 ± 0.5 SD). Clutch size seems to increase towards the north-east (Fig. 4B), but only longitude was found to significantly explain the spatial pattern in clutch size (Tables 2, A.37 and A.38).

3.5. Population trend

Population trends were evaluated in 37 countries (BirdLife International, 2017). In 53.8 % of the countries the population was stable and in 5.1 % it was fluctuating (Fig. 4C). Tawny Owl populations were decreasing in 15.4 % of the countries. In 25.6 % of the countries, the population trend was unknown. Southern Europe was the region with seemingly the most stable populations but there are some major knowledge gaps in Europe, with several neighbouring countries having no population trend estimates.

3.6. Dispersal

There were 23,970 entries from 20 countries in our ringing dataset. The range of juvenile-adult and adult-adult ringing distances across Europe was between 0 and 917 km, and their mean was 18.2 km (±36.3 SD). Overall,

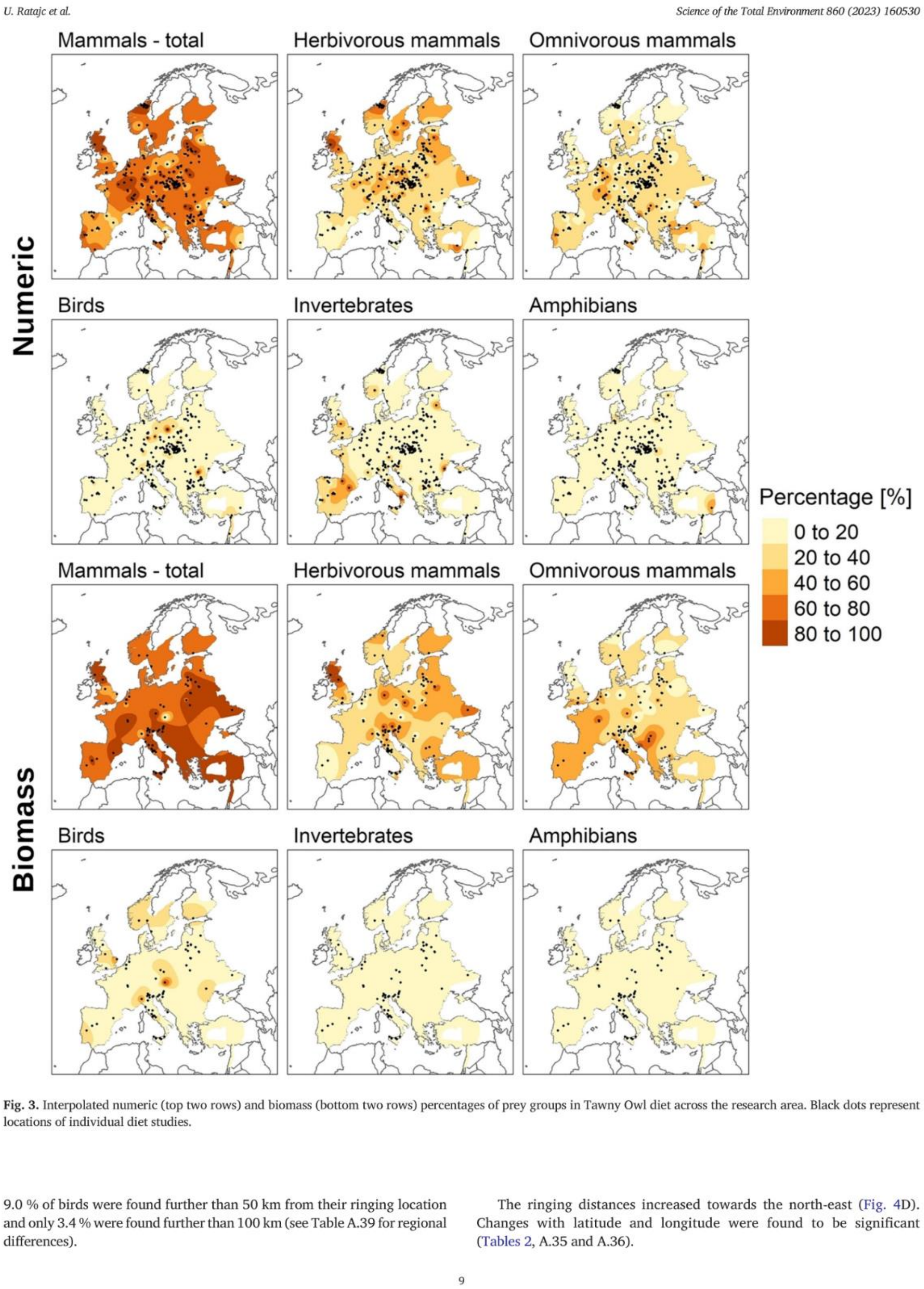

Fig. 3. Interpolated numeric (top two rows) and biomass (bottom two rows) percentages of prey groups in Tawny Owl diet across the research area. Black dots represent locations of individual diet studies.

9.0 % of birds were found further than 50 km from their ringing location and only 3.4 % were found further than 100 km (see Table A.39 for regional differences).

The ringing distances increased towards the north-east (Fig. 4D). Changes with latitude and longitude were found to be significant (Tables 2, A.35 and A.36).

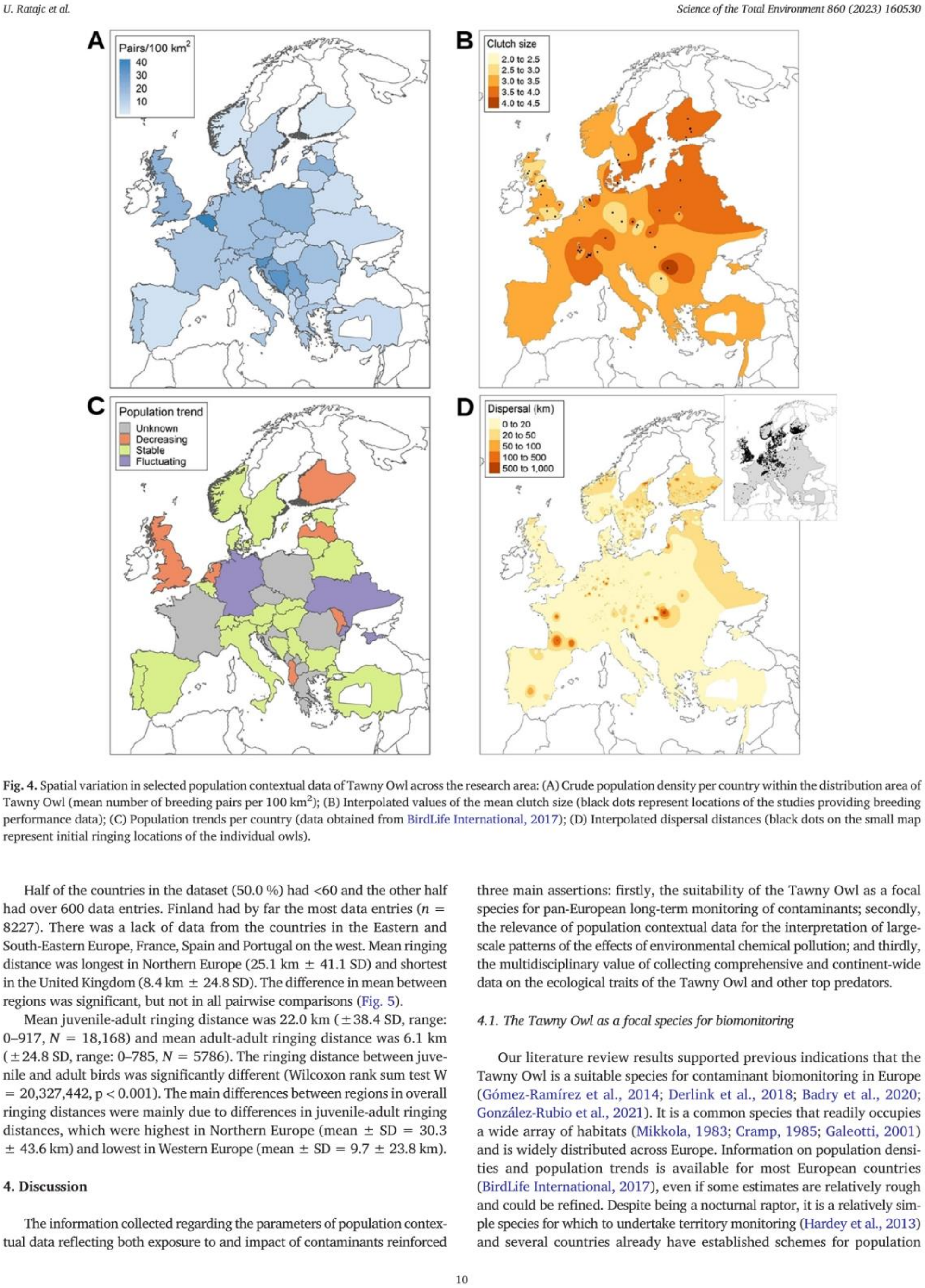

Fig. 4. Spatial variation in selected population contextual data of Tawny Owl across the research area: (A) Crude population density per country within the distribution area of Tawny Owl (mean number of breeding pairs per 100 km^2); (B) Interpolated values of the mean clutch size (black dots represent locations of the studies providing breeding performance data); (C) Population trends per country (data obtained from BirdLife International, 2017); (D) Interpolated dispersal distances (black dots on the small map represent initial ringing locations of the individual owls).

Half of the countries in the dataset (50.0 %) had <60 and the other half had over 600 data entries. Finland had by far the most data entries (n = 8227). There was a lack of data from the countries in the Eastern and South-Eastern Europe, France, Spain and Portugal on the west. Mean ringing distance was longest in Northern Europe (25.1 km ± 41.1 SD) and shortest in the United Kingdom (8.4 km ± 24.8 SD). The difference in mean between regions was significant, but not in all pairwise comparisons (Fig. 5).

Mean juvenile-adult ringing distance was 22.0 km (±38.4 SD, range: 0–917, N = 18,168) and mean adult-adult ringing distance was 6.1 km (±24.8 SD, range: 0–785, N = 5786). The ringing distance between juvenile and adult birds was significantly different (Wilcoxon rank sum test W = 20,327,442, $p < 0.001$). The main differences between regions in overall ringing distances were mainly due to differences in juvenile-adult ringing distances, which were highest in Northern Europe (mean ± SD = 30.3 ± 43.6 km) and lowest in Western Europe (mean ± SD = 9.7 ± 23.8 km).

4. Discussion

The information collected regarding the parameters of population contextual data reflecting both exposure to and impact of contaminants reinforced three main assertions: firstly, the suitability of the Tawny Owl as a focal species for pan-European long-term monitoring of contaminants; secondly, the relevance of population contextual data for the interpretation of large-scale patterns of the effects of environmental chemical pollution; and thirdly, the multidisciplinary value of collecting comprehensive and continent-wide data on the ecological traits of the Tawny Owl and other top predators.

4.1. The Tawny Owl as a focal species for biomonitoring

Our literature review results supported previous indications that the Tawny Owl is a suitable species for contaminant biomonitoring in Europe (Gómez-Ramírez et al., 2014; Derlink et al., 2018; Badry et al., 2020; González-Rubio et al., 2021). It is a common species that readily occupies a wide array of habitats (Mikkola, 1983; Cramp, 1985; Galeotti, 2001) and is widely distributed across Europe. Information on population densities and population trends is available for most European countries (BirdLife International, 2017), even if some estimates are relatively rough and could be refined. Despite being a nocturnal raptor, it is a relatively simple species for which to undertake territory monitoring (Hardey et al., 2013) and several countries already have established schemes for population

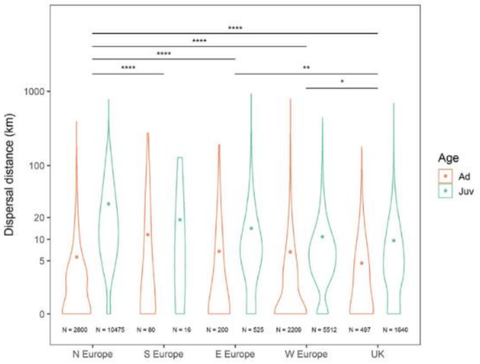

Fig. 5. Tawny Owl ringing distances in Europe by region and age (Juv - juvenile-adult ringing distance, Ad - adult-adult ringing distances). Y-axis is in logarithmic scale. The dots represent the arithmetic means. The significant pairwise comparisons between regions are shown (Kruskal-Wallis = 2270, df = 2, $p < 0.001$; post-hoc Dunn test with Bonferroni correction for multiple comparisons). $^{*}p < 0.05$, $^{**}p < 0.01$, $^{****}p < 0.0001$.

density and trend monitoring (Derlink et al., 2018). Additionally, diet studies are already numerous and distributed in many countries, making available background data for contributing to large-scale biomonitoring studies of contaminants. The Tawny Owl's generalistic nature shows in its ability to use a variety of nest structures (tree cavities, tree stumps, caves, cliffs, nest-boxes and buildings; Mikkola, 1983; Galeotti, 2001; Marchesi et al., 2006). Nest monitoring is rarely based on natural nesting sites, because it requires a very large sampling effort and nests are very difficult to find (Southern, 1970; Wendland, 1972; Zuberogoitia and Campos, 1998; Avotinš, 2004). It is, however, possible to determine breeding productivity with relatively high precision without accessing the nest, as juveniles throughout the post-fledging dependency period keep together and vocalise quite vigorously (Southern, 1970; Sunde and Markussen, 2005; Sunde and Naundrup, 2016). On the other hand, use of nest-boxes can be a very cost-efficient method for obtaining data on various other breeding productivity measures, including clutch size (Southern, 1970; Saurola and Francis, 2004). In a number of European countries nest-box monitoring is already established: Norway (Overskaug et al., 1999), Sweden (Ericsson et al., 2014), Finland (Saurola, 2012), Estonia (Nellis, 2012), Latvia (Reihmanis, 2012), Lithuania (Grašytė et al., 2016), Ukraine (Yatsiuk, 2010), Poland (Gryz et al., 2019), Czech Republic (Luka and Riegert, 2018), Slovakia (Karaska, 2007), Hungary (Sasvári and Hegyi, 1998), Slovenia (Vrezec and Bertoncelj, 2018), Italy (Sacchi et al., 2004), Switzerland (Roulin et al., 2011), Germany (Mammen et al., 2017), France (Baudvin and Jouaire, 2003), Denmark (Jensen et al., 2012), and United Kingdom (Petty et al., 1994). While monitoring studies based on nest-boxes may not be wholly representative of local populations, they enable reasonable comparisons of population contextual parameters between countries and regions of Europe.

Finally, spatial variation in the movements of the Tawny Owl in Europe confirmed previous notions (Southern, 1970; Sunde and Bølstad, 2004; Sunde, 2011) that the species is highly sedentary, which confirms it is a suitable sentinel species because it will serve to reflect the effects of contaminants mostly due to local exposure (Badry et al., 2020). Adult Tawny Owls are known to hold their territories even in poor prey abundance years and when not breeding (Sunde and Bølstad, 2004; Solonen, 2011; Vrezec and Bertoncelj, 2018; Ratajc et al., 2022). There are some exceptions, such as semi-nomadic behaviours of female in Northern Europe (Sunde et al., 2001). Although we found some tendency for longer dispersal distances in Northern Europe (see also Saurola, 2002) most owls did not disperse >50 km and <10 % of the individuals dispersed >100 km. In United Kingdom, for example, there were no records of Tawny Owls dispersing to the mainland and vice versa (Wernham et al., 2002), but there were a few cases of birds moving from Northern to Central Europe and from Central to Southern Europe and it seems that a few owls are capable of dispersing over the sea (Valkama et al., 2014) and colonising even remote islands (Vrezec and Jernejc Kodrič, 2021). As is often the case in birds, we found that juvenile-adult ringing distances were longer than adult-adult ringing distances. According to ringing recaptures in Finland, for example, there were about 25 % of young owls dispersing >100 km to their first nest (Saurola and Francis, 2004). Tawny Owls are territorial, long-lived and usually establish lasting territories early in life (Southern, 1970; Sunde, 2011), therefore adults are much more relevant for biomonitoring than juveniles due to their strict sedentary behaviour and thus representativeness of the local environment conditions. In other words, contaminant information from adult owls will be easier to interpret in relation to spatial exposure than that from independent juveniles that disperse further.

4.2. The importance of population contextual data for biomonitoring

Although movements seemed to have little large-scale effect, the exposure of Tawny Owl to environmental contaminants can potentially vary regionally due to spatial differences in diet composition. Food intake is one of the main pathways of contaminant exposure and contaminant transfer and bioaccumulation along food chains makes top predators particularly vulnerable to poisoning (Newton, 1979; Guigueno et al., 2012; Huang et al., 2021). The Tawny Owl is opportunistic in prey intake and easily adapts to local shifts in prey availability (Obuch, 2011; Gryz and Krauze-Gryz, 2016; Luka and Riegert, 2018). However, it is predominantly a mammal-eating predator, with other prey groups being of only rather local importance. For example, in urban areas the percentage of birds taken is generally higher (Goszczynski et al., 1993; Zalewski, 1994; Galeotti, 2001; Marchesi et al., 2006; Obuch, 2011; Gryz and Krauze-Gryz, 2019), which may increase local exposure to contaminants due to the consumption of prey from higher trophic levels (Newton, 1979; Palma et al., 2005; Lourenço et al., 2011b). Our data showed a distinct gradient of prey species taken at different trophic positions, where lower trophic level prey, i.e. herbivorous voles, are taken more frequently in the north, whereas higher trophic level prey, i.e. omnivorous mice, are taken more frequently in the south. Such latitudinal variation in the trophic levels of prey species is consistent with the dietary patterns of other similar small mammal eating predators (Birrer, 2009; Vrezec et al., 2018; Romano et al., 2020). In generalist predators, such as the Tawny Owl, the spatial variation in diet composition is greatly affected by prey availability (Petty, 1999; Grzędzicka et al., 2013). This dietary pattern can pose differential contaminant exposure risks across Europe, with higher bioaccumulative potentials being in general higher in Southern Europe. The diet of Tawny Owls exhibits not only spatial but also temporal variations. It reflects main prey population fluctuations (Gryz and Krauze-Gryz, 2016; Luka and Riegert, 2018), therefore seasonal and annual differences in exposure to contaminants can be expected (Ahrens et al., 2011; Christensen et al., 2012). In terms of population contextual data explaining contaminant levels in the tissues of Tawny Owls, it is important to differentiate seasonal/annual shifts in diet composition changes (Kirk, 1992; Jedrzejewski et al., 1994) from long-term dietary shifts as a response to environmental changes in populations of prey species (Grašytė et al., 2016).

Population density in Tawny Owl is limited and regulated by food supply, nest site availability, competitive interactions, habitat quality and climate (Southern, 1970; Wendland, 1984; Redpath, 1995; Vrezec and Tome, 2004; Brambilla et al., 2020). Spatial variation in density (and similarly, temporal variation in population trend) can thus indicate effects of a variety of factors and their individual contributions can be difficult to determine and require detailed research (Becker, 2003). For example, lower density can occur due to larger home ranges (Sunde et al., 2001), which may increase the risk of exposure to contaminants (e.g. higher exposure to anticoagulant rodenticides in urban and rural areas, López-Perea and Mateo, 2018) and a sudden drop in raptor population density can occur due to lethal levels of pollution in the area (Newton and Haas, 1984; Shore and Taggart, 2019).

However, Becker (2003) emphasised that productivity parameters are even better as "early warning" against detrimental effect of contaminants than population trend, because a response to sublethal levels of pollution is immediate in the reproduction, but delayed in the population size. Breeding attempts, clutch size, brood size, and survival of fledglings mostly depend on prey availability (Southern, 1970; Jedrzejewski et al., 1996; Coles and Petty, 1997; Solonen et al., 2015; Hoy et al., 2016). In years, when primary prey populations are low (mice and voles) and the owls rely on alternative prey (birds, amphibians, and shrews; Southern, 1970; Jedrzejewski et al., 1996; Petty, 1999), this reflects in lower breeding success and juvenile survival (Petty and Thirgood, 1989; Luka and Riegert, 2018; Ratajc et al., 2022). Decreased breeding success can thus be due to either dietary shifts to less favourable prey or high contaminant levels in tissues, which also correlate to the diet. Egg failure in raptors can relate to poor food quality due to contaminant exposure or due to low level of essential nutrients in food resulting in thinner egg shells or embryo anomalies (Newton, 1979; van den Burg, 2009; Yoccoz et al., 2009; Shore and Taggart, 2019), although these effects so far had not been extensively studied in Tawny Owl. Impact of contaminants on different populations should be assessed very carefully, and any major conclusions should be made only after considering all of the above mentioned natural drivers of the spatial and temporal variation in breeding success.

4.3. The potential contributions of ecological contextual data to knowledge advancement in large-scale and multidisciplinary studies

As shown in this review, most ecological studies are focused on a single or very few topics. There is still a considerable lack of integration of topics in multidisciplinary approaches to understand relationships between species traits, especially at a large-scale. Gathering existing data and harmonising the collection of new ecological information on the Tawny Owl and other top predators has the potential to open new research avenues by allowing unprecedented integrative analysis. Therefore, besides contributing to better understanding of environmental contamination patterns and processes, the effort to make available a large amount of ecological data from across Europe may also contribute to advances in many research topics, including a deeper understanding of predator-prey relationships (Luka and Riegert, 2018; Ratajc et al., 2022), unravelling the importance of biological control by top predators (Murano et al., 2019) and exploring the interactions between diet and morphological, physiological and behavioral traits (Karell et al., 2013, 2017, 2021).

4.4. Limitations of the currently available contextual ecological data on the Tawny Owl

Despite diet being the most studied trait in the Tawny Owl, there was a complete lack of available diet studies from some countries in the Balkans (Bosnia and Herzegovina, Albania, Kosovo and Macedonia) and only few studies in some other parts of Southern, Northern and Eastern Europe. We also acknowledge that there can be considerable limitations in assessing Tawny Owl contaminant exposure from published studies that were conducted mainly by conventional inspection for prey remains in pellets or nest material. These methods may underestimate some prey groups, particularly soft-bodied organisms, such as earthworms (Southern, 1969) and slugs, which can pose a significant part of Tawny Owl prey in some regions and years (Yalden, 1985; Kirk, 1992; Manganaro et al., 2000; Gaggi and Paci, 2009; Obuch, 2011; Sand, 2016; Vik, 2017). Since earthworms are macroconcentrators of contaminants (Rabitsch, 1995; Lukkari et al., 2004; Al Sayegh Petkovšek et al., 2015), a high consumption of this prey group could increase exposure of predators to contaminants at least on a local scale. The importance of earthworms in the diet of Tawny Owl should be assessed in future studies using advanced next-generation monitoring techniques, i.e. environmental DNA (Pompanon et al., 2012; Verkuil et al., 2022).

There are several possible biases in estimating dispersal distances, e.g. due to unequal sampling effort, lack of recaptures in some countries, differential recovery rate of dead ringed birds found in the field due to remoteness or low citizen science capacity, and not taking the proportions of unsuitable habitats in the area into the account, which can underestimate actual dispersal distances (Saurola and Francis, 2004). The currently available European ringing dataset in EURING database is extremely biassed in terms of the amount of data towards some countries, especially to Northern and Western Europe, while other countries have much less information available. This is probably a consequence of the lack of initial ringing of adults and chicks in most European countries (Derlink et al., 2018). According to the available ringing totals from some European countries, there is a huge discrepancy in Tawny Owl ringing intensity from about 30,000 or more ringed birds per country in the Northern and Central Europe and UK (Wernham et al., 2002; Fransson et al., 2008; Bairlein et al., 2014; Valkama et al., 2014) to only 2000 or less ringed birds per country in Southern Europe (Spina and Volponi, 2008; Božič, 2009; Šere, 2009; Kralj et al., 2013; Stanković et al., 2018). Considering the average recovery rate of ringed Tawny Owls in Europe, which is 8.7 ± 10.9 % of all ringed birds (calculated from ringing data in Wernham et al., 2002; Fransson et al., 2008; Spina and Volponi, 2008; Kralj et al., 2013; Valkama et al., 2014), this means that in practice 82–573 owls should be ringed for one recovery over 50 km, and 212–1910 ringed owls for one recovery over 100 km (calculated from data in Table A.39), which exceeds ringing totals of Tawny Owls in many European countries. A detailed review of EURING data is also showing differences in recovery reporting among countries since many countries apparently reported only long-distance and cross-border recoveries, and not short-distance and local recoveries (Spina et al., 2022), which are essential for a non-migratory species such as Tawny Owl. In general, overall dispersal patterns of the Tawny Owl in Europe are still insufficiently understood due to a small proportion of published studies (Fig. 2), particularly in Eastern and Southern Europe.

Compared to Tawny Owl population contextual data indicating exposure to contaminants, there was much less data published on contextual data that would indicate contaminant impact. Population trend was found relatively poorly known with many spatial gaps, which might be a consequence of a general lack of monitoring schemes for nocturnal raptors in Europe (Vrezec et al., 2012; Derlink et al., 2018). According to recent trend estimates, most European countries reported stable population trends (BirdLife International, 2017), however these seem to be very rough estimates due to discrepancies found in published literature sources. For example, BirdLife International (2017) reported a decreasing population trend for Finland, although the species population seems to be stable for decades (Saurola, 2012). On the other hand, in southern and central Europe, the population of the Tawny Owl was reported stable (BirdLife International, 2017), but recent detailed studies indicated that the Tawny Owl population is increasing with expected range expansion also to higher elevations according to climate change effects (Vrezec and Bertoncelj, 2018; Brambilla et al., 2020).

We noticed a large spatial gap in available clutch size data from Southern Europe. In Tawny Owl, nest monitoring is rarely conducted by counting begging nestlings and fledglings at natural nesting sites (Southern, 1970; Sunde and Markussen, 2005), even though it enables an estimation of fledgling survival (number of fledged begging young divided by number of nestlings). Monitoring of installed nest-boxes is more common, but few countries have resources for establishment of long-term field data collection (Derlink et al., 2018). Therefore, breeding productivity monitoring of brood size appeared to be much more feasible than clutch size due to avoidance of sensitive incubation period (Hardey et al., 2013) and since direct access to the nest is not necessary when counting begging young (Sunde and Markussen, 2005). As indicated in our review, there were more reports on the brood than clutch size in the literature, but the standardisation of measures for brood size (e.g. brood size per active territory or per active nest) is strongly needed.

Considering all these limitations, it is relevant to harmonise monitoring methods and establish a minimal scheme that could ensure the long-term

collection of data to be used in multiple large-scale studies related to the biology and ecology of the Tawny Owl.

4.5. Conclusions and perspectives

The feasibility of collecting population contextual data varies significantly due to different amounts of skill, manpower and funds needed to carry out the fieldwork. Surveying elusive nocturnal raptors requires several labour-intensive monitoring methods, which makes collecting some data very difficult and costly. Our results show that besides the diet, most studies monitored breeding population density and breeding productivity. Point counts/line transects and nest search were identified as the most popular systematic raptor monitoring methods (Derlink et al., 2018). Territory monitoring using the playback method requires relatively little field effort and was found to be a reliable approach for assessing population trends of Tawny Owl, particularly at large scale and in remote areas (Vrezec and Bertoncelj, 2018). However, nest monitoring, even though it is a labour-intensive field method, enables in addition to productivity data also collection of other valuable population contextual data (diet, survival, morph variation etc.).

Since all of the mentioned methods require a fair amount of capacity building, good coordination, funds and legal permissions, e.g. permits for accessing the nests and handling living birds (Vrezec et al., 2012; Dulsat-Masvidal et al., 2021), a comprehensive monitoring scheme for Tawny Owl can be very costly in most countries. Therefore, a basic more feasible and cost-effective scheme is needed to establish a pan-European population contextual data monitoring. We propose here a Minimal Recommended Raptor Monitoring Scheme (MRRMS), measuring internationally comparable parameters. Currently the monitoring schemes for breeding Tawny Owl are established in 13 countries (32 % of all European countries; Derlink et al., 2018) and our results confirmed that there are still large gaps to be covered with population monitoring of the species. In the scope of MRRMS, we propose one parameter indicating species exposure to contaminants and two indicating contaminant impact on the species, i.e. early warning of contaminant problems (Table 3). All proposed population contextual data also indicate population status and development of the target species and are essential also for overall conservation assessments. The proposed MRRMS for Tawny Owl is aimed to assist in the establishment of Tawny Owl monitoring schemes in the countries where no species monitoring is established yet as a starting point. Through time, the MRRMS has the potential to be elaborated using more sophisticated and costly approaches of integrated monitoring, if training can be provided and more experienced volunteers become available, for example allowing the additional collection of highly indicative demographic data such as population structure, related seasonal survival rate and lifetime reproduction (Saurola and Francis, 2018).

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CRediT authorship contribution statement

Urška Ratajc: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Rui Lourenço:** Conceptualization, Methodology, Validation, Investigation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Silvia Espín:** Conceptualization, Methodology, Project administration. **Pablo Sánchez Virosta:** Conceptualization, Methodology, Writing – review & editing, Project administration, Funding acquisition. **Simon Birrer:** Investigation, Data curation, Writing – review & editing. **Dani Studler:** Investigation, Data curation. **Chris Wernham:** Conceptualization, Methodology, Writing – review & editing, Project administration, Funding acquisition. **Al Vrezec:** Conceptualization, Methodology, Validation, Investigation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 3
Overview of focal population contextual data to be provided within a suggested Minimal Recommended Raptor Monitoring Scheme (MRRMS) for breeding populations of Tawny Owl in Europe.

Focal population contextual data	Contaminant indication	Derived data	Rational and conventional methodological approaches	Method advancement for rapid assessment in monitoring
Population trend	Impact	Annual population indices	The key approach is to determine presence/absence of the species at surveyed location or territory. There are many methodological approaches of territory survey with or without playback and/or nest survey (Hardey et al., 2013; Vrezec and Bertoncelj, 2018; Zuberogoitia et al., 2020).	Acoustic monitoring using field autonomous sound recorders proved to be effective soundscape bird survey method performed as point count (Darras et al., 2018), also for owls (Marín-Gómez et al., 2020), and should be further explored for Tawny Owl population monitoring using citizen science and automated identification tools.
Breeding productivity per territory	Impact	Annual indices of successful breeding per territory	The proportion of territories that produced at least one young in a year. More methodological approaches are possible from more simple, such as survey of vocalising fledged young to more detailed assessments of the young in the nests, which require additional skills and tools (i.e. nest boxes) (Sunde and Markussen, 2005; Saurola and Francis, 2018).	Nest-box cameras are increasingly used research tool for studying breeding biology of birds (Stevens et al., 2008; Williams and DeLeon, 2020; Surmacki and Podkowa, 2022), but can be also applied for monitoring of nest occupancy and productivity including clutch size and chick survival (Hereward et al., 2021).
Diet	Exposure	Periodical 5-year reports on the diet composition for main prey groups	Tawny Owl diet can be assessed from different types of prey remains; from pellets (Balčiauskienė et al., 2006; Gryz and Krauze-Gryz, 2019), food remains (Petty, 1999; Solonen et al., 2017) and stomach content (Overskaug et al., 1995; Villarán Adánez, 2000). For monitoring purposes, the diet structure can be evaluated at the level of main prey groups' proportions.	Molecular analysis using environmental DNA approach for diet assessments proved to be a promising tool (Pompanon et al., 2012; Verkuil et al., 2022), but not yet tested for owl diet by analysing eDNA in pellets, excrements or nest material.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160530.

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Chapter 3

Intertrophic Interactions: Responses to Prey Population Fluctuations

This chapter details our contributions to understanding the fluctuations of different small mammal populations and their effects on territory occupancy and breeding activity of Tawny Owl and other coexisting owls, Boreal *(Aegolius funereus)* and Ural Owl *(Strix uralensis)*. Responses of forest owls to small mammal fluctuations have so far been studied only in populations from Northern or Central Europe (e.g. Jedrzejewski et al., 1996; Luka & Riegert, 2018; Solonen & Karhunen, 2002). This is the first such study in Southern Europe and provides an insight into a possible large-scale gradient of owl adaptations. We used advanced methods (machine learning methods) to discover the relationships with small mammal population dynamics, which was a complete novelty in ornithological research area.

The research was organized in a paper, published in Ibis (Ratajc et al. 2022; Supporting information is given in Appendix B) and is included in this chapter. From the hypotheses defined in Chapter 1.2, it addresses the following:

H3 There is a key small mammal species in the Dinaric forest assemblage that triggers owl breeding responses.

H4 Prey decline always leads to a numerical response in forest owl species, but at different breeding stages in different owl species, i.e. territory vs. nest occupancy vs. productivity, and magnitudes.

H5 In temperate mixed forests of Dinaric Mountains, boreal zone owl species exhibit higher sensitivity to prey fluctuations than temperate zone owl species.

All three hypotheses were confirmed. The dominant species in the small mammal assemblage and the species that has the key role in determining predator responses is the Yellow-necked Mouse (*Apodemus flavicollis*). We found that populations of different owl species respond to low prey abundances at different stages and with different magnitudes, depending on their life-histories and survival strategies. In years with low populations of prey, the survival strategy in Boreal Owl is to abandon territories in search of prey-rich areas, in Ural Owl to suppress breeding and wait in the territory for better conditions, and in Tawny Owl to decrease the breeding activity slightly, but sustain it by relaying on alternative prey. Thus, as is reflected in more detrimental responses, the boreal species (Boreal and Ural Owls) are more sensitive to small mammal fluctuations than the temperate zone species (Tawny Owl) in the temperate mixed forest of southern European mountains.

I participated in designing the research and was included in the fieldwork on collecting data on owl breeding productivity and on small mammal densities (in the period 2017-2020). I cleaned the dataset for analysis, analyzed the data and prepared the figures. I wrote the original draft and revised it following the feedback from co-authors and the reviewers.

3.1 Differential Responses of Coexisting Owls to Annual Small Mammal Population Fluctuations in Temperate Mixed Forest

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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, Zárybnická *et al.* 2015, Yatsiuk & Filatova 2017, Luka & Riegert 2018, Tumiel & 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, Zárybnická *et al.* 2013, Tumiel & 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 & Bertoncelj 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, Zárybnická *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, Zárybnická *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 °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^2 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), 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).

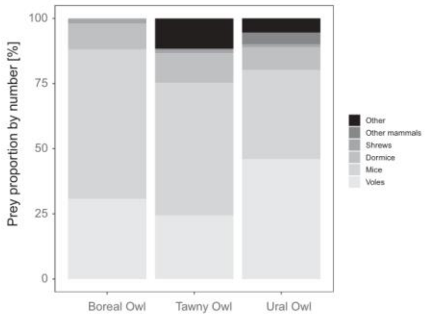

Figure 1. Summary of the available data on the breeding diet composition (proportion of prey item groups by number (%)) of the coexisting forest owls, i.e. the Boreal, Tawny and Ural Owls, in the Dinaric forests of Mount Krim, Slovenia.

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 Bertoncelj (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 nestbox monitoring (Vrezec & Bertoncelj 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 ± 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

$$\underset{c}{\operatorname{argmax}}\, Variance(S) - Variance_c(S1) - Variance_c(S2),$$

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

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

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).

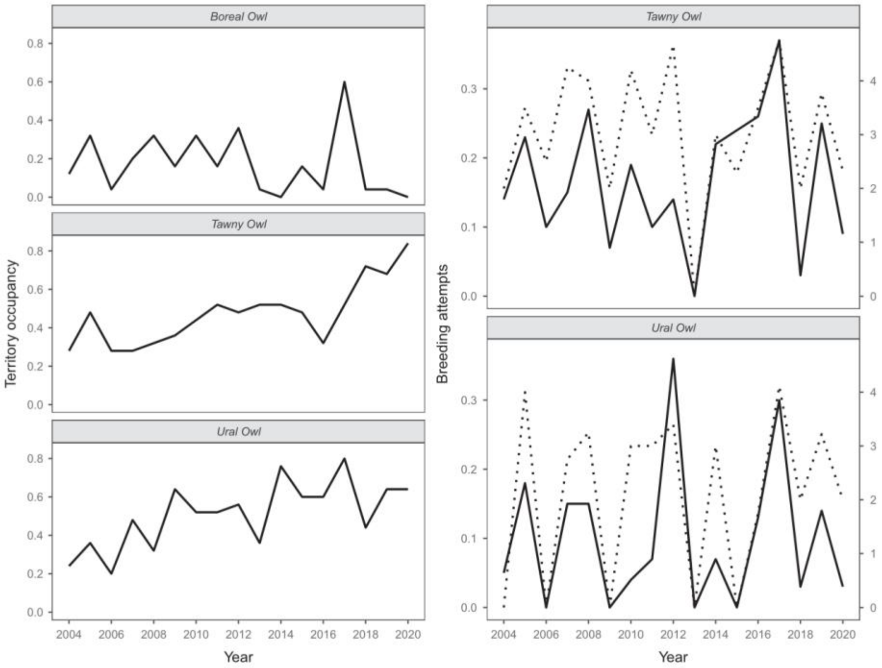

Figure 2. Population dynamics of owls on Mount Krim in the period from 2004 to 2020. Relative abundances of owls are given as the number of active territories per survey point (territory occupancy) and as the proportion of occupied nestboxes (breeding attempts). The dotted line represents between-year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

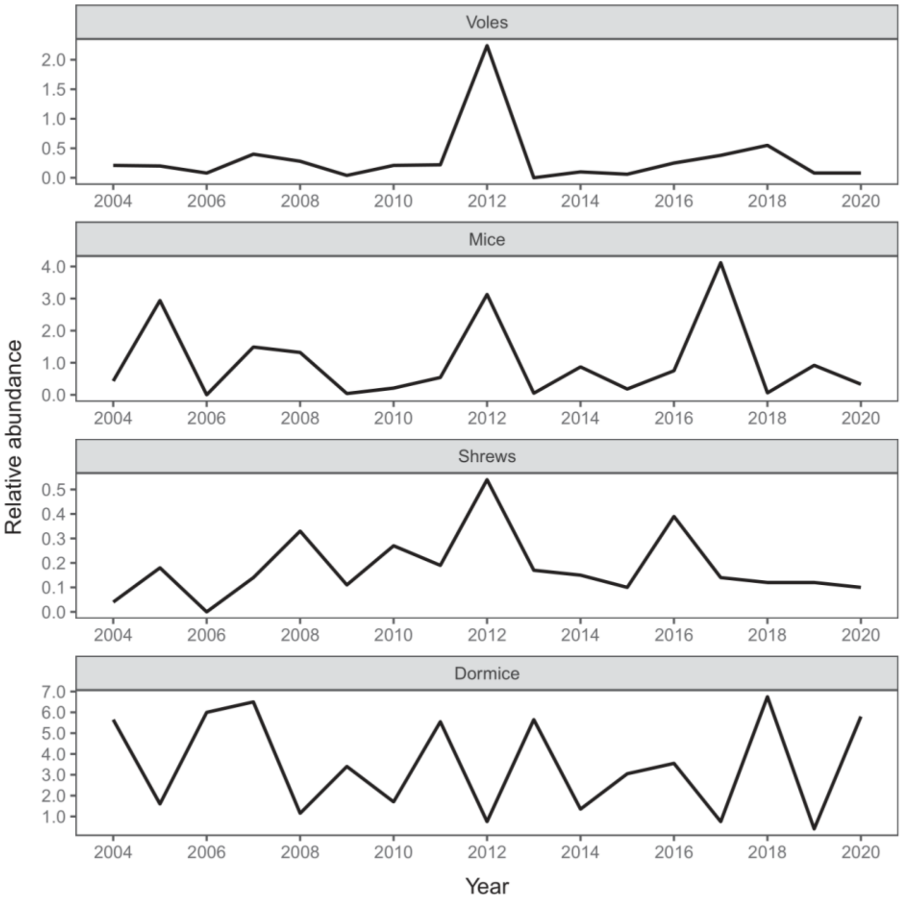

Figure 3. Population dynamics of small mammals on Mount Krim in the period from 2004 to 2020. Relative abundances of voles, mice and shrews are given as the number of trapped individuals per 10 trap-nights, and the relative abundance of dormice as the number of vocalizing individuals per survey point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

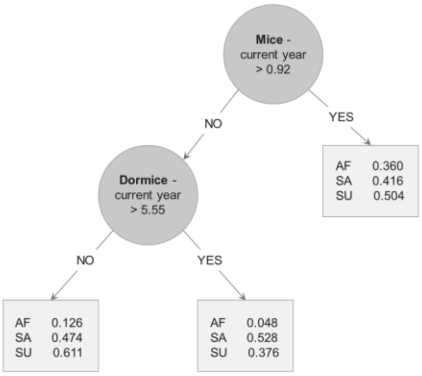

Figure 4. A PCT predicting territory occupancy rates for the three forest owl species (AF, Boreal Owl; SA, Tawny Owl; SU, Ural Owl) from the abundances of small mammals in the current and previous years.

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.

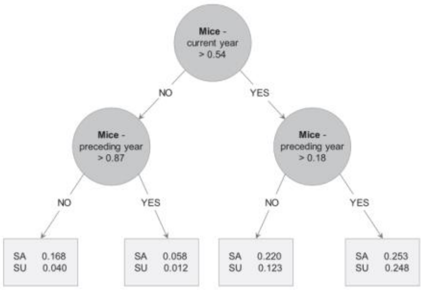

Figure 5. A PCT predicting the breeding attempt rate of Tawny Owl (SA) and Ural Owl (SU).

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).

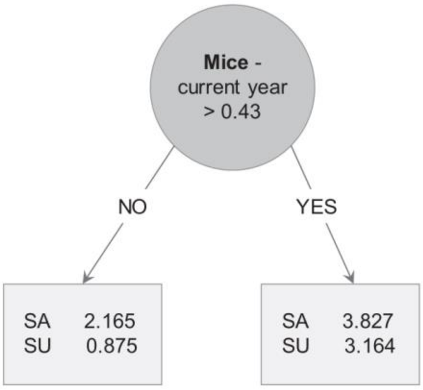

Figure 6. A PCT predicting the clutch size of Tawny Owl (SA) and Ural Owl (SU).

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.

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 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, hemi-boreal 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	Territory occupancy		Breeding attempts		Clutch size	
Data source	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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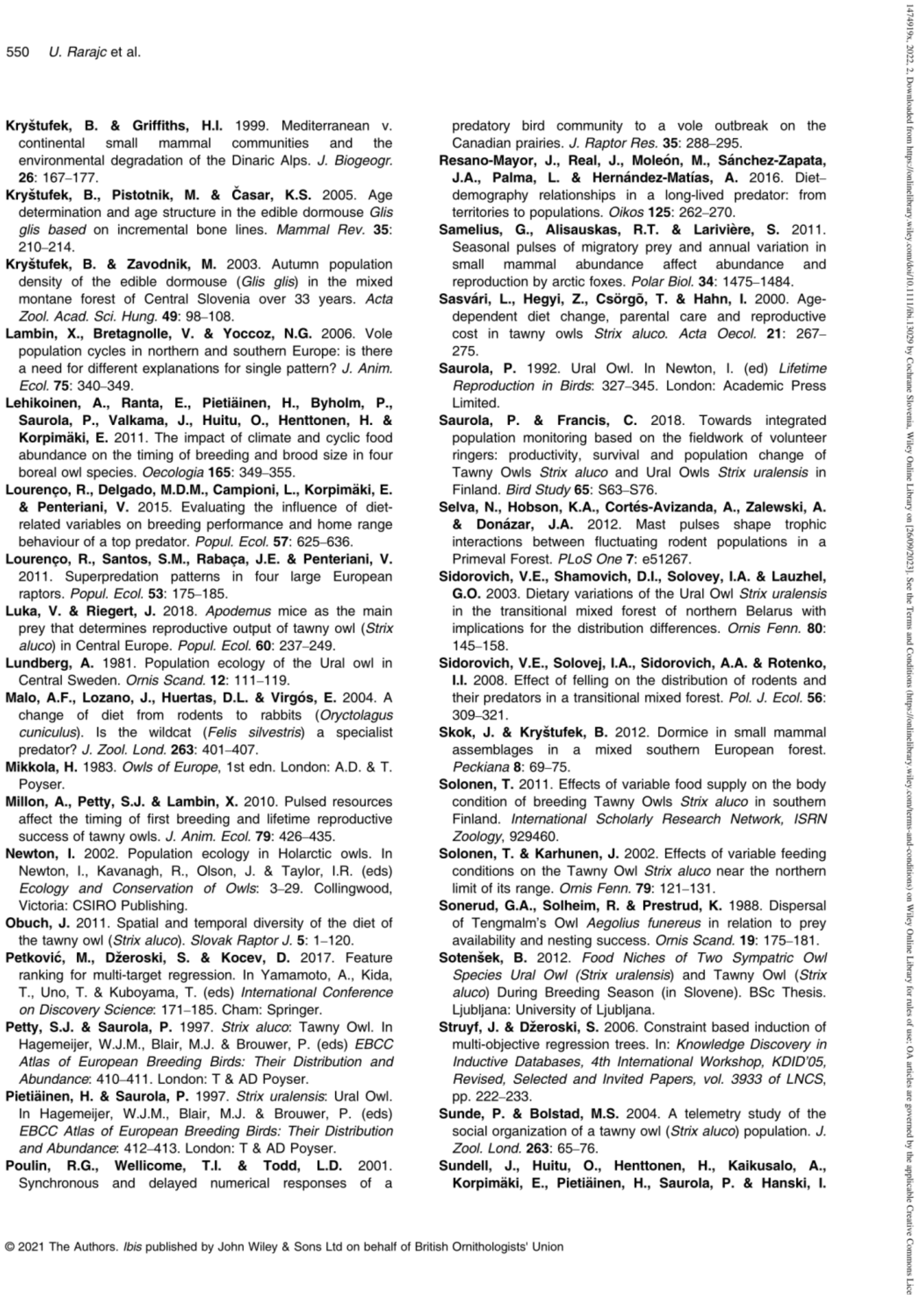

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SUPPORTING INFORMATION

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.

Chapter 4

Intratrophic Interactions: Competition with the Ural Owl

In this chapter, the Tawny Owl population trends and its interactions with competitive species from the same guild, the Ural Owl, were analysed. We were the first to test the assumptions and conclusions from predictive distribution models in the light of future climate change from the Alps (Brambilla et al., 2020), and investigated whether these predicted processes are already going on in the montane forests in the Northern Dinaric region. We used data from our long-term territory and nest-box monitoring to evaluate the local expansion rate in both species. The results revealed that intensified competitive intraguild interactions might lead to potential selection pressure towards increased body size in both species, which could be important for interpretation of regional size ratio differences between sympatric and allopatric areas, and for building predictions for future scenarios under ongoing global changes.

The following manuscript investigates the last three hypotheses defined in Chapter 1.2:

H6 Tawny Owl population in Dinaric forests is increasing due to expanding its range towards higher elevations.

H7 Tawny Owl intrusion into Ural Owl dominated areas in Dinaric forests increases intraguild interactions, notable in competition for nest-sites.

H8 Intensified intraguild interactions adversely affect breeding productivity of both species in Dinaric forests.

The first two hypotheses (H6 and H7) were confirmed. Tawny Owl population in our research area exhibits an overall moderate positive trend, but on account of a strong trend at higher altitudes. At the same time, the Ural Owl population is also increasing and the intraguild competitive interactions are getting stronger, which is evident based on the increasing competition for nest-boxes and displacement from the nests. The last hypothesis (H8) was rejected. We did not find any significant differences in breeding productivity in any of the species between nests in the absence and nests on territories overlapping territories of competitive species.

I contributed to the conceptualization of the research together with my co-author and was included in the fieldwork on collecting data on owl fitness and breeding productivity (2017-2021). I cleaned and analyzed the data, prepared figures, and drafted the manuscript together with my co-author.

4.1 Climate Change is Intensifying Intraguild Interactions Between Top Predators and Creating New Potential Evolutionary Pathways

Running head: Top predator interactions and climate change

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Abstract

Adaptations of coexisting species to climate-driven environmental changes might not necessarily lead to extinctions, but rather to niche shifts and trait variations that generate new competitive hierarchies in ecosystems. Top predators have a pivotal role as indicators or even generators of high biodiversity in ecosystems, but effects of climate change on top predators have not been sufficiently explored. We used long-term data on the territory and breeding dynamics of two coexisting, ecologically similar and closely related forest raptors, the temperate zone Tawny Owl *(Strix aluco)* and the boreal zone Ural Owl *(S. uralensis)*, in an area that has experienced significant climate change (>1°C mean temperature increase) but not habitat change in the last 20 years. We analysed the population dynamics of both species along an altitudinal gradient by measuring changes in territory overlap and nest displacement rate as well as effects on species breeding productivity and body size. As a result of concurrent population growth and range expansion, we observed a gradual intensification of competition for space and nest sites, including direct nest displacements of the smaller Tawny Owl by the larger Ural Owl. This close coexistence and intensified interaction can result in (1) increased disease transmission with possible new zoonotic outbreaks (direct nest displacements and shared territories), (2) a higher frequency of hybridization (mixed clutches) and (3) morphological changes of coexisting individuals. We observed that breeding Ural Owl females became significantly larger in shared territories with Tawny Owls compared to those in unshared territories. From an evolutionary-ecological perspective, this size disparity could bolster the Ural Owl's dominance over the Tawny Owl. However, it could also pose long-term risks for the Ural Owl, as the advantages of larger size come with increased energy demands and reduced hunting agility. This study highlights that, beyond theoretical model predictions, robust long-term monitoring data are urgently needed to capture the actual changes taking place in changing ecosystems and to reveal the hidden and trait-based adaptations of coexisting species and unforeseen drivers of extinction.

Key words: ecological trait, raptor, long-term study, concurrent population increase, population trend, territory overlap, nest displacement, selection pressure, size shift

4.1.1 Introduction

Climate change is one of the most potent drivers of global biological response (Parmesan, 2006). Changes in biotic interactions driven by climate change appear to be the primary catalyst of species declines, extinctions and subsequent alterations in ranges (Walther et al. 2002, Cahill et al. 2013). Biotic interactions therefore play a pivotal role in predicting the future distribution patterns of species (Van der Putten et al. 2010, Byholm et al. 2012). Recently, Carroll et al. (2023) proposed that biodiversity is changing through adaptive community dynamics. Existing communities become maladapted to new environmental conditions and must adapt to achieve the best fit of organism traits. This introduces new selection pressures, forcing the selection of certain genotypes and/or species (Carroll et al. 2023). Adaptations of coexisting species in changing environments might not necessarily lead to extinctions, but rather to niche shifts (Antão et al. 2022) and trait-based coexistence arising from trait variations that generate competitive hierarchies (Adler et al. 2013). The effects of climate change on biotic interactions have primarily been studied at lower trophic levels (Araújo & Luoto 2007; Stiling & Corelissen, 2007; Urban et al. 2013) owing to the heightened complexity of interactions at higher trophic levels, which involve both inter- and intraguild interactions.

The dependency of predators, particularly top predators, on the fluctuations of their main prey is well documented and understood. Such fluctuations can impact their reproductive patterns, survival rates, dispersal and habitat selection strategies (Sonerud et al., 1988; Brommer et al., 2002; Karell et al., 2009; Saurola & Francis, 2018; Mougeot et al. 2020). However, even predators within the same guild (Root 1967) can adopt different response strategies to prey scarcity (Newton, 2002; Ratajc et al., 2022). An increase in prey abundance can positively affect predator populations (Korpimäki, 1994; Brommer et al., 2002; Karell et al., 2009; Therrien et al., 2014), yet it also induces a reduction in proximity between neighbours, intensifying both intra- and interspecific interactions (Newton 2017). Apart from competing for food, nest sites and space, intraguild predation exerts a particularly strong effect on predator assemblages through the elimination of subordinate competitors, either through direct killing or non-lethal effects such as avoidance of dominant predators (Sergio & Hiraldo 2008). This can push subordinate predators to refugial areas or even drive them to extinction (Hakkarainen & Korpimäki 1996, Vrezec & Tome 2004a, Sergio et al. 2003, 2007, Dugger et al. 2011). An example of such competitive dynamics is a pair of ecologically equivalent species (Norberg 1987), the Northern Spotted Owl (*Strix occidentalis caurina*) and the Barred Owl (*S. varia*) in North America (Haig et al. 2004; Long & Wolf, 2019; Yakulic et al. 2019), where new contact zones have recently been established. Populations of the smaller species (Northern Spotted Owl) started to decline with the expansion of the larger and more aggressive Barred Owl (van Lanen et al. 2011). In addition to ongoing competitive interactions, hybridization has been observed, with the rate of hybridization events believed to negatively affect the viability of subordinate species populations (but see Kelly & Forsman 2004). However, hybridization has the potential to be a creative force contributing to speciation and overall species diversity (Elgvin et al. 2017).

Climate conditions exert a particularly strong influence on the spatial distribution of species. This is very well expressed on the local scale through the spacing of species along elevation gradients (Lurgi et al. 2012). On the level of communities, it is reflected in species turnover (McCain & Grytnes, 2010; de Groot & Vrezec 2019), where lowland generalists are succeeded by differently traited highland specialists at higher elevations (Žagar et al. 2018). Even among top predators, species can be altitudinally segregated due to different traits and intraguild interactions (Vrezec & Tome 2004a, b). The impact of climate change on elevation gradients follows a pattern wherein high-elevation communities become maladapted and gradually transform to a state of more optimal trait-environment matching (Carroll et al. 2023). This dynamic gives rise to two possible outcomes: (1) high-elevation specialists might become locally extinct or, if conditions allow, expand their ranges to higher elevations, constituting a retreat of high-elevation specialists (Lurgi et al. 2012), or (2) high-elevation specialists may persist within the newly adapted community through trait differentiation that enables survival in the altered environment and coexistence with expanding lowland species, thus establishing a new competitive hierarchy (Adler et al. 2013). This could also entail evolutionary and genetic changes (Turbek et al. 2023), which is a well-known and understood phenomenon in cases of strong biotic interactions between coevolving species, i.e. predator-prey or parasite-host interactions (Tokeshi 1999), but less so in intraguild interactions (Dhondt 2012).

To study climate-induced alterations of intraguild interactions among top predators, we focused on two sympatric and closely related raptors, the Tawny Owl *(Strix aluco)* and the Ural Owl *(Strix uralensis)*, in a sustainably managed temperate mixed forest in Slovenia, in the southern part of Central Europe. Since the late 20th century, average temperatures in the area have increased twice as much as the global or Northern Hemispheric average (Auer et al., 2007). Slovenia is a part of a wider geographical area identified as a “warming band” of mean annual temperatures, which extends from SW to NE Europe (Schönwiese and Janoschitz 2008). This provides a valuable opportunity to study climate change effects in an area with a moderate elevational gradient where both owl species coexist (Vrezec 2003). Both species belong to the guild of forest hole-nesting, small mammal-eating, nocturnal raptors (König & Weick 2008) and have been shown to produce fertile hybrids in in-situ experiments (Scherzinger 2017). However, their historical origins differ considerably. The Tawny Owl is an adaptable mesopredator of the temperate climate zone that expanded across the whole of Europe after the last glaciation from refugia in southern Europe (Brito 2005, Ratajc et al. 2023). Conversely, the Ural Owl is a boreal species, with isolated glacial relict populations inhabiting the southern temperate montane forests of Eastern and Southeastern Europe (Pietiäinen & Saurola 1997, Vrezec et al. 2018). In southern montane regions, Tawny and Ural Owls are altitudinally segregated, with the larger Ural Owl competitively excluding the smaller Tawny Owl from higher elevations (Vrezec & Tome 2004b). Similar habitat displacements have also been observed in other areas of sympatry (Bolboacă et al., 2013, Kajtoch et al. 2015). In parts of European Russia, the Tawny Owl even experienced a decline following the colonization of the Ural Owl (Keller et al. 2020). Current data suggest the substantial competitive dominance of the Ural Owl over the Tawny Owl, although the latter appears to be more adaptable to prey fluctuations than the Ural Owl, particularly in southern regions with small mammal assemblages dominated by mice (Muridae) (Ratajc et al. 2022). Over its European range, the Ural Owl is a vole (Arvicolinae) eating predator (Vrezec et al. 2018), which might make it less adapted to warmer, low-elevation mice-dominated temperate broadleaf forests (Ratajc et al. 2022). Climate models predict a strong concurrent increase in population sizes for both species in the Alps, with the range overlap expected to more than double in the future (Brambilla et al., 2020). Nevertheless, these modelled predictions warrant field investigation, as predictions regarding competitive interactions can be uncertain in modelled scenarios. It is known that Ural Owls can adopt different interaction patterns with coexisting raptor competitors in different types of environments (Fedyń et al. 2022).

To explore the predicted climate-driven expansion of range overlap between Tawny and Ural Owls (Brambilla et al. 2020), we used local, long-term territory and nest monitoring data. Our aim was to assess the changes in overlapping territories and the possible consequences of intensified interspecific competition on the breeding productivity of both *Strix* species. We hypothesized that in temperate montane forests, milder winter conditions are enabling the Tawny Owl to expand to higher elevations, thus intensifying interactions with the Ural Owl, particularly with respect to competition for nest sites. We anticipate that altered intraguild interactions adversely affect breeding productivity and selection pressures in populations of both species, albeit with varying degrees and directions depending on their respective traits.

4.1.2 Methods

4.1.2.1 Study area and regional velocity of climate change

The study area was Mount Krim (14°25´E 45° 58´N), a medium-high mountain of the north Dinaric Alps, ranging from 290 to 1107 m above sea level. The area is situated 10 km south of Ljubljana, central Slovenia (Southern Europe). The area of 140 km^2 predominantly consists of continuous mixed forests characterized by European Beech *(Fagus sylvatica)* and Silver Fir *(Abies alba)* as the dominant tree species (Vrezec et al. 2018). Agricultural and forest clearings are small and dispersed (Vrezec & Tome 2004a). Settlements are scarce and mostly in the lowlands and cover only 3% of the area, which is designated as a Natura 2000 site. Forests in 76% of the area are in the old growth phase with trunk diameters of 30 cm or more at breast height (Zavod za gozdove Slovenije & ZaVita 2022), which is an optimal habitat for large tree-hole nesting birds (Vrezec 2003). Forest management is consistent with no detected major landscape or forest habitat changes in the past 20 years (Zavod za gozdove Slovenije & ZaVita 2022). However, notable changes have occurred in the climatic parameters. Mean temperatures increased in total by 1.1°C from 1998 to 2021 (fitted values), which is a 0.05°C annual increase ($F = 10.2$, $p = 0.004$). The total number of days with frost in this same period decreased in total by 13.3 days, which is a trend of -0.6 frost days per year ($F = 4.9$, $p = 0.038$; Fig. 1) (data from an automatic climate station, Nova vas na Blokah, 720 m a.s.l., 10 km south of the core research area; Slovenian Environment Agency 2022).

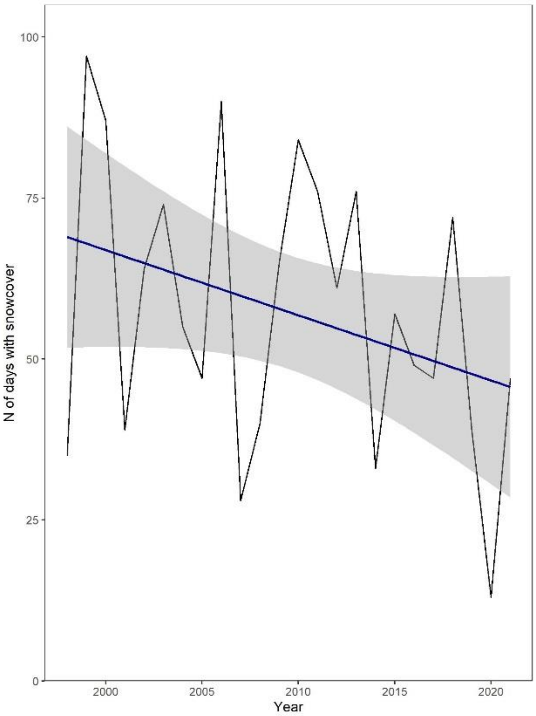

Figure 1: Total number of frost days (i.e. with T below 0°C) in the period from 1998 to 2021 in close proximity to and at the mean elevation of the study area of Mt. Krim. The trendline is a linear regression model (No. of frost days ~ year), and the shaded area represents the 95% confidence interval.

4.1.2.2 Study species

The Tawny Owl (*Strix aluco*) and Ural Owl (*Strix uralensis*) are sympatric in southern Fennoscandia, Central, South-East and Eastern Europe and further east to SW Siberia. However, a substantial portion of Ural Owl populations in eastern and northern Eurasia are parapatric (König & Weick 2008). Despite the moderate size difference between these species (Fig. 2), they appear to be very similar in many aspects of their ecological niche (Korpimäki, 1986). Therefore, strong competitive interactions have been observed between them (Vrezec & Tome, 2004b), including intraguild predation (Mikkola 1983), which leads to nest displacement, competitive exclusion and pronounced spatial segregation (Lundberg 1980; Vrezec & Tome, 2004b; Bolboacă et al., 2013; Kajtoch et al. 2015; Scherzinger 2017, Saurola 2023). Their diets largely consist of mice and voles, which determine their population fluctuations and reproduction (Saurola & Francis 2018). However, they exhibit different functional responses to prey scarcity (Ratajc et al. 2022), possibly shaping their population dynamics and range expansion patterns amidst changing environmental conditions (Brambilla et al. 2020, Avotins et al. 2023). The Ural Owl, as the larger, dominant species, can force the smaller, subordinate Tawny Owl to occupy less favourable habitats (Vrezec & Tome, 2004b; Bolboacă et al., 2013). Conversely, the Tawny Owl can offset its competitive disadvantages through higher overall productivity, achieved by adapting its diet during periods of low small mammal abundance (Ratajc et al. 2022). Prey availability has been observed to be more limiting for the predominantly vole-eating Ural Owl, while the Tawny Owl is more limited by climatic conditions (Pavón-Jordán et al., 2013; Vrezec et al. 2018; Solonen 2022; Avotins et al. 2023). In Northern Europe and at higher elevations, deep snow cover and severe winter conditions affect the hunting success and survival rates of the Tawny Owl, but less so for the Ural Owl, which is a highly tolerant species regarding altitudinal distribution (Vrezec 2003; Francis & Saurola 2004, Sasvári & Hegyi, 2005; Lehikoinen et al., 2011, Pavón-Jordán et al., 2013). Therefore, milder winters may prompt the Tawny Owl to expand towards higher latitudes and elevations (Kopij, 2011; Brambilla et al., 2020). Both Ural and Tawny Owls are regarded as capital breeders, relying on stored energy reserves during the pre-breeding period (Lehikoinen et al., 2011). Therefore, rising pre-laying temperatures stimulate the production of earlier and larger clutches in both species. Recent studies have revealed population growth and expansion trends in Ural Owls across the majority of their European range, even extending into lowlands (Bashta, 2009; Saurola 2009; Bylicka et al. 2010; Kopij 2011; Vrezec, 2019). However, the species was once more widely distributed in Western Europe, becoming extinct in the mediaeval period (Goffette et al. 2016), and 100 years ago also in parts of Central Europe, probably due to persecution (Scherzinger 2006). More recently, local declines have also been recorded in areas marked by significant reductions in small mammal populations (Avotins et al. 2023). Meanwhile, the European population of Tawny Owls has remained relatively stable across its range (Ratajc et al. 2023).

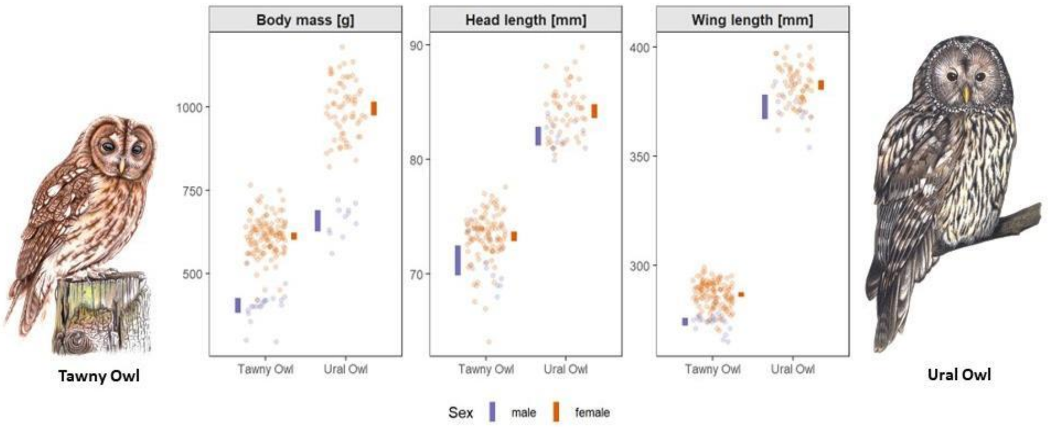

Figure 2: Intra- and interspecific body differences between sexes in coexisting Tawny and Ural Owls in Slovenia, captured and ringed during the breeding season. The lines represent 95% confidence intervals for the population mean. Significant differences in means between sexes and species are observed in all three body measurements (Mann-Whitney U test, $p<0.005$).

4.1.2.3 Field work

We used two field datasets in our research, one stemming from territory monitoring in the period 1998 to 2021, and the other from nest-box monitoring in the period 2004 to 2021. Playback surveys targeting the territories of Tawny and Ural Owls were conducted annually across a network of 65 survey points, from the foothills to the summit of Mount Krim (for a detailed description of the survey method, see Vrezec 2003 and Vrezec & Bertoncelj 2018). Out of these, 25 points were visited regularly every year. We considered the territory as occupied in the current breeding season if we recorded a response within a radius of 500 m from the survey point during any of the visits. A minimum two visits with Tawny Owl responses and three visits with Ural Owl male call playback were required. Simultaneously, during the spring months (March to May), we inspected all installed nest boxes for the presence of breeding owls. We used the same nest-box type for Tawny and Ural Owls to facilitate competitive interactions between the species (see nest-box details in Vrezec et al. 2018). Nest boxes on Mount Krim were first set up before the 2004 breading season, numbering between 22 and 32 from 2004 to 2018. In the fall and winter before the 2019 season, an additional 40 nest boxes were installed. The nest boxes were positioned in close proximity to survey points. Every occupied nest box was inspected at least twice in the season, during which clutch and brood sizes were recorded. Incubating females in the nest boxes were caught annually, measured (wing and head length, weight) and ringed or checked for ring identification. In 2019, in a mixed clutch in a Ural Owl nest, a Tawny Owl fledgling was fitted with a VHF radio tag to track chick survival two months after leaving the nest. The position of the chick was recorded weekly as well as its condition.

4.1.2.4 Data analysis

Territory occupancy (as a relative measure of territory density) in every season was assessed as the total number of territorial males of each species divided by the number of survey points checked in that year. We calculated territory occupancy separately for the area below 700 m a.s.l. (low elevations) and the area above 700 m a.s.l. (high elevations) using territory monitoring data from the regular 25 survey points. The elevation of 700 m divided the elevational range of the survey points in half (the mean was 714 m a.s.l.). The same dataset was used to calculate the trend of territory occupancy for each species using the “rtrim” package (version 2.1.1, van Strien et al. 2000). We used the linear trend option (model 2) with overdispersion and serial correlation, and missing data were taken into account. We weighted the estimated indices by the proportion of forest area below and above 700 m a.s.l. (= 1.43) of Mt. Krim.

Regular survey points in each year were assigned a category based on the results of the playback survey. If the response of only one of the species was recorded, then the survey point was assigned either to the category “Tawny Owl only” or “Ural Owl only”. If both species were territorial at the survey point in that year, the category “both” was assigned. If neither of the species was found during territory survey, the category “none” was assigned to the survey point. We used these categorical data to make an alluvial plot (using package “ggalluvial”, version 0.12.3, Brunson 2020) showing the changes in proportions between the statuses of survey points from 1998 to 2021. The trend in the number of unoccupied survey points (category “none”) and overlapping territories (category “both”) was calculated using the “rtrim” package, following the same settings used for calculating territory occupancy trends (see above).

Nest-box categories were assigned based on occupancy in the entire research period. Nest boxes in which both of the species had nested at least once were assigned the category of “both”. The proportions between the categories were calculated separately for the areas below and above 700 m a.s.l. and before and after 2009, which marked the midpoint of the research period (1998-2021). We calculated nest-box occupancy time-lags as the number of years between the nest-box setup and it’s first occupancy by the species. A nest box set up in the autumn of the previous year and occupied in the subsequent season was considered as one-year time-lag.

To analyse the relationship between clutch size and the presence of competitive *Strix* species, a subset of the nest-box monitoring dataset was used. We only included data from nest boxes at survey points where territories were surveyed for both species in that season. The differences in nest-box occupancy time-lags, clutch size and measurements (body mass, head length, wing length) of breeding females were examined using estimation statistics and graphically presented by Data Analysis with Bootstrap-coupled ESTimation (DABEST) plots (R package “dabestr”, version 0.3.0; Ho et al., 2019). These plots illustrate the raw data (swarmplot) against the mean difference between two groups (zero and test group), with the effect size as a bootstrap 95% confidence interval (95% CI) of the mean difference between the test group and the null. The mean difference is compared against zero using 5,000 bootstrap resamples. The bold black dot and the associated ticks represent the effect size and its 95% confidence interval (CI). The shaded curve indicates the bootstrapped effect size sampling-error distribution. Instead of an accept/reject dichotomy typical in null-hypothesis significance testing, estimation statistics emphasize effect quantification (Ho et al. 2019).

All statistical analyses were carried out using R 4.2.2 statistical software (R Core Team, 2022) in RStudio (RStudio Team, 2022), with visualizations generated using the "ggplot2" package (version 3.4.0, Wickham, 2022) and "patchwork" (version 1.1.2, Pedersen, 2022).

4.1.3 Results

4.1.3.1 Territory dynamics

We compared the population dynamics and trends of the number of occupied territories in both species at 25 survey points that were annually surveyed during the period 1998 to 2021. The number of territories for each species fluctuated and differed between species in the upper and lower area of Mt. Krim (Figure 3 and S1). Tawny Owl territory occupancy fluctuated between 0.4 and 1.0 territories per survey point (mean = 0.7) at low elevations and from 0.0 to 0.7 territories per survey point (mean = 0.3) at high elevations. The Ural Owl territory occupancy fluctuated between 0.0 and 0.7 territories per survey point (mean = 0.2) at low elevations and from 0.1 to 1.0 territories per survey point (mean = 0.6) at high elevations.

Log-linear trend models from the rtrim package estimated for the territory occupancy of both species were not rejected (goodness-of-fit in the Tawny Owl: LR = 291.43, df = 541, p = 1.00; in the Ural Owl: LR = 314.98, df = 564, p = 1.00). The overall trend of Tawny Owl territory occupancy on Mt. Krim increased moderately (Figure 4, 2.6% annual increase, $p<0.05$). Tawny Owl territory occupancy at low elevations increased by 1.3% annually, and significantly more, by 9.0% annually, at high elevations (Wald-test, $p<0.001$). The overall trend of Ural Owl territory occupancy on Mt. Krim indicated a moderate increase (Figure 4, 5.2% annual increase, $p<0.01$). Ural Owl territory occupancy increased by 7.1% annually at low elevations and by 4.2% at high elevations (the slope parameters did not differ significantly; Wald-test, p = 0.144).

Long-term territory monitoring also showed a moderate increase in the number of overlapping territories (Figure 4; goodness-of-fit LR = 241.09, df = 496, p = 1.00). This increase amounted to 11.0% annually and was statistically significant ($p<0.05$). The annual increase at low elevations was 10.8%, while at high elevations it was 11.3%. However, the difference between them was not significant (Wald-test, p = 0.89). The log-linear trend model estimated for unoccupied territories (goodness-of-fit LR = 334.3, df = 564, $p<0.05$) decreased moderately (9.0% annual decrease; Figure 4), with no significant difference between elevations (below 700 m a.s.l.: 6.2% annual decrease, above 700 m a.s.l.: 9.8% annual decrease; Wald-test, p = 0.14).

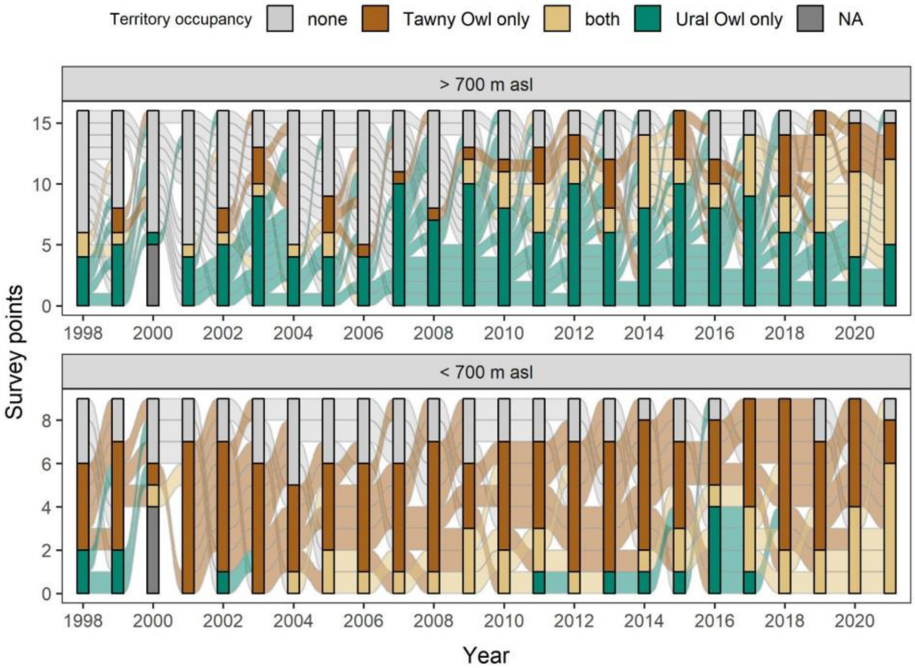

Figure 3: Territory occupancy of the Tawny Owl and Ural Owl in the period 1998-2021 at high and low elevations on Mt. Krim.

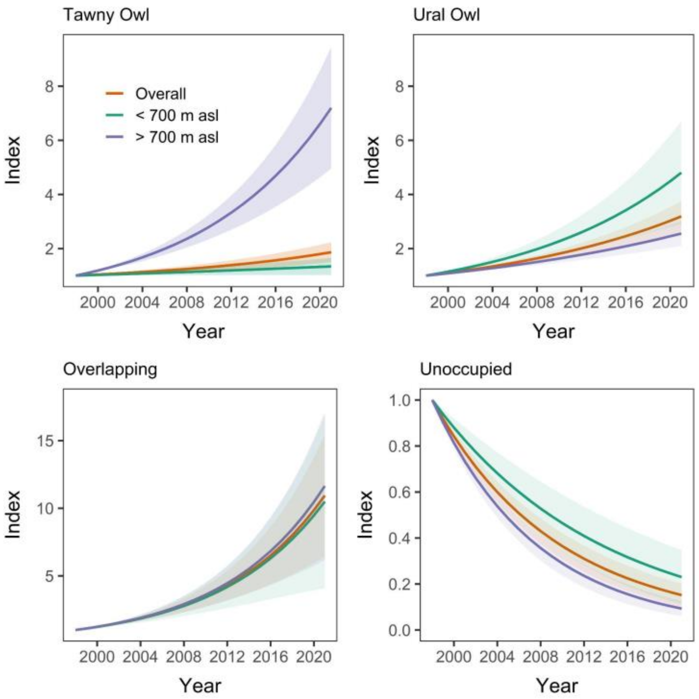

Figure 4: Model-based indices illustrating Tawny and Ural Owl territory occupancy, both overall and within two different elevational belts. The same representation is provided for overlapping territories (category "both") and unoccupied survey points (category "none"). Shaded areas represent standard errors. The first year, 1998, was chosen as the base year.

4.1.3.2 Breeding dynamics

In total, the Tawny Owl occupied a nest box 3.3 years (median = 3) after it was first set up, while the Ural Owl took 4.9 years on average (median = 3). However, these nest-box occupancy time-lags differed in both species before and after 2010 (Figure 5). Prior to 2010, the Tawny Owl occupied a nest box after 4.6 years on average, while after 2010, this time-lag was only 2.2 years on average (mean difference of -2.5, 95% CI = -4.8 to -0.9). Similarly, the time-lag for the Ural Owl decreased from 7.1 years before 2010 to 2.5 years on average after 2010 (mean difference of -4.6, 95% CI = -8.0 to -2.1). The overall minimum time-lag in nest-box occupancy by either of the species was one year. Throughout the study, the Tawny Owl nested in 35 different nest boxes, while the Ural Owl occupied 24. Additionally, in six nest boxes, the owl species alternated in different years. The Tawny Owl dominated nest boxes at low elevations and the Ural Owl at high elevations (Figure 6). The first cases of nest boxes being shared by both species in different breeding seasons occurred in 2012, and the proportion of shared nest boxes was higher above 700 m a.s.l. (Figure 6).

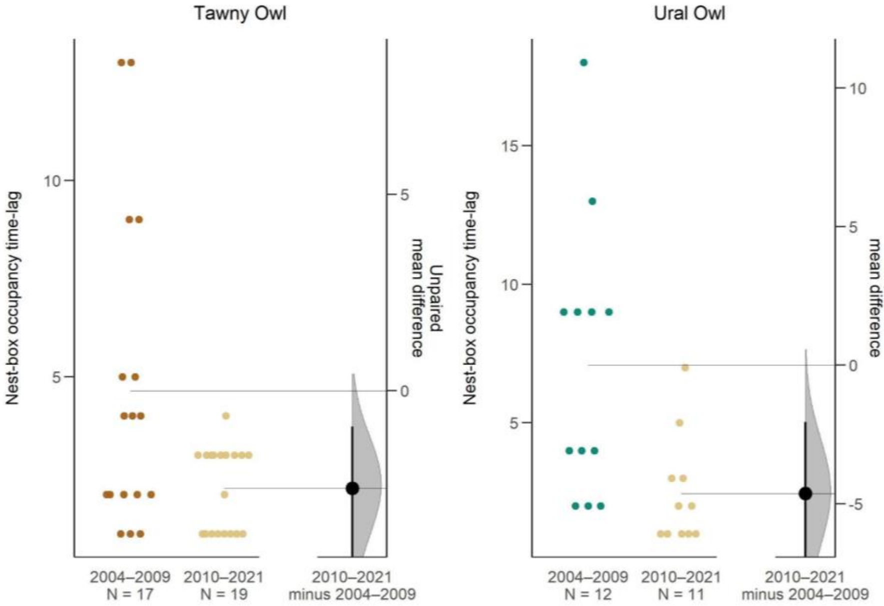

Figure 5: The effect size illustrating the differences in the time-lag of nest-box occupancy from its set up before and after 2010 by Tawny and Ural Owls. The left panel in each plot shows raw data for each group (before or after 2010), with the horizontal line indicating the group mean. In the right panel, the bold black dot and vertical ticks represent the mean difference and the associated 95% confidence interval, respectively. The shaded curve represents the sampling-error distribution, all derived from 5,000 bootstrapped resamples.

We recorded 32 cases of nesting in overlapping territories. At low elevations, 93% of the nest boxes occupied by the Tawny Owl were in overlapping territories. In contrast, at high elevations only 28% of nest boxes occupied by the Tawny Owl in were overlapping territories. In seven nest boxes, the breeding species was displaced by the competitive species, and in six of these cases, the Ural Owl displaced the Tawny Owl. In three cases, the displacement of the Tawny Owl was direct, in the same breeding season (in 2017, 2019 and 2020, in two different nest-boxes), where the Ural Owl took over the nest and clutch of the Tawny Owl. In two of three nesting attempts, one Tawny Owl chick was hatched and raised by the Ural Owl (Figure 7). In 2019, we found that the Ural Owl parents cared for a radio-tagged Tawny Owl fledgling even after it left the nest box. The fledgling was still alive and in good condition at the age of 83 days, or 54 days after leaving the nest.

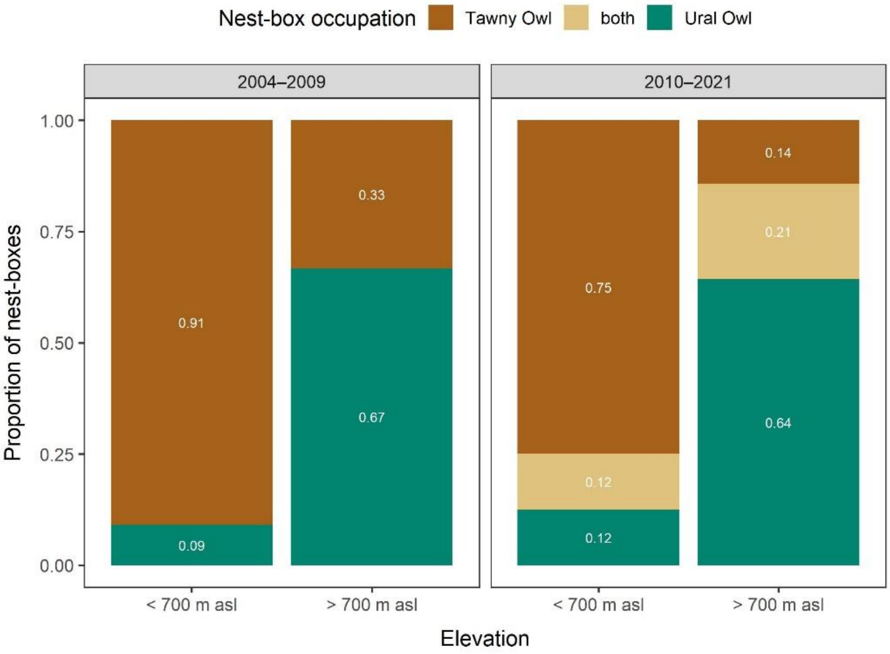

Figure 6: Proportions of nest boxes occupied by either the Tawny or Ural Owl, or by both, during periods before and after 2010 and at low (<700 m a.s.l.) and high (>700 m a.s.l.) elevations.

Figure 7: Ural (left) and Tawny Owl young (right) raised in the same Ural Owl nest at Mt. Krim in 2017.

Female Tawny Owls nesting at high elevations had significantly larger heads (mean = 74.8 mm) than females nesting at low elevations (mean = 72.8 mm). The mean difference was 2.04 mm (95% = 0.9 mm to 3.8 mm, Figure 8A). In Ural Owls, no such significant difference in the head length of females at high elevations (84.1 mm) compared to low elevations (84.7 mm) was found (mean difference of -0.6 mm, 95% CI = -2.2 mm to 0.9 mm, Figure 8B). In both species and at all elevations, the combined mean head length of incubating females on overlapping territories was greater than on territories without the competing owl (Figure 8). In Tawny Owls, the mean head length on overlapping territories was 73.6 mm and similar to 72.8 mm in the absence of the Ural Owl (mean difference of 0.8, 95% CI = -0.4 to 2.6; Figure 8C). In Ural Owls, however, the mean head length in overlapping territories was significantly larger (84.6 mm) compared to the territories without the Tawny Owl (83.5 mm; mean difference of 1.1, 95% CI = 0.0 to 2.1; Figure 8D). No significant differences in female body mass (Figure S1) or wing length (Figure S2) between elevations or in the absence/presence of the territorial interspecific competitor owl were found. In both studied species, clutch and brood size did not differ significantly in the presence of the territorial interspecific owl competitor near the nest (Figure S3).

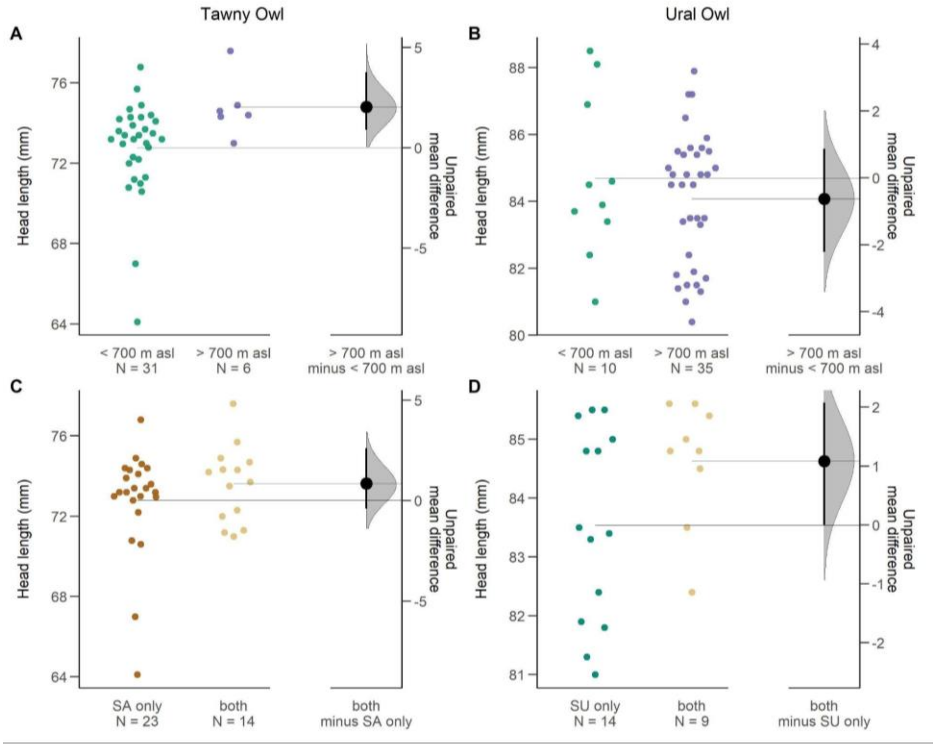

Figure 8: Differences in incubating female head length in Tawny and Ural Owls at different elevations (A and B) and in the absence/presence of the territorial interspecific competitor owl (C and D). The left panel in each plot shows raw data for each group, with the horizontal line representing the group mean. The bold black dot and vertical ticks in the right panel indicate the mean difference and the associated 95% confidence interval, respectively. The shaded curve represents the sampling-error distribution, all derived from 5,000 bootstrapped resamples.

4.1.4 Discussion

Our results are in line with the model forecasts of Brambilla et al. (2020), who predicted that climate change would increase the population size of Tawny and Ural Owls in montane temperate forests in South Central Europe. This concurrent population increase was reflected in a gradual increase in Ural Owl territories towards saturation in high-elevation forests and their expansion into low-elevation forests already saturated with Tawny Owl territories. On the other hand, the growth of the Tawny Owl population primarily resulted from the colonization of high-elevation forests that were traditionally occupied only by the Ural Owl (Vrezec & Tome 2004b). Brambilla et al. (2020) speculated that these changes would probably amplify the importance of interaction effects for these species at the regional scale. Our long-term data revealed that this concurrent population increase indeed intensified interactions, particularly the competition for nest sites, which are typically a limiting habitat structure for large tree-hole nesting owls (Lõhmus 2003). This competition led to direct nest displacements of the smaller Tawny Owl by the larger Ural Owl. However, these increased interspecific interactions did not appear to affect reproductive success, but rather promote micro-evolutionary changes in size due to altered selection pressures, as has been observed in insectivorous tits (Dhondt 2012).

4.1.4.1 Concurrent population increase of large *Strix* owls

The previously well-defined elevational segregation between Tawny and Ural Owls (Vrezec 2003, Vrezec & Tome 2004a, b) has recently become less distinct due to the robust population growth of both species. For the Tawny Owl, harsh winter conditions and interspecific competition have been found to be the primary factors limiting its distribution (Francis & Saurola 2004, Sasvári & Hegyi, 2005, Sunde, 2005; Sergio et al., 2007, Pavón-Jordán et al., 2013). Winter climate affects the physiological condition and breeding productivity of both *Strix* owls. Snow cover in particular affects the availability of small mammalian prey (Jedrzejewski et al. 1994; Solonen & Karhunen 2002; Solonen 2022). It serves as protection for ground small mammals during winter, making them less accessible to predators (Sasvári & Hegyi 1998, Solonen & Karhunen 2002). However, the Ural Owl is known to be able to detect and prey upon voles beneath snow cover, provided the cover is not too deep and there is no ice crust (Sonerud 1986; Korpimäki & Sulkava 1987, Suzuki et al. 2013). No such foraging behaviour has been described in the Tawny Owl. In harsh winters, it shifts its diet towards alternative prey, primarily birds (Sasvári & Hegyi 1998, Sasvári & Hegyi 2011), but also small mammals of open habitats (Yatsiuk & Filatova 2017). It tends to hunt in areas with thinner snow cover (Sunde et al. 2001), and extended snow cover periods could increase mortality within its population (Solheim 2009; Pavón-Jordán et al., 2013). At higher latitudes and elevations where winter conditions are more extreme, the larger Ural Owl frequently outcompetes the Tawny Owl (Korpimäki 1986; Vrezec & Tome 2004b). However, global warming has facilitated the expansion of the Tawny Owl, a food and habitat generalist (Ratajc et al. 2023), because milder winter conditions increase its competitive advantage against the larger Ural Owl. Its expansion has been observed not only towards higher elevations (Brambilla et al. 2020, this study), but also to higher latitudes (Sunde et al. 2001; Francis & Saurola, 2004, Grandans et al. 2009). We suggest that this expansion has been made possible by milder winters (Figure 1B).

Conversely, our results show that the Ural Owl is also expanding its population, particularly in low-elevation forests. The formation of territories in areas not previously inhabited by the species has also been observed in East-Central Europe (Bashta, 2009;

Kopij, 2011; Wasiński et al. 2022). Similarly, in Italy and Austria, the Ural Owl is expanding at the southwestern border of its Alpine range (Kleewein & Malle 2020, Vrezec et al. 2020). There are at least two possible explanations for this. It could be a consequence of growing and expanding populations in nearby montane forests (Kopij, 2011; Wasiński et al. 2022) or a positive response to a diminishing limiting factor, such as the availability of the main prey. Beech seeds are a key food source for small mammals in temperate mixed forests (Nopp-Mayr et al. 2012), and small mammal populations are able to respond to increased resource availability very rapidly (Jensen 1982; Pucek et al. 1993). Evidence from several studies suggests that in recent decades the mast frequency in European Beech, a major forest-forming tree in temperate Europe, has increased (Hacket-Pain & Bogdziewicz 2021). Masting cycles regulate seed predator abundances by satiation and starvation, and changes in mast seeding patterns may disrupt this regulation (Bogdziewicz et al. 2020). Both *Strix* owls respond positively to small mammal population peaks in terms of breeding productivity (Brommer et al. 2002; Lehikoinen et al. 2011; Luka & Riegert 2018; Ratajc et al., 2022). Increased breeding frequency and productivity could lead to positive long-term trends in owl population densities (Saurola & Francis 2018). Additionally, better prey availability could result in smaller territories (Schoener, 1968, Zabel et. al., 1995), facilitating increased territory densities and lower near-neighbour distances.

4.1.4.2 Intensification of interspecific interactions

The increasing territory density in both coexisting *Strix* species has led to an intensification of interspecific interactions. This is reflected in the increased proportion of overlapping territories at both high and low elevations. On the other hand, unoccupied territories without detected territorial owls, which represented half of all territories at the beginning of the study period (53.1% on average in the first 5 years), almost vanished by the end of the study (8.0% on average in the last 5 years; Figs. 3, 4). The upward trajectory of the number of owl territories was also reflected in nest-box occupancy time-lags, which were significantly shorter in the last years of the study period. This suggests a substantial demand for increased owl populations to secure suitable nest sites. Our results revealed that as both owl populations concurrently increased, competition for nest sites intensified. In the first half of the study period, when population density was low, no nest displacements were recorded. However, in the second half of the study period, nest displacements, i.e. shared nest sites occupied by different owl species in different years, occurred at both high and low elevations (Fig. 6). Nearly half of these displacements (43%) were direct, where the larger Ural Owl took over the nest box already occupied by Tawny Owl in the same season. In two cases, the Ural Owl even assumed care for the existing Tawny Owl clutch and incubated it with its own eggs. Nonetheless, despite the emergence of overlapping territories and increased interference interactions, clutch sizes did not decrease in either species (Fig. S3). This supports the assumption that clutch size is more affected by prey availability than actual competitor presence (Ratajc et al. 2022).

Such close coexistence and intensified interactions could potentially alter selection pressures and even have evolutionary consequences by favouring individuals better adapted to competition (Burton et al. 2010, Cadotte 2017, Carroll et al. 2023). At the interspecific level, these changes could result in (1) an increased likelihood of disease transmission, potentially leading to new zoonotic outbreaks due to more frequent direct contact between the two species, (2) a higher frequency of hybridization and (3) morphological changes of coexisting individuals. While diseases have been relatively less studied in owls, current studies have shown instances of differential susceptibility to herpesvirus that infects the Ural but not the Tawny Owl (Žlabravec et al. 2021). Closer contacts between species increases the potential of parasite transmissions to new hosts, especially if they are closely related, possibly leading to novel epidemic zoonoses (Gailbreath & Oaks 2008, Cunningham et al. 2017).

Mixed clutches are often observed in hole-nesting species, particularly when competition for nesting sites is severe (Shy 1982). Since sexual imprinting in nestlings plays such an important role in the development of mating preferences (Cate & Vos 1999), individuals from mixed clutches could potentially prefer the foster parent species (Bird et al. 1985), potentially leading to increased hybridization. So far, fertile Ural-Tawny Owl hybrids have only been documented in captivity (Scherzinger 2017, McCarthy 2006). Morphologically distinctions can be made at the F1 generation, but they become much less apparent in later generation crossbreeds in one of the species lines (Scherzinger 2017). Therefore, genetic studies of wild owl populations in sympatric areas are needed to reveal the level of natural hybridization (Haig et al. 2004) and to reveal the evolutionary implications of hybridization in contact zones between the Ural and Tawny Owl, particularly in rapidly changing environments that might even increase the adaptive potential of the species (Chan et al. 2019).

Micro-evolutionary morphological effects of competition have been described in tits, which compete for nest sites in a manner akin to owls. For instance, in the case of tits, the smaller Blue Tit *(Cyanistes caeruleus)* coexisting in high densities with its larger competitor, the Great Tit *(Parus major)*, gradually increased in size (Dhondt 2012). In our study, we have found that female Ural Owls inhabiting overlapping territories with Tawny Owls had larger heads than females from non-overlapping territories. Additionally, higher elevations, which are typically dominated by Ural Owls, were colonized by larger breeding female Tawny Owls. However, the presence of larger Tawny Owls at higher elevations could also be attributed to individuals at the expanding front, which are generally larger (Aulus-Giacosa et al. 2021), and might not necessarily reflect the effects of competition with the Ural Owl. This could explain why, overall, we did not find a difference in size of Tawny Owls between overlapping territories and non-overlapping territories. Unlike the findings in tits (Dhondt 2012), we found a clear increase in size among the larger rather than the smaller competitor in owls. The Ural Owl has two main advantages over the Tawny Owl: better adaptation to harsh winter conditions and a larger body size (Vrezec 2003; Francis & Saurola 2004, Sasvári & Hegyi, 2005; Lehikoinen et al., 2011, Pavón-Jordán et al., 2013). However, the advantage of effectively coping with adverse weather in winter is apparently diminishing due to global warming. Therefore, larger body size could become the decisive factor in this competitive interaction. According to Cope's rule, natural selection pressures in strong competitive environments favour larger and more competitive dominant individuals (Brown & Maurer 1986). As shown, the increasing density of Tawny Owls at higher elevations in the core of the Ural Owl population is comprised of larger individuals at the expansion front. This, in turn, further intensifies competitive pressure on Ural Owls, since larger female Tawny Owls are expected to be better defenders of their nest-sites. We also found similar size differentiation patterns between Ural Owl populations that are sympatric or allopatric to the Tawny Owl. Ural Owl size does not follow Bergmann's rule, where larger individuals are expected in the north (Norberg 1987), but depends on the presence or absence of the Tawny Owl. Populations allopatric to the Tawny Owl are at least 10% smaller than those in sympatric populations, regardless of latitude. Since a similar pattern is not evident in the Tawny Owl (Table 1), this might indicate that the Tawny Owl has an overall impact on Ural Owl size through intensive interspecific interactions, which selects for larger and competitively more successful Ural Owl individuals.

Table 1: Ratio of wing length (calculations based on minimum and maximum values per subspecies) between allopatric and sympatric (allopatric:sympatric) populations of Tawny Owl *(Strix aluco)* and Ural Owl *(Strix uralensis)*. Considered subspecies include: allopatric Tawny Owls (*bidulphi, harmsi, sanctinicolai, sylvatica, wilkonskii*), sympatric Tawny Owls (*aluco, siberiae)*, allopatric Ural Owls (*fuscescens, hondoensis, japonica, nikolskii, yenisseensis)* and sympatric Ural Owls *(macroura, liturata, uralensis)*. Data sources: Kohl 1977, König & Weick 2008.

Species/Sex	Tawny Owl	Ural Owl
Male	1.02 ± 0.10	0.87 ± 0.08
Female	1.03 ± 0.11	0.90 ± 0.07

4.1.4.3 Conclusions

To our knowledge, we have described the first micro-evolutionary example in top predators driven by intensified intraguild interactions enhanced by climate change. The expansion of both competitive species is expected to continue in the future, with expansion into montane areas towards Western Europe (Brambilla et al. 2020), but probably also to lowland forests, as indicated by studies in Eastern Europe (Bashta, 2009; Bylicka et al. 2010; Kopij 2011; Vrezec, 2019). Our study has revealed that the concurrent increase in populations has altered the competitive environment for both predators, leading to increasing body size at least in larger Ural Owl females. From an evolutionary-ecological perspective, this could enhance the Ural Owl's dominance over the Tawny Owl. However, it could also pose long-term risks for the Ural Owl by increasing viability costs, as large size demands higher energy intake and reduces agility (Blanckenhorn 2000). This could result in lower hunting success in habitats dominated by mice, which are more agile and better equipped to evade owl capture compared to voles (Derting & Cranford 1989). For example, the large Great Grey Owl *(Strix nebulosa)*, a vole specialist, can only thrive in highly productive vole-dominated boreal forests (Korpimäki 1986, Sulkava & Huhtala 1997), showing great nomadism in response to vole population fluctuations (Solheim & Stefansson 2016). In contrast, the Ural Owl is a sedentary species with low dispersal power (Saurola & Francis 2004, Valkama et al. 2014). Thus, a further increase in its body size might lead to extinction (McLain 1993) rather than competitive dominance, at least in the southern range of its current expansion (see also long-term predictions in Huntley et al. 2007). The ecological effects of microevolutionary morphological changes under intensified biotic interactions driven by rapid climate change therefore require more attention in future studies (Turbek et al. 2023).

Top predators have been recognized as indicators or even generators of high biodiversity (Sergio et al. 2005) through complex ecosystem interactions with both prey and non-prey species, i.e. predator-mediated species coexistence or the introduction of new indirect interactions between coexisting species (Hakkarainen & Korpimäki 1996, Bonsall & Hassell 1997, Tokeshi 1999, Vrezec & Tome 2004a). We have shown that recent climate changes are also inducing rapid changes in top predator assemblages, which is just the tip of the iceberg in terms of our understanding of establishment of new ecosystem dynamics. In addition to model predictions, there is an urgent need for robust long-term monitoring data to capture the actual changes taking place in altering ecosystems and to reveal hidden and trait-based adaptations of coexisting species and unforeseen extinction drivers (Dornelas et al. 2014). Therefore, comprehensive and integrated monitoring programs that include continuous measurements of species traits, demography, evolutionary adaptations and interaction dynamics at multiple trophic levels are urgently needed for advancing science, promoting biological conservation and fostering sustainable development (Arneth et al. 2020).

4.1.5 References

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Chapter 5

Conclusions

In the thesis, we presented aspects of Tawny Owl ecology that could enhance its use as an indicator species. Tawny Owl was previously identified as a suitable sentinel species (Badry et al., 2020), and we argue that Tawny Owl could also reflect the population state of its prey species, competitors and potentially some other environmental changes. Our research emphasizes the value of long-term data and monitoring schemes by demonstrating how climate-induced changes at different trophic levels can reflect at the level of an apex predator. Studies unraveling the complexity of interactions in communities based on trait studies of indicator species can provide invaluable key information for management on issues such as setting objectives for protected areas, predicting and controlling invasion of a certain species, or minimizing risks for contamination issues and disease outbreaks (Begon et al., 2006).

In this chapter, we summarize the main scientific contributions of the dissertation and outline several directions for further work.

5.1 Contributions to Science

We found considerable variation in availability of published and unpublished contextual data across Europe and several spatial knowledge gaps about the species ecology and biology. Our study is the first in evaluating different Tawny Owl traits on a large, continent- wide scale. Our findings led to the proposal of a minimal recommended scheme for monitoring of Tawny Owl population contextual data as one of the first steps toward a pan-European monitoring. The scheme would not only provide crucial data to improve interpretation of biomonitoring results, but also indicate population status and other essential information for overall conservation assessments.

We have shown that despite diverse small mammal assemblage in Dinaric forests the predator responses are governed only by one dominant small mammal species. Additionally, we described how Tawny Owl and coexisting predators do not respond to small mammal fluctuations equally, but that there are marked differences in sensitivity among the species. The Tawny Owl was found to be the most adapted species with respect to small mammal fluctuations in temperate mixed forests. In general, the boreal type predators appeared to be more sensitive to prey fluctuations than Tawny Owl, a temperate predator. The novelty of research is that we provided completely new insights into the owl-small mammal interactions, which were so far studied mainly in boreal forests and not in southern temperate mixed forests, from where such studies were lacking. The owl differential responses could define their population dynamics and range expansion/shift patterns in the changing environment (Avotins et al., 2023; Brambilla et al., 2020).

We analyzed long-term data on territory and nest-box occupancy to explore the trends and gradual changes in competitive dynamics between Tawny and Ural Owl. Our results are in line with the modelled forecasts of Brambilla et al. (2020), who predicted that climate change would increase the population size of both species in South Central Europe. We were the first to explore in the field whether there are already some noticeable changes in the long-term population trends in the area. Our data also revealed an increasing potential for hybridization between the species because of direct displacements in the nests. Against expectations, we did not find any effects of the breeding success, but our results do suggest micro-evolutionary changes in size due to changed selection pressures. Not only does Ural Owl not follow the Bergmann's rule (Norberg, 1987), its size may depend on the presence or absence of the Tawny Owl, meaning the subordinate species in the guild, not the dominant one, is intensifying the competitive pressure and consequently the selection of larger individuals in both species. In evolutionary-ecological perspective, this could enhance Ural Owl's dominance over Tawny Owl. On the other hand, it could pose certain long-term risks for the Ural Owl by increasing viability costs since large size demands higher energy intake and reduces agility (Blanckenhorn, 2000). This could reflect in lower hunting success in mice-dominated habitats, since mice tend to be more agile than voles and are better equipped to evade owl capture (Derting & Cranford, 1989). To our knowledge, we described the first known micro-evolutionary example in top predators driven by intensified intraguild interactions enhanced by climate change.

5.2 Further Work

Our findings represent a good foundation for further research on Tawny Owl populations and its interactions in a community. The review of its ecological traits offers numerous new starting points for detailed studies of individual traits and integrative research on correlations between them under the influence of environmental change. For example, the results revealed that Tawny Owl population trend, natal and breeding dispersal, genetic variation, range change, eggshell thickness and post-breeding dispersal are among the most understudied parameters. The proposed minimal monitoring scheme is an attempt to harmonize monitoring methods, to initiate or enhance existing monitoring schemes, fill in the spatial gaps and to ensure that the long-term collection of data could be used in multiple large-scale studies related to the biology and ecology of the Tawny Owl. There are still many steps to take before we reach a functional pan-European monitoring scheme.

A broader continental-scale approach is also urgently needed in future studies to reveal some general patterns in the ecology of other forest owls and small mammals. As climate change influences primary production, keystone herbivores (including voles) and consequently, apex predators, we need to understand their interactions to effectively predict the outcomes and adjust the management and conservation actions accordingly. Small mammal cycles affect not only the intraspecific interactions of their predators, but also the interspecific interactions and population dynamics in the predator guild. For example, our results revealed a particular sensitivity of the Boreal Owl to cyclic food availability. As this species is also subjected to intraguild predation by competitive owls, especially Tawny Owl, with which the range overlap is predicted to increase significantly (Brambilla et al., 2020), this threatened species might be facing some major challenges in the changing environment in the future. Our results agree with predictions that Tawny Owl populations are expanding towards higher elevations, which so far suited Boreal Owl the most; temperature and habitat-wise (Brambilla et al., 2020; Vrezec, 2003). A large-scale research is needed to evaluate the capacity of low-elevation forests in Central and

Southern Europe to sustain a viable population of Boreal Owl under ongoing climate change.

The size difference in Tawny and Ural Owl under the influence of climate-driven intensification in intratrophic competition is one of the major findings of this thesis and calls for additional research. In buzzards, the predation risk by goshawks is reduced in more southern latitudes where they have more similar body sizes (Rebollo et al., 2017). Will the intraguild predation effects disappear with increasingly smaller difference in the size of Tawny and Ural Owl individuals too (Sergio & Hiraldo, 2008)? Additional studies of microevolutionary morphological or physiological changes driven by environmental change and their ecological effects are urgently needed. We also still need to confirm and describe in detail the mechanistic drivers of population increase in both species. Is movement of individuals important in the process? How heritable is body size as a trait? What is the effect of longevity in both species in terms of microevolution? These are just a few of the questions that still need to be answered and would require a much larger sample size.

No effects of competition on breeding success were found, but this is a trait that should be studied further. After all, as Pianka (2011) said “The only currency of natural selection is differential reproductive success”. Further increase in body size in Tawny Owl might bring a new advantage in tolerating adverse winter conditions, since larger individuals are more capable of storing fat (Overskaug et al., 1997). In Ural Owl, however, increasing body size and increasing viability costs (Blanckenhorn, 2000) could be proportionately disadvantageous. Since the female body condition in spring is of crucial importance for breeding productivity (Lamarre & Franke, 2017; Pietiainen & Kolunen, 1993; Solonen, 2011), we might still expect some productivity and population changes in the near future.

The risks of increasing hybridization also remain an open question. A genetic research could help assess the magnitude of interspecific gene flow and its trend. More fieldwork is needed to answer at least some of the following questions: (1) to what degree do the young birds from mixed broods imprint on vocal cues and calls of the foster parents; (2) when reaching maturity, do they tend to pair with an individual of its own species or individual of foster family species; (3) are the potential hybrids fertile; (4) how do intensified interactions between competitive species impact disease transfer. In general, the knowledge on diseases in owls is still quite limited (but see Žlabravec et al., 2021). Displacements from nest-boxes mean increasing instances of close contact between the species, therefore we should also pay more attention to the danger of disease transmission and possible novel epidemic zoonoses.

The effects of global change are complex and understanding or predicting the consequences demands excellent knowledge of the indicator species role in the ecosystem and the dynamics of its interactions in the community. Therefore, additional research of Tawny Owl interactions with a multritrophic approach needed – one that would include other forest predators (e.g. mustelids), other prey groups (e.g. birds), and lower trophic levels (e.g. ground beetles). The primary focus of multitrophic interactions research is to understand the characteristics of organisms that influence non-adjacent trophic levels and to determine the relative importance of bottom-up and top-down effects (van Nouhuys & Hanski, 2008). Such multitrophic predictive models could thus even further improve predictions of species distribution, population trends and community response under future climate change.

Appendix A

The Importance of Population Contextual Data for Large-Scale Biomonitoring Using an Apex Predator: The Tawny Owl (*Strix aluco*) – Supplementary Data

Table A.1: Categorisation by trophic level of the mammal species found in the diet of European Tawny Owls according to the literature review (see Methods section).

Family	Species/Taxa	Category
Cricetidae	*Alexandromys oeconomus*	herbivore
Cricetidae	*Arvicola amphibius* (= *Arvicola terrestris*)	herbivore
Cricetidae	*Arvicola sapidus*	herbivore
Cricetidae	*Chionomys nivalis*	herbivore
Cricetidae	*Clethrionomys glareolus*	herbivore
Cricetidae	*Clethrionomys rufocanus*	herbivore
Cricetidae	*Cricetulus migratorius*	herbivore
Cricetidae	*Dinaromys bogdanovi*	herbivore
Cricetidae	*Lemmus lemmus*	herbivore
Cricetidae	*Microtus agrestis*	herbivore
Cricetidae	*Microtus arvalis*	herbivore
Cricetidae	*Microtus cf. socialis*	herbivore

Cricetidae	*Microtus guentheri*	herbivore
Cricetidae	*Microtus liechtensteini*	herbivore
Cricetidae	*Microtus lusitanicus*	herbivore
Cricetidae	*Microtus multiplex*	herbivore
Cricetidae	*Microtus rossiaemeridionalis*	herbivore
Cricetidae	*Microtus subterraneus*	herbivore
Cricetidae	*Microtus tatricus*	herbivore
Cricetidae	*Nothocricetulus migratorius*	omnivore
Dipodidae	*Sicista betulina*	omnivore
Erinaceidae	*Erinaceus concolor*	insectivore
Erinaceidae	*Erinaceus europaeus*	insectivore
Gliridae	*Dryomys nitedula*	omnivore
Gliridae	*Eliomys quercinus*	omnivore
Gliridae	*Glis glis*	herbivore
Gliridae	*Muscardinus avellanarius*	herbivore
Leporidae	*Lepus europaeus*	herbivore
Leporidae	*Lepus timidus*	herbivore
Leporidae	*Oryctolagus cuniculus*	herbivore
Leporidae	Non-identified Leporidae	herbivore
Muridae	*Acomys cahirinus*	omnivore
Muridae	*Acomys dimidiatus*	omnivore
Muridae	*Apodemus agrarius*	omnivore
Muridae	*Apodemus cf. uralensis*	omnivore
Muridae	*Apodemus flavicollis*	omnivore
Muridae	*Apodemus mystacinus*	omnivore
Muridae	*Apodemus* spp.	omnivore
Muridae	*Apodemus sylvaticus*	omnivore
Muridae	*Apodemus witherbyi*	omnivore

Muridae	*Dipodillus dasyurus*	omnivore
Muridae	Subfamily Gerbillinae	omnivore
Muridae	*Meriones sacramenti*	herbivore
Muridae	*Meriones tristrami*	herbivore
Muridae	*Micromys minutus*	omnivore
Muridae	*Mus cf. domesticus*	omnivore
Muridae	*Mus cf. macedonicus*	omnivore
Muridae	*Mus cf. musculus*	omnivore
Muridae	*Mus spretus*	omnivore
Muridae	*Rattus norvegicus*	omnivore
Muridae	*Rattus rattus*	omnivore
Muridae	Non-identified Muridae	omnivore
Mustelidae	*Martes martes*	carnivore
Mustelidae	*Mustela nivalis*	carnivore
Sciuridae	*Sciurus vulgaris*	herbivore
Soricidae	*Crocidura leucodon*	insectivore
Soricidae	*Crocidura russula*	insectivore
Soricidae	*Crocidura* spp.	insectivore
Soricidae	*Crocidura suaveolens*	insectivore
Soricidae	*Neomys anomalus*	insectivore
Soricidae	*Neomys fodiens*	insectivore
Soricidae	*Neomys* spp.	insectivore
Soricidae	*Neomys teres*	insectivore
Soricidae	*Sorex alpinus*	insectivore
Soricidae	*Sorex araneus*	insectivore
Soricidae	*Sorex coronatus*	insectivore
Soricidae	*Sorex minutus*	insectivore
Soricidae	*Sorex* spp.	insectivore

Soricidae	*Suncus etruscus*	insectivore
Spalacidae	*Nannospalax ehrenbergi*	herbivore
Talpidae	*Talpa caeca*	insectivore
Talpidae	*Talpa europaea*	insectivore
Talpidae	*Talpa* spp.	insectivore
	Non-identified bats (Order Chiroptera)	insectivore
	Non-identified shrews/moles (Order Eulipotyphla; = Insectivora)	insectivore

Table A.2: A list of fitted models and the abbreviations/names used for each. lat - latitude, lon - longitude, x - dependent variable (see the list in Table 3), s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

Model name	formula
M0	gam(x ~ 1)
M1	gam(x ~ lat + lon)
M2	gam(x ~ s(lat) + lon)
M3	gam(x ~ lat + s(lon))
M4	gam(x ~ s(lat) + s(lon))

Table A.3: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the numeric percentage of mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M1	3	0.0268	3.35	-1300.592	2609.3	0.00	0.247
M2	4	0.0268	3.35	-1300.592	2609.3	0.01	0.246
M3	4	0.0268	3.35	-1300.591	2609.3	0.01	0.246
M4	4	0.0268	3.35	-1300.592	2609.3	0.01	0.247
M0	2	0	0	-1305.562	2615.2	5.84	0.013

Table A.4: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the numeric percentage of mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M1		Estimate	SE	t	p	p signif.
	intercept	33.08699	11.09521	2.982	0.00311	**
	lat	0.69469	0.22056	3.150	0.00181	**
	lon	0.07078	0.13768	0.514	0.60760	
M2		Estimate	SE	t	p	p signif.
	intercept	66.69485	2.45473	27.170	< 0.001	***
	lon	0.07078	0.13768	0.514	0.608	
		edf	Ref.df value	F	p	p signif.
	s(lat)	1.002	1.004	9.886	0.00183	**
M3		Estimate	SE	t	p	p signif.
	intercept	34.1867	10.7412	3.183	0.00162	**
	lat	0.6946	0.2206	3.149	0.00181	**
		edf	Ref.df	F	p	p signif.
	s(lon)	1.003	1.006	0.261	0.61	
M4		Estimate	SE	t	p	p signif.
	intercept	67.789	1.224	55.39	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.001	1.003	9.896	0.00182	**
	s(lon)	1.000	1.000	0.264	0.60777	

Table A.5: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the biomass percentage of mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc − second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M1	4	0.0395	6.65	-306.005	620.6	0.00	0.210
M2	4	0.0395	6.65	-306.005	620.6	0.00	0.210
M3	4	0.0395	6.65	-306.005	620.6	0.00	0.210
M4	4	0.0395	6.65	-306.005	620.6	0.00	0.210
M0	1	0	0	-308.483	621.1	0.53	0.161

Table A.6: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) numeric percentage of birds in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc − second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M2	9	0.078	9.84	-368.342	756.6	0.00	0.541
M4	10	0.0789	10.0	-368.055	757.2	0.59	0.402
M1	3	0.036	4.27	-377.102	762.3	5.76	0.030
M3	5	0.0423	5.21	-375.662	762.6	5.98	0.027
M0	2	0	0	-383.467	771.0	14.39	0.000

Table A.7: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) numeric percentage of birds in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M2		Estimate	SE	t	p	p signif.
	intercept	1.903041	0.103013	18.474.	< 0.001	***
	lon	0.021785	0.005804	3.753	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	5.433	6.59	2.039	0.0691	
M4		Estimate	SE	t	p	p signif.
	intercept	2.23975	0.05062	44.25	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	5.387	6.536	1.930	0.08919	
	s(lon)	1.334	1.597	7.708	0.00113	**

Table A.8: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) biomass percentage of birds in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M0	2	0	0	-103.187	210.5	0.00	0.332
M1	4	0.0137	4.14	-101.663	211.9	1.38	0.167
M2	4	0.0137	4.14	-101.663	211.9	1.38	0.167
M3	4	0.0137	4.14	-101.663	211.9	1.38	0.167
M4	4	0.0137	4.14	-101.663	211.9	1.38	0.167

Table A.9: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) numeric percentage of invertebrates in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M4	11	0.213	23.3	-442.943	909.3	0.00	0.595
M2	9	0.201	21.8	-445.723	910.6	1.31	0.309
M3	7	0.187	19.9	-449.223	913.0	3.76	0.091
M1	3	0.159	16.5	-455.305	918.7	9.46	0.005
M0	2	-2.22e-16	0.00	-481.645	967.3	58.05	0.000

Table A.10: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) numeric percentage of invertebrates in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - p < 0.05, ** - p < 0.01, *** - p < 0.001), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M4		Estimate	SE	t	p	p signif.
	intercept	1.8631	0.0655	28.44	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	4.936	6.031	8.795	< 0.001	***
	s(lon)	2.536	3.179	3.088	0.0259	*
M2		Estimate	SE	t	p	p signif.
	intercept	2.127948	0.134025	15.88	< 0.001	***
	lon	-0.017138	0.007548	-2.27	0.0239	*
		edf	Ref.df	F	p	p signif.
	s(lat)	5.154	6.283	11.09	< 0.001	***

Table A. 11: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) biomass percentage of invertebrates in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M3	6	0.164	20.5	-70.155	153.7	0.00	0.526
M4	6	0.171	21.6	-69.670	154.5	0.82	0.350
M1	3	0.073	9.91	-74.674	157.9	4.21	0.064
M2	4	0.0802	1.11	-74.186	158.6	4.83	0.047
M0	2	0	-1.91e-14	-78.430	161.0	7.30	0.014

Table A.12: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) biomass percentage of invertebrates in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M3		Estimate	SE	t	p	p signif.
	intercept	1.83934	0.68717	2.677	0.00933	**
	lat	-0.02622	0.01421	-1.845	0.06939	
		edf	Ref.df	F	p	p signif.
	s(lon)	2.512	3.146	3.939	0.011	*
M4		Estimate	SE	t	p	p signif.
	intercept	0.57953	0.07773	7.456	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.361	1.630	1.785	0.1231	
	s(lon)	2.523	3.152	3.914	0.0113	*

Table A.13: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) numeric percentage of amphibians in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M2	10	0.29	30.9	-400.367	823.2	0.00	0.5
M4	10	0.29	30.9	-400.367	823.2	0.00	0.5
M3	9	0.245	26.2	-409.830	840.4	17.15	0.0
M1	3	0.202	20.8	-420.297	848.7	25.51	0.0
M0	1	0	0	-454.277	912.6	89.37	0.0

Table A.14: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) numeric percentage of amphibians in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M2		Estimate	SE	t	p	p signif.
	intercept	0.834206	0.115924	7.196	< 0.001	***
	lon	0.028932	0.006544	4.421	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	6.651	7.792	12.51	< 0.001	***
M4		Estimate	SE	t	p	p signif.
	intercept	1.28137	0.05663	22.63	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	6.651	7.792	12.51	< 0.001	***
	s(lon)	1.000	1.001	19.53	< 0.001	***

Table A.15: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) biomass percentage of amphibians in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M3	9	0.607	64.2	-61.961	146.0	0.00	0.479
M4	9	0.607	64.2	-61.961	146.0	0.00	0.479
M2	7	0.556	58.4	-67.350	151.0	4.98	0.040
M1	3	0.489	50.3	-73.783	156.2	10.18	0.003
M0	2	0	-2.16e-14	-98.961	202.1	56.11	0.000

Table A.16: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) biomass percentage of amphibians in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M3		Estimate	SE	t	p	p signif.
	intercept	-2.69820	0.71845	-3.756	< 0.001	***
	lat	0.07602	0.01488	5.110	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lon)	5.331	6.434	2.958	0.00928	**
M4		Estimate	SE	t	p	p signif.
	intercept	0.95481	0.07115	13.42	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.000	1.000	26.100	< 0.001	***
	s(lon)	5.331	6.434	2.958	0.00928	**

Table A.17: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) numeric percentage of reptiles in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M4	10	0.205	22.4	-123.774	269.6	0.00	0.545
M2	8	0.195	21.0	-126.348	269.9	0.38	0.451
M3	7	0.163	17.7	-132.274	279.8	10.24	0.003
M1	3	0.128	13.4	-139.788	287.7	18.15	0.000
M0	2	0	1.38e-14	-160.730	325.5	55.94	0.000

Table A.18: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) biomass percentage of amphibians in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M4		Estimate	SE	t	p	p signif.
	intercept	0.18214	0.02193	8.304	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	3.987	4.928	9.366	< 0.001	***
	s(lon)	2.925	3.643	3.594	0.00784	**
M2		Estimate	SE	t	p	p signif.
	intercept	0.064925	0.044667	1.454	0.14718	
	lon	0.007584	0.002513	3.018	0.00277	**
		edf	Ref.df	F	p	p signif.
	s(lat)	4.335	5.346	11.16	< 0.001	***

Table A.19: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) biomass percentage of reptiles in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M0	2	0	0	-45.305	94.8	0.0	0.313
M1	3	0.0161	4.38	-43.691	96.0	1.2	0.172
M2	4	0.0161	4.38	-43.691	96.0	1.2	0.172
M3	4	0.0161	4.38	-43.691	96.0	1.2	0.172
M4	4	0.0161	4.38	-43.691	96.0	1.2	0.172

Table A.20: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the numeric percentage of herbivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M2	11	0.226	24.4	-1572.171	3168.2	0.00	0.502
M4	11	0.226	24.4	-1572.166	3168.3	0.02	0.498
M3	7	0.17	18	-1587.058	3188.9	20.66	0.000
M1	4	0.157	16.2	-1591.165	3190.4	22.20	0.000
M0	2	0	0	-1623.724	3251.5	83.24	0.000

Table A. 21: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the numeric percentage of herbivorous mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M2		Estimate	SE	t	p	p signif.
	intercept	33.1193	2.0225	16.376	< 0.001	***
	lon	0.0486	0.1111	0.437	0.662	
		edf	Ref.df	F	p	p signif.
	s(lat)	7.655	8.542	12.81	< 0.001	***
M4		Estimate	SE	t	p	p signif.
	intercept	33.9106	0.9044	37.49	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	7.655	8.542	12.811	< 0.001	***
	s(lon)	1.006	1.012	0.191	0.668	

Table A.22: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the biomass percentage of herbivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M1	3	0.0348	5.49	-431.640	871.7	0.00	0.241
M3	4	0.0348	5.49	-431.640	871.7	0.00	0.241
M2	4	0.0377	6.02	-431.368	872.2	0.45	0.192
M4	4	0.0377	6.01	-431.370	872.2	0.45	0.192
M0	2	0	0	-434.379	872.9	1.17	0.134

Table A.23: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the numeric percentage of omnivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M3	11	0.182	20.1	-1528.057	3079.8	0.00	0.574
M4	13	0.187	20.9	-1526.329	3080.4	0.59	0.426
M2	6	0.11	11.9	-1546.230	3105.1	25.34	0.000
M1	4	0.0954	10	-1550.052	3108.2	28.43	0.000
M0	2	0	0	-1569.560	3143.2	63.37	0.000

Table A. 24: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the numeric percentage of omnivorous mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M3		Estimate	SE	t	p	p signif.
	intercept	84.1566	8.3265	10.11	< 0.001	***
	lat	-1.1617	0.1672	-6.95	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lon)	7.557	8.474	4.493	< 0.001	***
M4		Estimate	SE	t	p	p signif.
	intercept	26.56	0.80	33.2	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	2.315	2.921	17.552	< 0.001	***
	s(lon)	7.460	8.402	3.998	< 0.001	***

Table A. 25: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the biomass percentage of omnivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M1	3	0.294	30.9	-413.791	836.0	0.00	0.283
M3	4	0.294	30.9	-413.791	836.0	0.00	0.283
M2	4	0.297	31.4	-413.413	836.5	0.53	0.217
M4	4	0.297	31.4	-413.414	836.5	0.53	0.217
M0	2	0	0	-431.701	867.5	31.51	0.000

Table A.26: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the biomass percentage of omnivorous mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M1		Estimate	SE	t	p	p signif.
	intercept	128.4433	14.5596	8.822	< 0.001	***
	lat	-1.8339	0.3040	-6.033	< 0.001	***
	lon	-0.3368	0.2230	-1.510	0.134	
M2		Estimate	SE	t	p	p signif.
	intercept	40.6264	3.5668	11.390	< 0.001	***
	lon	-0.3332	0.2226	-1.497	0.138	
		edf	Ref.df	F	p	p signif.
	s(lat)	1.321	1.582	21.67	< 0.001	***
M3		Estimate	SE	t	p	p signif.
	intercept	123.761	14.657	8.444	< 0.001	***
	lat	-1.834	0.304	-6.033	< 0.001	***
		edf	Ref.df	F	p	p signif.

	s(lon)	1.001	1.002	2.279	0.135	
M4		Estimate	SE	t	p	p signif.
	intercept	35.994	1.774	20.29	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.319	1.579	21.71	< 0.001	***
	s(lon)	1.000	1.001	2.24	0.138	

Table A.27: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) numeric percentage of insectivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M3	7	0.121	13.2	-476.116	967.2	0.00	0.501
M4	7	0.121	13.2	-476.116	967.2	0.01	0.498
M1	3	0.0765	8.15	-486.622	981.4	14.18	0.000
M2	4	0.0765	8.15	-486.622	981.4	14.18	0.000
M0	2	0	0.00	-502.310	1008.7	41.47	0.000

Table A.28: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the numeric percentage of insectivorous mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M3		Estimate	SE	t	p	p signif.
	intercept	-0.563048	0.450314	-1.250	0.212	
	lat	0.052870	0.009035	5.852	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lon)	3.591	4.424	4.737	< 0.001	***

M4		Estimate	SE	t	p	p signif.
	intercept	2.05817	0.04612	44.62	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.001	1.001	34.206	< 0.001	***
	s(lon)	3.591	4.424	4.737	< 0.001	***

Table A. 29: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) biomass percentage of insectivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	wi
M3	6	0.125	15.8	-114.698	242.9	0.00	0.380
M4	6	0.125	15.8	-114.698	242.9	0.00	0.380
M1	3	0.0705	8.98	-118.455	245.3	2.40	0.115
M2	4	0.0705	8.98	-118.455	245.3	2.40	0.115
M0	2	0	0	-123.020	250.2	7.22	0.010

Table A. 30: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) biomass percentage of insectivorous mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M3		Estimate	SE	t	p	p signif.
	intercept	-0.05343	0.71242	-0.075	0.9404	
	lat	0.03214	0.01479	2.174	0.0323	*
		edf	Ref.df	F	p	p signif.
	s(lon)	2.586	3.269	1.827	0.132	
M4		Estimate	SE	t	p	p signif.

	intercept	1.48480	0.08212	18.08	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.000	1.001	4.721	0.0323	*
	s(lon)	2.586	3.269	1.827	0.1319	

Table A. 31: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) numeric percentage of carnivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M1	4	0.055	6.01	302.785	-597.5	0.00	0.276
M3	4	0.055	6.01	302.785	-597.5	0.00	0.276
M2	4	0.0559	6.18	303.114	-597.0	0.41	0.224
M4	4	0.0559	6.18	303.113	-597.0	0.42	0.224
M0	2	0	0	291.343	-578.7	18.81	0.000

Table A.32: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) numeric percentage of carnivorous mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M1		Estimate	SE	t	p	p signif.
	intercept	-0.2113946	0.0520349	-4.063	< 0.001	***
	lat	0.0047324	0.0010332	4.580	< 0.001	***
	lon	0.0008420	0.0006369	1.322	0.187	
M3		Estimate	SE	t	p	p signif.
	intercept	-0.197686	0.051529	-3.836	< 0.001	***
	lat	0.004732	0.001033	4.580	< 0.001	***
		edf	Ref.df	F	p	p signif.

	s(lon)	1.000	1.001	1.746	0.187	
M2		Estimate	SE	t	p	p signif.
	intercept	0.0231357	0.0117841	1.963	0.0504	
	lon	0.0008478	0.0006380	1.329	0.1847	
		edf	Ref.df	F	p	p signif.
	s(lat)	1.287	1.522	12.64	< 0.001	***
M4		Estimate	SE	t	p	p signif.
	intercept	0.036939	0.005565	6.638	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.286	1.522	12.644	< 0.001	***
	s(lon)	1.000	1.001	1.764	0.185	

Table A.33: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on the (log transformed) biomass percentage of carnivorous mammals in Tawny Owl diet. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M2	4	0.473	52.0	27.788	-30.5	0.00	0.501
M4	10	0.473	52.0	27.788	-30.5	0.01	0.499
M1	3	0.103	12.1	-1.530	11.5	42.01	0.000
M3	10	0.103	12.1	-1.530	11.5	42.01	0.000
M0	2	0	0	-7.803	19.7	50.25	0.000

Table A.34: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on the (log transformed) biomass percentage of carnivorous mammals in Tawny Owl diet. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M2		Estimate	SE	t	p	p signif.
	intercept	0.025570	0.041118	0.622	0.536	
	lon	0.003604	0.002607	1.383	0.170	
		edf	Ref.df	F	p	p signif.
	s(lat)	7.615	8.473	9.836	< 0.001	***
M4		Estimate	SE	t	p	p signif.
	intercept	0.07566	0.01944	3.893	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	7.615	8.473	9.836	< 0.001	***
	s(lon)	1.000	1.000	1.911	0.17	

Table A.35: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on Tawny Owl's dispersal distances (log transformed). df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc - second order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M4	18	0.12	12.1	-39472.06	78981.3	0.00	1
M2	11	0.119	11.9	-39494.73	79013.0	31.74	0
M3	11	0.115	11.5	-39552.18	79127.7	146.37	0
M1	3	0.111	11.1	-39599.36	79206.7	225.42	0
M0	2	0.00	0	-41015.56	82035.1	3053.82	0

Table A.36: Results of the best model (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on Tawny Owl's dispersal distances (log transformed). SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M4		Estimate	SE	t	p	p signif.
	intercept	2.047296	0.008114	252.3	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	8.525	8.930	74.896	< 0.001	***
	s(lon)	7.247	8.268	8.117	< 0.001	***

Table A.37: Parameters of the models compared using an information-theoretic model selection approach to analyse the effects of longitude and latitude on Tawny Owl's mean clutch size. df - degrees of freedom; R^2 - R-squared value, dev. expl. - deviance explained (%), logLik - loglikelihood value; AICc – second-order Akaike information criterion; ΔAICc - difference in AICc value; w_i = Akaike weight.

Model	df	R^2	dev. expl.	logLik	AICc	ΔAICc	w_i
M3	7	0.344	38.7	-27.906	72.6	0.00	0.492
M4	7	0.344	38.7	-27.906	72.6	0.00	0.491
M1	3	0.214	23.6	-35.925	80.4	7.89	0.010
M2	5	0.23	25.9	-34.810	81.0	8.43	0.007
M0	2	0	0	-45.759	95.7	23.14	0.000

Table A.38: Results of the best models (ΔAICc<2) selected for the analysis of the effect of longitude and latitude on Tawny Owl's mean clutch size. SE - standard error; t - t-test value; p - p value, p. signif. - p statistical significance level (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$), edf - effective degrees of freedom, Ref.df - original degrees of freedom, F - F-test value, lat - latitude, lon - longitude, s - smooth factor applied to the explanatory variable [s(lon);s(lat)].

M3		Estimate	SE	t	p	p signif.
	intercept	3.173284	0.780869	4.064	< 0.001	***
	lat	0.002936	0.014861	0.198	0.843962	

		edf	Ref.df	F	p	p signif.
	s(lon)	3.726	4.572	8.500	< 0.001	***
M4		Estimate	SE	t	p	p signif.
	intercept	3.32734	0.04324	76.95	< 0.001	***
		edf	Ref.df	F	p	p signif.
	s(lat)	1.000	1.000	0.039	0.844	
	s(lon)	3.726	4.572	8.500	< 0.001	***

Table A.39: Percentage of birds found further than 50 or 100 km away from the initial ringing location. Only countries with more than 600 records were included. N = number of recoveries and recaptures.

Region	> 50 km	> 100 km	N	Included countries (N)
Northern Europe	14.0%	5.4%	13182	Finland (8227), Sweden (2586), Norway (1754), Denmark (619)
Eastern Europe	3.2%	1.1%	663	Czech Republic (663)
Western Europe	2.7%	1.1%	7718	Netherlands (2275), Switzerland (2178), Germany (1880), Belgium (1396)
United Kingdom	2.0%	0.6%	2137	United Kingdom (2137)

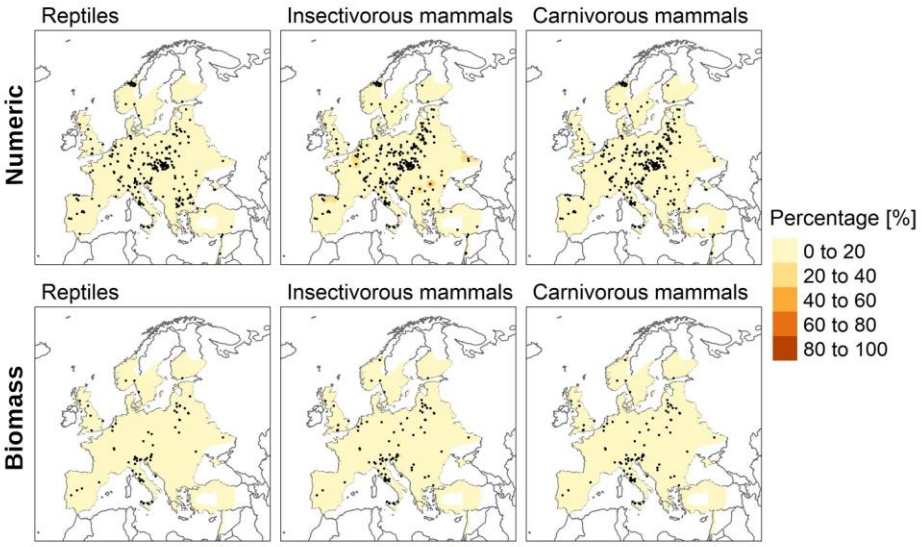

Figure A.1: Interpolated numeric (top row) and biomass (bottom row) percentages of prey groups in Tawny Owl diet across the research area. Black dots represent locations of individual diet studies.

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Appendix B

Differential Responses of Coexisting Owls to Annual Small Mammal Population Fluctuations in Temperate Mixed Forest – Supporting Information

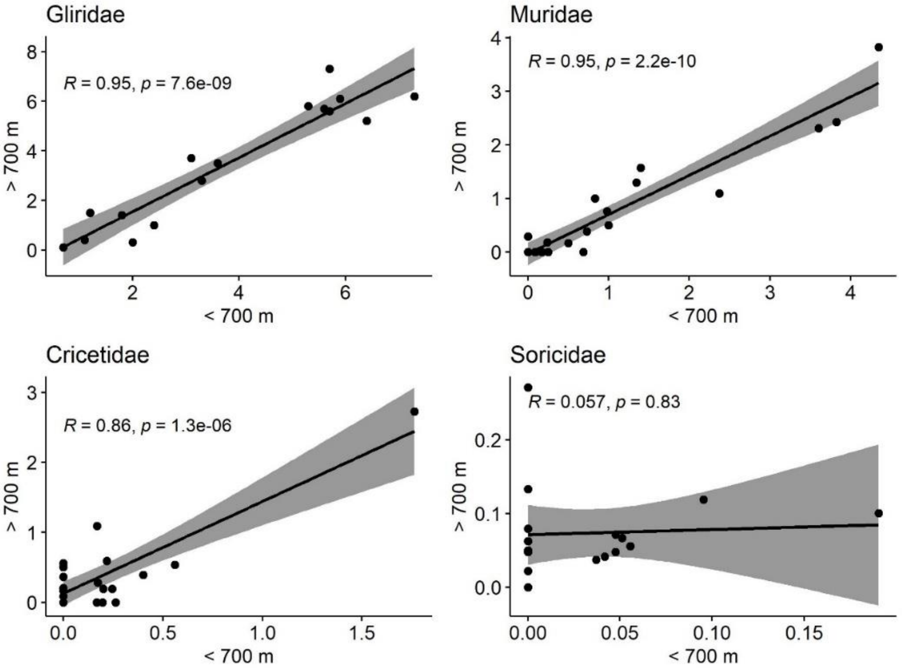

Figure S.1: Correlation of small mammal population densities (dormice, Gliridae; mice, Muridae, voles, Cricetidae; shrews, Soricidae) at low (< 700 m asl) and high altitudes (> 700 m asl) on Mt Krim (*R*, Pearson's coefficient).

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. Units: [1], number of active territories per survey point; [2], proportion of occupied nestboxes; [3], number of trapped individuals per 10 trap-nights; [4], number of vocalizing individuals per survey point.

Taxa	**Min**	**Q1**	**Mean**	**Q3**	**Max**
Boreal Owl					
Territory occupancy [1]	0.00	0.04	0.17	0.32	0.60
Tawny Owl					
Territory occupancy [1]	0.28	0.32	0.47	0.52	0.84
Breeding attempts [2]	0.00	0.10	0.17	0.24	0.37
Mean clutch size	0.00	2.29	3.05	4.00	4.75
Ural Owl					
Territory occupancy [1]	0.20	0.36	0.51	0.64	0.80
Breeding attempts [2]	0.00	0.03	0.10	0.15	0.36
Mean clutch size	0.00	0.00	2.09	3.22	4.11
Muridae [3]	0.00	0.18	1.02	1.32	4.12
Cricetidae [3]	0.00	0.08	0.32	0.28	2.24
Soricidae [3]	0.00	0.11	0.18	0.19	0.54
Gliridae [4]	0.4	1.35	3.50	5.65	6.75

Table S2: Attribute/feature rankings in terms of their importance for owl territory occupancy in the Boreal, Tawny and Ural Owl. Attributes denoted with an asterisk collectively carry enough discriminative information to predict the owl population densities within acceptable margins of error. GENIE3 importance scores and respective rankings are given for each species separately and overall.

Attribute	**Overall**		**Boreal Owl**		**Tawny Owl**		**Ural Owl**	
	rank	score	rank	score	rank	score	rank	score
Mice - current year *	1	0.0748	1	0.1045	3	0.0447	2	0.0752
Shrews - current year	2	0.0644	4	0.0332	2	0.0553	1	0.1047
Dormice - current year	3	0.0504	2	0.0618	5	0.0364	3	0.0530
Dormice - preceding year	4	0.0396	6	0.0224	1	0.0781	6	0.0184
Mice - preceding year	5	0.0374	5	0.0235	4	0.0377	4	0.0510
Voles - current year	6	0.0349	3	0.0459	6	0.0333	5	0.0256
Voles - preceding year	7	0.0194	7	0.0160	7	0.0244	7	0.0179
Shrews - preceding year	8	0.0182	8	0.0159	8	0.0214	8	0.0171

Table S3: Attribute rankings in terms of their importance for breeding attempts rates in the Tawny and Ural Owl. Attributes denoted with an asterisk collectively carry enough information to train a model to predict breeding attempts rates without substantial increase in the error rates. GENIE3 importance scores and respective rankings are given for each species separately and overall.

Attribute	**Overall**		**Tawny Owl**		**Ural Owl**	
	rank	score	rank	score	rank	Score
Mice - current year *	1	0.0545	1	0.0433	1	0.0657
Dormice - current year	2	0.0200	2	0.0205	2	0.0195
Dormice - preceding year	3	0.0167	4	0.0186	4	0.0148
Mice - preceding year	4	0.0147	3	0.0203	5	0.0091
Voles - current year	5	0.0120	6	0.0070	3	0.0169
Voles - preceding year	6	0.0055	5	0.0071	8	0.0038
Shrews - preceding year	7	0.0047	7	0.0028	6	0.0067
Shrews - current year	8	0.0042	8	0.0023	7	0.0062

Table S4: Attribute rankings in terms of their importance for clutch sizes in the Tawny and Ural Owl. Attributes denoted with an asterisk collectively carry enough information to train a model to predict clutch sizes without substantial increase in the error rates. GENIE3 importance scores and respective rankings are given for each species separately and overall.

Attribute	Overall		Tawny Owl		Ural Owl	
	rank	score	rank	score	rank	Score
Mice - current year *	1	7.6544	1	5.9074	1	9.4014
Shrews - current year	2	4.2335	2	2.6707	2	5.7963
Dormice - preceding year	3	3.2117	3	2.5967	4	3.8267
Dormice - current year	4	3.0804	6	2.0637	3	4.0970
Voles - current year	5	2.7032	4	2.4018	5	3.0047
Mice - preceding year	6	2.3361	5	2.2116	6	2.4606
Voles - preceding year	7	0.7506	7	0.6347	7	0.8665
Shrews - preceding year	8	0.5742	8	0.3984	8	0.7501

Appendix C

Does Intraguild Competition Reflect in Body Size and Productivity?

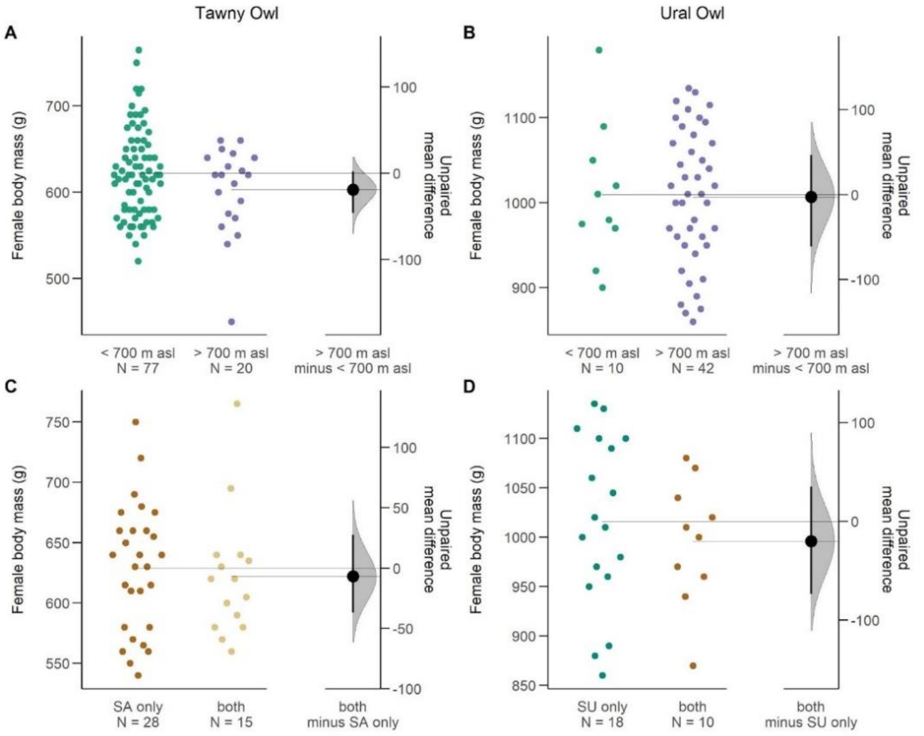

Figure S1: Differences in incubating female body mass in Tawny and Ural Owl at different altitudes (top row) and in the absence/presence of territorial interspecific competitor owl (i.e. the other *Strix* species; bottom row) on Mt Krim in the period 2004-2021. SA - Tawny Owl (*Strix aluco*), SU - Ural Owl (*Strix uralensis*). The left panel in each plot shows raw data for each group, horizontal line - group mean. Right panel; bold black dot and vertical ticks - mean difference and the associated 95% confidence interval; shaded curve - sampling-error distribution; all derived from 5,000 bootstrapped resamples.

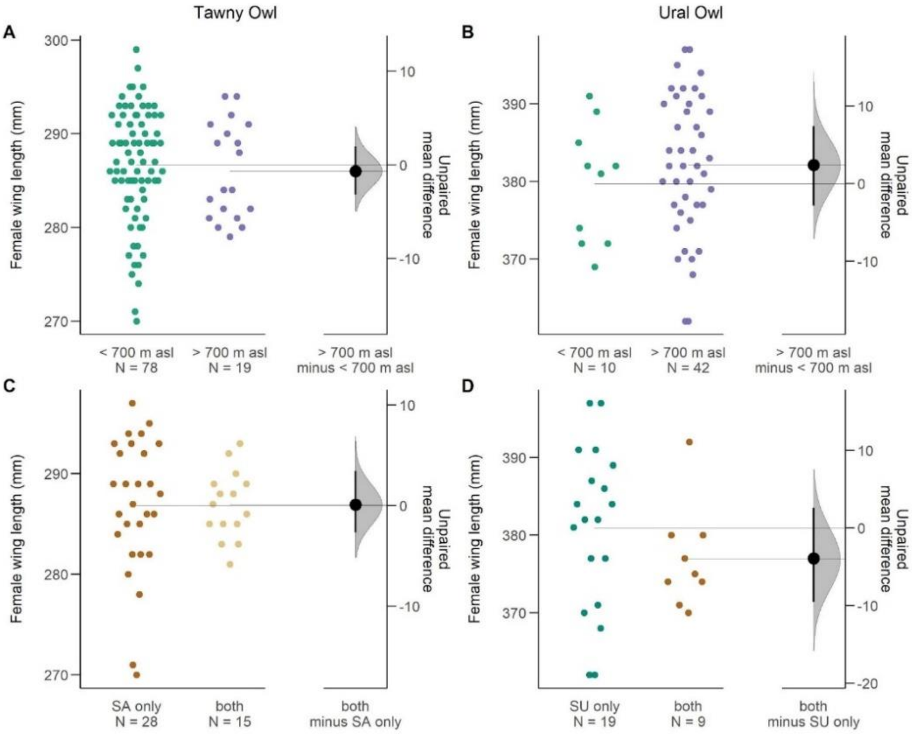

Figure S2: Differences in incubating female wing length in Tawny and Ural Owl at different altitudes (top row) and in the absence/presence of territorial interspecific competitor owl (i.e. the other Strix species; bottom row) on Mt Krim in the period 2004-2021. SA - Tawny Owl (*Strix aluco*), SU - Ural Owl (*Strix uralensis*). The left panel in each plot shows raw data for each group, horizontal line - group mean. Right panel; bold black dot and vertical ticks - mean difference and the associated 95% confidence interval; shaded curve - sampling-error distribution; all derived from 5,000 bootstrapped resamples.

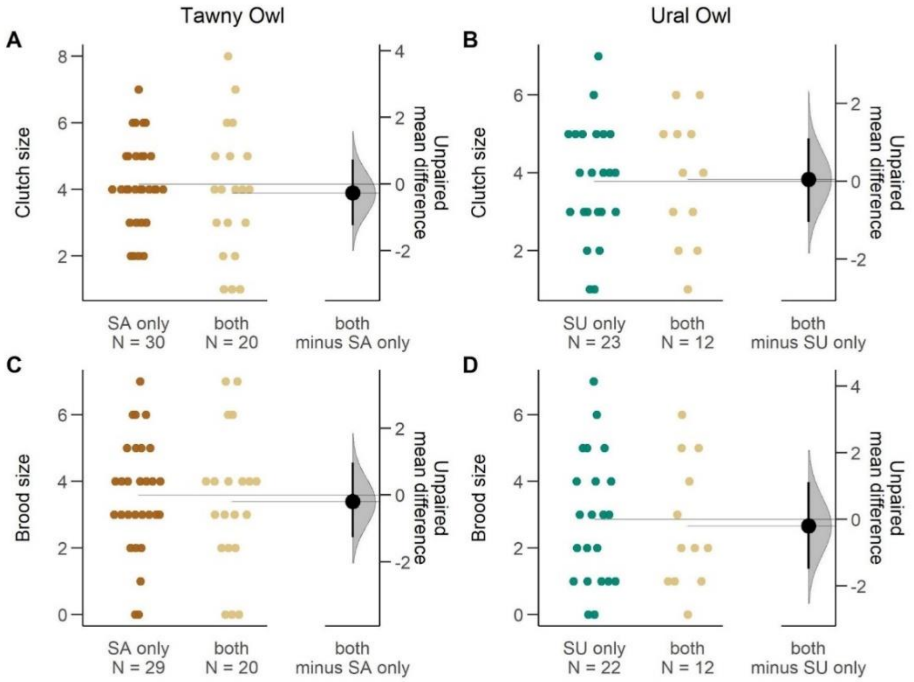

Figure S3: Clutch and brood size in Tawny and Ural Owl in the absence or presence of territorial interspecific competitor owl (i.e. the other *Strix* species) on Mt Krim in the period 2004-2021. SA - Tawny Owl (*Strix aluco*), SU - Ural Owl (*Strix uralensis*). The left panel in each plot shows raw data for each group, horizontal line - group mean. Right panel; bold black dot and vertical ticks - mean difference and the associated 95% confidence interval; shaded curve - sampling-error distribution; all derived from 5,000 bootstrapped resamples.

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Journal Articles

Ratajc, U., Lourenço, R., Espín, S., Virosta, P. S., Birrer, S., Studler, D., Wernham, C., & Vrezec, A. (2023). The importance of population contextual data for large-scale biomonitoring using an apex predator: The Tawny Owl (*Strix aluco*). Science of the Total Environment, 860, 160530. https://doi.org/10.1016/j.scitotenv.2022.160530

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Publications Related to the Thesis

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Ratajc, U., Lourenço, R., Vrezec, A., Espín, S., Sánchez Virosta, P., Birrer, S., Studler, D., Wernham, C. (2022). Overview of key ecological traits of tawny owl *Strix aluco* in Europe for their use in contaminant monitoring. In: *EOU 2022: 13th European Ornithologists' Union Congress*, Online.

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Biography

Urška Ratajc was born on July 26th, 1991, in Celje, Slovenia. She finished primary school in Griže, and secondary school in Celje. In 2010, she started her bachelor studies in biology at the Faculty of Biotechnology at the University of Ljubljana. After graduation in 2013, she started her master's studies in Ecology and Biodiversity at the same faculty. During her final year of master studies, she did one semester of Erasmus+ exchange traineeship at the institute ENKI, Třebon, Czech Republic, where she learned more about the effects of landscape management on water quality, biodiversity and local climate. She graduated in 2017 with the defence of the master's thesis entitled "Historical aspects of ground beetles (*Carabus*) and large diving beetles (Dytiscinae) distribution in Slovenia", under the mentorship of Assist. Prof. Dr. Al Vrezec. In the same year, she started working at the Department of Organisms and Ecosystems Research, National Institute of Biology, received a Young Researcher grant from the Slovenian Research Agency and enrolled in the PhD study programme Ecotechnologies at the Jožef Stefan International Postgraduate School.

Her research is mostly in the field of forest ecology. The PhD thesis focuses on the ecology of Tawny Owl and its interactions with other forest owl species and with small mammals in Dinaric forests. She is also interested in ecology of certain groups of beetles (ground beetles, diving beetles, saproxylic beetles) and has extensive experience in Natura 2000 beetle species monitoring programmes. She has published several papers and has presented her work at numerous international conferences, workshops and project meetings.