# Estimating age-specific survival rates of tawny owls—recaptures versus recoveries

**CHARLES M. FRANCIS<sup>1</sup> & PERTTI SAUROLA<sup>2</sup>**, <sup>1</sup>Bird Studies Canada, PO Box 160, Port Rowan, Ontario, Canada and <sup>2</sup>Ringing Centre, Zoological Museum, PO Box 17, FIN-00014 University of Helsinki, Finland

ABSTRACT We compared estimates of annual survival rates of tawny owls (Strix aluco) ringed in southern Finland from several different sampling methods: recoveries of birds ringed as young; recaptures of birds ringed as young; recoveries of birds ringed as adults as well as young; combined recoveries and recaptures of birds ringed as young, and combined recoveries and recaptures of birds ringed as adults and young. From 1979 to 1998, 18040 young owls were ringed, of which 983 were recaptured as breeders in subsequent years during this period, and 1764 were recovered dead at various locations. In addition, 1751 owls were ringed as adults, of which 612 were later recaptured and 199 were recovered dead. First-year survival rates estimated using only recoveries of birds ringed as young averaged 48%, while apparent survival rates estimated using only recaptures from birds ringed as young averaged 10-13%. Use of combined recapturerecovery models, or supplementary information from recoveries of birds ringed as adults, produced survival estimates of 30-37%. Survival estimates from young-recoveries-only models were biased high, because of violation of the assumption of constant recovery rates with age: birds dying in their first-year were one-third less likely to be found and reported than older birds. In contrast, recaptures-only models confounded emigration with mortality. Despite these differences in mean values, annual fluctuations in estimated first-year survival rates were similar with all models. Estimates of adult survival rates were similar with all models, while those for second-year birds were similar for all models except recaptures-only. These results highlight the potential biases associated with analysing either recaptures or recoveries alone of birds ringed as young, and the benefits of using combined data.

Correspondence: C. M. Francis, Bird Studies Canada, P.O. Box 160, Port Rowan, Ontario, Canada NOE 1M0. E-mail: cfrancis@bsc-eoc.org

# 1 Introduction

Models to estimate survival rates based only on recoveries of birds ringed as young were formally developed by Cormack (1970) and Seber (1971). Such models have considerable intuitive appeal, because the age of all birds is known, and hence the methods seem appropriate for estimating age-specific demographic parameters. However, several authors have shown that the assumptions of these early models are violated for most data sets (Anderson *et al.*, 1981, 1985; Burnham & Anderson, 1979; Nelson *et al.*, 1980), and the sampling covariances among estimates mean that many of the survival estimates were unreliable (Lakhani & Newton, 1983).

A number of improvements have been suggested for these models (e.g. Morgan & Freeman, 1989; Freeman & Morgan, 1992), allowing recovery and survival rates to vary over time, thus making more realistic assumptions while enhancing the reliability of the estimates. Such models usually still require the assumption that recovery rates (here defined as the proportion of dead birds that are found and their bands reported)<sup>1</sup> do not vary with age. Nevertheless, these models continue to be used because, in many cases, the assumption appears plausible, and recoveries of birds ringed as young provide the only data available for the analysis of demography of a species (e.g. Houston & Francis, 1995; Catchpole *et al.*, 1999).

Catchpole *et al.* (1995) noted that certain models that allow for age-specific variation in recovery rates are not, in fact, singular, and can be fitted. However, many of these models require the assumption that recovery rates do not vary with time (an unlikely assumption) and, in any case, they often perform badly (Catchpole *et al.* 1995); sampling covariances among parameter estimates may be very high, leading to unreliable results.

The validity and generality of the assumption of equal recovery rates for different age classes has rarely been tested. Because recovery rates incorporate finding rates, the assumption may be violated if young birds die from different causes or in different locations from older birds, such that they are more or less likely to be found. Potts (1969) found that the recovery rates of adult shags (Phalacrocorax aristotelis) were about half those of young birds, possibly due to differences in cause or location of death. However, his estimates were based on an-hoc analyses of recaptures, recoveries and resightings, and it would be valuable to re-examine his data using modern statistical methods. Freeman & Morgan (1992) compared recovery rates between young and adults for two data sets for hunted species of ducks, and concluded that differences were relatively small, although they did find them large enough to bias survival estimates in at least one case. Francis (1995) showed that first-year and adult recovery rates for lesser snow geese (Anser caerulescens) not only differed, but were changing in different patterns over time. He showed that none of the biologically important conclusions about this population could have been deduced solely from recoveries of birds ringed as young. Nevertheless, the population of that species was rather unusual, in that the population was rapidly increasing, which led to density-dependent increases in non-hunting mortality of juveniles on the breeding grounds or early on migration (due to deteriorating habitat and food supplies), concurrently with decreased adult mortality due to a smaller proportion of the population being shot. Because virtually all recoveries came from birds dying from a single source of mortality (hunting), this led to differential changes in the recovery rates by age class.

The majority of bird species are not hunted, and little is known of whether, or how, recovery rates of such species vary with age, or whether this might affect estimates of survival rates. One data set that has been used several times for developing models based only on recoveries of birds ringed as young is for tawny owls in Finland (e.g. Rinne *et al.*, 1990, 1993). Such models have suggested that survival rates may continue to differ with age for up to the first three years of life (Rinne *et al.* 1993), but the assumption of age-invariant recovery rates has not been tested. This data set has two other sources of information available. First, in addition to nestlings, adults have also been ringed in the same areas, many of which have subsequently been recovered. Also, many of the nestlings have subsequently been recaptured as breeding adults (some of which have, in turn, later been recovered).

These data thus give the opportunity to evaluate and compare a number of different approaches for estimating age-specific survival rates for comparison with models based only on recoveries of nestlings. Use of ringing and recovery data from both adults and young allows application of many of the standard recovery models (Brownie et al., 1985). Such models are usually relatively unaffected by emigration (but see Francis & Cooke, 1992), but have the disadvantage that estimates of age-specific mortality rates are limited to age classes identified during ringing. Although tawny owls can potentially be aged to two or three years of age, based on moult patterns, the majority of birds in the data set, especially from earlier years, were classed either as nestling or +1, indicating they are older than their first year. Recapture data, for birds ringed as young, are more flexible in this respect, because the age of all birds is known, thus allowing estimation of agespecific survival rates for as many age classes as the data can support. However, survival estimates from recapture data may be biased by emigration, because birds leaving the initial study area are generally much less likely to be recaptured, and are confounded with birds that die. Combining the best features of both types of data, Burnham (1993) proposed a model for jointly analysing recapture and recovery data to estimate fidelity (the complement of permanent emigration) in addition to survival, recovery and recapture parameters.

In this paper, we compare estimates of annual survival rates and other parameters for tawny owls, using five different combinations of data: recoveries-only of birds ringed as young; recaptures-only of birds ringed as young; recoveries-only of birds ringed as young and as adults; recoveries and recaptures of birds ringed as young; and recaptures and recoveries of birds ringed as both young and adults. We show that estimates from the first two of these are substantially different from those produced from any of the latter three models, and discuss some of the biological and statistical reasons for these differences.

# 2 Methods

# 2.1 Data set

Tawny owls have been ringed for many years in Finland, both as nestlings and as adults by members of the Finnish bird ringing scheme working throughout much of the species' breeding range in southern Finland (Saurola, 1997). Ringers locate nests of the species, many of which are in nest boxes, and ring the young shortly before they are ready to leave the nests. A concerted effort is also made to capture breeding adults at or around the nest boxes, especially the females—efforts to ring males have been less consistent. From 1968 to 1998, about 27 000 tawny owls (*Strix aluco*) were ringed as nestlings in southern Finland, of which over 1300 have been recaptured as breeders in subsequent years and nearly 3000 have been recovered dead at various locations. In addition, approximately 2500 owls were ringed as adults (also mostly at nest boxes), of which 870 have been recaptured, and 335 recovered dead. Since 1986, many adults have been aged to second-year, third-year, or older, but because the sample sizes are fairly small in each age class, and many birds, especially prior to 1986, were not aged, we have not used that information in the present analysis.

# 2.2 Data analysis

For this paper, we restricted analyses to birds ringed and recovered during the 20year period between 1979 and 1998 to make the models smaller and more tractable. Recovery data included only birds reported as dead, excluding birds that were injured but still alive, or for which their condition (live or dead) was not reported. Virtually all ringing and recapture data were of birds caught during the breeding season, at or near their nesting site. To set up the capture histories, all ringing and recapture data were assigned to the calendar year in which they took place. The approximate median ringing date was 1 June, so recoveries were assigned to years based on the time period from 1 June (or the time of ringing/recapture, if this was earlier) to 31 May of the following year.

All models were implemented using program MARK (White & Burnham, 1999), and terminology and parameterization follows that program:  $\Phi$  is estimated survival rate, r is recovery rate (probability that a bird that dies will be found and its ring reported), p is the capture rate (probability that a bird alive and in the population will be captured) and f is 'fidelity' (probability that a bird alive in the population will return to a study area where it may be recaptured). The term r has often been called 'reporting rate' (e.g. by Catchpole et al., 1995), but White & Burnham (1999, p. S122) use both 'recovery rate' and 'reporting rate' for this parameter on the same page. Francis (1995) suggested that because r incorporates both the probability of finding a bird and of reporting it, that the term recovery rate was more appropriate, so we use that term here. In recapture models, the term  $\Phi$ usually incorporates both the effects of permanent emigration and mortality ('apparent survival'), whereas in recovery models and joint recapture-recovery models, it is usually considered to estimate the true survival rate. Interpretation of f as fidelity in joint models is dependent upon this assumption (Burnham, 1993). However, depending on the geographical distribution of recoveries, even recovery models may be biased by emigration to areas where the birds are less likely to be recovered (Francis & Cooke, 1992), especially if most recoveries occur on or near the breeding grounds (e.g. for non-migratory species). Throughout this paper, we use the term 'estimated survival rate', but note that for models involving recoveries, this is likely to be less biased by emigration and more closely estimate true survival (if other model assumptions are met). Note that because ringing and recapture took place at many locations throughout southern Finland, the 'fidelity' parameter must be treated with some caution-it overestimates the probability that a bird returned to the same site as its original capture, because some birds were recaptured even if they emigrated to a new location.

All model parameters were initially allowed to vary with time and with age for two age-classes. The only exceptions were recovery parameters in young-only recovery models, which were either allowed to vary with time (following the other models) or with age (following Catchpole *et al.*, 1995), because they become non-identifiable if age- and time-specific variation are both allowed. For models involving only birds ringed as young, we also fitted models allowing for variation in apparent survival with three age-classes. We then fitted models with each of the parameters constrained to be constant over time, or with temporal variation assumed to vary in parallel for each age class.

Within each data set, we selected the most parsimonious way to model time variation in each parameter, based upon AIC<sub>c</sub>. Because AIC<sub>c</sub> values cannot be compared among data sets, we only present those values (as differences) that are relevant for comparison of the 3-age-class with the 2-age-class models. For each data set, the most general model fitted was tested for goodness-of-fit using the omnibus bootstrap goodness-of-fit test provided by MARK. In no case was there any evidence for lack-of-fit (P > 0.10,  $\hat{c} < 1.1$ ) so we did not apply quasi-likelihood or other methods for dealing with overdispersion (Anderson & Burnham, 1999). Estimates of mean survival rates were calculated for the years 1979-1996 (which could be estimated from all models) based upon random-effects models, with shrinkage estimators used to reduce the influence of sampling error on estimates of annual survival rates (Burnham, 2002, this issue). Shrinkage estimates were also used for graphing annual variation in survival rates.

## 3 Results

#### 3.1 Model selection and comparison of mean values

In all cases where data permitted their estimation, the most parsimonious models allowed survival, recovery, and capture rates to vary among years and with at least two age classes (Tables 1, 2). Estimated first-year survival rates were substantially higher based on models using only recoveries of birds ringed as young, and substantially lower based on models using only recaptures of young, than for any of the models using multiple data sources (Table 1). Models with multiple data sources indicate that recovery rates varied with age, with young birds having recovery rates about one third lower than adults (Table 1; Z-test comparing recovery rates: P < 0.0001 for all models).

Modelling young-only recovery data with recovery rates varying with age, and not with time, as used by Catchpole *et al.* (1995), was strongly rejected by AIC ( $\Delta AIC_c > 100$ ) in comparison with a model allowing temporal but no age-specific variation. Furthermore, the absolute value of sampling correlations between recovery rate estimates and first-year survival estimates from this model averaged 0.93, indicating that none of the estimates are reliable. The estimates provided by MARK were highly unrealistic, with recovery rates of young estimated to be 0.20, compared with 0.09 for adults (the reverse order of that demonstrated with more data), and mean first-year survival rate estimated at 0.69, similar to that of adults.

Despite variation among models in first-year survival estimates, mean adult survival estimates were similar from all models, at about 70% per year. Much of the data from all data sets came from birds that were adults, with 37% of recoveries and 47% of recaptures of birds ringed as young happening more than one year after ringing.

Data sets based on birds ringed as young indicate that models allowing survival rates to vary with age for at least three age classes provide a better fit than 2-age-

		Surviva	al rates	Recove	ry rates	Recaptu	re rates
Data set	Final model <sup>1</sup>	1 st-year	'Adult'	1st-year	'Adult'	l st-ye ar	'Adult'
Recoveries only—young	$\Phi\left(a;t,c ight)r(t)$	$47.8 \pm 3.1$	$69.9 \pm 1.3$	$12.2 \pm 0.8$		N/A	N/A
Recaptures only-young	$\Phi(a^{\star}t)p(a^{\star}t)$	$10.1 \pm 1.1$	$70.4 \pm 4.2$	N/A	N/A	$19.9 \pm 3.8$	$35.9 \pm 2.5$
Recoveries only-young & adults	$\Phi(a^{\star}t)r(a+t)$	$37.3 \pm 3.7$	$72.2\pm1.7$	$10.1 \pm 0.8$	$14.7 \pm 1.3$	N/A	N/A
Recoveries & recaptures-young <sup>2</sup>	$\Phi(a^{\star}t)r(a+t)\rho(a^{\star}t)f(a)$	$30.4 \pm 3.6$	$69.9\pm1.8$	$9.3 \pm 0.8$	$15.9\pm1.8$	$19.0\pm3.4$	$35.7 \pm 2.4$
Recoveries & recaptures-young & adults <sup>3</sup>	$\Phi(a^{\star}t)r(a^{\star}t)p(a^{\star}t)f(a)$	$33.7 \pm 3.7$	$71.1 \pm 2.4$	$9.2\pm0.8$	$13.6 \pm 1.1$	$20.6 \pm 3.6$	$39.1 \pm 2.3$

TABLE 1. Mean parameter estimates (% ± SE) for 2-age-class models for tawny owls ringed in Finland from 1979-1996 based on four different combinations of data.

 $^2\mathrm{Estimated}$  mean 'fidelity' parameters were  $32.3\pm2.9$  for 1st-years, and  $97.0\pm1.2$  for adults.

 $^3$ Estimated mean 'fidelity' parameters were  $30.7\pm2.0$  for 1st-years, and  $94.1\pm1.2$  for adults.

		Apparent survival estimate			
Data set	Final model <sup>1</sup>	1st-year	2nd-year	'Adult'	$\Delta AIC_{c}^{2}$
Recoveries only—young	$\Phi(3a:t,c,c)r(t)$	$48.2\pm3.4$	$64.4\pm1.9$	$74.9\pm1.6$	22.0
Recaptures only—young Recoveries & recaptures—young	$\Phi(3a^{\star}t)p(a^{\star}t) \Phi(3a^{\star}t)r(a+t)p(a^{\star}t)f(a)$	$13.0 \pm 1.4$ $31.3 \pm 3.7$	$44.6 \pm 3.4$ $62.2 \pm 2.2$	$72.9 \pm 2.8$ $73.3 \pm 2.2$	20.9 33.2

TABLE 2. Mean parameter estimates ( $\% \pm SE$ ) for 3-age-class models for tawny owls ringed as young in Finland from 1979-1996 based on three different combinations of data sets

<sup>1</sup>Model notation as in Table 1, except that  $\Phi$  parameters were modelled with three age classes. Recovery and recapture parameters were modelled with only two age classes. Their mean values were nearly identical to those in Table 1, so they are not presented.

 $^{2}$ Improvement in AIC<sub>c</sub> relative to the equivalent model with only 2 age classes for survival (in Table 1). Note that AIC<sub>c</sub> values cannot be compared among rows on the table, because the data sets differ.

class models (Table 2). Estimates for adult annual survival rates were very similar from all three models (and from the 2-age-class models), but estimates of second-year survival rates were substantially lower based just on recaptures, than if recovery data were also included.

## 3.2 Annual variation in survival, recapture and recovery rates

Despite differences in means, annual variation in estimated survival rates was similar based on all five combinations of data sets (Fig. 1), and estimated standard errors were low relative to annual variation in survival rates. The correlation between first-year annual survival rates for data from recaptures-only and those from recoveries-only for birds ringed as young, which are thus sampled completely independently, was 0.74 (n = 18, P < 0.001). First-year recovery rates also showed strong temporal patterns, with an apparent long-term decline over the course of the study (Fig. 2(a)). In contrast, recapture rates showed marked fluctuations on a 3-4 year cycle (Fig. 2(b)), but no long-term changes.

# 4 Discussion

We found that recovery rates of young tawny owls differed from those of adults, which was probably the main source of bias in the survival estimates from models that incorporate only recoveries of birds ringed as young. In this respect, our results are similar to those of most other studies that have tested for age-specific variation in recovery rates (Potts, 1969; Cavé, 1977; Francis, 1995; Freeman & Morgan, 1992). Without supplementary data from other sources, such as radio-tagged birds, for which the fate can be determined exactly, we can only speculate on reasons why recovery rates of young birds averaged lower than those of adults. One possibility is that many young birds may die soon after independence, perhaps near the nest where they are hard to find. Another possibility is that some young birds may emigrate to areas where they are less likely to be recovered than if they remained near their natal sites. This could potentially bias estimates of survival rates from recovery models (Francis & Cooke, 1992), although to a lesser extent than the bias due to emigration in recapture models.

Unfortunately, if recovery rates vary with age, young-only recovery models, which cannot reliably model that variation, are likely to produce biased estimates of first-year survival rates, as found in this paper. Simulation studies would be



FIG. 1. Estimated annual first-year survival rates of tawny owls in Finland from 1979 to 1996 based on various data sets: (A) birds ringed as young, using only recovery data; (B) birds ringed as young using only recapture data; (C) birds ringed as either young or adults, using only recovery data; (D) birds ringed as young using both recaptures and recoveries; and (E) birds ringed as adults or young using both recaptures and recoveries. Models as in Table 1.

valuable to determine the extent of that bias in relation to the difference between adult and first-year recovery rates, the true values of the survival rates, and the magnitude of annual variation in those rates. It is possible that under some circumstances the bias may be less of a problem than in others.

Apparent annual survival estimates for both of the first two years of life (Tables 1 and 2), based solely on recaptures of birds ringed as young, averaged substantially lower than those from other models. If we assume that models based on recovery data are unaffected by emigration, then  $\Phi$  from the joint adult and young recovery model, or the recaptures and recoveries combined model, should estimate true survival rates. Under this assumption, the combined recaptures and recoveries model of Burnham (1993) estimates the difference between  $\Phi$  from the recaptures only models, and  $\Phi$  from the recoveries model as a fidelity parameter. If this difference is due to permanent emigration, the fidelity parameters suggest that about two-thirds of young birds emigrate, while virtually none of the adults



FIG. 2. Estimated annual first-year recapture and recovery rates from a model allowing survival, recapture and recovery rates to vary with two age classes and time, based on combined recapture and recovery data for birds ringed as young.

emigrate (Saurola, 1987). However, this 'fidelity' parameter must be interpreted cautiously, because ringers are operating through much of the breeding range of the species. Although many young birds were recaptured by the original ringing team at breeding sites within 30 km of their natal site (P. Saurola, unpublished data), some birds were recaptured long distances away. To be interpreted as a meaningful biological parameter, fidelity needs to be defined in the context of a limited area. In this study, it could better be interpreted as the probability a young bird that survives will nest in an area where a ringer is working. Although this is more likely to happen near the ringing site, some birds that move long distances, and hence are not site faithful, could still potentially be recaptured.

The extent of the difference in survival estimates based solely on recaptures and those based on recoveries will depend on the biology of the species and the design of the study area. Francis & Cooke (1993) showed that apparent survival rates of lesser snow geese based on recaptures for females (which are fairly site faithful) were only slightly lower than survival estimates from recoveries, while those of males were substantially lower, due to emigration. Catchpole *et al.* (1998) used both recaptures and recoveries to estimate survival rates of Shags but did not include a 'fidelity' parameter in the model, apparently assuming that emigration did not occur, or would bias both recoveries and recaptures equally. Conversely, Francis & Cooke (1992) showed that emigration could also bias survival estimates from recoveries, if birds emigrate to areas where they are less likely to be recovered.

Additional data, either from recoveries of birds ringed as adults or from recaptures of birds ringed as young, can be used to supplement recoveries of birds ringed as young to provide survival estimates that are robust to variation in recovery rates with age. Recaptures and recoveries of birds ringed as young have the advantage that age-specific survival (and recovery) rates can be estimated beyond the ageclasses that can be readily identified in the field. Nevertheless, either type of data could be useful, depending upon the relative effort required to collect the data. If both types of data are available, the combined model, incorporating all the data (i.e. both recaptures and recoveries of birds ringed both as adults and as young), makes use of the maximum amount of information. However, this is not appropriate for estimating age-specific survival rates beyond two age classes, because of the lack of precise information on ages of most birds ringed as 'adults.'

Despite differences in mean values, estimated annual fluctuations in first-year survival rates from all analyses were remarkably similar (Fig. 1). Considering that the recaptures-only and recoveries-only data sets are statistically independent, these similarities suggest that much of this variation reflects real annual changes in the underlying survival rates and is not an artefact of any estimation procedure. Elsewhere, we will explore the possible relationships between first-year survival rates and external factors such as winter severity, large-scale climate fluctuations, and prey availability.

Recapture rates in many cases could be considered 'nuisance' parameters, which need to be modelled only for correctly interpreting survival estimates. However, in this study, because effort within each study area has been fairly consistent over time, variation in recapture rates can potentially be interpreted, with some cautions, in terms of variation in breeding propensity. The lower first-year recapture rates suggest that yearlings are less likely to breed than older birds (Table 1). The 3-4 year fluctuations in capture rates (Fig. 2) may reflect lower breeding propensity and/or lower breeding success in years when prey availability is low.

The apparent long-term decline in recovery rates (Fig. 2) could be due to a decline in the probability that members of the public finding a bird will report it. An alternative explanation is that changes in the causes of death have led to changes in the probability that dead birds will be found. As in many other parts of the world, changing attitudes among the public may lead to fewer owls being shot, trapped or otherwise persecuted (Houston & Francis, 1995). Owls dying of natural causes are less likely to be found, and hence recovery rates may decline if fewer birds are killed by humans.

## Acknowledgements

We thank all of the Finnish bird ringers who have participated in ringing and recapturing tawny owls, as well as everybody who has reported a recovery to the scheme. Ted Catchpole and an anonymous reviewer provided helpful comments on the manuscript.

# REFERENCES

- ANDERSON, D. R. & BURNHAM, K. P. (1999) Understanding information criteria for selection among capture-recapture or ring recovery models, *Bird Study*, 46, pp. S14-S21.
- ANDERSON, D. R., BURNHAM, K. P. & WHITE, G. C. (1985) Problems in estimating age-specific survival rates from recovery data of birds ringed as young, *Journal of Animal Ecology*, 54, pp. 89-98.
- ANDERSON, D. R., WYWIALOWSKI, A. P. & BURNHAM, K. P. (1981) Tests of the assumptions underlying life table methods for estimating parameters from cohort data, *Ecology*, 62, pp. 1121-1124.

- BROWNIE, C., ANDERSON, D. R., BURNHAM, K. P. & ROBSON, D. S. (1985) Statistical Inference from B and Recovery Data: a Handbook, 2nd edn. US Fish and Wildlife Service Resource Publication 156.
- BURNHAM, K. P. (1993) A theory for joint analysis of ring recovery and recapture data. In: J.-D. LEBRETON & P. M. NORTH (Eds) Marked Individuals in the Study of Bird Population, pp. 199-213 (Basel, Birkhäuser).
- BURNHAM, K. P. & ANDERSON, D. R. (1979) The composite dynamic method as evidence for agespecific waterfowl mortality, *Journal of Wildlife Management*, 43, pp. 356-366.
- CATCHPOLE, E. A., FREEMAN, S. N. & MORGAN, B. J. T. (1995) Modelling age variation in survival and reporting rates for recovery models, *Journal of Applied Statistics*, 22, pp. 597-609.
- CATCHPOLE, E. A., FREEMAN, S. N., MORGAN, B. J. T. & HARRIS, M. P. (1998) Integrated recovery/ recapture data analysis, *Biometrics*, 54, pp. 33-46.
- CATCHPOLE, E. A., MORGAN, B. J. T., FREEMAN, S. N., & PEACH, W. J. (1999) Modelling the survival of British Lapwings *Vanellus vanellus* using ring-recovery data and weather covariates, *Bird Study*, 46, pp. S5-S13.
- CAVÉ, A. J. (1977) Pitfalls in the estimation of age-dependent survival rates of birds from ringing and recovery data, *Die Vogelwarte*, 29, pp. 160-171.
- CORMACK, R. M. (1970) Statistical appendix to Fordham's paper, *Journal of Animal Ecology*, 39, pp. 24-27.
- FRANCIS, C. M. (1995) Estimating survival rates from recoveries of birds ringed as young: a case study, *Journal of Applied Statistics*, 22, pp. 567-577.
- FRANCIS, C. M. & COOKE, F. (1992) Sexual differences in survival and recovery rates of Lesser Snow Geese, *Journal of Wildlife Management*, 56, pp. 287-296.
- FRANCIS, C. M. & COOKE, F. (1993) A comparison of survival rate estimates from live recaptures and dead recoveries of Lesser Snow Geese. In: J.-D. LEBRETON & P. M. NORTH (Eds) The Use of Marked Individuals in the Study of Bird Population Dynamics: Models, Methods and Software, pp. 169-183 (Basel, Switzerland, Birkhäuser Verlag).
- FREEMAN, S. N. & MORGAN, B. J. T. (1992) A modelling strategy for recovery data from birds ringed as nestlings, *Biometrics*, 48, pp. 217-236.
- HOUSTON, C. S. & FRANCIS, C. M. (1995) Survival of Great Horned Owls in relation to the snowshoe hare cycle, *The Auk*, 112, pp. 44-59.
- LAKHANI, K. H. & NEWTON, I. (1983) Estimating age-specific bird survival rates from ring-recoveries: can it be done? *Journal of Animal Ecology*, 52, pp. 82-91.
- MORGAN, B. J. T. & FREEMAN, S. N. (1989) A model with first-year variation for ring-recovery data, *Biometrics*, 45, pp. 1087-1102.
- NELSON, L. J., ANDERSON, D. R., & BURNHAM, K. P. (1980) The effect of band loss on estimates of annual survival, *Journal of Field Ornithology*, 51, pp. 30-38.
- POTTS, G. R. (1969) The influence of eruptive movements, age, population size and other factors on the survival of the Shag (*Phalacrocorax aristotelis* (L.)), *Journal of Animal Ecology*, 38, 53-102.
- RINNE, J., LOKKI, H. & SAUROLA, P. (1990) Survival estimates of nestling recoveries: forbidden fruits of ringing? *The Ring*, 13, pp. 255-270.
- RINNE, J., LOKKI, H. & SAUROLA, P. (1993) Extensive parameterisation of survival models for recovery data analysis. In: J.-D. LEBRETON & P. M. NORTH (Eds) Marked Individuals in the Study of Bird Population, pp. 65-75 (Basel, Birkhäuser).
- SAUROLA, P. (1987) Mate and nest-site fidelity in Ural and tawny owls. In: R. W. NERO, R. J. CLARK, R. J. KNAPTON & R. H. HAMRE (Eds) Biology and Conservation in Northern Forest Owls: Symposium Proceedings, pp. 81-86, 3-7 February; Winnipeg, Manitoba. Gen. Technical Report RM-142. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Co.
- SAUROLA, P. (1997) Monitoring Finnish owls 1982-1996: methods and results. In: J. R. DUNCAN, D. H. JOHNSON & T. H. NICHOLLS (Eds) Biology and Conservation of Owls of the Northern Hemisphere: Second International Symposium, pp. 363-380, 5-9 February, Winnipeg, Manitoba. USDA Forest Service General Technical Report NC-190.
- SEBER, G. A. F. (1971) Estimating age-specific survival rates for birds from bird-band returns when the reporting rate is constant, *Biometrika*, 58, pp. 491-497.
- WHITE, G. C. & BURNHAM, K. P. (1999) Program MARK: survival estimation from populations of marked animals, *Bird Study*, 46, S120-S139.