Estimating components of variance in demographic parameters of Tawny Owls, *Strix aluco*

C. M. Francis & P. Saurola

Abstract

Estimating components of variance in demographic parameters of Tawny Owls, Strix aluco.— Survival rates of Tawny Owls (*Strix aluco*) were estimated using recapture and recovery data from approximately 20,000 nestling and adult owls ringed between 1980 and 1999 in southern Finland. Survival rates averaged 33% in the first year of life, 64% in the second, and 73% in subsequent years, but varied dramatically among years. Approximately 50% of annual variation in survival could be explained by stage of the vole cycle and severity of winter weather. Capture probabilities, an index of breeding propensity, varied dramatically among years, and could almost entirely be explained by the vole cycle, superimposed on a long–term increase in capture effort. Matrix models based on mean values in each year of the vole cycle, predict that in 2 out of 3 years, the population would decline by 13%–15% per year, offset by a large increase in the 3rd year. Numbers of nesting pairs are predicted to be low in one of three years, with no long–term trend, consistent with observed estimates of active nests.

Key words: Population fluctuations, Voles, Winter weather, Survival estimation, Matrix models.

Resumen

Estimación de los componentes de la varianza en los parámetros demográficos del cárabo común, Strix aluco.— Se calcularon las tasas de supervivencia del cárabo común (*Strix aluco*) utilizando datos de recaptura y recuperación correspondientes a unos 20.000 cárabos comunes —entre polluelos y adultos—, anillados entre 1980 y 1999 en el sur de Finlandia. Las tasas de supervivencia alcanzaron un promedio del 33% en el primer año de vida, del 64% en el segundo y del 73% en los años subsiguientes, variando de forma espectacular entre los distintos años. Alrededor del 50% de la variación anual en la supervivencia pudo ser explicada por el estadio en que se encontraba el ciclo poblacional de los micrótidos y el rigor del clima invernal. Las probabilidades de captura —que representan un índice de la propensión a la reproducción— variaron considerablemente entre los distintos años, pudiendo explicarse en su práctica totalidad por el ciclo de los micrótidos, superpuesto a un aumento a largo plazo del esfuerzo de captura. Según los modelos matriciales basados en los valores promedio correspondientes a cada año del ciclo de los micrótidos, predicen que en dos de cada tres años la población disminuirá entre un 13% y un 15% anual, aunque ello se verá compensado por un considerable aumento durante el tercer año; asimismo, se calcula que el número de parejas nidificantes será bajo uno de cada tres años, sin ninguna tendencia a largo plazo, lo que concuerda con las estimaciones observadas acerca de los nidos activos.

Palabras clave: Fluctuaciones poblacionales, Ratones de campo, Clima invernal, Estimación de supervivencia, Modelos matriciales.

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

Introduction

Populations of many animal species fluctuate in response to changing environmental conditions. For example, breeding populations of some seabirds are affected by multi–annual fluctuations in oceanographic patterns such as the El Niño Southern Oscillation, which affect food supply and hence both breeding success and survival (Nur & Sydeman, 1999). In other species, irregular severe weather events may cause substantial mortality at a particular time of year, such as for Grey Herons *Ardea herodias* overwintering in Britain (Freeman & North, 1990).

Of particular interest, from the perspective of variability, are the multi–year population cycles of small mammals and their associated predator communities. These have attracted considerable research attention, both studying the impact of small mammals on predators (e.g. Brand & Keith, 1979) and the impact of predators on small mammals (e.g., Korpimäki et al., 2003). Intensive long–term studies of the 10–year cycle of the Snowshoe Hare (*Lepus americanus*) and its associated predators in northern Canada suggest that this system is driven largely intrinsically, by predator–prey dynamics, with dispersal of predators, and possibly large–scale climatic factors, helping to synchronize the cycle (Krebs et al., 2001). In contrast, there is still considerable controversy about the factors driving the three to four year cycles of small rodents, particularly voles, in northern Europe (e.g., Oli, 2003; Korpimäki et al., 2003).

Ruesink et al. (2002) emphasized the importance of accurate demographic data for understanding population cycles. Among the predators involved in these northern forest systems, are several species of owls. Breeding propensity, clutch size, nesting success, movement patterns and survival rates of Great Horned Owls (*Bubo virginianus*) have all been shown to vary in relation to the 10–year cycle in Snowshoe Hare (Houston & Francis, 1995; Rohner et al., 2001). Breeding success and emigration patterns of several European owl species have also been shown to fluctuate in response to the 3–4 year cycle of many microtine rodents (Saurola, 1997). Dispersal distances of many Finnish owls are greater in years of low vole abundance (Saurola, 2002). Survival rates of male Tengmalm's Owls (*Aegolius funereus*) vary dramatically in response to vole abundance with estimated survival decreasing from 50–75% in peak years to only 30–35% in poor years (Hakkarainen et al., 2002). In addition, surviving males were less likely to breed in low vole years, as indicated by lower recapture rates. Breeding success and survival also vary dramatically among years in the Ural Owl (*Strix uralensis*) (Brommer et al., 2002).

Tawny Owls (*Strix aluco*) breed throughout much of Europe. In Finland, the Tawny Owl is a relative newcomer, with the first record in 1875, and the distribution still largely restricted to the south (Saurola, 1995). The Tawny Owl may be restricted from expanding farther north by winter tempera-

tures and snow conditions. Like most other owls in Finland, Tawny Owls feed on voles when these are abundant, but as generalist feeders, they can also feed on other prey when voles are scarce (Saurola, 1995; Sunde et al., 2001; Solonen & Karhunen, 2002). Nevertheless, numbers of occupied territories, numbers of nesting pairs, and numbers of young per nesting attempt have been found to vary in response to vole abundance (Saurola, 1997).

Changes in population numbers with the vole cycle could be influenced by variation in breeding success (productivity), variation in survival rates, or a combination of both. To determine the relative importance of these factors requires estimates of annual variation in each of these parameters. Data from large–scale, coordinated ringing in Finland provide an opportunity to examine the impact of vole abundance, as well as other environmental factors such as winter weather, on demographic parameters of this species, and to estimate the impact of these factors on population dynamics of the owls.

In this paper, joint analyses of recapture and recovery data of Tawny Owls ringed throughout southern Finland (Francis & Saurola, 2002) are used to estimate annual variation in age–specific survival probabilities of this species and the proportion of variation that can be explained by the vole cycle and by winter weather conditions. Annual variation in recapture parameters of yearlings and adults is also estimated. Because most adults are captured as breeders, capture probabilities can be considered an index of the proportion of pairs that are breeding (breeding propensity), after allowing for any variation in capture effort. Finally, the results of these analyses are put into a simple demographic model to estimate the overall impact of fluctuations in vole abundance on population size of these owls.

Methods

Field data

Especially since the early 1970s, bird ringers in Finland have been strongly encouraged to ring nestlings and capture adults of several species of birds of prey (Saurola, 1997; Saurola & Francis, 2004). As a consequence of this activity, a very large data base of ringing, recapture and recovery data has been accumulated for several species of owls. For the Tawny Owl, ringing has taken place during the breeding season throughout much of the species breeding range in Finland. Many individuals now breed in nest boxes, mostly installed by ringers and inspected regularly during the breeding season. At successful nests, the nestlings are ringed when they are of sufficient age. In addition, most ringers also attempt to trap and ring the adult female and many also trap the male at each nest.

In this paper, data from the 20 year period from 1980 to 1999 were selected for analysis. The sample sizes during this period (including only breeding

season captures) were 18,166 nestlings ringed, leading to 1,737 recaptures and 1,655 recoveries, along with 1,742 adults ringed which generated 1,278 recaptures and 190 recoveries.

Small mammal abundance varies dramatically among years, with variation in abundance of voles between high and low points in the population cycle up to two orders of magnitude (Brommer et al., 2002; Hanski et al., 1991). Quantitative measures of vole abundance were only available from some areas of Finland. Previous analyses have shown that these are generally well–correlated at broad spatial scales with a 3–year cycle in most of southern Finland (Sundell et al., 2004). By combining these quantitative observations with casual observations in the field, years were readily classified into one of three categories, here labelled based on the potential impact for survival of owls over the coming year: Poor – voles are at their peak at the beginning of the year, but crash over the course of the year, such that owls have very few voles available for food during the year, especially in the following winter; Medium – voles are low at the start of the year, but gradually increase over the course of the year; Good – voles are moderately abundant at the beginning of the year and increase to a peak over the summer and following winter.

Winter severity was indexed by two measures: mean daily temperature over the winter, derived from the mean monthly temperatures between December and March, and mean monthly snow depth during the same period. Both measures were taken as the mean of data from five weather stations of the Finnish Meteorological Institute in southern Finland: 1,201 Jokioinen (60° 49' N, 23° 30' E); 1,303 Hattula Leteensuo (61° 04' N, 24° 14' E); 1,304 Hattula Lepaa (61° 08' N, 24° 20' E); 1,306 Pälkäne Myttäälä (61° 20' N, 24° 13' E); 1,403 Lammi, Biological station (61° 03' N, 25° 03' E).

Statistical analyses

Survival probabilities were estimated using joint recapture and recovery models (Burnham, 1993). Previous analyses have shown that these combined models allow estimation of age–specific survival rates with little apparent bias due to emigration from the study area (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 breeding population will be captured 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. This "fidelity" parameter is often considered as the probability that an individual will not emigrate from the study area (Burnham, 1993), but this interpreta-

tion is dependent on several assumptions: recapture effort is concentrated in a particular study area; all animals present in the study area are equally likely to be captured; and all individuals that have left the study area are equally like to be recovered. For Tawny Owls, even individuals that emigrate from a particular area can potentially be recaptured, because capture effort occurred throughout the species range in Finland. Also, although individuals from anywhere in the country can potentially be recovered, the probability may vary geographically with human population densities. Finally, in some areas, capture probabilities of males were probably lower than those of females, with the result that males may appear to have "emigrated" from the study area (note that Tawny Owls were not sexed as nestlings nor on recovery, so this is not easily modelled). For these reasons "fidelity" parameters can not reliably be interpreted in any biological context, and we do not present the estimates.

Initially, a series of models was tested with 2 or 3 age classes for each parameter, and annual variation in all parameters except "fidelity" parameters, which were constrained to be constant within each age class. For models with more than 2 age classes, birds ringed as "adults" were treated as if they were all in the highest age class. In practice, these likely included some birds in their second year which were not distinguished from adults. While these are unlikely to be a large percentage of birds captured (because of the lower nesting probability of yearlings), this may cause a slight downwards bias in the adult estimates.

Goodness of fit was tested for the most general model examined (with three age classes for survival and recapture probabilities, two age classes for recovery, and three for "fidelity", the first three all varying among years) using a generalized bootstrap goodness of fit within MARK (White & Burnham, 1999). This indicated some residual lack of fit, which was dealt with through quasi–likelihood approaches, using an overdispersion parameter $\hat{c}$ = 1.2. QAICc was then used for selection among these models.

All model selection and parameter estimation was performed using MARK; however, because of the complexity involved with editing the large Parameter Index Matrices and the Design Matrix, the input files for the analyses were created using custom–written SAS programs (SAS Institute, 2001). Models were also checked, and in many cases rerun, from within the MARK interface. This was particularly necessary for some constrained parameter models that converged on a local maximum of the likelihood and had to be rerun with alternative starting values.

Two approaches were selected to estimate annual variation in survival and recapture parameters (the latter being related to breeding propensity because only breeding birds were captured). The first approach was to use the Variance Components option within MARK, modelling annual variation in age–specific survival as a random effect. This es-

sentially involves modelling residual variation in the annual estimates, after correcting for sampling error, using the variance–covariance matrix of the estimates (White & Burnham, 1999). This was done with no covariates except the mean (to measure total variance), then with voles as a covariate (treated as a class variable with 3 unranked levels to avoid imposing any assumptions about the nature of the response of different parameters to the vole cycle), with weather as covariates (including both snow depth and temperature, each standardized to a range between +1 and –1), and with both together.

The second approach involved using ultrastructural models to incorporate covariates directly into the estimation procedure. First, a model constraining survival to be constant over time was fitted to the data and the difference in deviance (–2 * Likelihood) between this model and the year–specific model was taken as an index of total variation in annual survival rates. Then models were fitted constraining survival rates to vary in relation to voles, weather, or both, using the same coding as above. The percent reduction in the deviance, relative to the difference between constant and year–specific models, was used as a measure of the total variance in annual survival rates that could be explained by the covariates. This procedure was carried out separately for first–year survival (allowing adult and yearling survival to vary among years) and for survival of older age classes (which varied in parallel, while allowing first–year survival to vary independently among years).

The variance components approach was also used to estimate the percentage of variance in capture probabilities that could be explained by the vole cycle. In addition, as there appears to have been an increase in trapping effort for adults over time, a model incorporating year as a linear covariate, as well as voles, was also fitted.

Mean productivity estimates (nestlings per active nest) were derived from the Raptor Questionnaire (Saurola & Francis, 2004) that is completed by all active ringers in Finland.

Population modelling

A complete analysis of the impacts of both voles and winter weather on population dynamics of Tawny Owls, through stochastic simulation models, is beyond the scope of this paper. However, as a preliminary evaluation of the potential impact of the vole cycle, a deterministic, 2–stage, pre–breeding matrix model was developed, based on mean parameter values during each of the three stages of the vole cycle. The two stages were yearlings and adults, with transition probabilities from yearlings to adults and adults to adults represented by second year and adult survival probabilities respectively, while transitions to yearlings were estimated by the product of age–specific breeding propensity (probability a bird will breed), mean nestlings per nest (divided by 2 to allow for the fact that two adults are associated with each nest), and first–year survival probabilities (fig.

1). Breeding propensity for yearlings and adults at each stage of the vole cycle was estimated assuming that it was directly proportional to estimated mean recapture rates at each stage of the cycle and that 90% of adults breed during peak years of vole abundance. This 90% estimate was based on general impressions of the numbers of non–breeders during field work ringing owls, and is similar to peak estimates of percentage breeders of Ural Owls (Brommer et al., 2002).

Three separate matrices were developed, one for each year of the three stages of the vole cycle. The dominant eigenvalue of each matrix was used to estimate what population growth rate would have been, if population parameters had remained unchanged at those values. Population growth over the vole cycle, assuming that it continues as a regular three year cycle, can be estimated by analysing the matrix generated by multiplying the three matrices together in reverse order (Caswell, 2001). Age ratios at each stage of the cycle, as well as realized population growth rates in each year of the cycle, were determined by iteratively multiplying the matrices until the age distributions stabilized.

Results

Model selection indicated that survival probabilities varied for at least three age classes, whereas capture parameters could be adequately modelled with two age classes (table 1). This apparent discrepancy is, in fact, consistent with a model that allows different parameters for nestlings, yearlings and adults, because the first capture parameter actually refers to capture at one year of age (capture probabilities of nestlings are not included in the models). For the survival parameters, a model in which adult and yearling survival parameters are constrained to vary in parallel (on a logit scale) was found to be an adequate fit, and hence was used for all further analyses.

Survival rates varied considerably among years in all age classes (fig. 2), but the variance of first–year survival rates was about 40% higher than that of adults (table 2). Variance components analysis indicated that stage of the vole cycle could explain about 39% of annual variation in first–year survival, but only 11% of variation in adult survival (table 2). In contrast, winter severity, as measured by snow depth and temperature, explained only 35% of variation in first–year survival, but about 58% of variation in adult survival. Collectively, voles and winter weather explained approximately 50% and 58% of total variation in survival for young and adults respectively (table 2, fig. 2).

Estimates of variance components based upon changes in the deviance of ultra–structural models produced very similar results, with overall variance explained by all covariates estimated at 54% and 63% for young and adults respectively (table 3).

Annual survival rates for both age classes increased with warmer winter temperatures (fig. 3)
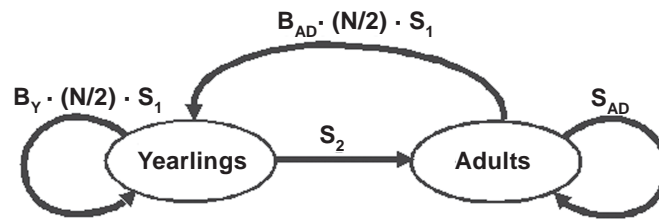
Fig. 1. Life cycle diagram for a pre–breeding, stage–based matrix model of Tawny Owls in Finland: B_Y. Proportion of yearlings (one–year old birds) that breed; B_{AD}. Proportion of adults that breed; N. Mean number of nestlings fledged per nesting attempt (assumed the same for yearlings and adults); S_1. Survival probability of owls in their first year, from fledging to the following breeding season; S_2. Survival probability of owls over their second year; S_{AD}. Annual survival probability of adults.

Fig. 1. Diagrama del ciclo vital según un modelo de matrices por etapas para la pre–reproducción del cárabo común en Finlandia: B_Y. Proporción de aves de un año de vida que se reproducen; B_{AD}. Proporción de adultos que se reproducen; N. Promedio de polluelos volantones por cada intento de anidación (presuponiendo lo mismo para aves de un año de vida y para adultos); S_1. Probabilidad de supervivencia del cárabo común durante su primer año de vida, desde la fase de volantones hasta la siguiente estación de reproducción; S_2. Probabilidad de supervivencia del cárabo común durante su segundo año de vida; S_{AD}. Probabilidad de supervivencia anual de los adultos.

and with reduced winter snow depth (fig. 4). However, both of these weather variables were strongly correlated, and after taking into account temperature, snow depth explained little residual variation. Mean winter temperatures varied by nearly 10°C among years over the study period. The predicted impact on the owls was most dramatic for first–year survival, with a predicted increase from only 20% annual survival in the coldest years, up to 40% in warmer years. Adult survival was predicted to vary from 60% up to 80% over the same temperature range (fig. 3).

Table 1. Results of initial model selection process to estimate annual variation in age–specific survival and recapture probabilities: Model parameters represent probabilities for survival (Φ), recapture (p), recovery (r) and "fidelity" (F) (see text for definitions). In each column, letters refer to variation modeled in first, second, and third age classes (if present) (Y. Year–specific; C. Constant; Y+Y. Different intercepts, but parallel —on a logit scale— annual variation in the 2nd and oldest age classes). $\hat{c}$ was estimated at 1.2 from a parametric bootstrap procedure.

Tabla 1. Resultados del proceso de selección inicial de modelos para estimar la variación anual en la supervivencia específica dependiente de la edad y las probabilidades de recaptura: "Model parameters" representan la probabilidad de supervivencia (Φ), recaptura (p), recuperación (r) y fidelidad (F) (ver el texto para las definiciones). En cada columna las letras se refieren a la variación modelada en la primera, segunda y tercera clases de edad (Y. Anual; C. Constante; Y+Y. Distintas intercepciones, pero variación anual paralela —en escala logit— en la segunda y superiores clases de edad). $\hat{c}$ se calcula a 1,2 a partir de un proceso bootstrap paramétrico.

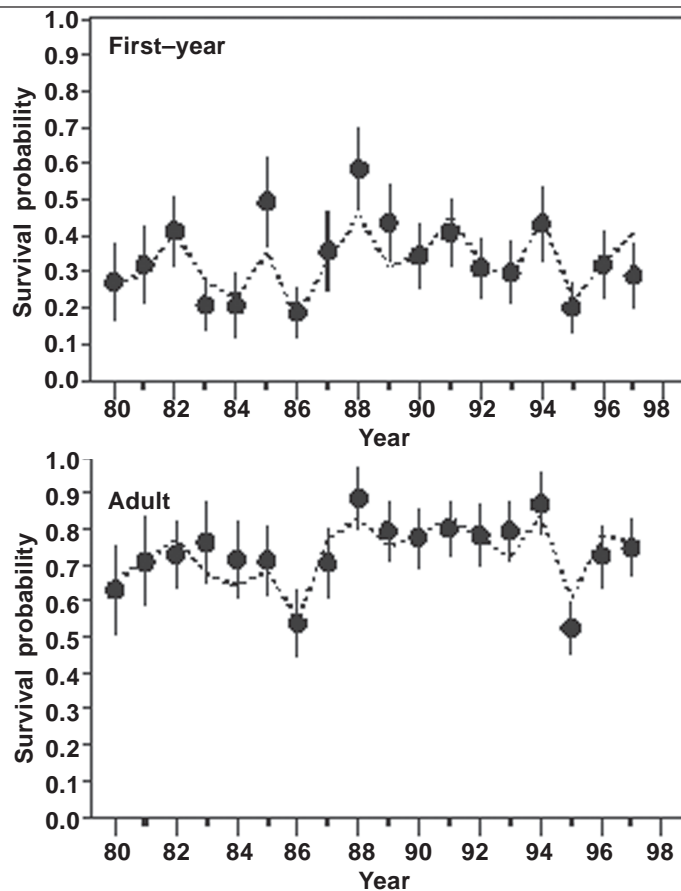| Model parameters				Model fit		
Φ	p	r	F	$\Delta AIC(\hat{c})$	# Parm.	Deviance
Y,Y+Y	Y,Y	Y,Y	C,C,C	0.00	120	3270.65
Y,Y+Y	Y,Y,Y	Y,Y	C,C,C	7.43	137	3243.70
Y,Y,Y	Y,Y	Y,Y	C,C,C	14.04	136	3252.33
Y,Y,Y	Y,Y,Y	Y,Y	C,C,C	21.67	151	3229.58
Y,Y	Y,Y	Y,Y	C,C	34.84	117	3311.57
Y,Y	Y,Y	Y,Y	Y,Y	56.70	141	3284.87

Fig. 2. Estimated annual survival probabilities with 95% confidence intervals for Tawny Owls in their first year of life (top) and as adults (bottom), from 1980 to 1997. Note that second–year survival probabilities were modelled as fluctuating in parallel (on a logit scale) with adult survival, but averaged about 13% lower. Dashed lines show predicted survival rates based on a regression model incorporating stage of the vole cycle and two measures of severity of winter weather.

Fig. 2. Estimaciones de las probabilidades de supervivencia anual, con intervalos de confianza del 95%, del cárabo común durante su primer año de vida (parte superior) y como adulto (parte inferior), desde 1980 hasta 1997. Obsérvese que las probabilidades de supervivencia durante el segundo año se modelaron como si fluctuaran en paralelo (en una escala logit) con la supervivencia de los adultos, pero el promedio fue alrededor de un 13% inferior. Las líneas discontinuas indican las tasas de supervivencia previstas basadas en un modelo de regresión que incorpora la etapa del ciclo de los micrótidos y dos medidas de rigor invernal.

Capture probabilities also varied dramatically among years, especially for yearlings (fig. 5). In this case, stage of the vole cycle explained nearly all of the variation in capture probabilities for yearlings, with only minimal additional variation explained by a linear trend variable (table 4). For adults, stage of the vole cycle, on its own, explained only 64% of variation in capture probabilities, but addition of a trend variable, possibly reflecting increased effort in recent years, brought this up to nearly 95% as well. Weather variables explained no additional variation.

Considering only the impact of the vole cycle, mean survival rates in poor and good years ranged from 26% to 43% in first–year, 57% to 71% in second year, and 67% to 79% in older owls (table 5). Capture probabilities, which can be considered an index of breeding propensity as only nesting birds were captured, were lowest in years following poor survival, dropping to only 4% for yearlings and 29% for adults. For yearlings, the next lowest years were in periods when voles crashed, presumably because the crash starts just before or during the breeding cycle. In contrast, for adults, there was little difference in breeding propensity between good years and years when voles crashed.

Data on nesting productivity from 1986–1997 (Saurola & Francis, 2004) indicate that nest suc-

Table 2. Components of variance in annual survival probabilities for first year birds and older birds, based on using the variance components option within program MARK for survival estimates from model Φ(Y,Y+Y) p(Y,Y) r(Y,Y) F(C,C,C) from table 1. Residual variance in this model is estimated after adjusting for variance due to sampling error. Voles were modelled as a class variable with three states, and weather variables (snow depth and temperature) were modelled as continuous covariates.

Tabla 2. Componentes de varianza en las probabilidades de supervivencia anual para las aves de un año de vida y las de más edad, a partir de la opción de componentes de varianza en el marco del programa MARK para estimaciones de supervivencia a partir del modelo Φ(Y,Y+Y) p(Y,Y) r(Y,Y) F(C,C,C) de la tabla 1. En este modelo la varianza residual se estima tras haber ajustado la varianza como consecuencia del error de muestreo. Los ratones de campo se modelaron como una variable de clases con tres estados, mientras que las variables climáticas (profundidad de la nieve y temperatura) se modelaron como covariantes continuas.

Covariates	First–Year		Yearling/adults	
	Residual variance	% Reduction in variance	Residual variance	%Reduction in variance
No covariates	0.01130	0.0	0.00802	0.0
Voles alone	0.00691	38.8	0.00712	11.2
Weather variables alone	0.00730	35.4	0.00335	58.3
Voles and weather variables	0.00566	50.0	0.00340	57.6

Table 3. Estimates of the percent of total variance in annual survival probabilities for first year birds and older birds, based on fitting ultra–structural models with various constraints placed on first year survival, starting with model Φ(Y,Y+Y) p(Y,Y) r(Y,Y) F(C,C,C) from table 1. All constraints were based on logit–link models, with voles modelled as a class variable with three states, and weather variables (snow depth and temperature) modelled as continuous covariates. In all models, the other age classes were allowed to vary among years.

Tabla 3. Estimaciones del porcentaje de la varianza total en las probabilidades de supervivencia anual para las aves de un año de vida (parte superior) y las aves de más edad (parte inferior), tras haber ajustado modelos ultraestructurales con varias restricciones en la supervivencia del primer año, empezando con el modelo Φ(Y,Y+Y) p(Y,Y) r(Y,Y) F(C,C,C) de la tabla 1. Todas las restricciones se basaron en modelos logit-link, con los ratones de campo modelados como una variable de clases con tres estados, mientras que las variables climáticas (la profundidad de la nieve y la temperatura) se modelaron como covariantes continuas. En todos los modelos se permitió que las otras clases de edad variaran entre los distintos años.

| Model	Deviance	ΔDeviance	% Variance explained
First–year survival			
Year–specific	3270.653	0.00	100
Voles and weather variables	3311.691	41.04	54
Weather variables alone	3328.888	58.23	35
Voles alone	3334.364	63.71	29
No covariates (constant survival)	3360.361	89.71	0
Yearling and adult survival			
Year–specific	3270.653	0.00	100
Voles and weather variables	3302.467	31.81	63
Weather variables alone	3309.923	39.27	55
Voles alone	3349.046	78.39	9
No covariates (constant survival)	3357.027	86.37	0
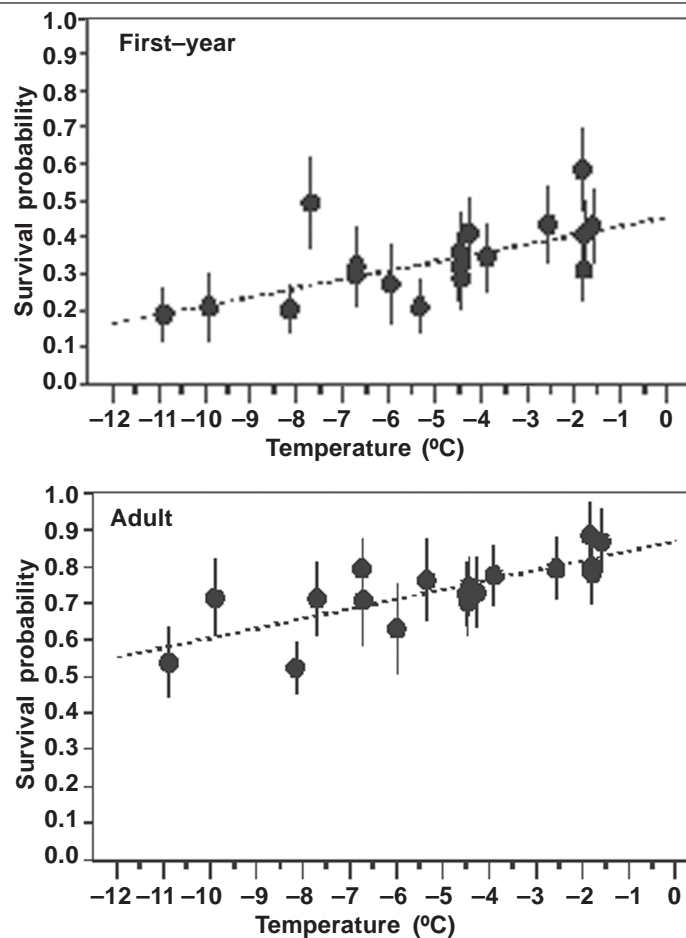
Fig. 3. Estimated annual survival probabilities with 95% confidence intervals for Tawny Owls in their first year of life (top) and as adults (bottom), from 1980 to 1997 plotted in relation to mean winter temperature. Dashed line shows a simple linear regression.

Fig. 3. Estimaciones de las probabilidades de supervivencia anual, con intervalos de confianza del 95%, del cárabo común durante su primer año de vida (parte superior) y como adulto (parte inferior), desde 1980 hasta 1997, representadas gráficamente con relación a la temperatura media invernal. La línea discontinua indica una regresión lineal simple.

cess, among active nests, parallels breeding propensity of yearlings, with lowest productivity (2.30 young per active nest) in years following a crash, medium productivity (2.76 young/nest) in years when the crash actually occurred, and highest productivity (3.03 young/nest) in years when voles were abundant and increasing.

These values were used to construct population projection matrices based on the model in figure 1 for each of the three phases of the vole cycle (table 6).

The lower entries in each of the component 2 x 2 matrices represent survival probabilities for yearlings and adults (table 5). The upper values represent the product of the number of young produced and the first year survival rate, calculated as $B_x \cdot (N/2) \cdot S_1$, where B_x is estimated by

$P_x \cdot (0.90/P_{AD-peak})$. For example, the number of new yearlings produced by yearlings in poor years is estimated at:

$$0.189 \cdot (0.90/0.469) \cdot (2.76/2) \cdot 0.26 = 0.130.$$

The dominant eigenvalues of these matrices suggest that, if parameters were to remain stable at each of those levels, conditions of poor and medium years of the vole cycle would lead to a 10% to 12% decline per year, whereas conditions for good years would lead to an increase of about 26% (table 6). Such analyses do not, however, reflect actual population changes over the cycle, because the age ratio changes through the cycle.

The projection matrix over the complete vole cycle indicates that, over a 3–year period, the popu-
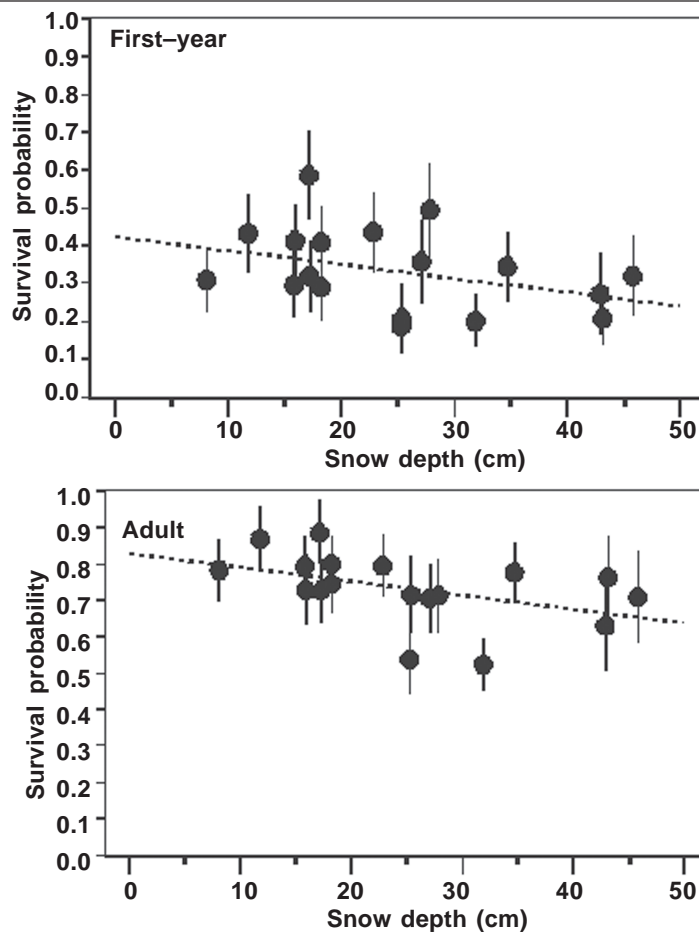
Fig. 4. Estimated annual survival probabilities with 95% confidence intervals for Tawny Owls in their first year of life (top) and as adults (bottom), from 1980 to 1997 plotted in relation to mean snow depth. Dashed line shows a simple linear regression.

Fig. 4. Estimaciones de las probabilidades de supervivencia anual, con intervalos de confianza del 95%, del cárabo común durante su primer año de vida (parte superior) y como adulto (parte inferior), desde 1980 hasta 1997, representadas gráficamente con relación a la profundidad media de la nieve. La línea discontinua indica una regresión lineal simple.

lation would be approximately stable (at least within the uncertainty of the parameter estimates), but fluctuations in numbers of birds are greater than suggested by the eigenvalues. The overall population drops by 13% in the first year, another 15% in the second year, but then increases by 32% in the third year (table 6). Much of this variation arises as a result of changes in the age ratio, with a large surge in production of young in the third year. Population changes for adults lag one year behind, and are less extreme: the number of adults in the population increases by 7.4% over the poor year (as the large number of yearlings produced in the previous good year matures), then decreases by 1.7% in the medium year, and 6.3% in the good year. Based on these models, and taking into account the breeding probability of each age class, the model predicts that

the number of active nests should be lowest at the beginning of a medium year, increase by 74% by the start of a good year, then increase by a further 5% at the start of a poor year before dropping again.

Discussion

These analyses indicate that all aspects of the demography of Tawny Owls in Finland vary substantially among years, including survival probabilities, capture probabilities (an index of breeding propensity) and nesting success.

The variance components analysis suggests that more than half of the variation in survival rates for all age classes can be explained by a combination of vole abundance and winter weather.
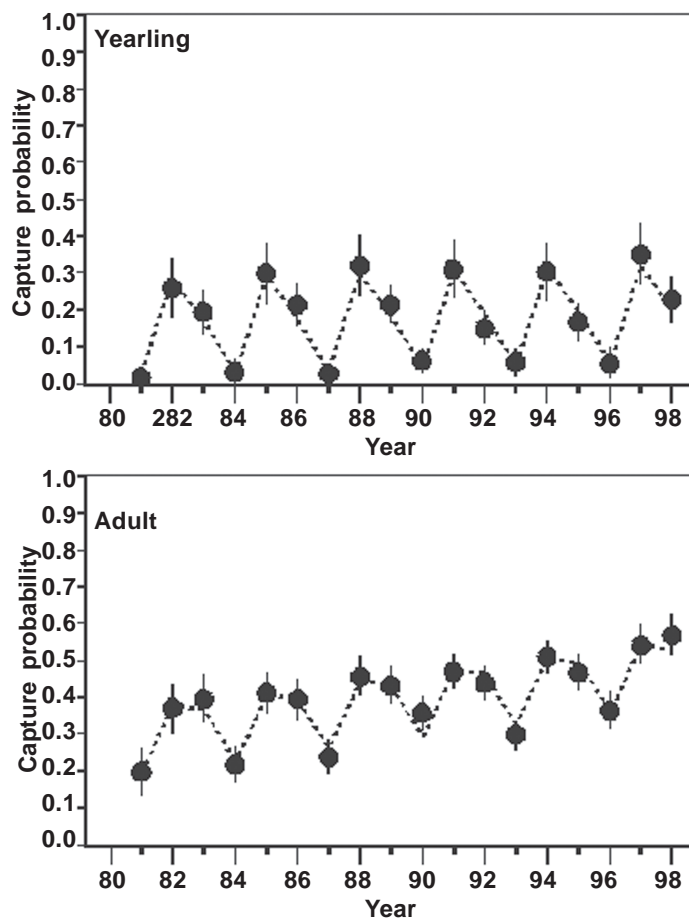
Fig. 5. Estimated capture probabilities with 95% confidence intervals for yearling (top) and adult (bottom) Tawny Owls in Finland from 1981 to 1998. Dashed lines show predicted capture probabilities based on a regression model incorporating stage of the vole cycle and year as a linear covariate.

Fig. 5. Estimaciones de las probabilidades de captura, con intervalos de confianza del 95%, del cárabo común durante su primer año de vida (parte superior) y como adulto (parte inferior), en Finlandia, desde 1981 hasta 1998. Las líneas discontinuas indican las probabilidades de captura previstas a partir de un modelo de regresión que incorpora la etapa del ciclo de los micrótidos y el año como una covariante lineal.

Both approaches to estimating variance components produced similar estimates, though there were some slight differences, presumably reflecting the fact that both methods involve approximations and asymptotic assumptions. The variance components approach (White & Burnham, 1999) produces the apparent anomaly of a poorer fit when both weather and voles are considered together, than with just weather effects. This may be due to the small number of years for estimating variance (18) relative to the number of parameters (4), and changes in the estimated error variance with reduced degrees of freedom as more dependent variables are added. The approach using ultrastructural models is robust to this particular limitation, but has other limitations, including the

fact that only one set of parameters can be modelled at a time without introducing bias. Bayesian approaches, using Markov Chain Monte Carlo (MCMC) would allow more robust estimates of variance components (Link & Barker, 2004), for both strictly random effects models as well as for mixed effects models such as this one, and should be considered for future analyses.

An examination of the individual survival estimates (fig. 2) suggests that a substantial amount of the residual variation, after accounting for voles and weather, is due to particularly high survival, especially for first–year birds, in two peak vole years in 1985 and 1988. Anecdotal evidence suggests that voles were exceptionally abundant in those two years, despite the fact that capture prob-

Table 4. Components of variance in annual capture probabilities for yearling and older birds, based on using the variance components option within program MARK for recapture estimates from model $\Phi(Y,Y+Y)$ p(Y,Y) r(Y,Y) F(C,C,C). Residual variance in this model is estimated after adjusting for variance due to sampling error. Voles were modelled as a class variable with three states, while year was modelled as a linear covariate.

Tabla 4. Componentes de varianza en las probabilidades de captura anual para las aves de un año de vida y de más edad, a partir de la opción de componentes de varianza en el marco del programa MARK para estimaciones de recaptura a partir del modelo $\Phi(Y,Y+Y)$ p(Y,Y) r(Y,Y) F(C,C,C). En este modelo, la varianza residual se estima tras haber ajustado la varianza como consecuencia del error de muestreo. Los ratones de campo se modelaron como una variable de clases con tres estados, mientras que el año se modeló como una covariante lineal.

	Yearlings		Adults	
Covariates	Residual variance	% reduction in variance	Residual variance	% reduction in variance
No covariates	0.01324	0.0	0.01048	0.0
Voles alone	0.00061	95.4	0.00375	64.2
Voles and year	0.00061	95.4	0.00068	93.5

abilities, which fluctuate almost perfectly in synchrony with the vole cycle (fig. 5) show nothing exceptional about those years. Different responses of survival and breeding propensity to quantitative variation in vole abundance might be expected, because the limiting factors are at different times of year. Breeding activity is influenced mainly by vole abundance early in the season and may plateau at moderate levels of vole abundance. Survival, in contrast, is likely to be limited later in the year, especially in winter, and may not asymptote at the same level. Unfortunately, the quantitative data re-

Table 5. Estimates of mean survival rates (S) and capture probabilities (p) with their standard errors in relation to the vole cycle, estimated from the model $\Phi(Y,Y+Y)$ p(Y,Y) r(Y,Y) F(C,C,C). Stages of the vole cycle are labelled with respect to their predicted impact on survival probabilities. Because the main impact of the crash is after the breeding season, the relative impacts on capture probabilities (assumed proportional to breeding propensity) are different from those on survival.

Tabla 5. Estimaciones de las tasas de supervivencia media (S) y probabilidades de captura (p), con sus errores estándar con relación al ciclo de los micrótidos, estimadas a partir del modelo $\Phi(Y,Y+Y)$ p(Y,Y) r(Y,Y) F(C,C,C). Los estadios del ciclo de los micrótidos se determinan en función del impacto esperado sobre la probabilidad de supervivencia. Dado que el principal impacto se da después de la estación de reproducción, los impactos relativos sobre las probabilidades de captura (asumidos proporcionales a la propensión de reporducirse) son diferentes a los de la supervivencia.

	Stage of the vole cycle					
	Poor		Medium		Good	
Parameter	Mean	SE	Mean	SE	Mean	SE
S_1	26.0	4.2	30.1	4.4	42.7	4.8
S_2	57.3	5.6	64.6	5.7	70.6	5.4
S_{AD}	67.1	4.5	73.8	4.5	79.2	4.3
$P_{Yearling}$	18.9	2.2	3.9	1.4	30.5	3.7
P_{AD}	45.8	3.0	28.9	3.0	46.9	3.1

Table 6. Projection matrices, their dominant eigenvalues (λ), and estimated population change (ΔN) for Tawny Owls in Finland during each year of the vole cycle, based on the model in figure 1. The "whole cycle" matrix represents the projection from one good year to the next good year (see text), and as such λ and ΔN for this matrix refers to a 3–year period. Change in population size from the beginning of a particular phase of the vole cycle to the start of the next phase (ΔN) and the percentage of yearlings at the end of the cycle (% Yearlings), calculated through iterative deterministic modelling.

Tabla 6. Matrices de proyección, sus valores propios dominantes (λ), y cambio poblacional estimado (ΔN) para el cárabo común en Finlandia durante cada año del ciclo de los micrótidos, a partir del modelo de la figura 1. La matriz del "ciclo completo" representa la proyección de un año bueno hasta el siguiente año bueno (véase el texto) y, por consiguiente, en esta matriz, λ y ΔN se refieren a un período de 3 años. Cambio en el tamaño de población desde el inicio de una determinada fase del ciclo de los micrótidos hasta el inicio de la siguiente fase (ΔN) y el porcentaje de individuos de un año al final del ciclo (% Yearlings) calculado mediante un modelo determinístico itarativo.

Stage of vole cycle		Projection matrix		λ	ΔN	%Yearlings
		Yearling	Adults			
Poor	Yearling	0.130	0.315	0.904	0.869	27.5
	Adults	0.573	0.671			
Medium	Yearling	0.026	0.192	0.883	0.859	17.0
	Adults	0.646	0.738			
Good	Yearling	0.378	0.582	1.259	1.324	41.3
	Adults	0.706	0.792			
Whole cycle	Yearling	0.338	0.458	0.989	0.989	—
	Adults	0.482	0.650			

quired to test this hypothesis, on variation among cycles both in vole abundance and in how this changes across seasons, are lacking.

The relationship between capture probabilities and the vole cycle, after allowing for the long–term increase, is almost unbelievably close —it is important to note that all of the estimates in figure 5 were derived from unconstrained year–specific parameter estimates. This relationship is unlikely to be affected by ringing effort, which is believed to be quite independent of the stage of the vole cycle. Most ringers check every nest box in their territory every year, and make a concerted effort to trap nesting birds at all occupied nest boxes. However, the long–term increase in capture probabilities suggests that efforts by the ringing office to encourage ringers to capture more adults, especially males, have been successful. In this analysis, we did not consider differences in capture probabilities between the sexes, which are likely to differ based on the fact that nearly three times as many adult females as males are ringed (unpublished data). Unfortunately, sex can only be determined for adults, and thus is unknown for nearly all nestlings that were not subsequently recaptured, including most of those that were later recovered without being recaptured. It would be possible to develop models that allow sex–specificity in some parameters such as capture probabilities, but only by making explicit assumptions about other parameters that are not estimable because of missing information. In any case, it is quite likely that the main difference between the sexes is in capture probability, rather than either breeding propensity or survival.

Matrix models indicate that the abundance of voles has a dramatic impact on the demography of Tawny Owls, with populations declining for two years out of every three, and then bounding back in the 3rd year, such that the long–term trend is for a roughly stable population (table 6). Although total population size is predicted to show two years of decline followed by an increase, the numbers of nesting pairs are predicted to show low breeding numbers in medium years followed by 2 years of increases. This latter pattern agrees at least qualitatively with observed numbers of nesting pairs estimated from the Raptor Census from 1982–1997 (Saurola, 1997; Saurola & Francis, 2004 —note that 1984 was a medium year). The matrix model suggests a slight long–term decline, of 1% every 3 years, but a slight change in some of the parameter estimates, such as the percentage of adults that attempt to breed in a good year,

could shift this to a stable or slightly increasing population. In any case, a change this small would not be detectable over a 20 year period. Observed population data show no sign of any long–term trend over the study period.

The impact of the vole cycle on this species is surprisingly great, considering that the Tawny Owl is a generalist feeder and can switch to other species of prey when voles are scarce (Saurola, 1995; Sunde et al., 2001; Solonen & Karhunen, 2002). The limited effect of vole abundance on adult survival (table 5) suggests that adults are able to use alternative prey to survive, although their breeding propensity is influenced by vole abundance. In contrast, young birds appear to be strongly dependent on small rodents both for survival over their first year, and for breeding in the subsequent year, if they do survive. Previous analyses of data from Tengmalm's Owl (Hakkarainen et al., 2002), which is relatively specialized on voles, indicate a more dramatic effect on adult survival, with nearly a 50% reduction in survival during years of low vole abundance, in addition to reduced breeding propensity. Survival probabilities of Ural Owls also vary considerably among years for both young and adults. Brommer et al. (1998, 2002) found that adult survival of Ural Owls ranged from a low of 60% to as high as 90%, while first–year survival estimates ranged from a low of 0% to as high as 75%, but only some of that variation could be explained by vole abundance. However, sample sizes were fairly small for some years, such that a substantial portion of that variance may be due to sampling variance.

The strong correlation between survival, of all age classes, and mean winter temperature supports the hypothesis that the northward spread of this species may be limited by severe winter weather. This suggests several directions for further research. One is to develop stochastic matrix models that consider the interaction between the vole cycle and winter weather patterns and their impact on projected population growth rates. These models would benefit from improved estimates of the variance components, derived from Bayesian approaches (Link & Barker, 2004). Such models could be used to determine whether the observed relationships between survival and temperature are consistent with the current northern limits of this species in southern Finland based on winter isoclines of temperature and snow depth. Predictions from such a model could be tested by looking for geographic variation in survival rates of this species within Finland because the geographic location of each territory is available as an individual covariate. Finally, such models could also be used to predict the potential impacts of various climate change scenarios on this species.

Such detailed demographic models, especially if similar models can be developed for some of the other owl species such as Ural Owl, can be used to enhance understanding of the extent to which these owls may actually be driving the population cycles of the voles, as opposed to merely responding to them.

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