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Towards integrated population monitoring based on the fieldwork of volunteer ringers: productivity, survival and population change of Tawny Owls *Strix aluco* and Ural Owls *Strix uralensis* in Finland

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ABSTRACT

Capsule: Monitoring of demographic parameters by volunteer ringers provides insight into the factors driving population changes in owls.

Aims: To assess the value of national ringing, recapture and recovery data from volunteers to understand population dynamics.

Methods: We analysed 49 years of ringing, recapture and recovery data from throughout Finland for Tawny Owls *Strix aluco* and Ural Owls *Strix uralensis* and compared them with annual population and productivity indices from other volunteer-based surveys.

Results: Volunteer-based ringing data show that all aspects of the demography of Ural and Tawny Owls fluctuate dramatically in relation to an approximately three-year cycle of voles. When voles are abundant, a high proportion of owls breed and many young are produced; however, few of those young survive because vole populations crash the following winter. Survival of adults fluctuates less than that of young, suggesting that adults are better able to survive on alternative prey. In 2005, when vole populations remained high two years in row, many young were produced and survived, leading to a peak in owl breeding populations four years later at the top of the next vole cycle. This was immediately followed by a crash in populations suggesting a density-dependent interaction with vole abundance. Changing climate could affect owls both directly, by influencing winter survival, as well as indirectly through impacting prey availability.

Conclusion: Encouraging similar, volunteer-based national-scale ringing efforts for owls elsewhere in Europe, especially for Tawny Owls which occur in most countries, would be a cost-effective way to understand how factors such as changing prey availability, climate and habitat availability are influencing the population levels of this and other raptors.

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Well-planned long-term ecological monitoring programmes provide the foundation for effective conservation and management of our natural world (Baillie 1990). Humans have an enormous capacity to change the physical, chemical and biological environment of the Earth. Many human activities have negative effects on animal and plant populations. Short-sighted focus on immediate economic and social gain often leads to longer term negative impacts not only on ecosystems, but also on the interests of future human generations. Effective ecological monitoring programmes can be used to identify potential concerns before they become irreversible and also to provide information necessary to identify potential approaches to addressing concerns. Reliable information on changes in animal and plant populations is also important to evaluate the effectiveness of conservation and management actions, and adjust them as necessary (Williams 2011).

Monitoring of diurnal and nocturnal raptors can be used to provide information on the overall state of the environment, as well as directly benefiting conservation of the species concerned (Newton 1979). Because raptors are at the top of their food chains, changes in their numbers, productivity and survival may reflect changes in the ecosystem that also affect many other species including humans (Sergio *et al.* 2006). For example, dramatic declines in populations of several raptor species including Peregrine Falcons *Falco peregrinus* and Ospreys *Pandion haliaetus* provided strong evidence of the serious negative impacts of organic pesticides such as DDT (Dichlorodiphenyltrichloroethane) on ecosystems (Newton 1979, Risebrough 1986), which motivated efforts to control their use. Consequently, raptors have

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been proposed for use as environmental sentinels (Helander *et al.* 2008). In addition, many raptors have suffered from other environmental contaminants, habitat destruction, persecution and other negative impacts caused by humans (Newton 1979), with a result that many species have become endangered.

While many monitoring programmes focus on trends in population size, monitoring of demographic parameters such as survival and productivity can provide information on the underlying causes of population change (Baillie 1990, 1995, Baillie & Schaub 2009, Robinson *et al.* 2014). Among raptors, one of the most intensive studies has been the 30-year study in the northwestern United States of the demography of the Northern Spotted Owl *Strix occidentalis*. This very intensive (and hence expensive) study involved monitoring a range of demographic parameters with a large team of professional researchers, providing detailed information on the causes of population change to inform conservation planning for this threatened species (Forsman *et al.* 2011).

In this paper, we show how data collected by volunteers at a national scale can provide similar insight into raptor population dynamics. Many ecological monitoring programmes depend heavily upon the efforts of volunteers, often under the guidance of a government programme. For example, the North American Breeding Bird Survey, which now provides the foundation for much landbird conservation planning in North America, depends heavily upon volunteer field surveyors (Downes *et al.* 2016). Similarly, many programmes run by the British Trust for Ornithology and other programmes elsewhere in Europe depend upon the efforts of volunteers (Baillie 1995, Baillie & Schaub 2009, Vrezec *et al.* 2012, Robinson *et al.* 2014, Derlink *et al.* 2018).

In Finland, an exceptional network of volunteers has developed to monitor a range of demographic parameters for both diurnal and raptor species for more than half a century. Pioneering fieldwork in the early 1950s on both diurnal and nocturnal raptors by a well-known nature philosopher and voluntary ringer, Pentti Linkola, provided the stimulus and motivation for extensive voluntary work carried out by bird ringers and other bird watchers interested in raptors (Linkola & Myllymäki 1969). Since the early 1970s, the Finnish Ringing Centre has encouraged ringers to ring nestlings and to ring or recapture breeding adults at the nests of raptors for analysing annual survival and dispersal (Saurola 1987a). In 1982, a raptor monitoring project, the *Raptor Grid*, was started to obtain information from volunteer ringers on annual fluctuations and long-term changes in breeding populations of diurnal and nocturnal birds of prey, based on 10×10 km study plots (Saurola 1985). Further, in 1986 a *Raptor Questionnaire* project was started to obtain additional information on numbers of occupied territories, active nests, clutch and brood sizes (Saurola 2006).

This tremendous volunteer effort has been complemented by research and analyses by university and government researchers. Following Linkola's stimulus, long-term local population studies were started by a series of professional researchers, including many on two species of owls: the Tawny Owl *Strix aluco* and Ural Owl *Strix uralensis*. These included local studies starting in the 1960s on both species (Saurola 1987b, 1989); further studies started in the 1970s on the Ural Owl (Pietiäinen *et. al.* 1984, 1986, Pietiäinen 1988, Brommer *et al.* 2002, Pavón-Jordán *et al.* 2013) and Tawny Owl (Karell *et al.* 2009); and more in the early 1990s on the Tawny Owl (Solonen 2005, Solonen & af Ursin 2008). In addition, a number of studies have examined population change and demographic parameters of both Tawny and Ural Owls at a national scale using the large-scale databases of the Finnish Ringing Centre (Francis & Saurola 2002, 2004, 2009, Saurola & Francis 2004, Saurola 2007, 2008, 2009, 2012, Lehikoinen *et al.* 2011; see also Sundell *et al.* 2004).

These combined efforts have produced an exceptional database that can be used to estimate the full range of demographic parameters of these two species of owls, far exceeding data available elsewhere in Europe. In a recent review of raptor monitoring in Europe, Derlink *et al.* (2018) found that the breeding performance of the Tawny Owl has been monitored regularly (at least 10 years) in 12 of the 41 European countries (32%) where it breeds. Similarly, the breeding performance of the Ural Owl has been monitored in 8 of the 22 European countries (36%) where it breeds. In contrast, Newton *et al.* (2016) found in a recent review only four published studies on survival estimates of the Tawny Owl (three of which were from Finland) and one of the Ural Owl (also from Finland).

The objectives of our paper are (1) to provide details on the tremendous amount of demographic information that can be gained on raptors by combining the extensive field effort of dedicated amateur and professional bird-ringers with modern statistical analytical methods, using the Tawny Owl and Ural Owl as examples; (2) to encourage the national Ringing Schemes to use the 'free' and enthusiastic power of volunteer ringers for monitoring not only population size, but also demographic parameters of raptor populations elsewhere in Europe; and (3) to propose a Pan-European project for monitoring the demography of one or both of these species of owls. Expanding the geographic coverage of this project to cover much of the natural range of these species would be particularly valuable for assessing the impacts of new and emerging threats such as climate change.

Methods

Study species

The Tawny Owl and Ural Owl are both Palearctic medium-sized generalist predators. Although they can feed on a wide range of prey, for successful breeding both of them are highly dependent on microtine rodent populations, which tend to fluctuate more or less cyclically (Linkola & Myllymäki 1969). In Finland the most important species are the Field Vole *Microtus agrestis*, Bank Vole *Myodes glareolus* and Water Vole *Arvicola terrestris* (Saurola 1995). The Tawny Owl and Ural Owl are year-round residents and short-distance dispersers; about 90% of fledglings that were recaptured as breeders were found less than 50 km from their natal nest, and about 90% of breeders stay all their lives in the same territory (Saurola 1995, Saurola & Francis 2004).

Study area

The study area samples most of the breeding range of both Tawny and Ural Owls in Finland (Valkama *et al.* 2014). The Tawny Owl is a relatively recent arrival in Finland from the south, first recorded in 1875, with the first nest found a couple of years later (Saurola 1995). The present distribution of the Tawny Owl covers the southern quarter of Finland. The Ural Owl breeds throughout the mainland of the southern half of Finland but is rare along the southern and southwestern coastal areas (Saurola 1995). The nest-box programmes of ringers cover much of the Finnish distribution of both species (Saurola & Francis 2004).

Raptor grid

The *Raptor Grid* was started in 1982 by the Finnish Ringing Centre for monitoring all species of both diurnal and nocturnal raptors, with an emphasis on widespread and common species; prior to this, only selected endangered species were monitored (Saurola 2008). For the *Raptor Grid*, volunteer ringers devoted to raptors were asked to join in teams and select a 10 × 10 km study plot based on the Finnish National Grid. Within each plot, each year they try to locate all occupied territories of raptors and find as many active nests as possible (Saurola 1985). This provides information on the numbers of territorial pairs in the population, as well as the proportion of those that attempt to breed.

To accomplish this, volunteers: (1) listen for territorial hoots of owls; (2) watch for aerial displays of buzzards and hawks; (3) search for nests; (4) listen for fledged broods and (5) report all of their data in September to the Ringing Centre (Saurola 1985). Data reported include information on the numbers of observers and hours of effort expended in addition to the total numbers of birds, nests and broods detected. Most participants also provide information on the precise location of each nest, along with a nest record card providing details on the nest. To achieve fairly thorough coverage of all raptor species, about 300–500 person-hours/study plot/breeding season are needed in southern Finland with its mixture of boreal forest, agricultural land and lakes. Volunteers are encouraged to keep the effort within a study plot more or less the same from year to year; it is not necessary (or possible for some species) to have enough effort to detect every territorial raptor each year within each plot, but consistency over time in the amount of effort and spatial coverage is important.

The number of *Raptor Grid* study plots surveyed during 1982–2016 averaged 130 per year with, most recently, 142 in 2015 and 123 in 2016 (Meller *et al.* 2017).

Raptor questionnaire

Since 1986, additional information on productivity has been requested from bird ringers using the *Raptor Questionnaire* (Saurola 2006). Information requested includes: (1) the total numbers of potential territories and nests checked, including nest boxes and natural cavities for owls; (2) the total number of occupied territories found (including those where birds did not breed) as well as the number of active nests and (3) the productivity of occupied nests, in terms of clutch and brood sizes. At almost all of these nests, the young are also ringed. This information is collected both from *Raptor Grid* study plots, as well as from additional areas where ringers are working. The number of completed forms varies between years. In 2016, 226 individual ringers or teams filled 317 *Raptor Questionnaire* forms. To complete these forms, just for 2016, a total of 38 358 potential nest sites of raptors and owls were inspected, including 3241 nest boxes for Tawny Owls, 4121 for Ural Owls, 5190 for the Pygmy Owls *Glaucidium passerinum*, 4914 for the Boreal Owls *Aegolius funereus* and 1629 large and 1535 small natural cavities suitable for owls. Altogether 7627 occupied territories including 5406 active nests of common diurnal raptors and 4955 occupied territories including 3005 active nests of owls were found and reported (Meller *et al.* 2017).

Most raptor ringers survey their ringing territory with about the same intensity from year to year, which means that at least a part of the *Raptor Questionnaire*, which is a much larger data set than that of the *Raptor Grid*, is also comparable and useful for monitoring changes in the breeding population. In any case, the *Raptor Questionnaire* is a vital source of data for monitoring population trajectories of rare, northern and nomadic species and for monitoring productivity of all raptor species.

Ringing, recapture and recovery data

Particularly since the early 1970s, the Finnish Ringing Centre has encouraged ringers to ring nestlings and ring-and-recapture breeding adults at nests of all raptor species (Saurola 1987a). This has been particularly effective for both Ural and Tawny Owls, as most individuals of both species in Finland now nest largely in nest boxes provided by ringers. This makes it relatively easy to check the nests and to ring the young and to catch the female by trapping her inside the box. Some ringers make the additional effort to also capture the male (Saurola 1987b). Since the inception of the ringing scheme in the early 1900s until the end of 2016, a total of 66 404 Ural Owls have been ringed and 18 811 encounters recorded. Corresponding totals for the Tawny Owl are 54 561 and 14 604 (Valkama & Piha 2017).

In our survival analyses, for the period 1968–2006 inclusive, we used data from 60 500 Ural Owls ringed as nestlings and 5420 ringed as breeding adults. Of these, 5345 were recaptured at least once in subsequent years (for a total of 14 492 live recaptures including birds caught in multiple years), usually by ringers at a nest box, and 3244 were recovered dead, usually by members of the public (we included recoveries for which condition was not known, most of which were likely dead). For Tawny Owls, the totals were 46 791 ringed as nestlings and 5171 ringed as breeding adults, of which 4176 were recaptured alive at least once in subsequent years (with a total of 8258 live recaptures), and 5369 were recovered dead.

Statistical analysis

Population trends

Data from the *Raptor Grid* were used to estimate changes in population size. Calculations of the population indices were based on both occupied territories, called here the *territory-index*, and on numbers of active nests, called here the *nest-index*. While an effort was made to retain the same set of study plots over time, many plots became inactive and new ones emerged during 36 years, because of the voluntary basis of the fieldwork.

We used program TRIM (Pannekoek & van Strien 2004) to estimate the annual indices for each species, as has been done since 2007 (Saurola 2009, 2012). Program TRIM imputes missing values for sites that were not surveyed in every year, thus allowing inclusion of the complete data set. Within the program, the options *time effects*, *overdispersion* and *serial correlation* were selected. We used program PIA (Anders Bignert, Swedish Museum of Natural History; Bignert 2003) to estimate the average annual change per year in indices on the basis of ordinary log-linear regression.

Productivity

Average annual productivity was calculated on the basis of national data gathered by the *Raptor Questionnaire*. The total number of large young produced was related to (1) the total number of occupied territories, (2) the number of active nests (i.e. nests in which eggs were laid) and (3) the number of successful nests (i.e. nests in which large young were produced).

Survival analysis

We estimated survival, recapture and recovery probabilities using the joint recapture and recovery model of Burnham (1993) in a hierarchical Bayes framework, using the methods described by Francis & Saurola (2009). These combined models allow estimation of relatively precise age-specific survival probabilities with little apparent bias due to emigration from the study areas (Francis & Saurola 2002). These models estimate four classes of parameters: survival (Φ) – the probability that an animal alive at the beginning of the year (here defined as 1 June) will be alive the following year; recapture (p) – the probability that a marked individual alive and present in the study population will be recaptured in a particular year; recovery (r) – the probability that an individual that dies in a particular year will be found and its ring number reported to the ringing office and 'fidelity' (F) – the probability that a marked surviving individual that was in the local population the previous year is still in the population available for recapture. In this study, the fidelity parameter is difficult to interpret biologically because both recaptures and recoveries occurred over a large geographical area (Francis & Saurola 2004); hence it does not actually provide an estimate of fidelity to a particular breeding location. Rather, it estimates the probability that a bird will return to breed in an area where a ringer is working.

We used models in which survival and recapture probabilities were allowed to differ with age over four age classes, while recovery probabilities and fidelity parameters were allowed to differ only between young birds and older birds. Birds ringed as 'adults' were treated as if they were all in the highest age class, although a few of them were probably in their second or third year (Francis & Saurola 2002).

All parameters were assumed to vary between years and estimated with hierarchical Bayesian models fitted using the Markov chain Monte Carlo (MCMC) option in program MARK (White & Burnham 1999). For each set of age-specific parameters, we imposed a hierarchical structure to the annual parameters by defining hyper-distribution priors using a hyperdesign matrix (White *et al.* 2009; see Francis & Saurola 2009 for more details on the models). For the graphical analyses presented here, we assumed a simple normal prior, with the logit transformed annual survival, recapture, recovery and fidelity parameters for both first year and adults assumed to come from a normal distribution with a specific mean and variance but no covariates. This approach tends to shrink imprecise estimates towards the mean, thus reducing the impacts of annual variation in sample size. Following Francis & Saurola (2009), we modelled second and third year survival and recapture parameters to be equal to those of adults minus a difference parameter (on a logit scale). The difference parameters were allowed to vary among years, but with a prior hyper-distribution imposed on the differences, thus tending to reduce them towards the mean difference. This results in survival estimates for these age classes that tend to fluctuate in parallel with adults unless strong data indicate to the contrary.

We also ran models in which we added covariates to the hyper-distributions to estimate the impacts of vole abundance on survival and recapture probabilities, following Francis & Saurola (2009). Vole abundance in each year was classified into one of three categories. For capture probabilities, voles were modelled as Poor – scarce in spring; Moderate – moderately abundant in spring; and Good – abundant in spring. For survival, they were modelled as Poor – abundant in spring but crashing after the breeding season; Moderate – low at the start of the year, but gradually increasing over the year; and Good – moderate early in the year and increasing over the rest of the year. Years were categorized based on general field observations of voles throughout southern Finland (Meller *et al.* 2017), because long-term quantitative prey abundance data were only available from a few local studies. To complete the hierarchical model, standard non-informative priors were placed on the coefficients of the means and variance parameters (σ^2) for the hyper-distributions, as well as any parameters constrained to be constant over time, as described by White *et al.* (2009).

Because of the complexity involved with editing the large Parameter Index Matrices, the Design Matrix and the Hyperdesign Matrix, the input files for the analyses were created using custom-written programs in SAS 9.4 (SAS Institute 2003), and run using the MARK batch facility. All MCMC models were run with the default options in MARK, using a random starting point, 1000 burn-in samples, 4000 tuning samples, and 10 000 iterations in each chain with a minimum of two chains for each model. We have previously shown (Francis & Saurola 2009) that this is sufficient to get reliable estimates with 2 or 3 significant digits. We also used SAS to summarize the output from the MCMC coda files. We graph the resultant parameters together with their 95% posterior credible confidence intervals.

Results

Population trend

For the Ural Owl, during 1982–2016, the territory-indices fluctuated between 0.67 and 2.01 and the nest-indices between 0.29 and 2.07 (Figure 1, left). The cyclic pattern of fluctuations was as follows: five cycles of three years (two high years and one low), followed by two cycles of four years (three and one) and then two more cycles of three years. The index of breeding pairs reached an all-time peak in 2009, followed by a deep crash in 2010. Subsequently, the amplitude of annual fluctuations has been reduced. The nest-indices fluctuated much more than the territory-indices, indicating that even in years when few birds breed, many were still available to be counted on their occupied territories. Ordinary log-linear regression analysis shows that the territory-index increased by an average 1.1% ($P < 0.01$) and the nest-index by 1.6% ($P < 0.05$) per year during the last 36 years.

During 1986–2016, the annual totals of occupied territories (range = 422–1710), active nests (range = 198–1566) and successful nests (range = 168–1341) recorded by the *Raptor Questionnaire* for this species varied considerably. The much larger, but less consistent data from the *Raptor Questionnaire* gave the same pattern of fluctuations of both territory and nest-indices of Ural Owls during 1986–2016 as the *Raptor Grid* (correlation $r = 0.99$).

For the Tawny Owl, the territory-index fluctuated between 0.63 and 1.97 and the nest-index between 0.46 and 1.97, both without showing any long-term trends (Figure 1, right). As with the Ural Owl, the nest-index showed much larger fluctuations than the territory-index.

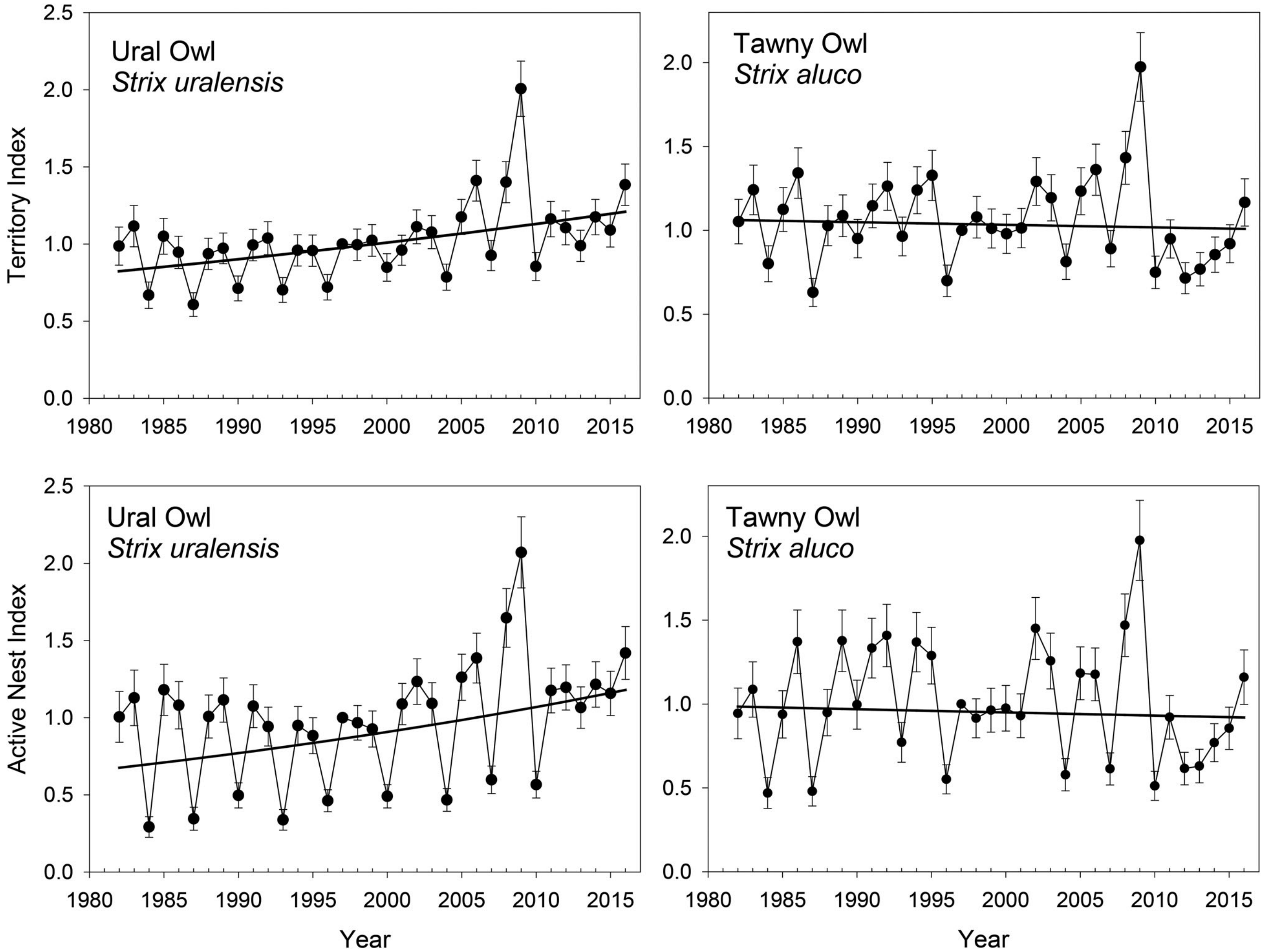

Figure 1. Annual population indices of Ural Owls (left) and Tawny Owls (right) in Finland calculated from the numbers of occupied territories (top) and active nests (bottom) recorded in the *Raptor Grid* study plots during 1982–2016. Vertical bars indicate standard errors. Thick line = log-linear regression line. Ural Owl: Annual change 1982–2016 of territory-index = 1.1% / year ($P < 0.01$ and of nest-index = 1.6% / year ($P < 0.05$). Tawny Owl: Annual change 1982–2016 of both territory and nest-indices = −0.2% / year (NS).

Annual totals of occupied territories (range = 287–857), active nests (range = 125–807), and successful nests (range = 98–681) of the Tawny Owl recorded by the *Raptor Questionnaire* in 1986–2016 varied largely as in the Ural Owl. Also, as in the Ural Owl, the *Raptor Questionnaire* data gave very precisely the same general pattern ($r = 0.99$) of the annual fluctuations of the Finnish Tawny Owl population indices during 1986–2016 as the *Raptor Grid*.

The time-series of both the territory-index ($r = 0.99$) and nest-index ($r = 0.96$) of the Tawny Owl are highly correlated with those of the Ural Owl. The synchrony of the two species is not surprising, as the data come from heavily overlapping study areas and the breeding performance of both species is highly dependent on cyclic vole populations. The lower fluctuations in the time-series of nest-indices for Tawny Owl suggest that this species is a bit less dependent on voles than the Ural Owl.

Productivity

The national time-series on the productivity of Ural and Tawny Owls (Figure 2) based on the *Raptor Questionnaire* data 1986–2016 resembled the general pattern of corresponding population indices (Figure 1). The correlation between the time-series of population indices and productivity (young per active nest) was quite high (0.74 in the Ural Owl and 0.71 in the Tawny Owl). Thus, when the number of breeding pairs was high, the number of young birds produced per breeding pair was also high. As a result, the total number of new individuals produced into the population was up to 10–15 times higher in a peak year than in a low year.

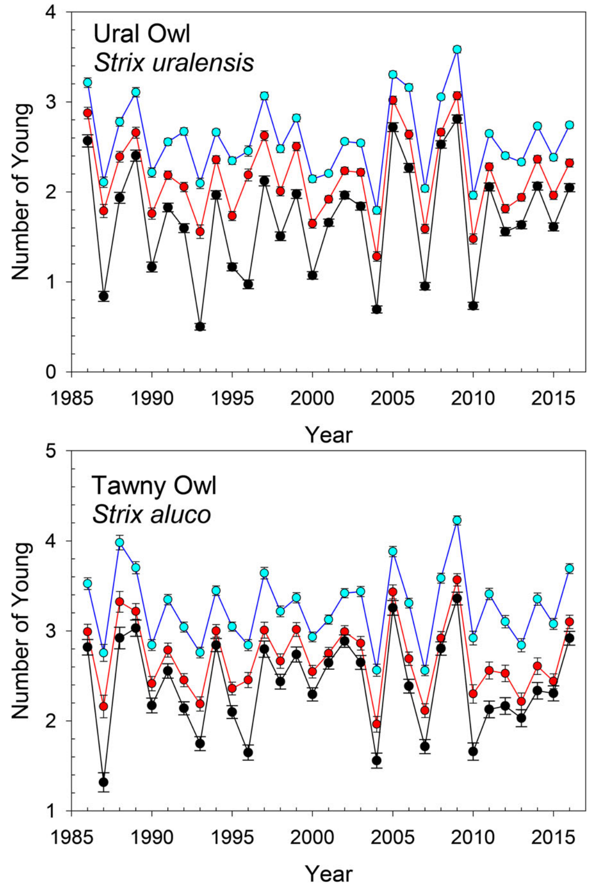

Figure 2. Average annual productivity (filled circles) of Ural Owls (top) and Tawny Owls (bottom) during 1986–2016 based on data from the *Raptor Questionnaire*. Blue = young per successful nest, red = young per active nest and black = young per occupied territory.

In the Ural Owl, the highest productivity in the study period was recorded in 2009, when the number of young produced was 2.8 per occupied territory, 3.1 per active nest and 3.5 per successful nest. The lowest annual numbers of young produced were 0.5 per occupied territory (1993), 1.48 per active nest (2010) and 1.79 per successful nest (2004). The annual total number of young produced by the Ural Owls recorded by the *Raptor Questionnaire* varied from 352 in 1993 to 4805 in 2009.

The productivity of the Tawny Owl also peaked in 2009 and was 3.35 per occupied territory, 3.57 per active nest and 4.23 per successful nest. The lowest numbers of young recorded per year were 1.32 per occupied territory (1987), 1.96 per active nest (2004) and 2.56 per successful nest (2004 and 2007). The total number of young produced per year varied from 270 in 1987 to 2879 in 2009.

No long-term trends in productivity were found in either species.

Survival

The time-series for ringing data extends back much earlier than that for the other monitoring programmes, allowing estimates of survival, recapture and recovery probabilities over a 49-year period (Figure 3).

Survival probabilities of all age classes of both species fluctuated considerably among years in a very similar fashion to each other, but with slightly different patterns than productivity. Fluctuations were greatest for first year survival, ranging from a high in 1988 of 65% for Ural Owl and 56% for Tawny Owl, to a low for both species in 2009 of 18% for Ural Owl and 15% for Tawny Owl. In most years, first year survival was lowest immediately following a year of high productivity, indicating that most of the young in those high productivity years failed to become breeders. In general, adult survival fluctuated much less than that of young, but adult survival of both species dropped substantially in 2009, the same year the first year survival was at its lowest level. Overall survival probabilities of Ural Owls were higher than those of Tawny Owls.

Capture probabilities

Recapture probabilities (probability that a bird alive in the population at that time was captured and ringed) can be considered as an index of breeding propensity, as most birds were captured in a nest box when they were breeding (Figure 3). Thus, non-breeders were very rarely captured.

First year recapture probabilities (probability a bird was recaptured breeding at the age of 1 year old, after surviving its first year) were generally much lower for Ural Owl (frequently less than 1% with only one year as high as 15%) than Tawny Owl (only a few years <10%, with the lowest year at 3%, and one year as high as 40%).

For both species, capture probabilities continued to differ at the age of 2 and 3 years from those of adults, especially for Ural Owls, indicating that it took at least four years before these species were able to breed regularly (Figure 3). Fluctuations in recapture probabilities for all age classes were highly synchronized, and generally matched those found in the *Raptor Questionnaire* (Figure 2) for years when we had data from both sources.

Recovery probabilities

Recovery probabilities, which represent the probability that a bird that has died will be found and reported, were higher for adults than for young (Figure 3), indicating that adults were more likely to die in places

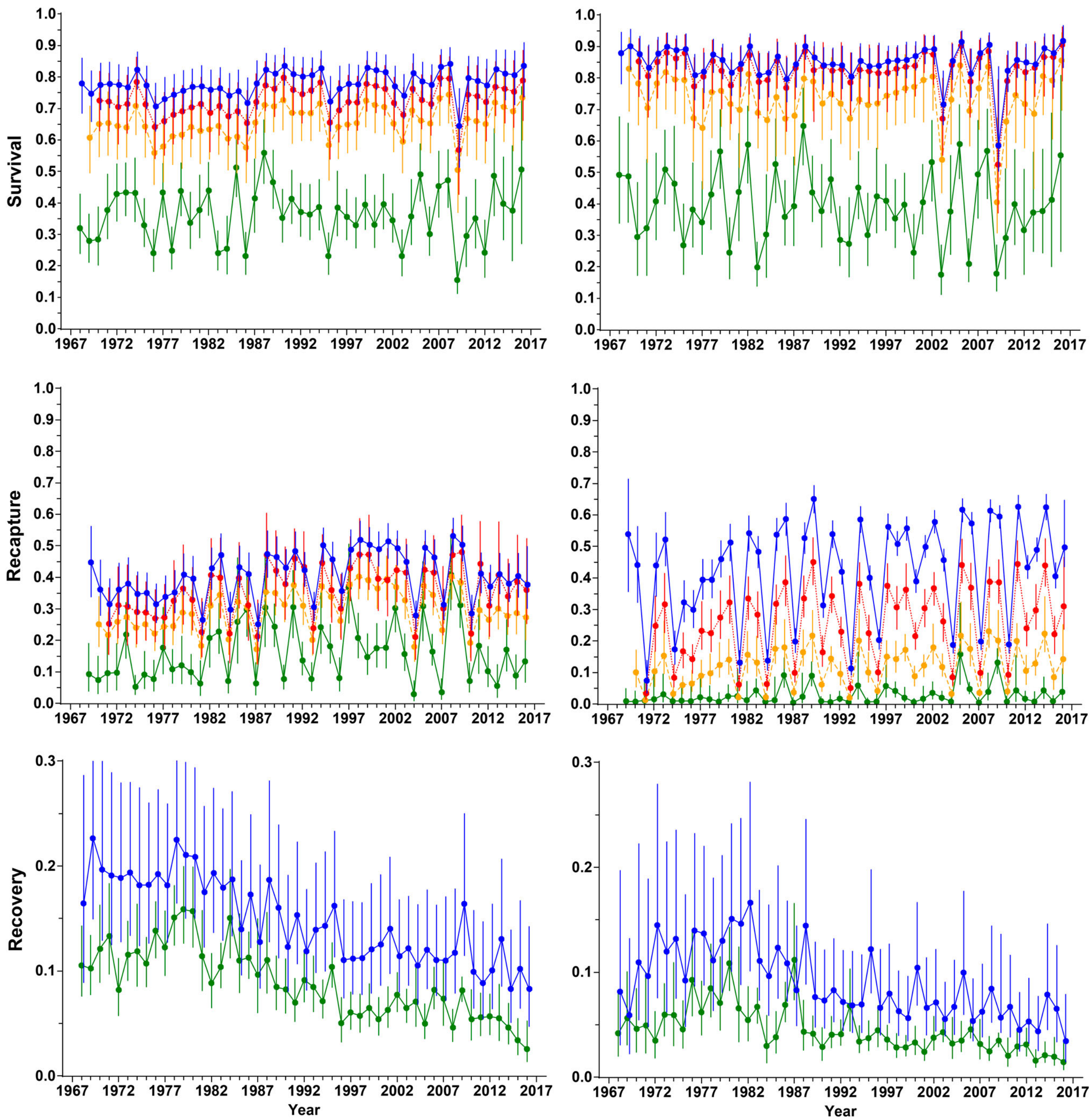

Figure 3. Estimated annual survival probabilities (top), recapture probabilities (middle) and recovery probabilities (bottom) with 95% credible intervals for Tawny Owls (left) and Ural Owls (right) during 1968–2016, in their 1st (green), 2nd (yellow), 3rd (red) and later (blue) years of life.

or at times where humans might find them. Recovery rates for both species showed a clear long-term decline, dropping in recent years to less than half of what they were in the late 1960s. Recovery rates of Ural Owls were generally somewhat lower than those of Tawny Owls.

Table 1. Mean (± standard error) proportion of occupied territories where nests were active (eggs laid), and mean number of young fledged per active nest for Tawny and Ural Owls in relation to abundance of voles during the breeding season (see Figure 4).

	Tawny Owl			Ural Owl		
	Low	Moderate	High	Low	Moderate	High
Nests/Territory	0.81 ± 0.03	0.92 ± 0.01	0.92 ± 0.01	0.63 ± 0.06	0.84 ± 0.03	0.88 ± 0.03
Young/Nest	2.38 ± 0.09	2.82 ± 0.09	2.93 ± 0.14	1.84 ± 0.11	2.23 ± 0.09	2.48 ± 0.16

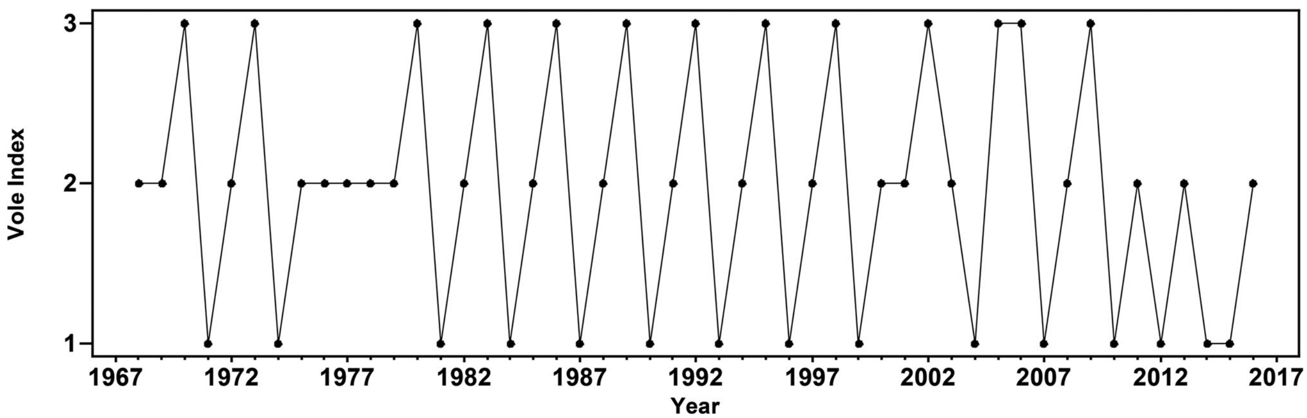

Figure 4. Annual variation in the abundance of voles at the time of nesting, where 1 = low, but increasing after the nesting season, 2 = moderate and usually (but not always) increasing after the nesting season and 3 = high, but usually (with the exception of 2005) crashing after the nesting season.

Vole cycles

A substantial portion of the annual variation in all demographic parameters can be explained by a simple index of vole abundance (Figure 4). Fluctuations in numbers of breeding pairs (Figure 1), productivity (Figure 2), and survival and recapture probabilities (Figure 3) generally match those of the voles (Figure 4), especially during periods of regular 3-year vole cycles. On average, the proportion of occupied territories that had nests and the mean number of young per nest were substantially lower in years when vole populations were low during the breeding season (Table 1). Similarly, capture probabilities were substantially lower in years of low prey abundance (Table 2) reflecting lower breeding probability. The differences between high and low vole years were greater in the Ural Owl, with nearly a two-fold average difference in capture probability (breeding propensity) of adults between Good and Poor years (Table 1). For both species, the differences were greatest for first year birds, for which capture probabilities in years of low prey abundance were about half those in high prey years, suggesting they were half as likely to attempt breeding in years when prey was scarce.

On average, first year survival was highest in years when voles started as moderate but increased over the year, and lowest in years when prey were abundant at the beginning of the season, then crashed (Table 2). Adult survival was similar in moderate and good years, but significantly lower in poor years when vole populations crashed.

Discussion

Our analyses show that it is possible to get very high-quality demographic monitoring data on raptors based largely on the efforts of dedicated volunteers. All demographic parameters, including population indices, breeding propensity, nest success and survival probabilities were estimated with high precision over a very long time period (Figures 1–3). Robinson *et al.* (2014) also demonstrated that volunteer-collected monitoring data from the UK, including population indices, productivity from nest records, and survival estimates from ringing and recovery data, can be used to generate integrated population models to understand population change for a range of species. They found that their model did not work as well for Tawny Owls as for many passerines, but they attributed this to the fact that their population monitoring was based on daytime surveys in the peak passerine breeding season, when owls are rarely detected. The demographic information on the Ural and Tawny Owls in Finland is exceptionally good because these are resident species (Saurola 2002, Saurola & Francis 2004), the population monitoring is designed specifically for raptors, and the Ringing Centre has encouraged ringers to collect data for capture–recapture analysis as well as nesting data (Saurola 1987a).

The results of our analyses are consistent with previous local and shorter term studies highlighting the pivotal importance of fluctuating vole populations in the demography of these two species in Fennoscandia (Francis & Saurola 2002, 2004, 2009, Saurola & Francis 2004, Solonen 2005, Solonen & af Ursin 2008, Karell *et al.* 2009, Millon *et al.* 2009, Pavón-Jordán *et al.* 2013). Similar fluctuations in demographic parameters have been found in other species of resident northern breeding owls that feed on cyclically fluctuating populations of rodents or lagomorphs (Newton 2002).

Our new, national-scale analyses highlight several aspects of the population dynamics of Ural and Tawny owls. Both species are highly affected, in similar ways,

Table 2. Mean (± standard error) survival (**Φ**) and capture (**P**) probabilities of first year and adult Tawny and Ural Owls in relation to changes in vole abundance (Figure 4). For survival: Poor years = voles were high during the breeding season, but crashed over the following winter; Medium years = voles were low or moderate during the breeding season, but increased to moderate over the following winter; Good years = voles were moderate during the breeding season and increased to abundant over the following winter. For capture probabilities, Poor, Medium and Good were determined based on vole abundance during the breeding season.

	Tawny Owl			Ural Owl		
	Poor	Medium	Good	Poor	Medium	Good
Φ adult	0.74 ± 0.02	0.81 ± 0.02	0.80 ± 0.02	0.81 ± 0.02	0.87 ± 0.015	0.88 ± 0.014
Φ young	0.28 ± 0.03	0.37 ± 0.03	0.42 ± 0.03	0.27 ± 0.03	0.39 ± 0.04	0.51 ± 0.04
P adult	0.36 ± 0.02	0.43 ± 0.02	0.43 ± 0.02	0.29 ± 0.03	0.49 ± 0.04	0.51 ± 0.04
P first year	0.09 ± 0.02	0.18 ± 0.03	0.18 ± 0.03	0.01 ± 0.003	0.02 ± 0.01	0.04 ± 0.01

by fluctuations in prey abundance, with high variation among years in the number of active nests (Figure 1) and in the number of young produced per active nest (Figure 2). There was much less variation in adult survival (Figure 3), indicating that many adults were still alive in years of low vole abundance, but did not breed. This is consistent with the lower variation in the territory-index (Figure 1).

The high productivity in years of high vole abundance did not usually result in a large increase in owl populations, because survival of these young was usually very low in the subsequent year, when vole densities were low. The one exceptional situation was in 2005, when there was very high productivity, but there was also very high survival of the young probably because vole populations remained high for a second year (Figure 4). This resulted in many surviving young available and ready to breed in 2009 when the vole populations next peaked. The result was exceptionally high production of young in 2009, followed by very high mortality of all age classes. The high mortality presumably reflects some level of density-dependent mortality (Saether *et al.* 2016), driven by a crash in prey populations and intense competition for remaining voles and other prey.

Information on recovery rates also provides insights into the cause of death of different age classes. The lower recovery probability for young seems counter-intuitive because, in general, slightly more birds ringed as young were recovered in their first year of life than later. The explanation is that many more birds die in their first year. On average, in years when prey was abundant at the beginning of the year (so many birds bred and lots of young were produced), survival was exceptionally low, with more than 70% of birds dying. Thus, although a smaller percentage was reported, the actual number was similar or higher. Recovery probabilities are a function of the bird being found by a human, and subsequently reported. It is unlikely that age of the bird would affect the reporting probability, so the difference indicates that the age classes die in different ways or places or at different times of year. The lower recovery rate of young owls suggests they are more likely to die of natural causes in the forest away from humans. This is consistent with the findings of Overskaug *et al.* (1999) in Norway and Sunde (2005) in Denmark who found that many radio-tracked young died near their nests, often from predation. In contrast, adults may be more likely to die in ways that humans might find them (e.g. from collisions on roads). The lower recovery probabilities for Ural Owl probably reflect its more northern distribution, slightly farther away from most humans.

One limitation of the population monitoring data is that they provide incomplete information on non-breeders. Younger birds that are not yet ready to breed are unlikely to defend territories and hence not included in the territory surveys. As such, their abundance can only be inferred indirectly based on survival models. However, there are several lines of evidence that fluctuations in the territory-index do represent fluctuations in the numbers of surviving older birds, and not just the number that breed. First, the territory-index fluctuates much less than the nest-index (Figure 1), indicating that many birds, even if they fail to breed, continue to occupy territories. The proportion of territorial birds that nest varies among years, particularly in relation to prey availability (Table 1). Second, we have previously shown that simple deterministic matrix models based on survival and productivity estimates in relation to the vole cycle produce fluctuations in adult populations that are similar to those observed in territory-indices, at least during periods of regular vole cycles (Francis & Saurola 2004). Finally, use of mark-recapture models to estimate population change using the models of Pradel (1996) indicated generally similar fluctuations to those observed in the territory-indices (Francis & Saurola, unpubl. data). Integrated population models (Schaub & Abadi 2011, Robinson *et al.* 2014) would provide a formal approach for estimating missing parameters, including the numbers of pre-breeders and the numbers of breeding adults that were not detected, but we have not yet implemented such models with these data.

Some of the most intensive demographic monitoring programmes have been associated with rare or endangered species. For these species, monitoring is needed to understand the factors that are driving, or have driven, population declines so that efforts can be made to reverse them. One of the most intensive studies of a wild raptor population has been the study, over more than 30 years, of the endangered Northern Spotted Owl in the northwestern United States, leading to a detailed report involving 27 leading specialists in population ecology and biostatistics (Forsman *et al.* 2011).

Monitoring of more common raptor species, which are not yet endangered, is also important for monitoring the health of ecosystems, for providing baseline data in case populations later decline, and for understanding interactions among organisms. Global climate change is currently leading to dramatic changes in ecosystems that are affecting populations of many wildlife species. For example, we have previously shown that survival of Tawny Owls (although not necessarily other demographic factors) is also influenced by the severity of winter weather (Francis & Saurola 2004), which has been changing rapidly in Finland. Variation in winter weather might directly affect their survival, through affecting ability to catch prey (which could be harder to detect or catch in deep snow), or indirectly by affecting the abundance of prey. Information from elsewhere in their range would be valuable for understanding the likely implications of these changes. Increasing populations of one species can potentially have negative impacts on others. For example, the rapid expansion of the distribution of a common species, the Barred Owl (*Strix varia*), has been shown to be one of the factors with negative effects on the endangered Spotted Owl (Forsman *et al.* 2011).

We believe that the examples based on the Finnish data on Tawny and Ural Owls presented here highlight the value of engaging dedicated volunteers in monitoring programmes. Bird ringers tend to be idealistic individuals prepared to conduct meticulous fieldwork needed for monitoring. They are well-trained *amateurs* i.e. 'lovers' of birds, with highly professional skills, equally or even more committed to their fieldwork than many paid biologists. Government agencies with responsibility for wildlife conservation could take advantage of this enthusiasm and skill to develop relatively low cost but very effective monitoring programmes for owls and other raptors. Only some extra administrative support is needed in the ringing centres – in addition to the costs of their normal routines – to develop effective monitoring programmes for these species. In Finland, the Ministry of Environment has paid the costs of one extra clerical staff member of the Ringing Centre responsible for the administration (including study design, encouragement of participation, data management and annual reporting of the results) of the *Raptor Grid, Raptor Questionnaire* and Project Pandion monitoring programmes based on the voluntary fieldwork of several hundred amateur ringers each year (see Saurola 2008, 2012).

Engagement of the broader public can also enhance the quality of the monitoring. For example, recoveries from the general public are important to ensure that survival estimates are not biased by local emigration, which is a common problem for many mark-recapture studies. The long-term decline in recovery rates suggests that people are now less likely to find and report rings than in the past (Saurola *et al.* 2013, Valkama *et al.* 2014). Efforts may be needed to encourage greater reporting rates. New technologies such as smart phones and web applications for reporting – and providing instant feedback – may attract younger generations to greater participation. Requesting photographs of recovered birds or rings, with GPS coordinates from smart phones can help to verify data and improve accuracy.

Concluding proposal

The high scientific and conservation value of the volunteer-based ringing of owls and other raptors in Finland, as shown in this paper, suggests there could be considerable value to expanding efforts throughout much of Europe. One of the objectives of EURAPMON, the ESF Research Networking Program 2010–15 was to establish a pan-European, dynamic network of raptor researchers (Vrezec *et al.* 2012). There were also discussions about developing a volunteer-based pan-European integrated monitoring project on some common and widespread raptor species. We suggest that the Tawny Owl would be a good candidate for such a coordinated pilot programme for several reasons. Encouraging ringers to participate in a continental programme for a single species could likely be done with existing staff in many ringing centres.

The Tawny Owl is a relatively common breeder all over Europe except Ireland and the northern parts of Fennoscandia and Russia (Petty & Saurola 1997). In addition, the Tawny Owl is a cavity breeder, which can be easily attracted to breed in nest boxes (Meller *et al.* 2017). Monitoring breeding success, through collecting data on eggs, nestlings and prey is much easier in nest boxes than in natural cavities. In addition, techniques are well established for capturing both adults in the nest box (Saurola 1987b). Both sexes of the Tawny Owl are relatively site faithful (Saurola 1987b), thus allowing high year-to-year recapture probabilities, improving data quality for estimating survival, in addition to productivity and population changes. However, some care is needed in studying the Tawny Owl, because it may desert the nest if disturbed too often during incubation (Kania 1992).

Such a continental-scale programme would be particularly valuable for understanding the impacts of changing environments, including climate change, on ecosystems, using the Tawny Owl as an indicator. Studying a species throughout its range allows understanding of population responses to different climatic scenarios, which is essential to model accurately the impacts of future change. The Tawny Owl also breeds in a range of environments, from natural wild habitats to areas close to human settlements. Monitoring a gradient of rural to urban habitats can provide valuable information on the condition of these environments and how they are changing over time (Solonen & af Ursin 2008).

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