

# Estimating population dynamics and dispersal distances of owls from nationally coordinated ringing data in Finland

P. Saurola & C. M. Francis

Saurola, P. & Francis, C. M., 2004. Estimating population dynamics and dispersal distances of owls from nationally coordinated ringing data in Finland. *Animal Biodiversity and Conservation*, 27.1: 403–

## Abstract

*Estimating population dynamics and dispersal distances of owls from nationally coordinated ringing data in Finland.*— Amateur bird ringers can collect data at a geographic and temporal scale that is rarely possible with professional field crews, thus allowing truly national analyses of population dynamics and dispersal. Since the early 1970s, bird ringers in Finland have been strongly encouraged to focus on birds of prey, especially cavity-nesting owls. In addition to ringing nestlings and adults, ringers also provide data on population trends and breeding success. The resultant data indicate that numbers of breeding pairs fluctuated with the 3–4 year microtine cycle, but without any long-term trend. Mean productivity per nest varied from 2.18 to 3.33 fledglings per active nest in Tawny Owls, 1.56 to 2.87 in Ural Owls and 1.78 to 4.32 in Tengmalm's Owls. Survival and breeding propensity also varied with the vole cycle and explained much of the observed variation in breeding populations. Observed median dispersal distances were 24 and 18 km for Ural and Tawny Owls respectively, but increased to 36 and 48 km, using a method presented here to adjust for uneven sampling effort, highlighting the importance of considering sampling effort when estimating dispersal.

Key words: Amateur ringers, Natal dispersal, Population modelling, Mark-recapture analysis, Tawny Owl, Ural Owl, Tengmalm's Owl.

## Resumen

*Estimación de la dinámica poblacional y de las distancias de dispersión en los búhos, efectuada utilizando datos de anillamiento de Finlandia coordinados a escala nacional.*— Los anilladores aficionados pueden recopilar datos a una escala geográfica y temporal que rara vez está al alcance de los equipos de campo profesionales, lo que permite llevar a cabo análisis de dinámica poblacional y de dispersión de alcance verdaderamente a escala nacional. Desde principios de la década de 1970, se ha recomendado encarecidamente a los anilladores de Finlandia que se centren en las aves de presa, en concreto, en los búhos que anidan en cavidades. Además de anillar a los pollos nidífugos y a los ejemplares adultos, los anilladores también aportan datos acerca de las tendencias poblacionales y el éxito de reproducción. Los datos resultantes indican que el número de parejas reproductoras fluctuó con el ciclo microtino de 3–4 años, pero no pudo observarse ninguna tendencia a largo plazo. La productividad media por nido varió de 2,18 a 3,33 volantones por nido activo en el cárabo común, de 1,56 a 2,87 en el cárabo uralense, y de 1,78 a 4,32 en la lechuza de Tengmalm. La supervivencia y propensión a la reproducción también experimentaron cambios con el ciclo de los micrótidos, lo que explicaría, en gran parte, la variación apreciada en las poblaciones reproductoras. Las distancias de dispersión medias observadas fueron de 24 y 18 km para el cárabo uralense y el cárabo común, respectivamente, si bien, mediante el método descrito en el presente estudio, aumentaron hasta alcanzar los 36 y 48 km. Dicho método permite ajustar los esfuerzos de muestreo desiguales, al tiempo que resalta su importancia a la hora de estimar la dispersión.

Palabras clave: Anilladores aficionados, Dispersión natal, Modelaje de la población, Análisis de marcaje-recaptura, Cárabo común, Cárabo uralense, Lechuza de Tengmalm.

*Pertti Saurola, Finnish Museum of Natural History, Univ. of Helsinki, P. O. Box 17, FIN-00014, Finland.— Charles M. Francis, Canadian Wildlife Service, National Wildlife Research Centre, Ottawa, Ontario, K1A 0H3, Canada.*

## Introduction

In Finland, as in many other places in the world, bird ringers are an extremely dedicated and skilled group of birdwatchers. The majority of ringers are real *amateurs* with the best meaning of the word — *lovers* of their hobby, contributing many hundreds of hours as volunteers each year to collect data on their passion—birds. As such, they are an important resource for science and conservation, and professional ornithologists can benefit enormously by making good use of their data.

This paper illustrates, through analysis of large-scale data sets on owls generated by ringers in Finland, the types of data that can be provided by ringers, some of the analyses that can be done with such data, and some of the statistical challenges that remain for working with these types of data, especially for analysis of dispersal. Specifically, this contribution has three main objectives: (1) to highlight to ringing schemes around the world, the value of coordinating amateur ringers on specialized projects, and of fully computerizing all of the data as precisely as possible; (2) to demonstrate how amateur ringing data can be used to study all aspects of the population dynamics of owls, providing background information for more detailed analyses presented elsewhere (Francis & Saurola, 2004); and (3) to encourage statisticians to develop new methods to estimate dispersal distances from data sets collected from large areas.

In many countries, data produced by amateur ringers have been used primarily for studies of bird migration (e.g. Bairlein, 2001; Wernham et al., 2002). While such studies are obviously valuable, they tap only a small percentage of the potential uses of these data. Increasingly, efforts are being made to use amateurs in programs such as constant-effort mist-netting programs to monitor population trends (e.g. DeSante et al., 1999; Peach et al., 1996). Nevertheless, the vast majority of scientific research on detailed aspects of the population ecology and dispersal of birds has been based on data gathered by professional ornithologists (see e.g. references in Newton, 1986). In many cases, these studies are limited to relatively small study areas, although there are some notable exceptions. For example, a very impressive population study on owls has been carried out in north-western USA on the endangered Spotted Owl *Strix occidentalis* (e.g. Forsman et al., 1996, 2002), but this was realized with a remarkable funding base that can only be dreamed of by the majority of researchers.

The Finnish owl data illustrate how, with dedicated volunteers, high quality data on all aspects of population biology can be collected by amateurs. Making maximum use of data from amateurs requires well organized, centralized computer files that incorporate all aspects of the data, as well as well-planned and coordinated data collection.

Although most ringing schemes now have all of their recoveries computerized, many still do not store the details of the original ringing records, nor

all of the recapture records in electronic form. Both of these types of data are required to estimate survival as well as dispersal, by providing information on the spatial and temporal distribution of ringing effort. Furthermore, in some ringing schemes, even if the data are computerized, the location data (ringing and encounters) are recorded only approximately (for example, in North America, they are recorded only to 10' of latitude and longitude), which severely limits the precision of many spatial analyses, including estimation of natal and breeding dispersal distances in birds.

In Finland, since the start of ringing in 1913, all dead encounters reported by the general public have been computerized and are available in electronic form. In addition, since 1974 (larger ring sizes since 1973), all ringing as well as all live encounter data (recaptures and resightings) have also been stored, with the location recorded to within 100m, in the central computer system of the Finnish Ringing Centre (Saurola, 1987a).

Gaining maximum value from amateur ringers also requires a well coordinated research design. For both scientific and conservation reasons, Finnish ringers have been, since 1974, especially encouraged by the Finnish Ringing Centre to work on birds of prey (Saurola, 1987a). Now, after 30 years of coordinated voluntary work involving several hundred active ringers, very large data sets have been accumulated on a scale that would be impossible to achieve for a normal research team of professional ornithologists. Not only are they recording birds that they ringed, but they are also tracking numbers of breeding pairs, active nests, and young per nest. These data sets are particularly critical for raptors which, being at the top of the food chain, are intrinsically much less common than many other bird species, and are also particularly vulnerable to environmental threats such as the accumulation of pesticides or other toxic chemicals (e.g. Newton, 1979).

The potential of these remarkable data sets for understanding the population dynamics of cavity-nesting owls is illustrated in this paper and a companion paper by Francis & Saurola (2004).

These same data can also be used to estimate dispersal, but that presents a number of still unsolved statistical challenges. Walters (2000) suggested that "lack of information about dispersal has begun to limit progress on several biological fronts". These limitations arise not just because of limited data, but also because of limited statistical methods for their analysis. Saurola (2002) presented information on sexual and annual variation in natal dispersal of Finnish Owls, but did not take into account potential geographic variation in ringing and recapture efforts. Thomson et al. (2003) presented a method that uses data on the distribution of ringing effort, combined with population data from breeding bird atlases to adjust the observed dispersal distributions. Here, an alternative, though related, method is presented, and applied to two species of owls. Adjusting for effort substantially increases estimated dispersal distances,

but also highlights a number of remaining challenges related to estimation of confidence limits and statistical comparisons among estimates.

#### Data collection methods

##### Ringings and recoveries

Since 1974, the Finnish Ringing Centre has encouraged ringers to ring birds of prey. To ensure data quality, candidates interested in ringing in Finland must pass a fairly demanding test in which they demonstrate skills in identifying all species of birds encountered in Finland, in completing all required reporting and documentation (preferably in electronic form), and in techniques for safely handling birds without injury, etc. In addition, the ringer has to make a "ringing plan", that outlines the ringing activities that would be undertaken if the application is accepted. All new ringing licences are usually restricted to a limited number of species that meet this plan. Because birds of prey have had high priority, candidates applying for a ringing licence for birds of prey have been given a high priority as well. Further details on the ringing program were given by Saurola (1987a).

Most ringers working on owls select a study area ranging from about 100 km<sup>2</sup> to over 1,000 km<sup>2</sup>. These are chosen in consultation with other ringers to avoid overlap or confusion in responsibility. Ringers then place nest boxes throughout suitable habitat within their area, of an appropriate size and design for the species of hole-nesting owls expected to be within their area. These boxes are checked regularly during the breeding season and, if a nest is found, the ringer returns on the appropriate date to ring the nestlings. In addition, most ringers attempt to catch the adults, especially females, which in most species are much easier to catch. A relatively effective but still laborious method for catching adult males of the Tawny Owl (*Strix aluco*) and Ural Owl (*Strix uralensis*) was developed in the early 1970s (Saurola, 1987b), but so far only some ringers have regularly caught adult males of these species.

##### Raptor Grid

In 1982, the Finnish Ringing Centre, with some support for administration from the Ministry of Environment, started a monitoring project called the Raptor Grid to monitor diurnal and nocturnal birds of prey (Saurola, 1986). The Raptor Grid program is completely based on voluntary field work by raptor ringers. Ringers are asked (1) to establish a study group; (2) to select a 10x10 km study plot based on 10-km squares of the Finnish National Grid; and (3) to try each year to find all the active nests or at least the occupied territories of all species of birds of prey in their study plot. The number of Raptor Grid study plots surveyed has averaged 120 per year (Saurola, 1997; Björklund et al., 2003). The amount of effort has varied considerably among study plots, but

ringers are asked to provide a measure of the effort on their plot. In general, effort within an individual plot has remained roughly the same from year to year (unpublished data).

##### Raptor Questionnaire

In 1982, a Raptor Nest Card (in addition to the traditional nest card available for all species) was introduced and ringers were asked to complete a card for all nests found. In 1986, after a relatively poor initial response rate, an alternative report, called a Raptor Questionnaire was introduced, which must be completed as a requirement in the annual reports of all ringers working on raptors. The Raptor Questionnaire summarises the total numbers of (1) potential nest sites checked, (2) active nests and occupied territories found, and (3) nests of different clutch and brood sizes verified by ringers. In addition, measures of effort are reported. These results are summarized for reporting based on the "territories" of all local ornithological societies in different parts of the country.

The main purpose of the Raptor Questionnaire is to collect data on annual breeding output. In addition, these data, although not precisely standardised from year to year, may be used with care to detect fluctuations and trends in population sizes, especially for areas where Raptor Grid data are too scanty.

#### Data analysis methods

##### Changes in population size

Data from the Raptor Grid were used for estimating changes in population size. While efforts have been made to retain the same set of study plots over time, in practice, some plots have become inactive and new ones have emerged, primarily because of changes in volunteers involved in the field work. Thus, analyses have to control for this potential variation in coverage among plots. To do this, for each year, population indices were calculated through pairwise comparisons of mean numbers in that year to those in a reference year for plots that were active in both years (cf. Baillie et al., 1986; Peach et al., 1996). For this analysis, 1997 was chosen as a reference year because it was a good year with many active plots and many data. Thus, only plots that were active in 1997 were included in this analysis. Two measures of abundance were examined: all occupied territories and active nests.

##### Population parameters

Productivity was estimated as the mean number of large nestlings (i.e. old enough to be ringed) produced per nest, for all active nests (i.e. nests in which eggs were laid) reported by ringers through the Raptor Questionnaire. Most of the owlets are ringed during the second half of the nestling period, when they were at least two weeks old, but prior to

fledging. Age at ringing is an appropriate metric, because mortality within the nest after this age is low and, in any case, first-year survival estimates are based from the age of ringing onwards.

Combined mark–recapture–recovery analyses, as implemented in program MARK (White & Burnham, 1999) were used to estimate age–specific survival rates (Francis & Saurola, 2002) as well as relative breeding propensity (based on annual and age–specific variation in capture probabilities). Details of the methods, as well as the results of those analyses are presented elsewhere (Francis & Saurola, 2004) and not repeated here.

### Natal dispersal distances

In principle, the distribution of natal dispersal distances, defined as the distance from the natal site to the first breeding location, can be estimated by ringing birds as nestlings and later recapturing them as breeding adults. In practice, however, this procedure may produce biased estimates because only some of the marked nestlings that survive to breed are ever recaptured as breeders. If the dispersal distances of the observed recruits are not representative of those of recruits that were not observed, then estimates of dispersal distances may be biased unless appropriate correction factors can be developed (Barrowclough, 1978; Van Noordwijk, 1984).

In many cases, the study area is smaller than the maximum dispersal distance, and distribution of potential dispersal distances is truncated, leading to an under–estimate of mean dispersal distances. Without any information on long–distance recruitment, no correction is possible.

In the case of species such as owls in Finland, ringing takes place over a very large area, so that the distribution (at least for most species) is unlikely to be truncated. However, ringing effort may vary throughout the area, such that owls in some parts of the country may be more likely to be captured and ringed than owls in other parts.

Thomson et al. (2003) presented a method for adjusting observed dispersal distances for effort, using data from breeding bird atlases combined with ringing totals. They estimated the relative probability of recapturing birds at different distances for each bird that was ringed. In this paper, an alternative, but related method is presented, first developed by Saurola & Taivalmäki (unpublished). This method involves studying dispersal in the reverse direction: for each first capture of a breeding adult originally ringed as a nestling (a recruit), calculating (a) the actual *observed* dispersal distance for that individual, and (b) the distribution of *potential* dispersal distances, which is defined as the distribution of distances from the recapture site to all birds ringed as nestlings in the same year as the observed recruit was first ringed. These represent birds that could have been detected if they had recruited to the site. These potential recruitment

distances are then used to estimate the density of ringed individuals at different distances from the observed recruit by dividing by the land area at each distance. If the density of breeding owls is similar throughout the range of the species, the relative density of ringed owls at each distance provides an index of the proportion of owls that were ringed at each distance category. By repeating this process for all owls, and averaging across individuals, these relative densities can be used to adjust the estimated dispersal probabilities.

Mathematically, this can be expressed as follows: *observed recruit*, a bird ringed as a nestling and caught for the first time as a breeding adult at the nest; *potential recruits*, birds ringed as nestlings in the same year as an observed recruit was ringed.

Let us define the following symbols:

$N_b^i$ . Number of observed recruits in distance category  $i$  in which the natal dispersal distance  $y$  is  $r_{i-1} < y < r_i$  where  $r_i$  is the radius of the outer and  $r_{i-1}$  the inner border of the distance category  $i$ .

$N_q^{ik}$ . Number of potential recruits in distance category  $i$  for the  $k^{\text{th}}$  capture. Distance is measured from the site of the capture to all the sites where nestlings were ringed in the same year as the observed recruit.

$N_p^i$ . Number of potential recruits in distance category  $i$  summed across all observed recruits.  $N_p^i$  can be calculated as follows:

$$N_p^i = \sum_{k=1}^m N_q^{ik},$$

where  $m$  is the total number of captures (= different individuals captured at their nest) in the distance category  $i$ .

Let us then define the density of potential recruits  $\delta$  in distance category  $i$ :

$$\delta_i = \frac{N_p^i}{A_i},$$

where  $A_i$  is the area of the distance category  $i$ . If the study area were large without boundaries, then  $A_i$  could be calculated as:

$$A_i = \pi \times (r_i^2 - r_{i-1}^2)$$

However, in most landscapes, this will overestimate the true area, because some parts of the distance band may be in the ocean or otherwise in unsuitable habitat for owls. For this paper, a GIS analysis was used to estimate the land area of each distance band (excluding both ocean and inland water bodies) from each observed recruit. This was done using the "Digital Chart of the World" at a 1:1,000,000 scale. The map was rasterized at a 500m pixel resolution for the analysis, and then overlaid with 10 km distance bands from each observed recruit, using an Arc/Info script to determine the land area in each band. Furthermore, land areas north of the breeding range of the species were also excluded (for Tawny Owl, areas north of 63.9°N were excluded, as well as the inland area of northwestern Finland with few records—see fig. 1;

for Ural Owl, areas north of 67.2°N were excluded). The area at each distance was then averaged across all recruits to generate  $A_i$ . This analysis was carried out separately considering only land areas within Finland, and also considering land areas in adjacent countries from which the species might also disperse.

The corrected proportion of individuals dispersing from each distance category can then be estimated as:

$$D_i = \frac{d_i}{\sum_{i=1}^{N_c} d_i}$$

where:

$$d_i = \frac{N_b^i}{\delta_i}$$

and  $N_c$  is the total number of distance categories.

Results

Ringing data

During 1913–2002, altogether 223,981 owls were ringed in Finland, predominantly of 5 different species (table 1).

Although the vast majority of these birds, for all species, were young birds, in the past 30 years most ringers attempted to catch the adults, at least the females, of hole nesting owls breeding in their nest-boxes. As a result of this effort, almost 10% of newly ringed birds for some species are of breeding adults (table 1). In addition, for these same species, a significant portion of the re-encounters represent birds recaptured alive at the nests in subsequent years. These data provide valuable information on the survival of older birds, and are also critical for capture–recapture and dispersal analyses, to determine what happens to the young birds. Unfortunately, only a few ringers have been systematically attempting to catch breeding males as well, owing to the substantially greater effort required.

The spatial distribution of the ringing effort for the Tawny Owl, Ural Owl and Tengmalm’s Owl coincides fairly well with the distribution of each species that has been mapped using data from all available sources in the Finnish Breeding Bird Atlas (Väisänen et al., 1998). Both nestlings and breeding adults of the Tawny Owl have been ringed only in the southern quarter of Finland (fig. 1). For the Ural Owl this extends to the southern half of the country, while Tengmalm’s Owls have been ringed all over the country (fig. 2). However, in all these species, the spatial distribution of ringing effort is somewhat patchy: in some areas the work has been much more intensive than elsewhere.

Demographic parameters

In the process of ringing these owls, Finnish ringers have also inspected very large numbers of nest sites each year. For example, in 2002, 44,650

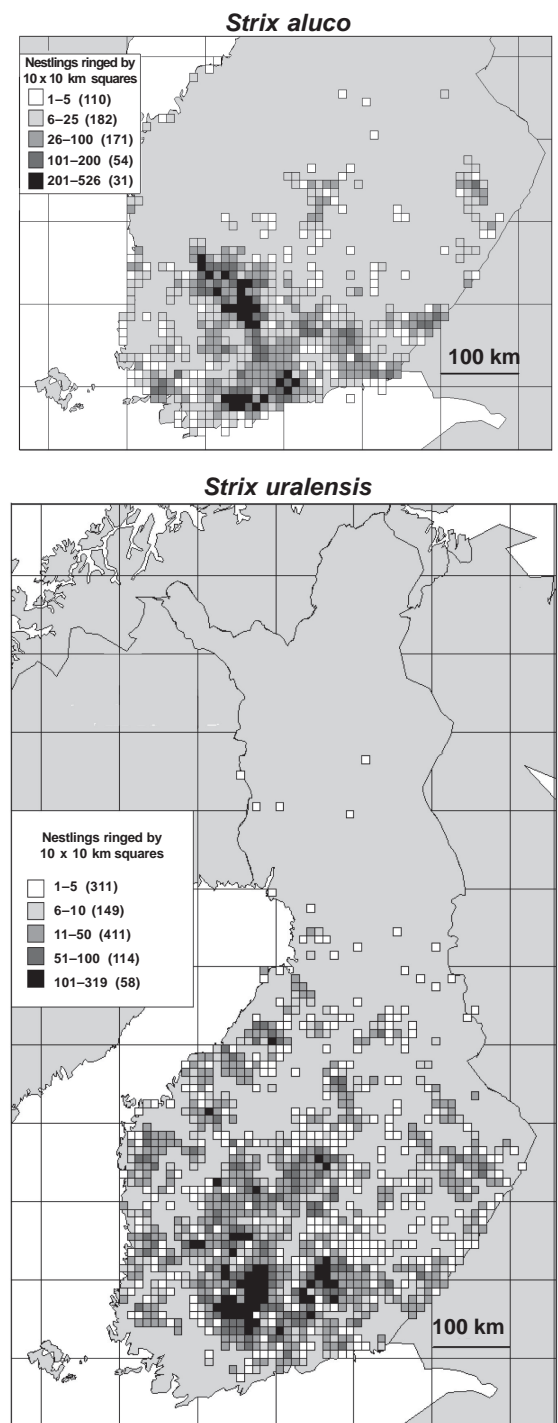


Fig. 1. Distribution of numbers of nestlings ringed for Tawny Owls (top) and Ural Owls (bottom) from 1973 to 2002 by 10 x 10 km squares of the Finnish National Grid.

Fig. 1. Distribución del número de pollos anillados, correspondiente al cárabo común y al cárabo uralense, desde 1973 hasta 2002, por cuadrados de 10 x 10 km de la Red Nacional del Sistema de Coordenadas de Finlandia.

Table 1. Accumulated ringing totals, since 1913, of five species of owls in Finland, along with the % of adults ringed of the total in 1993–2002 and the total number of recoveries and recaptures (the latter including only movements of at least 10 km or an elapsed time of at least 3 months): S. Species; RT. Ringing total; %A. Percentage of adults; R–R. Recaptures/recoveries; TeO. Tengmalm's Owl (*Aegolius funereus*); TaO. Tawny Owl (*Strix aluco*); UrO. Ural Owl (*Strix uralensis*); PyO. Pygmy Owl (*Glaucidium passerinum*); EaO. Eagle Owl (*Bubo bubo*).

Tabla 1. Total de anillamientos acumulados, desde 1913, con respecto a cinco especies de búhos en Finlandia, junto con el porcentaje de adultos anillados sobre el total correspondiente a 1993–2002 y el número total de recuperaciones y recapturas (estas últimas sólo incluyen movimientos de por lo menos 10 km, o un tiempo transcurrido mínimo de tres meses): S. Especies; RT. Total de anillamientos; %A. Porcentaje de adultos; R–R. Recapturas/recuperaciones; TeO. Lechuza de Tengmalm (*Aegolius funereus*); TaO. Cárabo común (*Strix aluco*); UrO. Cárabo uralense (*Strix uralensis*); PyO. Mochuelo chico (*Glaucidium passerinum*); EaO. Buho real (*Bubo bubo*).

S	RT	%A	R–R
TeO	96,263	11.5%	4,962
TaO	37,067	8.7%	9,880
UrO	35,615	8.4%	9,779
PyO	20,305	9.6%	1,253
EaO	13,058	3.4%	2,884

potential nest sites of all species of birds of prey were inspected and reported by 236 ringers/groups (Björklund et al., 2003). These included the following numbers of nest-boxes for owls: Tengmalm's Owl 9,264, Pygmy Owl 5,540, Ural Owl 4,338 and Tawny Owl 4,038. The corresponding numbers of active nests found in that year were 621, 578, 1,084 and 560. In addition to providing information on numbers of occupied territories, from most of these nests, data were also gathered on the number of nestlings produced per nest, an important measure of productivity.

Analyses of data from the Raptor Grids show major fluctuations in the numbers of breeding owls and occupied territories each year for both the Tawny Owl and Ural Owl (fig. 3). These fluctuations coincide strongly with the 3–4 year cycle of small mammals, especially voles, through the 1980s and early 1990s, although the correspondence does not

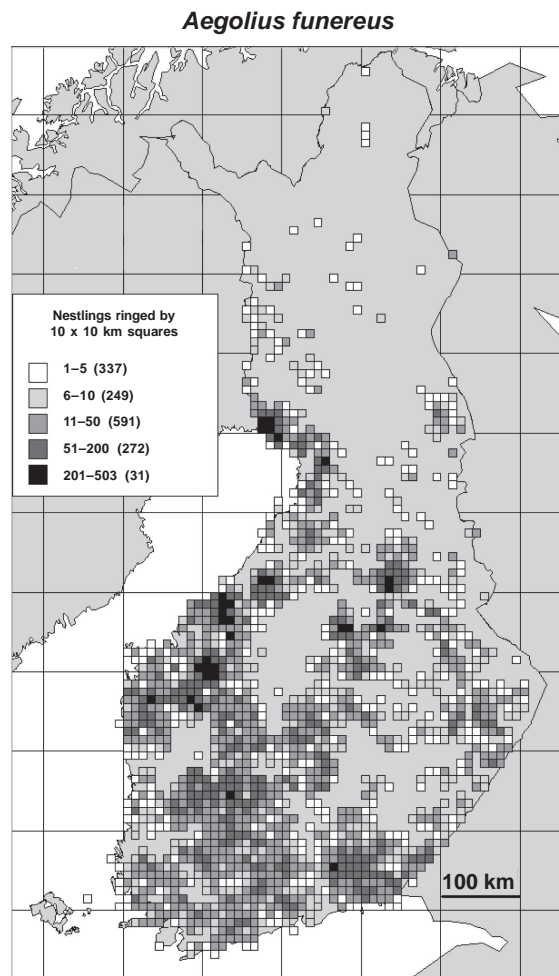


Fig. 2. Distribution of numbers of nestlings ringed for Tengmalm's Owls (*Aegolius funereus*) from 1973 to 2002 by 10 x 10 km squares of the Finnish National Grid.

Fig. 2. Distribución del número de pollos anillados, correspondiente a la lechuza de Tengmalm (*Aegolius funereus*), desde 1973 hasta 2002, por cuadrados de 10 x 10 km de la Red Nacional del Sistema de Coordenadas de Finlandia.

appear to be as strong during the past four years (see also Sundell et al. 2004). Furthermore, these data indicate that the populations of both species have remained at roughly the same mean levels during the last two decades, with no evidence of long-term trends. Sundell et al. (2004) used these data to demonstrate widespread spatial synchrony in the breeding patterns of the owls, apparently related to similar spatial synchrony in the cycle of microtine rodents

Data from the Raptor Questionnaire show that the reproductive success of the Tawny Owl and

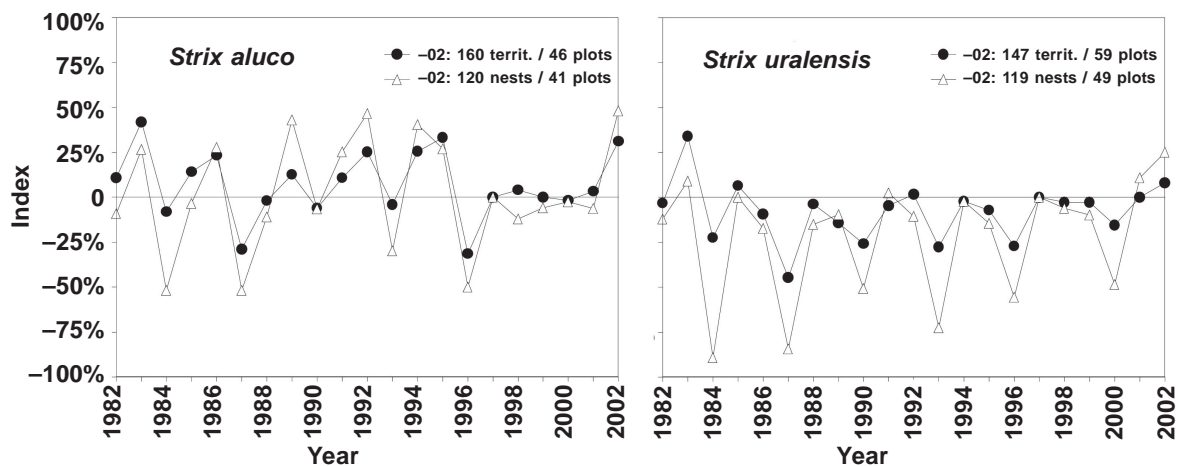


Fig. 3. Population indices of Tawny Owls (*Strix aluco*) and Ural Owls (*Strix uralensis*) during 1986–2002 in Finland, based on data from the Raptor Grid monitoring project. All indices represent the percent difference in population size relative to 1997 (index = 0%). Black dots, indices based on all occupied territories; white triangles, indices based on active nests.

Fig. 3. Índices poblacionales del cárabo común (*Strix aluco*) y del cárabo uralense (*Strix uralensis*) durante 1986–2002 en Finlandia, elaborados mediante datos extraídos del Proyecto de Observación del Sistema de Coordenadas para Aves Rapaces. Todos los índices representan la diferencia porcentual en el tamaño poblacional correspondiente a 1997 (índice = 0%). Puntos negros, índices basados en todos los territorios ocupados; triángulos blancos, índices basados en nidos activos.

Ural Owl fluctuated from one year to the next (fig. 4). In these more generalist feeders the amplitude of fluctuations was not as large as might be expected for the most specialized vole feeders (Saurola, 1995) but was still substantial. For example during 1986–2002, the average annual production of large nestlings per active nest varied from 2.18 to 3.33 in the Tawny Owl and from 1.56 to 2.87 in the Ural Owl (fig. 4). In the more specialized Tengmalm's Owl, production varied from 1.78 to 4.32 in the same time period.

Francis & Saurola (2004) showed that Tawny Owl survival rates for both adults and young also varied considerably among years. The vole cycle explained some of the variation, with lowest survival in years when voles crashed and remained at very low levels over the following winter. Even more variation was explained by the severity of winter weather, with lower survival in very cold winters. Recapture probabilities, an index of breeding propensity, varied dramatically in response to the vole cycle, with lowest breeding in years of low vole abundance. The variation was most extreme for one-year old owls.

#### Dispersal analyses

For three species of Finnish hole-nesting owls, the Tawny Owl, Ural Owl and Tengmalm's Owl, extensive data suitable for dispersal analysis are avail-

able for birds ringed as nestlings and later recaptured as breeding adults (figs. 5, 6).

For Tawny and Ural Owls, adjusting the observed dispersal distribution for the density of ringed birds (potential recruits) leads to an outward shift of the estimated distribution of dispersal distances, with a substantial increase in the estimated proportion of birds that moved very long distances (fig. 7). Assuming that each species occurs throughout the land areas in both Finland and adjacent countries, south of the northern limit of its breeding range, the estimated median dispersal distance increased from 18 to 48 km for Tawny Owls, and 24 to 36 km for Ural Owls (table 2). If the presence of unsuitable areas (e.g. water, including sea) is ignored, then the estimated dispersal distances are substantially higher, while if the species are assumed only to disperse within Finland, then the estimated dispersal distances are somewhat lower, especially for Tawny Owls (table 2). The adjusted estimates suggest that both recaptures and recoveries may underestimate dispersal distances, despite the fact that recoveries of birds found dead during the breeding season are generated from a sampling method that is fairly independent of the ringing data, being found by the general public (table 2). Adjusting the dispersal distances also leads to changes in the estimated differences between the sexes (table 2), although these may be biased due to the much more limited areas where males were trapped (fig. 5).

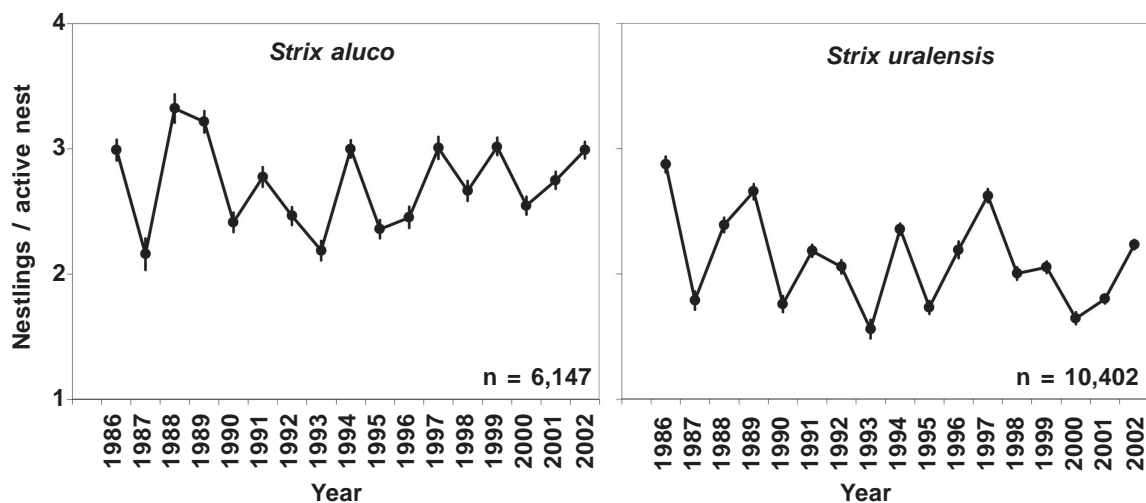


Fig. 4. Mean breeding output (large young per active nest) of Tawny Owls (*Strix aluco*) and Ural Owls (*Strix uralensis*) during 1986–2002, based on data from the Raptor Questionnaires. Standard errors are indicated by vertical bars.

Fig. 4. Promedio de resultados de reproducción (individuos jóvenes ya crecidos por nido activo) del cárabo común (*Strix aluco*) y del cárabo uralense (*Strix uralensis*) durante 1986–2002, obtenido a partir de datos extraídos de los Cuestionarios sobre Aves Rapaces. Los errores estándar se indican mediante barras verticales.

The Tengmalm's Owl presents a challenge to this analysis method, because several very long-distance movements were observed into Sweden (fig. 6). Analyses would be enhanced with information on the numbers of nestlings ringed every year in Sweden, as well as information on the distribution within Sweden. Nevertheless, it is likely that adjusting these estimates would lead to a substantial increase in the estimated proportion of very long distance movements for that species as well.

## Discussion

### The role of Finnish ringers in monitoring birds of prey

Ringers play a crucial role in monitoring birds of prey in Finland, for understanding all aspects of their population ecology, from changes in population size and range, to changes in demographic parameters. At one scale, field-work needed in special projects to monitor threatened species of birds of prey, is carried out by ringers. At another scale, monitoring of common birds of prey is totally based on voluntary work by ringers. The Finnish Ministry of Environment has provided only limited funding for this program, primarily for the administrative work needed to coordinate the field work, to file the data and to produce annual reports (see Björklund et al., 2003).

Because every ringer who rings birds of prey has to report his observations through the Raptor Ques-

tionnaire, in addition to providing ringing data, ringers also provide an extensive overview of the annual variation of the average breeding performance (clutch size, brood size and breeding success) of different species of birds of prey. This is very important, because otherwise only a relatively small fraction of nests and territories of birds of prey found by ringers would be reported at all. Motivation to complete a summary form seems to be much higher than to complete more detailed nest records cards, especially from the nests of a common species such as the Tawny Owl. While this reduces the detailed information available on such things as nest site selection, habitat, nest height, etc., the most critical information on annual productivity is provided.

### Demographic analyses

Both through ringing and through reporting nesting data and numbers of pairs, ringers in Finland provide information on all aspects of the life cycle of several species of owls. Survey data provide information on numbers of birds breeding and nesting success. Coordination of ringing effort by many ringers throughout Finland allows for much greater precision (through larger sample sizes) as well as a more representative national picture, than would be possible with only a few ringers, even though some of the most dedicated ringers have ringed over 1,000 owls each. Detailed analyses of survival rates for Tawny Owls (Francis & Saurola, 2004), indicate the



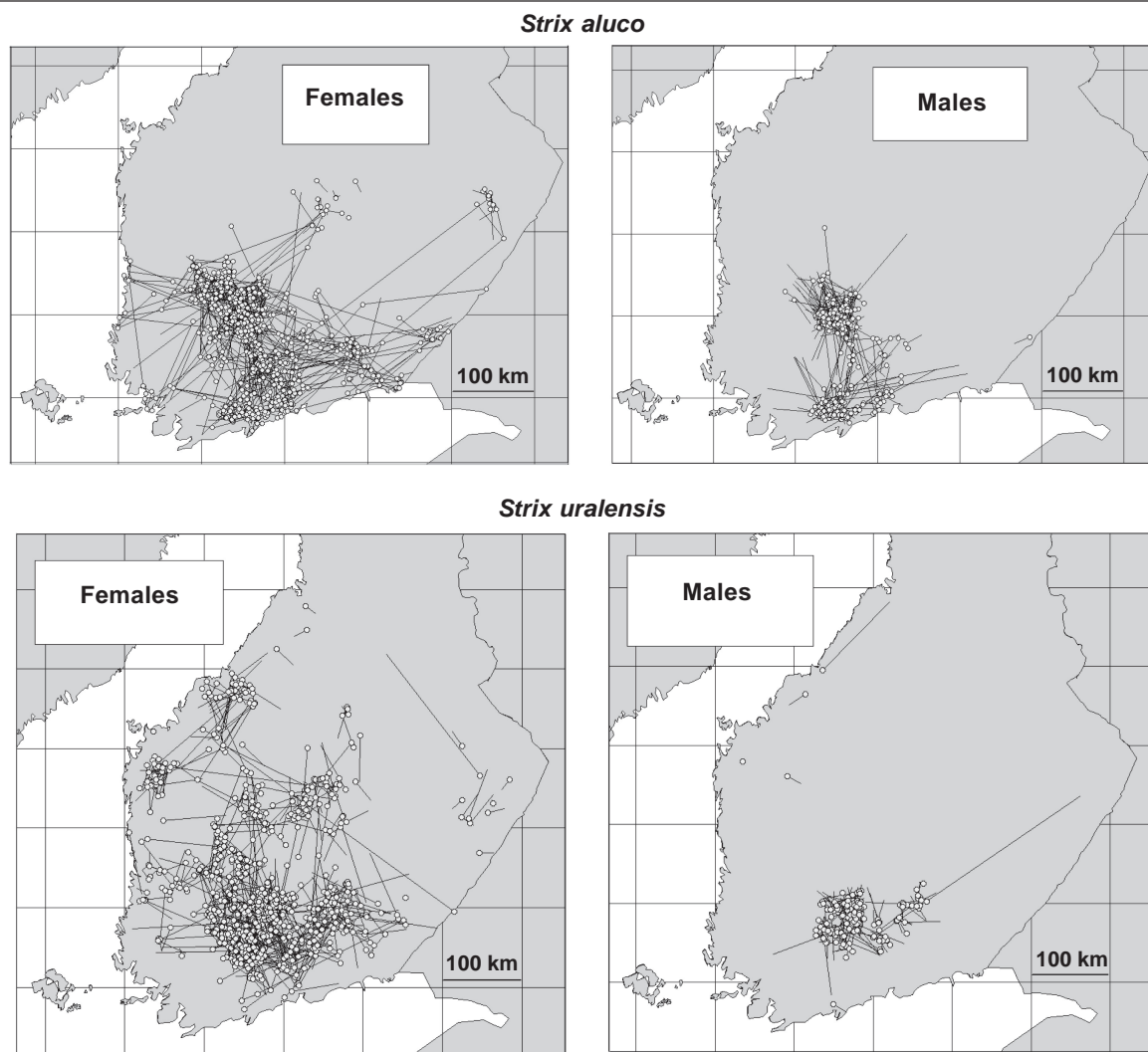


Fig. 5. Natal dispersal patterns of Tawny Owls (*Strix aluco*) and Ural Owls (*Strix uralensis*) for females (left) and males (right) from 1951 to 2002. The locations of nests where ringed nestlings were first captured as breeding adults are indicated by dots, connected to the corresponding natal sites by lines.

*Fig. 5. Pautas de dispersión natal del cárabo común (Strix aluco) y del cárabo uralense (Strix uralensis) para hembras (izquierda) y machos (derecha), desde 1951 hasta 2002. La situación de los nidos en los que los pollitos nidífugos fueron capturados por primera vez siendo adultos reproductores se indica a través de puntos, conectándose mediante líneas a los correspondientes lugares de nacimiento.*

data are sufficient to estimate annual variation in survival rates for three age classes with good precision, and to model that variation in relation to prey abundance and winter weather conditions. Because the ringing effort has been consistently high, annual variation in capture probabilities can also be used as an index of age-specific variation in breeding probabilities. Francis & Saurola (2004) were able to use these parameter estimates to develop a simple matrix model of the demography of this population that, even in a deterministic fashion, captured some of

the key variation in population numbers in relation to vole abundance. The data should also be sufficient to estimate spatial variation in demographic parameters such as survival, but such analyses have not yet been undertaken.

#### Natal dispersal distances

The analyses presented here indicate that the dispersal estimates in Saurola (2002) may be a substantial underestimate of true dispersal distances

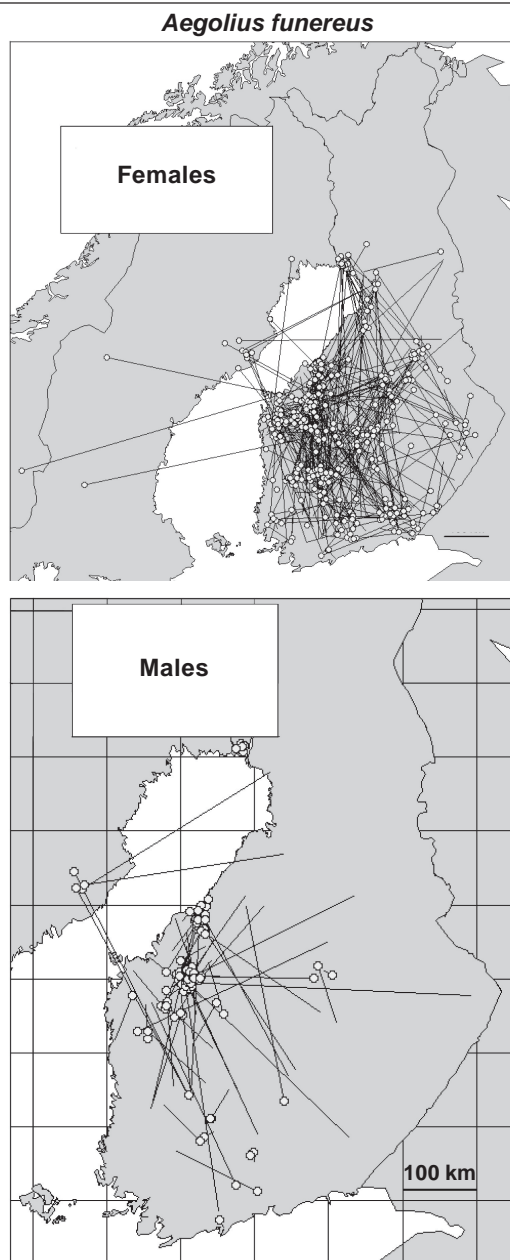


Fig. 6. Natal dispersal patterns of Tengmalm's Owl (*Aegolius funereus*), females and males, ringed in Finland from 1951 to 2002. The locations of nests where ringed nestlings were first captured as breeding adults are indicated by dots, connected to the corresponding natal sites by lines.

*Fig. 6. Pautas de dispersión natal de las lechuzas de Tengmalm (*Aegolius funereus*), hembras y machos, anilladas en Finlandia entre 1951 y 2002. La situación de los nidos en los que los pollos fueron capturados por primera vez siendo adultos reproductores se indica con puntos, conectándose mediante líneas a los correspondientes lugares de nacimiento.*

(fig. 7). The proportion of long-distance movements appears to be substantially underestimated based solely on observed recaptures, despite the fact that ringing took place throughout much of the range of the species in Finland. Even greater shifts can be anticipated for Tengmalm's Owls, given the numbers of very long distance movements, and the likelihood of a similar drop-off in density of marked individuals with distance.

These corrections can also potentially affect analyses of relative dispersal distance. For example, Saurola (2002) showed that if all recaptures at the nest of Ural Owls, Tawny Owls and Tengmalm's Owls ringed as nestlings from the entire country were included in the analysis, statistically significant difference between males and females were detected (figs. 5, 6). However, if the analyses were restricted only to intensive study areas, where both sexes were captured at the nest, the difference remained significant only in the Tengmalm's Owl. This suggests that at least some of the apparent differences between the sexes could be due to bias caused by geographic variation in dispersal distances: because most of the trapping of male owls took place within a few study areas (fig. 6), estimates of their dispersal distances may not have been comparable to those of females ringed throughout Finland. The analyses presented here indicate that the estimated differences between the sexes increase if the observed dispersal distances are adjusted for uneven sampling effort (table 2). However, these analyses did not consider the possibility of geographic variation in dispersal distances, and thus could still be biased. Further developments of the method are required to take that into account.

Saurola (2002) showed that observed median natal dispersal distances of the Tawny Owl were about three times longer in Finland than in Britain (Paradis et al., 1998) and in southwest Sweden (Wallin et al., 1988). However, the average distances between the nests were 3.2 and 2.7 times longer, suggesting that natal dispersal distances of owls from these three areas may be closely related to territory densities, with birds moving farther when territories are large (Saurola, 2002). Again, these analyses might be affected by adjusting for sampling effort, which would likely vary among the three countries.

This correction method depends on the assumption that the densities of owls are similar throughout their range. Furthermore, in order to apply this method, some assumptions are required about densities of each species outside of Finland. Comparison of the analysis methods (table 2) indicates that results for Tawny Owl are particularly sensitive to the assumptions, probably because its true breeding range is more restricted. An alternative assumption could be that the distribution of ringing records actually reflects the true distribution of owls, given the wide distribution of ringing activities. However, the estimated densities of ringed birds dropped off noticeably with distance, even over the first few

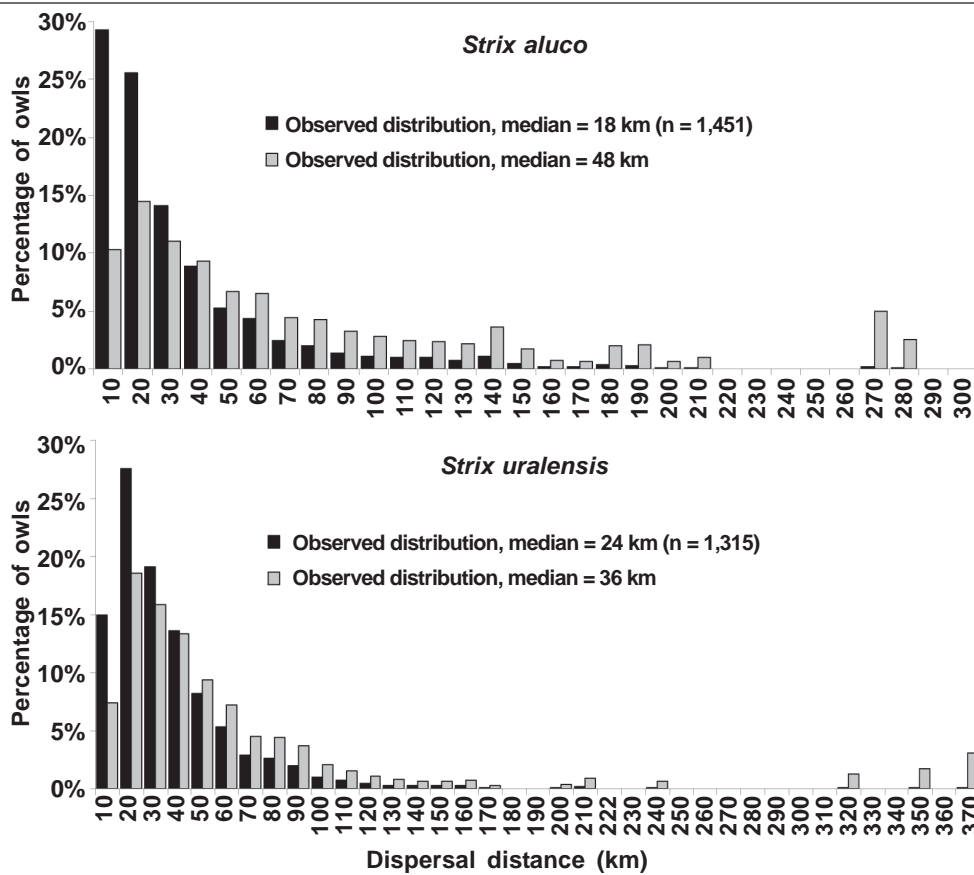


Fig. 7. Distribution of natal dispersal distances of Tawny Owls (*Strix aluco*) and Ural Owls (*Strix uralensis*) in Finland. Black columns, observed distribution of distances; grey columns, distribution corrected for density of ringed birds throughout their breeding range in Finland and adjacent countries (see Methods).

Fig. 7. Distribución de las distancias de dispersión natal del cárabo común (*Strix aluco*) y del cárabo uralense (*Strix uralensis*) en Finlandia: Columnas negras, distribución de distancias observada; columnas grises, distribución corregida para la densidad de aves anilladas a lo largo de toda su zona reproductora en Finlandia y países adyacentes (véase Métodos).

distance bands, probably reflecting the fact that ringing activities are clumped into individual study areas. Most likely, the true dispersal distances are somewhere in between these approaches—densities do vary through Finland, but not exactly proportional to ringing densities. Thomson et al. (2003) proposed a method involving the use of atlas data to estimate both the distribution and relative abundance of the species, to provide a more accurate correction. Given the availability of atlas data from much of Finland, such an approach should be explored in future with the Finnish ringing data.

An additional statistical challenge involves placing confidence limits on the estimates. These correction methods are particularly sensitive to long-distance movements, which are usually few in number, because the density of available ringed birds at longer distances is usually low. Much of the shift in the estimated median

dispersal distance for Tawny Owls arises because of a small number of observed movements > 250 km. Appropriate statistical methods, perhaps involving jack-knifing or randomization tests, are required to place confidence limits on these estimates. These must take into account not only the sampling characteristics, but also the uncertainty in estimates of the distribution of breeding owls. Furthermore, it is important to emphasize that ringing must take place over a wide enough area that at least some long-distance movements are observed—this method cannot adjust distance categories with no observed recoveries.

Since the inception of the EURING technical meetings, huge advances have been made in statistical development of models for estimating survival and movement probabilities. Similar developments are now required for the estimation of dispersal distances (cf. Van Noordwijk, 1993).

Table 2. Estimated median dispersal distances (km) from natal nest to site of first recapture during the breeding season for two species of owls in Finland, both unadjusted (Observed), and adjusted for variation in effort and area (see text); and distances between natal site and site of death for owls ringed as nestlings, and recovered dead in a subsequent year during the breeding season: <sup>1</sup> Adjusted based on the land area in the species' breeding range within Finland; <sup>2</sup> Adjusted based on the land area south of the northern limits of the species range in Finland and adjoining countries; <sup>3</sup> Adjusted based solely on the calculated surface area of each distance band; <sup>4</sup> Derived from Saurola (2002).

Tabla 2. Distancias de dispersión medias estimadas (km) desde el nido natal hasta el lugar donde se realizó la primera recaptura durante la estación reproductora para dos especies de búhos en Finlandia, indicándose tanto las no ajustadas (Observed), como aquellas ajustadas para la variación con respecto a los esfuerzos y al área (véase el texto); y distancias entre el lugar del nacimiento y el lugar de la muerte correspondiente a búhos que fueron anillados siendo pollos nidifugas y que se recuperaron muertos en un año posterior durante la estación reproductora: <sup>1</sup> Ajuste basado en el área dentro del rango reproductor de la especie en Finlandia; <sup>2</sup> Ajuste basado en el área situada al sur del límite norte de distribución de la especie en Finlandia y países cercanos; <sup>3</sup> Ajuste basado exclusivamente en la superficie del área calculada para cada banda de distancias; <sup>4</sup> Basado en Saurola (2002).

Specie	N	Recaptures			Recoveries	
		Observed	Adjusted <sup>1</sup>	Adjusted <sup>2</sup>	Adjusted <sup>3</sup>	Observed <sup>4</sup>
<b>Tawny Owl <i>Strix aluco</i></b>						
Males only	439	16	25	36	38	
Females only	999	19	45	51	56	
Both	1,451	18	42	48	58	22
<b>Ural Owl <i>Strix uralensis</i></b>						
Males only	213	17	26	27	32	
Females only	1,084	26	36	37	40	
Both	1,315	24	35	36	39	28

## Conclusions

These analyses demonstrate the enormous potential for ecological research through coordinated, large-scale volunteer-based ringing projects involving ringing of both nestlings and older age classes. These data can be further enhanced through collecting relevant auxiliary data such as nesting productivity data. In addition, and most importantly, all of the data must be centrally and efficiently computerized. Unfortunately, the majority of the Ringing Centres around the world have not yet started to file data on original ringing records and/or local recaptures in electronic form. Furthermore, in many cases the location information is only recorded to within 10–15 km, which is not sufficiently precise to allow accurate estimation of dispersal for many species (median dispersal distance in many species may even be smaller than this limit). Nevertheless, with appropriate encouragement and guidance, similar coordinated volunteer-based projects could no doubt be developed through enthusiastic ringers in many parts of the world, leading to greatly enhanced understanding of population dynamics and thus more effective management and conservation planning.

## Acknowledgements

We are grateful to Finnish ringers for their outstanding work, especially on birds of prey, to Jukka-Pekka Taivalmäki for fresh ideas in developing a new method to correct observed dispersal distances, to Heidi Björklund for producing ringing and recovery maps, and to Andrew Couturier of Bird Studies Canada for the GIS analyses required to help correct dispersal distances.

## References

- Baillie, S. R., Green, R. E., Boddy, M. & Buckland, S. T., 1986. *An evaluation of the Constant Effort Sites Scheme*. BTO Research Report 21, BTO. Thetford.
- Bairlein, F., 2001. Results of bird ringing in the study of migration routes. *Ardea*, 89(1) special issue: 7–19.
- Barrowclough, G. F., 1978. Sampling bias in dispersal studies based on finite area. *Bird Banding*, 49: 333–341.
- Björklund, H., Saurola, P. & Haapala, J., 2003.

- Breeding and population trends of common raptors and owls in 2002—many new records saw the daylight. *Linnut—vuosikirja, 2002*: 18–40. (In Finnish with extensive English summary).
- DeSante, D. F., O'Grady, D. R., & Pyle, P., 1999. Measures of productivity and survival derived from standardized mist-netting are consistent with observed population changes. *Bird Study*, 46 (suppl.): 178–188.
- Forsman, E. D., Anthony, R. G., Reid, J. A., Loschl, P. J., Sovern, S. G., Taylor, M., Biswell, B. L., Ellingson, A., Meslow, E. C., Miller, G. S., Swindle, K. A., Thairkill, J. A., Wagner, F. F. & Seaman, D. E., 2002. Natal and breeding dispersal of Northern Spotted Owls. *Wildlife Monographs*, 149: 1–35.
- Forsman, E. D., DeStefano, S., Raphael, M. G. & Gutiérrez, R. J. (Eds.), 1996. *Demography of the Northern Spotted Owl. Studies in Avian Biology No. 17*. Cooper Ornithological Society.
- Francis, C. M. & Saurola, P., 2002. Estimating age-specific survival rates of tawny owls—recaptures versus recoveries. *Journal of Applied Statistics*, 29: 637–647.
- 2004. Estimating components of variance in demographic parameters of Tawny Owls. *Animal Biodiversity and Conservation*, 27.1: 489–502.
- Newton, I., 1979. *Population ecology of raptors*. T. & A. D. Poyser. London.
- 1986. *The Sparrowhawk*. T. & A. D. Poyser. London.
- Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D., 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, 67: 518–536.
- Peach, W. J., Buckland, S. T. & Baillie, S. R., 1996. The use of constant effort mist-netting to measure between-year changes in the abundance and productivity of common passerines. *Bird Study*, 43: 142–156.
- Saurola, P., 1986. The *Raptor Grid*: an attempt to monitor Finnish raptors and owls. *Vår Fågelvärld. Suppl.*, 11: 187–190.
- 1987a. Bird ringing in Finland: status and guidelines. *Acta Reg. Soc. Sci. Litt. Gothoburgensis. Zoologica*, 14: 189–201.
- 1987b. Mate and nest-site fidelity in Ural and Tawny Owls. In: *Biology and conservation of northern forest owls. Symposium proceedings, February 3–7, 1987 Winnipeg, Manitoba*: 81–86 (R. W. Nero, R. J. Clark, R. J. Knapton & R. H. Hamre, Eds.). USDA Forest Service Gen. Tech. Rep. RM-142.
- 1995. *Suomen pöllöt. Owls of Finland*. Helsinki, Kirjayhtymä. (in Finnish with English summary).
- 1997. Monitoring Finnish Owls 1982–1996: methods and results. In: *Biology and conservation of owls of the northern hemisphere. 2<sup>nd</sup> International Symposium, February 5–9, 1997, Winnipeg, Manitoba, Canada*: 363–380 (J. R. Duncan, D. H. Johnson & T. H. Nichols, Eds.). USDA Forest Service Gen. Tech. Rep. NC.
- 2002. Natal dispersal distances of Finnish owls: results from ringing. In: *Ecology and conservation of owls*: 42–55 (I. Newton, R. Kavanagh, J. Olsen & I. Taylor, Eds.). CSIRO Publishing, Collingwood VIC, Australia.
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P., & Hanski, I., 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating predators. *Journal of Animal Ecology*, 73: 167–178.
- Thomson, D. L., Van Noordwijk, A., & Hagemeyer, W., 2003. Estimating avian dispersal distances from data on ringed birds. *Journal of Applied Statistics*, 30: 1003–1008.
- Van Noordwijk, A. J., 1984. Problems in the analysis of dispersal and a critique on its "heritability" in the Great Tit. *Journal of Animal Ecology*, 53: 533–544.
- 1993. On the role of ringing schemes in the measurement of dispersal. In: *Marked Individuals in the Study of Bird Population*: 323–328 (J.–D. Lebreton & P. M. North, Eds.). Birkhäuser Verlag, Basel.
- Väisänen, R., Lammi, E. & Koskimies, P., 1998. *Distribution, numbers and population changes of Finnish breeding birds*. Otava, Helsinki (In Finnish with English summary).
- Wallin, K., Carlsson, M. & Wall, J., 1988. Natal dispersal in female and male Tawny Owls (*Strix aluco*). In: *Life history evolution and ecology in the Tawny Owls (Strix aluco)* (Wallin, K.). Ph. D. Thesis, Univ. of Gothenburg.
- Walters, J. R., 2000. Dispersal behavior: an ornithological frontier. *Condor*, 102: 479–481.
- Wernham, C. V., Toms, M. F., 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.
- White, G. C. & Burnham, K. P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46: S120–S139