



## Review

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



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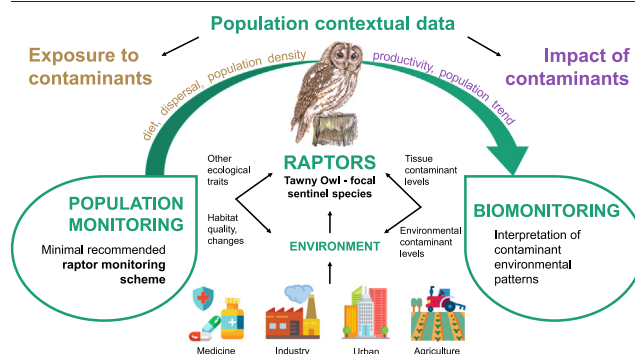
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## HIGHLIGHTS

- 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, biomagnifiable 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 A considerable variation in availability of published and unpublished contextual data across Europe was found, with diet being the most extensively studied trait.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, biomagnifiable 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; Vrežec 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; Hörmfeldt 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

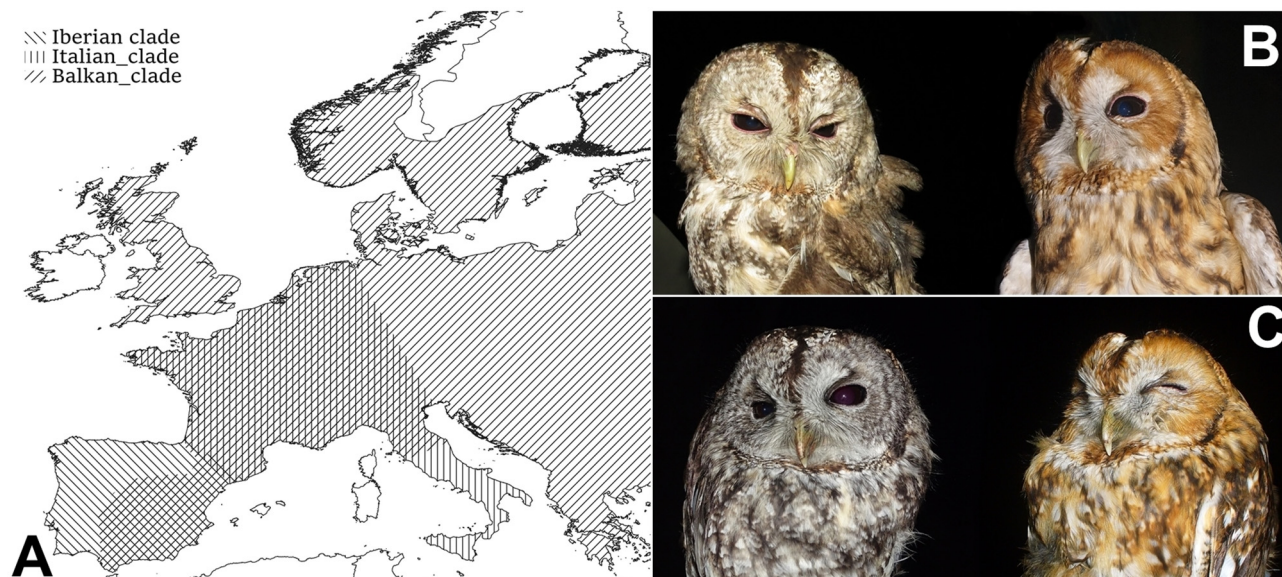
The study area was defined to encompass the 39 Member and Cooperating Member countries in the European Cooperation in Science and Technology network (COST <https://www.cost.eu/about/members/>), including the 27 member states of the European Union and the Near Neighbour and International Partner Countries 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. wilkenskii* (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; Ratajč 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 (Vrežec 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<sup>2</sup> (Ranazzi et al., 2001; Vrežec, 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; Vrežec, 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; Vrežec and Bertonec, 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 <sup>2</sup> )	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	Impact: Ratio between known nest

**Table 1 (continued)**

Contextual data parameter	Description and derived data	Value for contaminant studies
	hatch successfully and causes of failure	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
Threats (including persecution)	Information on the existence of threats to populations on a regional or national scale (qualitative data)	poisoning problems in the population (González et al., 2007; Isomursu et al., 2018; Alarcón and Lambertucci, 2018). 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

Table 1 (continued)

Contextual data parameter	Description and derived data	Value for contaminant studies
		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<sup>2</sup>).

Ringling data (recoveries and recaptures), were acquired from the EURING database (du Feu et al., 2009), to which we added ringling data for Slovenia from the Slovenian Bird Ringling Centre (Slovenian Museum of Natural History) database. The ringling dataset included data from 1910 to 2021. Some data entries had a doubtfully large time difference between ringling 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 ringling and retrapping (Coles and Petty, 1997; Sunde, 2011). Juveniles were considered as those birds which were ringling as nestlings or fledglings not able to fly, whereas adults were considered as those birds which were ringling as fully grown with age 2 y and more. Only maximum distance from the ringling location per ring ID and the coordinates of

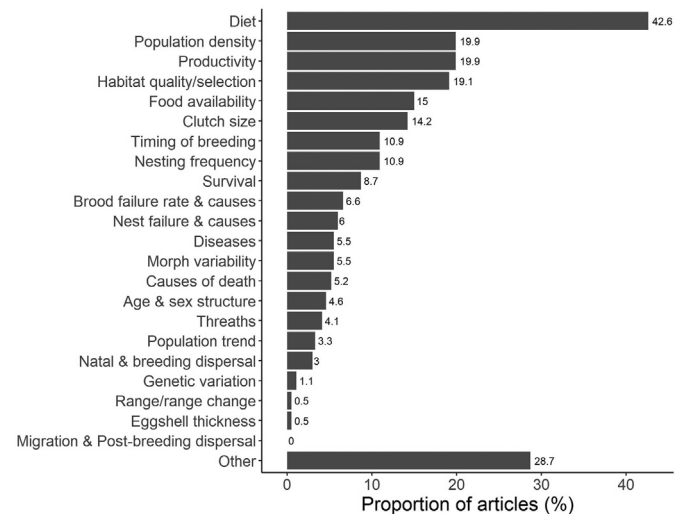


Fig. 2. Frequency of published articles covering the population contextual data of Tawny Owl in Europe (N = 366). Some articles offered data on several topics, thus the overall sum totals >100 %.

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  $\Delta AICc$  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  $0.2^\circ \times 0.2^\circ$  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 (%) $\pm$ SD	Range (%) (min-max)
N of mammals	lat, s(lat)	67.8 $\pm$ 21.2	4.4-100.0
N of birds	lon, s(lon)	12.9 $\pm$ 14.4	0.0-90.1
log transformed			
N of invertebrates	lon, s(lat), s(lon)	12.2 $\pm$ 16.6	0.0-95.6
log transformed			
N of amphibians	lon, s(lat), s(lon)	6.4 $\pm$ 10.7	0.0-60.4
log transformed			
N of reptiles	lon, s(lat), s(lon)	0.4 $\pm$ 1.8	0.0-27.2
log transformed			
N of herbivore mammals	s(lat)	33.9 $\pm$ 19.7	0.0-94.3
N of omnivore mammals	lat, s(lat), s(lon)	26.6 $\pm$ 17.0	0.0-96.7
N of insectivore mammals	lat, s(lat), s(lon)	10.6 $\pm$ 10.5	0.0-63.4
log transformed			
N of carnivore mammals	lat, s(lat)	0.05 $\pm$ 0.1	0.0-1.1
log transformed			
B of mammals	Null model	79.0 $\pm$ 17.7	14.0-100.0
B of birds	Null model	15.4 $\pm$ 16.2	0.0-76.0
log transformed			
B of invertebrates	s(lon)	1.5 $\pm$ 3.1	0.0-15.9
log transformed			
B of amphibians	lat, s(lat), s(lon)	3.2 $\pm$ 4.7	0.0-24.1
log transformed			
B of reptiles	Null model	0.4 $\pm$ 1.2	0.0-7.0
log transformed			
B of herbivorous mammals	Null model	38.6 $\pm$ 21.4	0.0-95.4
B of omnivorous mammals	lat, s(lat)	36.0 $\pm$ 20.8	0.0-98.8
B of insectivorous mammals	lat, s(lat)	5.4 $\pm$ 6.7	0.0-49.4
log transformed			
B of carnivorous mammals	s(lat)	0.1 $\pm$ 0.6	0.0-4.5
log transformed			

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<sup>2</sup> ( $n = 37$  countries, SD = ±9.9). The lowest densities were found in Moldova (0.2 pairs/100 km<sup>2</sup>) and Finland (0.7 pairs/100 km<sup>2</sup>) (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<sup>2</sup>, 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,



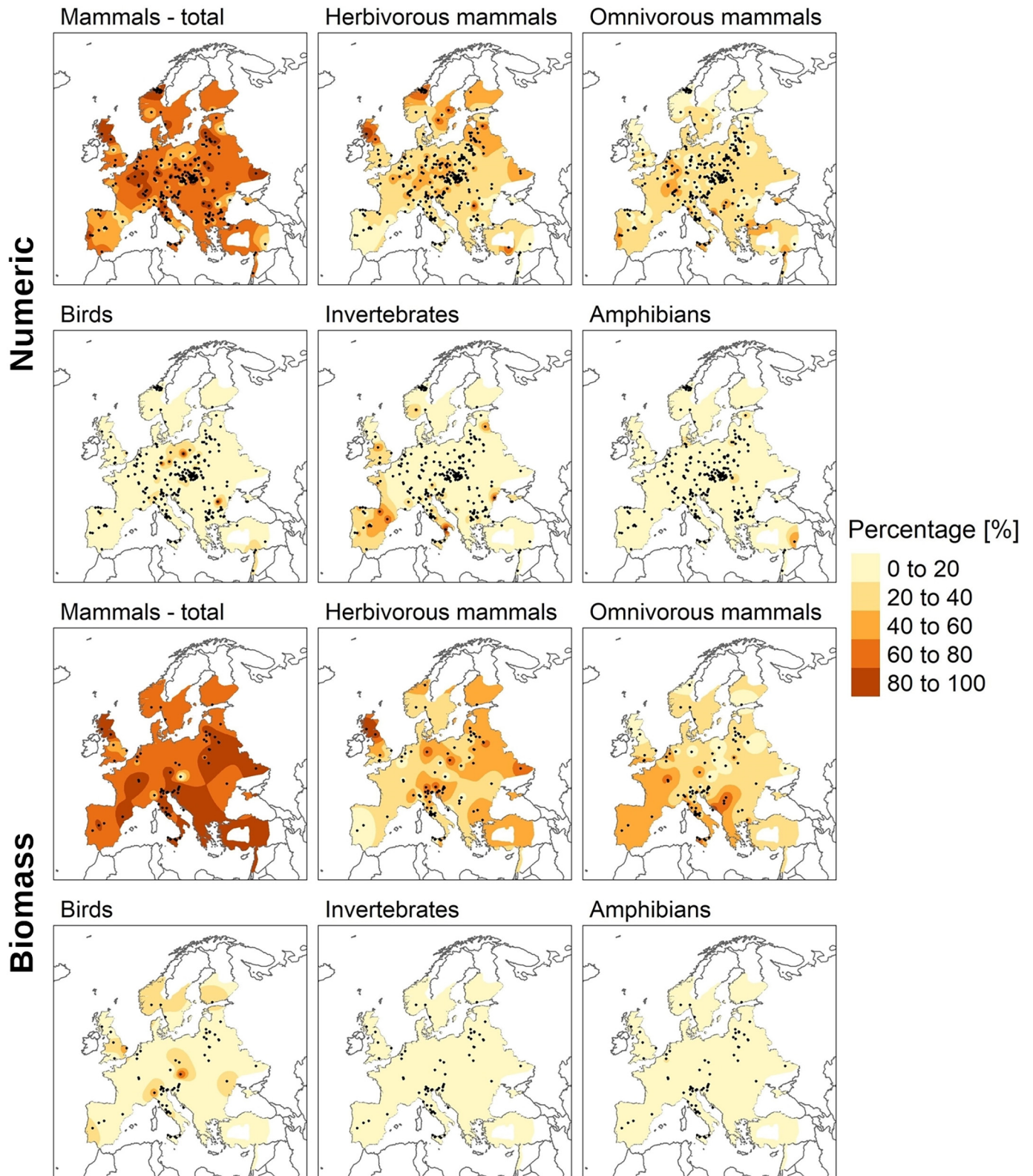
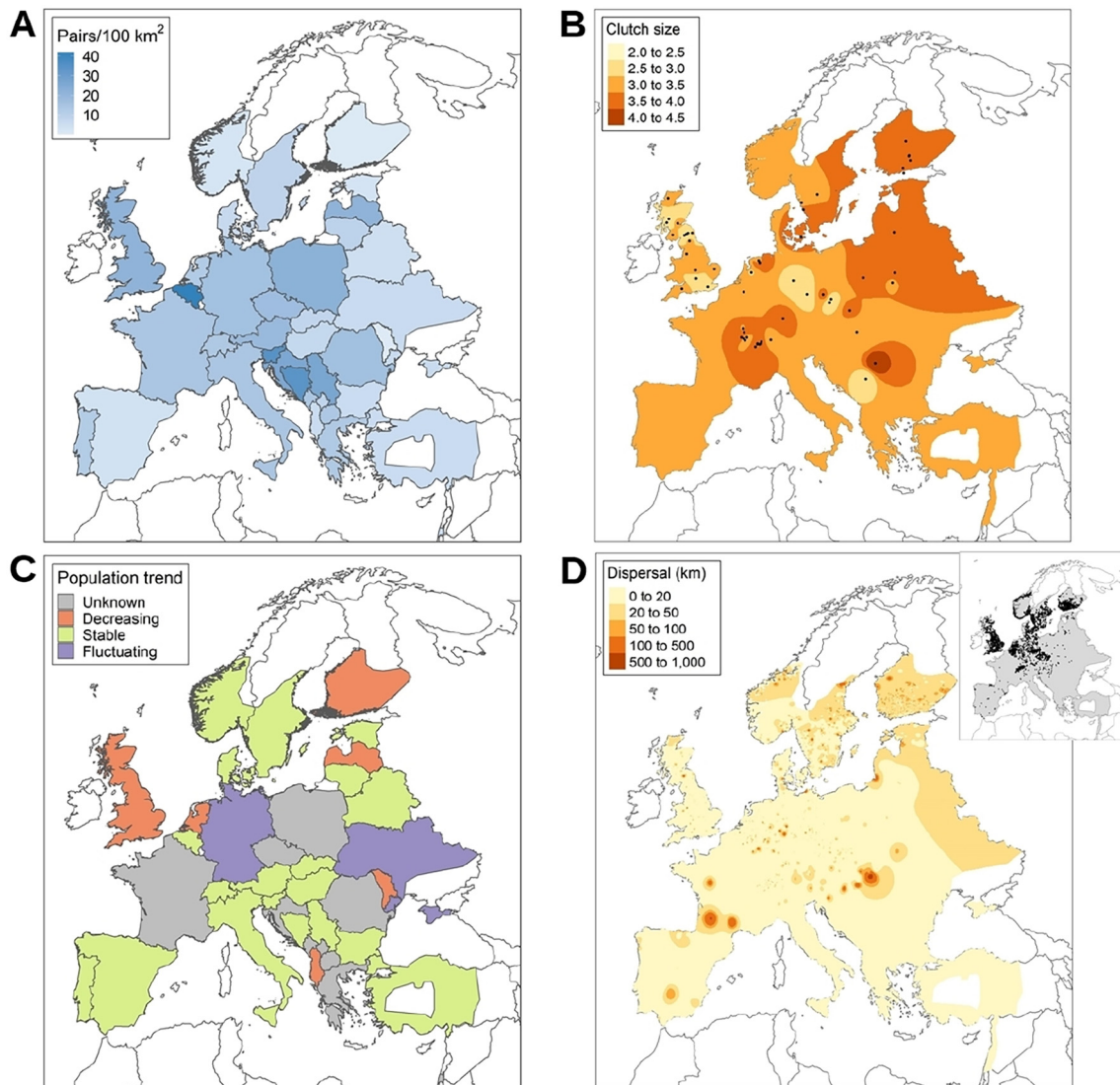


Fig. 3. Interpolated numeric (top two rows) and biomass (bottom two rows) percentages of prey groups in Tawny Owl diet across the research area. Black dots represent locations of individual diet studies.

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<sup>2</sup>); (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 ( $25.1 \text{ km} \pm 41.1 \text{ SD}$ ) and shortest in the United Kingdom ( $8.4 \text{ km} \pm 24.8 \text{ SD}$ ). The difference in mean between regions was significant, but not in all pairwise comparisons (Fig. 5).

Mean juvenile-adult ringing distance was  $22.0 \text{ km} (\pm 38.4 \text{ SD}, \text{ range: } 0\text{--}917, N = 18,168)$  and mean adult-adult ringing distance was  $6.1 \text{ km} (\pm 24.8 \text{ SD}, \text{ range: } 0\text{--}785, N = 5786)$ . 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  $\pm \text{SD} = 30.3 \pm 43.6 \text{ km}$ ) and lowest in Western Europe (mean  $\pm \text{SD} = 9.7 \pm 23.8 \text{ km}$ ).

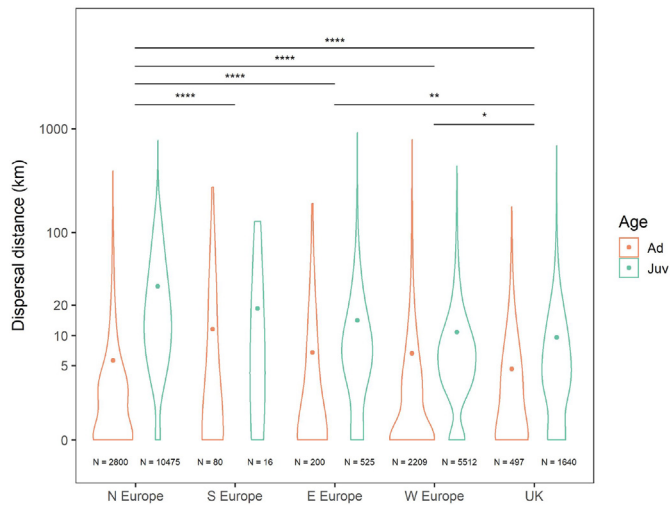
#### 4. Discussion

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; Milkola, 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; Zuberogioita 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 Bertoneclj, 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 Bertoneclj, 2018; Ratajč 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 (Goszczyński 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 biased 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  $8.7 \pm 10.9\%$  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 Bertoneclj, 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 Bertoncej, 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 Bertoncej, 2018; Zuberogitia 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 Podkova, 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

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## References

- Ahrens, L., Herzke, D., Huber, S., Bustnes, J.O., Bangjord, G., Ebinghaus, R., 2011. Temporal trends and pattern of polyfluoroalkyl compounds in tawny owl (*Strix aluco*) eggs from Norway, 1986–2009. *Environ. Sci. Technol.* 45, 8090–8097. <https://doi.org/10.1021/es103473v>.
- Al Sayegh Petkovič, S., Kopašar, N., Tome, D., Kryštufek, B., 2015. Risk assessment of metals and PAHs for receptor organisms in differently polluted areas in Slovenia. *Sci. Total Environ.* 532, 404–414. <https://doi.org/10.1016/j.scitotenv.2015.05.076>.
- Alarcón, P.A.E., Lambertucci, S.A., 2018. Pesticides thwart condor conservation. *Science* 360, 612. <https://doi.org/10.1126/science.aat6039>.
- Avotins, A., 2004. Tawny Owl's territory occupancy in Eastern Latvia. In: Anselin, A. (Ed.), *Bird Numbers 1995, Proceedings of the International Conference and 13th Meeting of the European Bird Census Council*, Pärnu, Estonia. 13. *Bird Census News*, pp. 167–173.
- Badry, A., Krone, O., Jaspers, V.L.B., Mateo, R., García-Fernández, A., Leivits, M., Shore, R.F., 2020. Towards harmonisation of chemical monitoring using avian apex predators: identification of key species for pan-European biomonitoring. *Sci. Total Environ.* 731, 139198. <https://doi.org/10.1016/j.scitotenv.2020.139198>.
- Badry, A., Palma, L., Beja, P., Ciesielski, T.M., Dias, A., Lierhagen, S., Jenssen, B.M., Sturaro, N., Euliers, I., Jaspers, V.L.B., 2019. Using an apex predator for large-scale monitoring of trace element contamination: associations with environmental, anthropogenic and dietary proxies. *Sci. Total Environ.* 676, 746–755. <https://doi.org/10.1016/j.scitotenv.2019.04.217>.
- Badry, A., Treu, G., Gkotsis, G., Nika, M.-C., Alygizakis, N., Thomaidis, N.S., Voigt, C.C., Krone, O., 2022. Ecological and spatial variations of legacy and emerging contaminants in white-tailed sea eagles from Germany: implications for prioritisation and future risk management. *Environ. Int.* 158, 106934. <https://doi.org/10.1016/j.envint.2021.106934>.
- Bairlein, F., Dierschke, J., Dierschke, V., Salewski, V., Geiter, O., Hüppop, K., Köppen, U., Fiedler, W., 2014. *Atlas des Vogelzugs: Ringfunde deutscher Brut- und Gastvögel*. AULA-Verlag, Wiebelsheim.
- Balčiauskienė, L., Jovaišas, A., Naruševičius, V., Petraška, A., Skuja, S., 2006. Diet of Tawny Owl (*Strix aluco*) and long-eared owl (*Asio otus*) in Lithuania as found from pellets. *Acta Zool. Lit.* 16, 37–45. <https://doi.org/10.1080/13921657.2006.10512708>.
- Bartolommei, P., Mortelliti, A., Pezzo, F., Puglisi, L., 2012. Distribution of nocturnal birds (Strigiformes and Caprimulgidae) in relation to land-use types, extent and configuration in agricultural landscapes of Central Italy. *Rend. Lincei* 24, 13–21. <https://doi.org/10.1007/s12210-012-0211-3>.
- Bartón, K., 2020. MuMIn: Multi-Model Inference v.1.43.17. Version 1.43.17. <https://cran.r-project.org/package=MuMIn>.
- Bauduin, H., Jouaire, S., 2003. Breeding biology of the Tawny Owl *Strix aluco* in the forests of Burgundy. *Vogelwelt* 124, 289–294.
- Becker, P.H., 2003. Biomonitoring with birds. Trace Metals and other Contaminants in the Environment. 6, pp. 677–736. [https://doi.org/10.1016/S0927-5215\(03\)80149-2](https://doi.org/10.1016/S0927-5215(03)80149-2).
- Bedrosian, B., Craighead, D., Crandall, R., 2012. Lead exposure in bald eagles from big game hunting, the continental implications and successful mitigation efforts. *PLoS One* 7, e51978. <https://doi.org/10.1371/journal.pone.0051978>.
- Berg, W., Johnels, A., Sjöstrand, B., Westermark, T., 1966. Mercury content in feathers of Swedish birds from the past 100 years. *Oikos* 17, 71–83.
- Birdlife International, 2017. *European Birds of Conservation Concern: Populations, Trends and National Responsibilities*. Birdlife International Cambridge, UK.
- Birrer, S., 2009. Synthesis of 312 studies on the diet of the long-eared owl *Asio otus*. *Ardea* 97, 615–624. <https://doi.org/10.5253/078.097.0430>.
- Blanco, G., Sergio, F., Frías, Ó., Salinas, P., Tanfema, A., Hiraldo, F., Barceló, D., Eljarrat, E., 2018. Integrating population connectivity into pollution assessment: overwintering mixing reveals flame retardant contamination in breeding areas in a migratory raptor. *Environ. Res.* 166, 553–561. <https://doi.org/10.1016/j.envres.2018.06.037>.
- Božič, I.A., 2009. Results of bird ringing in Slovenia: 1926–1982. *Scopolia Suppl.* 4, 23–110.
- Brambilla, M., Scridel, D., Bazzi, G., Ilahiane, L., Iemba, A., Pedrini, P., Bassi, E., Bionda, R., Marchesi, L., Genero, F., Teufelbauer, N., Probst, R., Vrezec, A., Kmecl, P., Mihelič, T., Bogliani, G., Schmid, H., Assandri, G., Pontarini, R., Braunisch, V., Arlettaz, R., Chamberlain, D., 2020. Species interactions and climate change: how the disruption of species co-occurrence will impact on an avian forest guild. *Glob. Chang. Biol.* 26, 1–13. <https://doi.org/10.1111/gcb.14953>.
- Brito, P.H., 2005. The influence of Pleistocene glacial refugia on tawny owl genetic diversity and phylogeography in western Europe. *Mol. Ecol.* 14, 3077–3094. <https://doi.org/10.1111/j.1365-294X.2005.02663.x>.
- Brommer, J.E., Ahola, K., Karstinen, T., 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proc. R. Soc. B Biol. Sci.* 272, 935–940. <https://doi.org/10.1098/rspb.2005.3052>.
- Brown, A.R., Hosken, D.J., Balloux, F., Bickley, L.K., LePage, G., Owen, S.F., Hetheridge, M.J., Tyler, C.R., 2009. Genetic variation, inbreeding and chemical exposure—combined effects in wildlife and critical considerations for ecotoxicology. *Philos. Trans. R. Soc. B Biol. Sci.* 364, 3377–3390. <https://doi.org/10.1098/rstb.2009.0126>.
- Bucciolini, G.L., Morosinotto, C., Ericsson, P., Nilsson, L.-O., Vrezec, A., Poprach, K., Öien, I.J., Koning, H.J., Karell, P., 2022. Early life climate effects on life history components and life expectancy across Europe in a color polymorphic species. In: Chamberlain, D., Schumm, Y. (Eds.), *EOU 2022, 13th European Ornithologists' Union Congress, Online Conference, 15 March 2022*. Scientific Programme Committee and the Local Organising Committee (Hessian Society for Ornithology and Nature Conservation (HGON) and Behavioural Ecology & Ecophysiology Group, Justus-Liebig University), pp. 91–92.
- Burgos, G., Zuberogaitia, I., 2020. A telemetry study to discriminate between home range and territory size in Tawny Owls. *Bioacoustics* 29, 109–121. <https://doi.org/10.1080/09524622.2018.1555717>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach*. 2nd ed. Springer, New York.
- Bustnes, J.O., Bårdsen, B.J., Bangjord, G., Lierhagen, S., Yoccoz, N.G., 2013. Temporal trends (1986–2005) of essential and non-essential elements in a terrestrial raptor in northern Europe. *Sci. Total Environ.* 458–460, 101–106. <https://doi.org/10.1016/j.scitotenv.2013.04.027>.
- Bustnes, J.O., Yoccoz, N.G., Bangjord, G., Herzke, D., Ahrens, L., Skaare, J.U., 2011. Impacts of climate and feeding conditions on the annual accumulation (1986–2009) of persistent organic pollutants in a terrestrial raptor. *Environ. Sci. Technol.* 45, 7542–7547. <https://doi.org/10.1021/es201786x>.
- Christensen, T.K., Lassen, P., Elmeros, M., 2012. High exposure rates of anticoagulant rodenticides in predatory bird species in intensively managed landscapes in Denmark. *Arch. Environ. Contam. Toxicol.* 63, 437–444. <https://doi.org/10.1007/s00244-012-9771-6>.
- Coles, C.F., 2000. Breeding, survival, movements and foraging of tawny owls *Strix aluco* in a managed spruce forest: a spatial approach. University of Durham PhD thesis.
- Coles, C.F., Petty, S.J., 1997. Dispersal behaviour and survival of juvenile tawny owls (*Strix aluco*) during the low point in a vole cycle. In: Duncan, J.R., Johnson, D.H., Nicholls, T.H. (Eds.), *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium*. USDA Forest Service, Manitoba, Canada, pp. 111–118.
- Comay, O., Ezov, E., Yom-Tov, Y., Dayan, T., 2022. In its southern edge of distribution, the Tawny Owl (*Strix aluco*) is more sensitive to extreme temperatures than to rural development. *Animals* 12, 641. <https://doi.org/10.3390/ani12050641>.
- Cramp, S., 1985. *The Birds of the Western Palearctic*. Vol. 4. Oxford University Press, Oxford, United Kingdom.
- Crick, H.Q.P., Ratcliffe, D.A., 1995. The Peregrine *Falco peregrinus* breeding population of the United Kingdom in 1991. *Bird Study* 42, 1–19. <https://doi.org/10.1080/0006365909477143>.
- Darras, K., Batáry, P., Furnas, B., Celis-Murillo, A., Van Wilgenburg, S.L., Mulyani, Y.A., Tschardt, T., 2018. Comparing the sampling performance of sound recorders versus point counts in bird surveys: a meta-analysis. *J. Appl. Ecol.* 55, 2575–2586. <https://doi.org/10.1111/1365-2664.13229>.
- Dauwe, T., Chu, S.G., Covaci, A., Schepens, P., Eens, M., 2003. Great tit (*Parus major*) nestlings as biomonitors of organochlorine pollution. *Arch. Environ. Contam. Toxicol.* 44, 89–96. <https://doi.org/10.1007/s00244-002-1243-y>.
- Delibes, M., Gaona, P., Ferreras, P., 2001. Effects of an attractive sink leading into maladaptive habitat selection. *Am. Nat.* 158, 277–285. <https://doi.org/10.1086/321319>.
- Derlink, M., Wernham, C., Bertoncelj, I., Kovács, A., Saurola, P., Duke, G., Movalli, P., Vrezec, A., 2018. A review of raptor and owl monitoring activity across Europe: its implications for capacity building towards pan-European monitoring. *Bird Study* 65, S4–S20. <https://doi.org/10.1080/00063657.2018.1447546>.
- Dimitriou, K.G., Kotsonas, E.G., Bakaloudis, D.E., Vlachos, C.G., Holloway, G.J., Yosef, R., 2021. Population viability and conservation strategies for the Eurasian black vulture (*Aegypius monachus*) in southeast Europe. *Animals* 11, 124. <https://doi.org/10.3390/ani11010124>.
- du Feu, C., Joys, A., Clark, J., Fiedler, W., Downie, I., van Noordwijk, A.J., Spina, F., Wassenaar, R., Baillie, S.R., 2009. EURING Data Bank geographical index 2009. <http://eurring.org/edb>.
- Dulsat-Masvidal, M., Lourenço, R., Lacorte, S., D'Amico, M., Albayrak, T., Andevski, J., Aradis, A., Baltag, E., Berger-Tal, O., Berny, P., Chores, Y., Duke, G., Espin, S., García-Fernández, A.J., Gómez-Ramírez, P., Hallgrímsson, G.T., Jaspers, V., Johansson, U., Kovacs, A., Krone, O., Leivits, M., Martínez-López, E., Mateo, R., Movalli, P., Sánchez-Virosta, P., Shore, R.F., Valkama, J., Vrezec, A., Xirouchakis, S., Walker, L.A., Wernham, C., 2021. A review of constraints and solutions for collecting raptor samples and contextual data for a European raptor biomonitoring facility. *Sci. Total Environ.* 793, 148599. <https://doi.org/10.1016/j.scitotenv.2021.148599>.
- Ericsson, P., Nilsson, L.-O., Haglund, K., Ericsson, D., 2014. Breeding biology of a Tawny Owl *Strix aluco* population in south-western Sweden - a 15 year survey. *Ornis Svecica* 24, 41–50. <https://doi.org/10.34080/os.v24.22563>.
- Eriksson, U., Roos, A., Lind, Y., Hope, K., Ekblad, A., Kärrman, A., 2016. Comparison of PFAS contamination in the freshwater and terrestrial environments by analysis of eggs from







- Sasvári, L., Hegyi, Z., 1998. Bird predation by tawny owls (*Strix aluco* L.) and its effect on the reproductive performance of tits. *Acta Oecol.* 19, 483–490. [https://doi.org/10.1016/S1146-609X\(99\)80002-2](https://doi.org/10.1016/S1146-609X(99)80002-2).
- Saurola, P., 2012. An overview of monitoring for raptors in Finland. *Acrocephalus* 33, 203–215. <https://doi.org/10.2478/v10100-012-0007-7>.
- Saurola, P., 2002. Natal dispersal distances of Finnish owls: results from ringing. In: Newton, I., Kavanagh, R., Olsen, J., Taylor, I. (Eds.), *Ecology and Conservation of Owls*. CSIRO Publishing, Collingwood, Australia, pp. 42–55.
- Saurola, P., Francis, C., 2018. Towards integrated population monitoring based on the field-work of volunteer ringers: productivity, survival and population change of Tawny Owls *Strix aluco* and Ural Owls *Strix uralensis* in Finland. *Bird Stud.* 65, 563–576. <https://doi.org/10.1080/00063657.2018.1481364>.
- Saurola, P., Francis, C.M., 2004. Estimating population dynamics and dispersal distances of owls from nationally coordinated ringing data in Finland. *Anim. Biodivers. Conserv.* 27, 403–415.
- Schipper, A.M., Wijnhoven, S., Baveco, H., van den Brink, N.W., 2012. Contaminant exposure in relation to spatio-temporal variation in diet composition: a case study of the little owl (*Athene noctua*). *Environ. Pollut.* 163, 109–116. <https://doi.org/10.1016/j.envpol.2011.12.020>.
- Seidensticker, J.C., Reynolds, H.V., 1971. The nesting, reproductive performance, and chlorinated hydrocarbon residues in the Red-tailed Hawk and Great Horned Owl in south-central Montana. *Wilson Bull.* 83, 408–418.
- Šere, D., 2009. A short report on birds ringed in Slovenia, 1983–2008. *Scopolia Suppl.* 4, 111–174.
- Sergio, F., Marchesi, L., Pedrini, P., Penteriani, V., 2007. Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Anim. Behav.* 74, 1607–1616. <https://doi.org/10.1016/j.anbehav.2006.10.022>.
- Shirihai, H., Dovrat, E., Christie, D.A., Harris, A., 1996. *The Birds of Israel*. Academic Press, London.
- Shore, R.F., Taggart, M.A., 2019. Population-level impacts of chemical contaminants on apex avian species. *Curr. Opin. Environ. Sci. Health* 11, 65–70. <https://doi.org/10.1016/j.coesh.2019.06.007>.
- Shore, R.F., Taggart, M.A., Smits, J., Mateo, R., Richards, N.L., Fryday, S., 2014. Detection and drivers of exposure and effects of pharmaceuticals in higher vertebrates. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 20130570. <https://doi.org/10.1098/rstb.2013.0570>.
- Silva, C.C., Lourenço, R., Godinho, S., Gomes, E., Sabino-Marques, H., Medinas, D., Neves, V., Silva, C., Rabaça, J.E., Mira, A., 2012. Major roads have a negative impact on the Tawny Owl *Strix aluco* and the Little Owl *Athene noctua* populations. *Acta Ornithol.* 47, 47–54. <https://doi.org/10.3161/000164512X653917>.
- Solonen, T., 2021. Does plumage colour signal fitness in the tawny owl *Strix aluco*? *J. Avian Biol.* 52, 1–7. <https://doi.org/10.1111/jav.02470>.
- Solonen, T., 2014. Timing of breeding in rural and urban Tawny Owls *Strix aluco* in southern Finland: effects of vole abundance and winter weather. *J. Ornithol.* 155, 27–36. <https://doi.org/10.1007/s10336-013-0983-y>.
- Solonen, T., 2011. Effects of variable food supply on the body condition of breeding tawny owls *Strix aluco* in southern Finland. *ISRN Zool.* 2011, 1–8. <https://doi.org/10.5402/2011/929460>.
- Solonen, T., af Ursin, K., 2008. Breeding of Tawny Owls *Strix aluco* in rural and urban habitats in southern Finland. *Bird Study* 55, 216–221. <https://doi.org/10.1080/00063650809461525>.
- Solonen, T., Ahola, K., Karstinen, T., 2015. Clutch size of a vole-eating bird of prey as an indicator of vole abundance. *Environ. Monit. Assess.* 187, 588. <https://doi.org/10.1007/s10661-015-4783-0>.
- Solonen, T., Karhunen, J., Kekkonen, J., Kolunen, H., Pietiäinen, H., 2017. Diet and reproduction in coastal and inland populations of the Tawny Owl *Strix aluco* in southern Finland. *J. Ornithol.* 158, 541–548. <https://doi.org/10.1007/s10336-016-1405-8>.
- Solonen, T., Lodenius, M., 1990. Feathers of birds of prey as indicators of mercury contamination in southern Finland. *Holarct. Ecol.* 13, 229–237. <https://doi.org/10.1111/j.1600-0587.1990.tb00613.x>.
- Southern, H.N., 1970. The natural control of a population of Tawny Owls (*Strix aluco*). *J. Zool.* 162, 197–285. <https://doi.org/10.1111/j.1469-7998.1970.tb01264.x>.
- Southern, H.N., 1969. Prey taken by tawny owls during the breeding season. *Ibis* 111, 293–299. <https://doi.org/10.1111/j.1474-919X.1969.tb02545.x>.
- Southern, H.N., Vaughan, R., Muir, R.C., 1954. *The behaviour of young Tawny Owls after fledging*. *Bird Study* 1, 101–110.
- Spina, F., Baillie, S.R., Bairlein, F., Ambrosini, R., Fattorini, N., Fiedler, W., Franks, S., Funghi, C., Thorup, K., 2022. *Eurasian-African Bird Migration Atlas*. EURING/CMS. <https://migrationatlas.org/>.
- Spina, F., Volponi, S., 2008. *Italian Bird Migration Atlas. Volume 2*. Ministero dell'ambiente e della tutela del territorio e del mare, Roma.
- Stanković, D., Punović, M., Raković, M., 2018. *Atlas of Migratory Birds and Bats of Serbia*, Knjiga. 46. ed. Ministarstvo zaštite životne sredine Republike Srbije, Ministarstvo kulture i informisanja Republike Srbije, Prirodnački muzej u Beogradu, Beograd.
- Steenhof, K., Newton, I., 2007. Assessing nesting success and productivity. In: Bird, D.M., Bildstein, K.L. (Eds.), *Raptor Research and Management Techniques*. Hancock House Publishers, Surrey, pp. 181–192.
- Stevens, D.K., Anderson, G.Q.A., Grice, P.V., Norris, K., Butcher, N., 2008. Predators of spotted flycatcher *Muscicapa striata* nests in southern England as determined by digital nest-cameras. *Bird Study* 55, 179–187. <https://doi.org/10.1080/00063650809461520>.
- Sunde, P., 2005. Predators control post-fledging mortality in tawny owls, *Strix aluco*. *Oikos* 110, 461–472. <https://doi.org/10.1111/j.0030-1299.2005.14069.x>.
- Sunde, P., 2008. Parent-offspring conflict over duration of parental care and its consequences in tawny owls *Strix aluco*. *J. Avian Biol.* 39, 242–246. <https://doi.org/10.1111/j.2008.0908-8857.04194.x>.
- Sunde, P., 2011. What do we know about territorial behaviour and its consequences in tawny owls? In: Zuberogoitia, I., Martínez, J.E. (Eds.), *Ecology and Conservation of European Forest Dwelling Raptors*. Departamento de Agricultura de la Diputación Foral de Bizkaia, Bilbao, pp. 253–260.
- Sunde, P., Bolstad, M.S., 2004. A telemetry study of the social organization of a tawny owl (*Strix aluco*) population. *J. Zool.* 263, 65–76. <https://doi.org/10.1017/S0952836904004881>.
- Sunde, P., Markussen, B.E.N., 2005. Using counts of begging young to estimate post-fledging survival in Tawny Owls *Strix aluco*. *Bird Study* 52, 343–345. <https://doi.org/10.1080/00063650509461409>.
- Sunde, P., Naundrup, P.J., 2016. Spatial and begging behaviours of juvenile Tawny Owls (*Strix aluco*) from fledging to independence under contrasting food conditions. *J. Ornithol.* 157, 961–970. <https://doi.org/10.1007/s10336-016-1344-4>.
- Sunde, P., Overskaug, K., Bolstad, J.P., Oien, L.J., 2001. *Living at the limit: ecology and behaviour of tawny owls Strix aluco in a northern edge population in Central Norway*. *Ardea* 89, 495–508.
- Surmacki, A., Podkowa, P., 2022. The use of trail cameras to monitor species inhabiting artificial nest boxes. *Ecol. Evol.* 12, 1–11. <https://doi.org/10.1002/ece3.8550>.
- Tenan, S., Adrover, J., Muñoz Navarro, A., Sergio, F., Tavecchia, G., 2012. Demographic consequences of poison-related mortality in a threatened bird of prey. *PLoS One* 7, e49187. <https://doi.org/10.1371/journal.pone.0049187>.
- Tennekes, M., 2018. tmap: thematic maps in R. *J. Stat. Softw.* 84, 1–39. <https://doi.org/10.18637/jss.v084.i06>.
- Thompson, D.R., Hamer, K.C., Furness, R.W., 1991. Mercury accumulation in great skuas *Catharacta skua* of known age and sex, and its effects upon breeding and survival. *J. Appl. Ecol.* 28, 672–684.
- Valkama, J., Saurola, P., Lehtikoinen, A., Lehtikoinen, E., Piha, M., Sola, P., Velmala, W., Forsman, D., Solonen, H., 2014. *The Finnish Bird Ringing Atlas. Volume II. LUOMUS - Finnish Museum of Natural History, Helsinki, Finland*.
- Van Den Burg, A.B., 2009. Limitations of owl reproduction in the wild: is there a role for food quality besides quantity. *Ardea* 97, 609–614. <https://doi.org/10.5253/078.097.0429>.
- van der Horst, S., Goytre, F., Marques, A., Santos, S., Mira, A., Lourenço, R., 2019. Road effects on species abundance and population trend: a case study on tawny owl. *Eur. J. Wildl. Res.* 65, 99. <https://doi.org/10.1007/s10344-019-1325-z>.
- van Oosten, H.H., van den Burg, A.B., Arlt, D., Both, C., van den Brink, N.W., Chiu, S., Crump, D., Jeppsson, T., de Kroon, H., Traag, W., Siepel, H., 2019. Hatching failure and accumulation of organic pollutants through the terrestrial food web of a declining songbird in Western Europe. *Sci. Total Environ.* 650, 1547–1553. <https://doi.org/10.1016/j.scitotenv.2018.09.138>.
- van Velden, J.L., Koeslag, A., Curtis, O., Gous, T., Amar, A., 2017. Negative effect of mite (*Knemidokoptes*) infection on reproductive output in an African raptor. *Auk* 134, 498–508. <https://doi.org/10.1642/AUK-16-134.1>.
- Varela, J., García-Seoane, R., Fernández, J.A., Carballeira, A., Aboal, J.R., 2016. Study of temporal trends in mercury concentrations in the primary flight feathers of *Strix aluco*. *Ecotoxicol. Environ. Saf.* 130, 199–206. <https://doi.org/10.1016/j.ecoenv.2016.04.006>.
- Verkuil, Y.I., Nicolaus, M., Ubels, R., Dietz, M.W., Samplonius, J.M., Galema, A., Kiebekos, K., de Knijff, P., Both, C., 2022. DNA metabarcoding quantifies the relative biomass of arthropod taxa in songbird diets: validation with camera-recorded diets. *Ecol. Evol.* 12, e8881. <https://doi.org/10.1002/ece3.8881>.
- Vik, J.O., 2017. *Diet and Diel Pattern in the Tawny Owl (Strix aluco)*. Norwegian University of Life Sciences, Faculty of Environmental Sciences and Natural Resource, Management MSc Thesis.
- Villafuerte, R., Viñuela, J., Blanco, J.C., 1998. Extensive predator persecution caused by population crash in a game species: the case of red kites and rabbits in Spain. *Biol. Conserv.* 84, 181–188. [https://doi.org/10.1016/S0006-3207\(97\)00094-3](https://doi.org/10.1016/S0006-3207(97)00094-3).
- Villarín Adánez, A., 2000. *Sex-specific comparative analysis of diet in the Tawny Owl Strix aluco in the Iberian Peninsula*. *Ardeola* 47, 203–213.
- Vrezec, A., 2003. Breeding density and altitudinal distribution of the Ural, Tawny, and Boreal owls in North Dinaric Alps (Central Slovenia). *J. Raptor Res.* 37, 55–62.
- Vrezec, A., Bertonec, I., 2018. Territory monitoring of Tawny Owls *Strix aluco* using playback calls is a reliable population monitoring method. *Bird Study* 65, S52–S62. <https://doi.org/10.1080/00063657.2018.1522527>.
- Vrezec, A., Duke, G., Kovács, A., Saurola, P., Wernham, C., Burfield, I., Movalli, P., Bertonec, I., 2012. Overview of raptor monitoring activities in Europe. *Acrocephalus* 33, 145–157. <https://doi.org/10.2478/v10100-012-0003-y>.
- Vrezec, A., Jernej Kodrič, M., 2021. Overview of owl fauna and the diet of the Tawny Owl (*Strix aluco*) at the remote island of Lastovo in the Adriatic Sea (southern Dalmatia, Croatia). *Larus-Godišnjak Zavoda za ornitologiju Hrvatske akademije znanosti i umjetnosti*. 56, pp. 56–66. <https://doi.org/10.21857/mlngc50ry>.
- Vrezec, A., Saurola, P., Avotins, A., Kocijančič, S., Sulkava, S., 2018. A comparative study of Ural Owl *Strix uralensis* breeding season diet within its European breeding range, derived from nest box monitoring schemes. *Bird Study* 65, S85–S95. <https://doi.org/10.1080/00063657.2018.1553026>.
- Vrezec, A., Tome, D., 2004. Altitudinal segregation between Ural Owl *Strix uralensis* and Tawny Owl *S. aluco*: evidence for competitive exclusion in raptorial birds. *Bird Study* 51, 264–269. <https://doi.org/10.1080/00063650409461362>.
- Weimeyer, S.N., Hoffman, D.J., 1996. Reproduction in eastern screech-owls fed selenium. *J. Wildl. Manag.* 60, 332–341. <https://doi.org/10.2307/3802232>.
- Wendland, V., 1984. The influence of prey fluctuations on the breeding success of the Tawny Owl *Strix aluco*. *Ibis* 126, 284–295. <https://doi.org/10.1111/j.1474-919X.1984.tb00251.x>.
- Wendland, V., 1972. Fourteen years observations on the reproduction of a Tawny Owl population. *J. Ornithol.* 113, 276–286.
- Wernham, C., Toms, C.V., Marchant, J.H., Clark, J.A., Siriwardena, G.M., Baillie, S.R., 2002. *The Migration Atlas: Movements of the Birds of Britain and Ireland*. T. & A. D. Poyser, London.
- Whitfield, D.P., McLeod, D.R.A., Watson, J., Fielding, A.H., Haworth, P.F., 2003. The association of grouse moor in Scotland with the illegal use of poisons to control predators. *Biol. Conserv.* 114, 157–163. [https://doi.org/10.1016/S0006-3207\(03\)00019-3](https://doi.org/10.1016/S0006-3207(03)00019-3).
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. v.3.3.3 (Version 3.3.3). <https://ggplot2.tidyverse.org/>.

- Williams, H.M., DeLeon, R.L., 2020. Deep learning analysis of nest camera video recordings reveals temperature-sensitive incubation behavior in the purple martin (*Progne subis*). *Behav. Ecol. Sociobiol.* 74, 1–12. <https://doi.org/10.1007/s00265-019-2789-2>.
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction With R*. 2nd ed. CRC Press/Taylor & Francis Group, Boca Raton.
- Yalden, D.W., 1985. Dietary separation of owls in the Peak District. *Bird Study* 32, 122–131. <https://doi.org/10.1080/00063658509476867>.
- Yatsiuk, Y., 2010. Usage of closed shelters by the Tawny Owl (*Strix aluco*) in the forest-steppe oak forest of the National Natural Park “Gomolshansky Forests” (Kharkov Region, Ukraine). *Branta* 13, 177–183.
- Yoccoz, N.G., Bustnes, J.O., Bangjord, G., Skaare, J.U., 2009. Reproduction and survival of tawny owls in relation to persistent organic pollutants. *Environ. Int.* 35, 107–112. <https://doi.org/10.1016/j.envint.2008.08.014>.
- Zalewski, A., 1994. Diet of urban and suburban tawny owls (*Strix aluco*) in the breeding season. *J.Raptor Res.* 28, 246–252.
- Zuberogoitia, I., Campos, L.F., 1998. Censusing owls in large areas: a comparison between methods. *Ardeola* 45, 47–53.
- Zuberogoitia, I., Martínez, J.E., González-Oreja, J.A., de Buitrago, C.G., Belamendia, G., Zabala, J., Laso, M., Pagaldai, N., Jiménez-Franco, M.V., 2020. Maximizing detection probability for effective large-scale nocturnal bird monitoring. *Divers. Distrib.* 26, 1034–1050. <https://doi.org/10.1111/ddi.13075>.