



CHICAGO JOURNALS



The University of Chicago

Estimating Population Size and Hidden Demographic Parameters with State-Space Modeling.
Author(s): Giacomo Tavecchia, Panagiotis Besbeas, Tim Coulson, Byron J. T. Morgan, and
Tim H. Clutton-Brock

Source: *The American Naturalist*, Vol. 173, No. 6 (June 2009), pp. 722-733

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/598499>

Accessed: 28/10/2014 13:34

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

Estimating Population Size and Hidden Demographic Parameters with State-Space Modeling

Giacomo Tavecchia,^{1,2,*} Panagiotis Besbeas,¹ Tim Coulson,² Byron J. T. Morgan,¹ and Tim H. Clutton-Brock³

1. Institute of Mathematics, Statistics, and Actuarial Science, University of Kent, Canterbury, Kent CT2 7NF, United Kingdom;

2. Department of Biological Sciences and the Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, United Kingdom; 3. Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom

Submitted May 2, 2008; Accepted February 2, 2009; Electronically published April 8, 2009

Online enhancement: appendix.

ABSTRACT: Recent research has shown how process variability and measurement error in ecological time series can be separated using state-space modeling techniques to combine individual-based data with population counts. We extend the current maximum likelihood approaches to allow the incorporation of sex- and age-dependent counts and provide an application to data from a population of Soay sheep living on the St. Kilda archipelago. We then empirically evaluate the performance and potential of the method by sequentially omitting portions of the data available. We show that the use of multivariate time series extends the power of the state-space modeling approach. The variance of measurement error was found to be smaller for males and the sex ratio of lambs to be skewed toward females and constant over time. Our results indicated that demographic parameters estimated using state-space modeling without relevant individual-based data were in close agreement with those obtained from mark-recapture-recovery analyses alone. Similarly, estimates of population size obtained when the corresponding count observations were unavailable were close to those from the entire data set. We conclude that the approach illustrated here has great potential for estimating hidden demographic parameters, planning studies on population monitoring, and estimating both historical and future population size.

Keywords: fecundity, hidden parameters, population dynamics, Soay sheep, state-space modeling, survival.

Introduction

Ecologists commonly use time series of population counts to derive inferences about the demographic processes underlying observed fluctuations (Cappuccino and Price 1995; Stenseth et al. 2004). However, changes in observed population size reflect both demographic variability and

measurement error (Clark and Bjørnstad 2004). A possible way to disentangle these two processes is through combining population counts with individual-based life-history data into a single analytical framework (Besbeas et al. 2002; Brooks et al. 2004; Buckland et al. 2004; Clark and Bjørnstad 2004; Newman et al. 2006). The basis of this framework is a state-space model for the population data, where the true but unknown size of the population is modeled with a state process and linked to the observed counts by an observation process. Assuming independence between data sets, a joint likelihood may be formed by multiplying the likelihood resulting from the count and the likelihoods from the demographic analyses. This methodology is termed “integrated population modeling” or “integrated analysis.” Parameter estimates that result from an integrated analysis provide a simultaneous description of all the data and are in principle more precise than those obtained from the analysis of count or individual-based information alone. There is a growing literature on fitting state-space models in both a classical and a Bayesian statistical framework (Wang 2007), in particular, in fish stock assessment and management (Newman 1998; Meyer and Millar 1999; Millar and Meyer 2000). State-space models have also recently been applied to questions concerning population change in birds (Besbeas et al. 2002, 2003) and mammals (Buckland et al. 2004; Thomas et al. 2005). A particularly useful feature of integrating counts and individual-based information in a single analysis is the potential to estimate demographic parameters that have not been measured directly (Besbeas et al. 2002; Newman et al. 2006; Besbeas and Freeman 2007). For example, by combining census and ring-recovery data of lapwings (*Vanellus vanellus*), Besbeas et al. (2002) provided an estimate of per capita fecundity that was not originally monitored in the field. We refer to the parameters that influence the population dynamics but that cannot be estimated from

* Corresponding author. Present address: Institut Mediterrani d'Estudis Avançats—Consejo Superior de Investigaciones Científicas/Universitat de les Illes Balears, 21 Miquel Marqués, 07190 Esporles, Spain; e-mail: g.tavecchia@uib.es.

Am. Nat. 2009. Vol. 173, pp. 722–733. © 2009 by The University of Chicago. 0003-0147/2009/17306-5042\$15.00. All rights reserved. DOI: 10.1086/598499

just the individual-based information or the time series of counts as “hidden.” The ability to estimate hidden parameters from a joint analysis is important in planning conservation studies when individual-based data on survival or fertility are too difficult or too expensive to collect.

Integrated modeling obviously has considerable potential to increase understanding in population biology; however, its flexibility and performance in estimating hidden parameters has not been fully examined using ecological data. The aim of this article is twofold. First, we use an integrated analysis to model the dynamics of a population of Soay sheep (*Ovis aries*) on the island of Hirta in the St. Kilda archipelago, Scotland (Clutton-Brock and Pemberton 2004). Fecundity, survival, and lamb sex ratio at birth can be directly estimated from detailed individual-based data collected from approximately one-third of the island population. Population size is estimated by a single, annual census of the whole island. This first analysis allowed us to estimate parameters previously unknown, specifically, the sampling variance within the census data and the sex ratio at birth. Second, we experimentally evaluated the flexibility and limitations of the integrated approach by omitting portions of the data and comparing the results from these “incomplete” data sets with those obtained from the entire data set and from the analysis of the mark-resighting-recovery data only. The deletions were chosen to correspond to realistic biological situations in which the state-space modeling approach could be applied. In particular, we have three objectives:

Objective 1: Estimating Measurement Error

Our first objective was to estimate the sampling variances within the census data. Census data are typically a univariate time series of total population size in a given area. In our case, three time series of census data are available, corresponding to adult males, adult females, and lambs of either sex. We extended existing methodology based on maximum likelihood model fitting to the simultaneous analysis of multivariate census data. We also investigated whether results were robust to the initial assumptions on sampling variance distribution and among-groups correlation in process errors by simulation.

Objective 2: Estimating Hidden Demographic Processes

Our second objective was to estimate unmeasured biological variables and, in particular, the proportion of female lambs on the island, ρ , and its temporal variation. This information cannot be collected during the whole island census because lamb sex cannot confidently be ascribed from a distance. We compared the estimates with those from the individual-based data resulting from a re-

stricted part of the island. We also investigated the performance of the method in estimating ρ using simulation. Subsequently, we generated subsets of the entire data set by excluding individual-based survival or fertility records. This had the effect of making, in addition to ρ , age-specific fertility and survival hidden parameters. In each case, resulting estimates were compared with those from the individual-based data. This was intended to empirically explore the robustness of the state-space approach when demographic parameters are estimated without the corresponding field data.

Objective 3: Estimating Population Size

Our third objective was to estimate population size when census data were missing. We first deleted three consecutive observed values to make population size a hidden parameter, which was then estimated. We also used the full state-space model to forecast the population size in a future year under a range of climatic conditions.

The Soay Sheep Population

Soay sheep are a rare breed thought to be similar to domestic Neolithic sheep introduced to Britain around 5,000 BC (Clutton-Brock 1999). The study population was introduced to the island of Hirta in 1932 from the neighboring island of Soay after the voluntary evacuation of the local human population in 1930 (Clutton-Brock and Pemberton 2004). The population of Soay sheep on Hirta exhibits a complex dynamic, with years of steady growth followed by periodic crashes in which up to 60% of the population might die (Coulson et al. 2000). Time series analyses (Grenfell et al. 1998; Stenseth et al. 2004) and studies at the individual level (Catchpole et al. 2000; Coulson et al. 2001) have shown that this peculiar dynamic results from the interplay of population density and climatic fluctuations and their differential effect on different age classes. Males suffer relatively high mortality, which results in an adult population that is highly skewed toward females (Clutton-Brock and Pemberton 2004). The large amount of information collected from this population (synthesized in Clutton-Brock and Pemberton 2004) provides a robust base of knowledge against which to empirically test the performance of the state-space approach.

Methods

Individual-Based Data and Estimation of Demographic Parameters

The individual-based data used in the article are recaptures and recoveries collected during the period 1986–2004

within Village Bay, an area covering about one-third of the island. Following previous analyses of early parts of the data (Catchpole et al. 2000; Stenseth et al. 2004), survival and fecundity rates, θ_{ji} , of individuals of age j in year i were modeled through logistic regressions of the general form

$$\text{logit}(\theta_{ji}) = \beta_{0j} + \beta_{1j}P_i + \beta_{2j}N_i + \beta_{3j}N_iP_i, \quad (1)$$

where the β 's are regression coefficients to be estimated and N and P are two external covariates—the North Atlantic Oscillation (NAO) index (Hurrell 1995) and the total island population size, respectively—that have been shown to affect both individual survival and fecundity (Coulson et al. 2001). We selected models using the Akaike Information Criterion (AIC; Burnham and Anderson 2002), calculated as model deviance plus twice the number of parameters in the model. Models with AIC values within two points of one another were considered to describe the data equally well.

Survival Probability. For the analysis of survival, we used observations on 1,589 females and 1,655 males collected in the Village Bay area. Data were coded in the form of individual encounter histories indicating for each year whether an animal was seen alive, not seen, or recovered dead (Burnham 1993). We will refer to these data as mark-recapture-recovery (MRR) data. Each encounter history can be written as a combination of three probabilities describing the different events that characterize the history (Catchpole et al. 1998): ϕ_{ji} , the probability that an individual of age j survives during the time interval $i, i + 1$; p_i , the probability that an individual known to be alive at occasion i is encountered; λ_i , the probability that a tag of an individual that died during the interval $i - 1, i$ is encountered.

Estimates of these probabilities can be derived from MRR data by maximum likelihood (Burnham 1993; Catchpole et al. 1998). Catchpole et al. (2000) provided an extensive analysis of MRR data collected between 1986 and 1996. They considered separate models for males and females, involving distinct age classes, and different models for the three probabilities above. They found that survival varied as a function of climatic variables, population size, and their interaction, while the probabilities p and λ varied as a function of time (Coulson et al. 2001). We updated this analysis incorporating observations from 1997 to 2004. In our models, we employed three age classes for females, corresponding to lambs (0–1 year old), yearlings (1–2 years old), and adults (2+ years old), while for males we considered only lambs (0–1 year old) and adults (1+ years old). This age structure is simpler than the one employed by Catchpole et al. (2000), which included an extra

age class for females aged 7 years and older and one for males older than 6 years. However, our simplification allows a robust analysis of the census data without substantially compromising biological realism. The survival probability in each age class was modeled as a function of N , P , and their interaction, $N \times P$, as in equation (1) (see also Tavecchia et al. 2005), whereas p and λ were modeled as functions of time. On the basis of these models, the likelihood function for the MRR data was derived and maximized using the program MARK (White and Burnham 1999).

Fecundity. For the analysis of fecundity, we used observations between lambing and the summer census (approximately May–July) on 2,226 lambs born to 1,972 marked females. Modeling sheep fecundity can be a complex procedure, since the sheep may twin, and the production of lambs can be a function of mother age and of external covariates such as winter weather and population density. We estimated the mean number of lambs, F_{ji} , at year i per female of age j that survive until the summer census as a product of three probabilities that were modeled independently. The F_{ji} is calculated as

$$F_{ji} = G_{ji}[w_{ji} + 2(1 - w_{ji})]S_{ji}, \quad (2)$$

where G_{ji} is the probability that a female of age j gives birth in year i ; w_{ji} is the conditional probability that a female sheep of age j gives birth to a single lamb in year i , given that it gives birth, so $1 - w_{ji}$ is the probability of giving birth to twins; and S_{ji} is the probability that a lamb born to a female of age j in year i would survive until the summer.

Standard errors for F_{ji} were obtained from combining the standard errors of G_{ji} , w_{ji} , and S_{ji} using the delta method (Morgan 2000, p. 109). In modeling fecundity, we found it natural to employ the same age structure as for female survival. Note that equation (2) does not include an effect of mother identity. In a study on the maternal effects on lamb early survival, Jones et al. (2005) found that models with maternal identity as a random effect were unstable and, because the majority of mothers contributed only a single lamb to the data set, that the individual effect should be negligible.

Census Data and the State-Space Model

We considered census data from 1986 to 2004, obtained from a summer count of the whole island population, each year recording the numbers of lambs, y_1 , and adult females and adult males, y_2 and y_3 , respectively. Note that sex information is not available for lambs. Thus, our census data form a multivariate time series, and in this respect, our

analysis extends previous analyses of total counts (Grenfell et al. 1998; Stenseth et al. 2004). We describe these multivariate data with a state-space model parameterized in terms of the age-by-sex demographic parameters described as a function of external covariates as in equation (1) (table 1). In particular, the model considers a postbreeding population vector with five sex-by-age classes, corresponding to female lambs, yearlings, and adults and male lambs and adults. If we denote the numbers of animals in these classes at year i by $n_{0,\text{f}}^{\text{f}}$, $n_{1,\text{f}}^{\text{f}}$, $n_{2+,\text{f}}^{\text{f}}$, $n_{0,\text{m}}^{\text{m}}$ and $n_{1+,\text{m}}^{\text{m}}$ respectively, then we can write the state-space transition equation as

$$\begin{bmatrix} n_{0,\text{f}}^{\text{f}} \\ n_{1,\text{f}}^{\text{f}} \\ n_{2+,\text{f}}^{\text{f}} \\ n_{0,\text{m}}^{\text{m}} \\ n_{1+,\text{m}}^{\text{m}} \end{bmatrix}_{i+1} = \begin{bmatrix} \rho F_{1,\text{f}} \phi_{1,\text{f}}^{\text{f}} & \rho F_{2,\text{f}} \phi_{2,\text{f}}^{\text{f}} & \rho F_{3+,\text{f}} \phi_{3+,\text{f}}^{\text{f}} & 0 & 0 \\ \phi_{1,\text{f}}^{\text{f}} & 0 & 0 & 0 & 0 \\ 0 & \phi_{2,\text{f}}^{\text{f}} & \phi_{3+,\text{f}}^{\text{f}} & 0 & 0 \\ (1-\rho)F_{1,\text{f}} \phi_{1,\text{f}}^{\text{f}} & (1-\rho)F_{2,\text{f}} \phi_{2,\text{f}}^{\text{f}} & (1-\rho)F_{3+,\text{f}} \phi_{3+,\text{f}}^{\text{f}} & 0 & 0 \\ 0 & 0 & 0 & \phi_{1,\text{m}}^{\text{m}} & \phi_{2+,\text{m}}^{\text{m}} \end{bmatrix} \begin{bmatrix} n_{0,\text{f}}^{\text{f}} \\ n_{1,\text{f}}^{\text{f}} \\ n_{2+,\text{f}}^{\text{f}} \\ n_{0,\text{m}}^{\text{m}} \\ n_{1+,\text{m}}^{\text{m}} \end{bmatrix}_i + \begin{bmatrix} \varepsilon_{0,\text{f}}^{\text{f}} \\ \varepsilon_{1,\text{f}}^{\text{f}} \\ \varepsilon_{2+,\text{f}}^{\text{f}} \\ \varepsilon_{0,\text{m}}^{\text{m}} \\ \varepsilon_{1+,\text{m}}^{\text{m}} \end{bmatrix}_i, \quad (3)$$

where ϕ_j^{m} , ϕ_j^{f} , and F_j are the primary demographic parameters of male survival, female survival, and fecundity at age j , respectively, and ρ is the proportion of female lambs at birth. The process error vector $\varepsilon_i = (\varepsilon_{0,\text{f}}^{\text{f}}, \dots, \varepsilon_{1+,\text{m}}^{\text{m}})'_i$ denotes a random error term incorporating demographic stochasticity. The components of ε_i are assumed to be independent and normally distributed, with variances given by suitable Poisson/binomial expressions as explained by Besbeas et al. (2002). However, we also investigated the effect of these assumptions by simulation (appendix in the online edition of the *American Naturalist*).

The population vector in equation (3) is not fully observed, but it can be related to the census data at time i by the measurement equation

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix}_i = \begin{bmatrix} 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} n_{0,\text{f}}^{\text{f}} \\ n_{1,\text{f}}^{\text{f}} \\ n_{2+,\text{f}}^{\text{f}} \\ n_{0,\text{m}}^{\text{m}} \\ n_{1+,\text{m}}^{\text{m}} \end{bmatrix}_i + \begin{bmatrix} \eta_1 \\ \eta_2 \\ \eta_3 \end{bmatrix}_i, \quad (4)$$

where $\eta_i = (\eta_1, \eta_2, \eta_3)'_i$ is a random error term included to account for census errors. The observation errors η_r , $r = 1, 2, 3$, are assumed to be independent and normally distributed, with variances $\sigma_{\eta_r}^2$. These variances, together

Table 1: Linear predictors retained on a logit scale (SE) of survival and fecundity from the analysis of individual-based data (mark-recapture-recovery)

Parameter	Intercept	N	P	$N \times P$
Survival:				
$\phi_{1,\text{f}}^{\text{f}}$.59 (.08)	-2.38 (.40)	-.34 (.02)	-.80 (.15)
$\phi_{2,\text{f}}^{\text{f}}$	2.69 (.31)	-5.85 (1.81)	-.32 (.05)	.48 (.44)
$\phi_{3+,\text{f}}^{\text{f}}$	2.41 (.10)	-2.05 (.47)	-.24 (.01)	-.48 (.15)
$\phi_{1,\text{m}}^{\text{m}}$	-.18 (.08)	-3.86 (.41)	-.34 (.02)	-.63 (.15)
$\phi_{2+,\text{m}}^{\text{m}}$	1.58 (.18)	-3.46 (.12)	-.31 (.03)	-.48 (.32)
Fecundity:				
$F_{1,\text{f}}^{\text{f}}$:				
$G_{1,\text{f}}$	-.73 (.18)	-1.73 (.77)	-.27 (.05)	NR
$w_{1,\text{f}}$	11 ^a	NT	NT	NT
$S_{1,\text{f}}$	-.37 (.21)	-3.02 (.92)	-.29 (.06)	NR
$F_{2,\text{f}}^{\text{f}}$:				
$G_{2,\text{f}}$.56 (.15)	NR	NR	NR
$w_{2,\text{f}}$	-7.2 (.01)	NT	NT	NT
$S_{2,\text{f}}$	1.58 (.38)	NR	-.24 (.08)	NR
$F_{3+,\text{f}}^{\text{f}}$:				
$G_{3+,\text{f}}$.99 (.06)	NR	NR	NR
$w_{3+,\text{f}}$	-9.5 (.01)	NT	NT	NT
$S_{3+,\text{f}}$	2.04 (.11)	-1.63 (.55)	-.09 (.03)	-.46 (.19)

Note: Survival parameters of sheep of age j in year i are denoted ϕ_{ji}^{f} and ϕ_{ji}^{m} for females and males, respectively. Fecundity of a female sheep aged j in year i is denoted F_{ji} . Note that F_{ji} has been estimated as the combination of three probabilities modeled separately, the probability of giving birth (G_{ji}), the probability of producing a singleton (w_{ji}), and the probability that the newborn survives until the summer census (S_{ji}). Models included population density (P), the North Atlantic Oscillation index (N), and their statistical interaction ($N \times P$) as predictors. In modeling survival and fecundity, only the model with the lowest AIC value was retained. NR = not retained, NT = not tested.

^a Fixed to 1.00 because 1-year-old mothers never twin.

with the demographic parameters in the matrix of equation (3), need to be estimated.

Collectively, equations (3) and (4) form a linear Gaussian state-space model. From this model, a likelihood for the census data— $L_c(\phi_{j,\text{f}}^{\text{f}}, \phi_{j,\text{m}}^{\text{m}}, F_{j,\text{f}}, \rho, \sigma_{\eta_r})$ —was derived by using the Kalman filter. The Kalman filter is a recursive algorithm that estimates the unknown states of a dynamic system from a series of incomplete and noisy measurements (de Valpine and Hastings 2002; Chatfield 2004). Given a starting value, the algorithm steps through the recursions, and at each time period it computes the optimal estimator of the state vector and its variance. These quantities contain all the information needed for inference. We started the recursive algorithm from the year 1986 using the observed proportions of animals in each class in the Village Bay area in the same year. The general forms of the Kalman filter recursions and likelihood function can be found in, for example, the study by Harvey (1989, chap. 3). The main advantages of a Kalman filter approach over a Bayesian alternative are its computational tractability and objectivity.

The Integrated Analysis

We combined the census and individual-based data in a joint likelihood, L_{joint} , formed by multiplying the census likelihood, L_c , and the MRR likelihoods, L_{mrr} , together. However, because the MRR likelihoods were derived by using specialist computer packages (e.g., MARK), they were approximated by multivariate normal distributions based on the maximum-likelihood estimates obtained from analyzing the individual-based data alone (Besbeas et al. 2002, 2003). Parameter estimates resulted, in general, from maximizing

$$L_{\text{joint}}(\phi_{ji}^f, \phi_{ji}^m, F_{ji}, \rho_i, \sigma_{ri}) = L_c(\phi_{ji}^f, \phi_{ji}^m, F_{ji}, \rho_i, \sigma_{ri}) \hat{L}_{\text{mrr}}(\phi_{ji}^f) \hat{L}_{\text{mrr}}(\phi_{ji}^m) \hat{L}_{\text{mrr}}(F_{ji}), \quad (5)$$

where \hat{L}_{mrr} denotes the multivariate normal density. The assumption of independence needed to multiply the component likelihoods together is not likely to be seriously violated here, since the individual-based data result from the Village Bay area of Hirta and form only a small part of the population data.

Objective 1: Estimating the Measurement Error. The use of multivariate counts allowed us to model the sampling variance σ_{ri}^2 of the observed census y_r at time i . We employed several models including constant and full time dependence, $\ln(\sigma_{ri}^2) = \beta_r$ and $\ln(\sigma_{ri}^2) = \beta_{ri}$, respectively, and a linear function of time on the log scale, $\ln(\sigma_{ri}^2) = \beta_{0r} + \beta_{1r}T$, where T indexes years, that is, a linear trend over time. The value of the proportion of females at birth, ρ , was assumed to be a constant but unknown number. Despite the fact that our interest was in modeling and estimating the measurement errors, all other parameters in equation (5) were estimated simultaneously.

Objective 2: Estimating Hidden Demographic Processes. Using the best model for the measurement error variances, we modeled ρ as a function of time t , population size P , and linear trend T through logistic regressions. Furthermore, we explored the performance of the integrated analysis in estimating an additional demographic parameter without the support of relevant MRR data. For example, using the retained structure of σ_{ri}^2 and ρ , we discarded all observations on individual reproductive success and estimated all parameters, including fecundity and birth sex ratio, by maximizing the likelihood of equation (5) without the component $L_{\text{mrr}}(F_{ji})$. This application is more challenging because now both ρ and F are hidden parameters. We repeated a similar procedure to estimate male lamb survival, ϕ_{1i}^m , from counts, fecundity, and male adult and female survival data only. In both cases, we compared the

estimates with those obtained from analyzing the corresponding individual-based data. In addition, the performance of the analysis was verified by simulation (appendix).

Objective 3: Estimating Population Size. To assess the performance of the integrated approach in estimating population size, we removed three consecutive censuses taken in 1998, 1999, and 2000. This particular period was chosen because of the crash in population size that occurred in the winter of 1998–1999. We were interested in verifying whether the integrated analysis would be able to detect such an abrupt change in population size. We also used the integrated approach to forecast the population size in 2005 using the information up to 2004 and assuming a range of NAO index values for this year.

Results*Objective 1: Estimating a Model for Measurement Error*

A model that assumed error-free counts was clearly rejected (table 2, model 1); the best-supported models found that the measurement error variances in female and lamb counts were equivalent but differed from that for male counts (table 2, model 5). There was no evidence of significant temporal variation or of a trend in any of the variances (table 2, models 7–13). As a consequence, we retained the simpler model 5 to test hypotheses about the temporal variation in the sex ratio at birth. According to this model, the measurement error standard deviation associated with the time series of males ($\hat{\sigma}_3 = 48.2$, SE = 8.79) was significantly smaller than that for the female and lamb time series ($\hat{\sigma}_2 = \hat{\sigma}_1 = 98.22$, SE = 12.48).

In equation (3), the process errors ε_i are assumed to be independent across groups. This assumption might not hold when environmental variability is large. Using the structure of the selected model (model 5), we verified whether a correlated processes error generated substantial changes in parameter estimates by simulation. We found that estimates were robust to the process versus observation variance partitioning and under moderate to high correlation in the process error and variance (appendix).

Objective 2: Estimating Hidden Demographic Processes

Models assuming a linear trend (model 15) in the sex ratio at birth or a covariation with population size (model 16) were within two points of AIC from model 5. However, we still retained model 5 assuming constant ρ and σ^2 values, since it is the one with the lowest number of parameters and the lowest AIC. According to this model, the proportion of female lambs is 0.59 (95% confidence limits

Table 2: Testing hypotheses about the variance of sampling error of lamb (σ_1), ewe (σ_2), and ram (σ_3) counts and about the sex ratio of newborn lambs (ρ)

Model	Notation	L_{joint}	n_p	AIC
Measurement errors:				
1	$\rho(\cdot)/\sigma_1 = \sigma_2 = \sigma_3 = 0$	1,009.49	37	2,092.98
2	$\rho(\cdot)/\sigma_2(\cdot), \sigma_1(\cdot), \sigma_3(\cdot)$	235.97	40	551.94
3	$\rho(\cdot)/\sigma_1(\cdot), \sigma_3(\cdot) = \sigma_2(\cdot)$	239.33	39	556.66
4	$\rho(\cdot)/\sigma_1(\cdot) = \sigma_3(\cdot), \sigma_2(\cdot)$	239.60	39	557.21
5 ^a	$\rho(\cdot)/\sigma_1(\cdot) = \sigma_2(\cdot), \sigma_3(\cdot)$	235.97	39	549.94
6	$\rho(\cdot)/\sigma_1(\cdot) = \sigma_2(\cdot) = \sigma_3(\cdot)$	240.42	38	556.83
7 ^a	$\rho(\cdot)/\sigma_1(\cdot) = \sigma_2(\cdot), \sigma_3(T)$	235.08	40	550.16
8 ^a	$\rho(\cdot)/\sigma_1(T) = \sigma_2(T), \sigma_3(\cdot)$	235.30	40	550.60
9 ^a	$\rho(\cdot)/\sigma_1(T) = \sigma_2(T), \sigma_3(T)$	234.43	41	550.85
10	$\rho(\cdot)/\sigma_1(\cdot) = \sigma_2(\cdot), \sigma_3(t)$	224.49	57	562.99
11	$\rho(\cdot)/\sigma_1(t) = \sigma_2(t), \sigma_3(\cdot)$	224.65	57	563.31
12	$\rho(\cdot)/\sigma_1(t) = \sigma_2(t), \sigma_3(t)$	213.08	75	576.17
13	$\rho = .5/\sigma_1(t), \sigma_2(t), \sigma_3(t)$	209.18	93	604.36
Proportion of females at birth:				
14	$\rho(t)/\sigma_1(\cdot) = \sigma_2(\cdot), \sigma_3(\cdot)$	228.87	56	569.75
15 ^a	$\rho(T)/\sigma_1(\cdot) = \sigma_2(\cdot), \sigma_3(\cdot)$	235.92	40	551.83
16 ^a	$\rho(P)/\sigma_1(\cdot) = \sigma_2(\cdot), \sigma_3(\cdot)$	235.88	40	551.75

Note: L_{joint} = maximum joint log-likelihood value (eq. [5]). $\hat{L}_{\text{mrr}}(\phi_{\text{f}}^t)$, $\hat{L}_{\text{mrr}}(\phi_{\text{f}}^m)$, and $\hat{L}_{\text{mrr}}(F_{\text{f}})$ in equation (5) are as in table 1; n_p = number of parameters in the model, Akaike Information Criterion (AIC) = $2L_{\text{joint}} + 2n_p$; t denotes full time dependence, T denotes a linear trend in time, and a period denotes a constant value.

^a Equally supported best models, with a difference in AIC values <2 points.

= 0.53–0.65), a value higher than but consistent with (z -test: $Z = 1.36$, $P = .09$) the average proportion of female lambs observed in the Village Bay sector during the period 1985–2003 (0.52; 95% confidence limits = 0.50–0.54). The use of models 7–9 instead of model 5 for the variances does not change the conclusion that ρ is constant (results not shown). Model 5 provided a good overall agreement between predicted and observed numbers of sheep in all three categories (fig. 1). However, in the early 1990s, the predicted number of females was higher than that observed. A mismatch is also evident in the number of lambs during the summers of 1996–1998 and 2001, when predicted numbers were lower than observed. Despite these differences, the total population size predicted by model 5 correlates strongly with the one observed ($R^2 = 0.77$), and parameter estimates are similar to those found from the MRR analysis (see tables 1, A1 [in the online edition of the *American Naturalist*]). In all previous models, data on ρ were not included in the analysis. Furthermore, this parameter was estimated by the joint analysis without using information on the observed sex ratio at birth in Village Bay. To further assess the performance of the integrated analysis in estimating primary demographic parameters without direct information, we alternatively estimated fecundity and survival through the maximization of the joint likelihood (eq. [5]) without the support of relevant individual-based information. For fecundity, a

single value of fecundity estimated in this way was 0.67 (95% confidence limits = 0.61–0.73; table 3, model 23), a value higher than but not significantly different from ($Z = 1.44$, $P = .07$) the corresponding estimate from the individual-based data alone (0.61; 95% confidence limits = 0.56–0.66). Models with age variation in fecundity returned unreasonable estimates (results not shown), suggesting a problem of parameter redundancy in the joint analysis in this case. The temporal variation of a single age-independent parameter was well explained by regressions involving the NAO index (models 19, 21). The model assuming a time-dependent fecundity, however, had the lowest AIC value (table 3, model 17). Fecundity values from this model were consistent with those observed except perhaps for the summers of 1995–1998, during which estimated values were noticeably higher than those observed (fig. 2). Despite a low correlation between the estimated and observed values of fecundity ($R^2 = 0.20$; fig. 2), the model increased the agreement between predicted and observed population sizes ($R^2 = 0.94$) compared with model 5 that included observations on individual reproductive success. Note that we used R^2 to illustrate an increase of model fit, but this point is also revealed by comparing the AIC values. In a similar way, we estimated survival parameters, specifically ϕ_{f}^m , without observations on male lamb survival (table 3, models 24–28). In this experiment, observations on reproductive success were in-

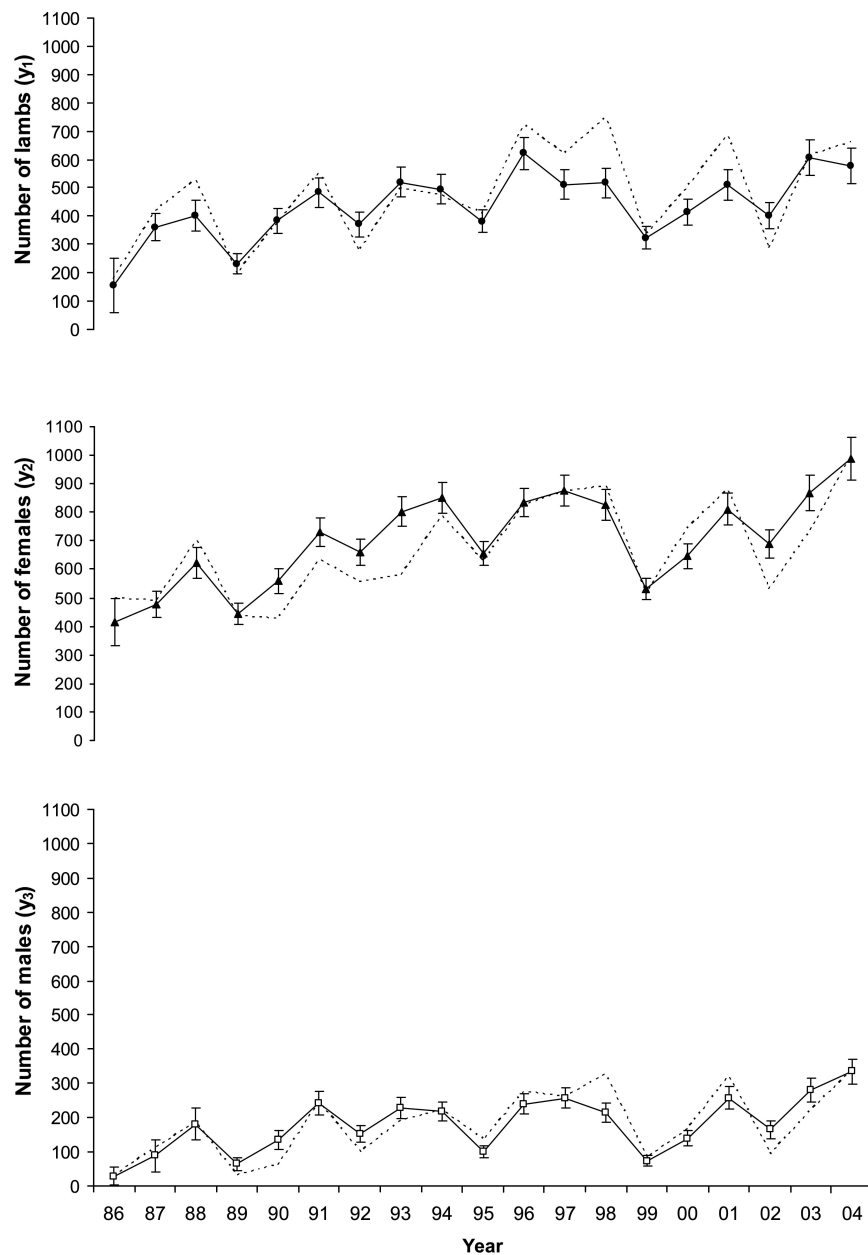


Figure 1: Observed (*dotted lines*) and predicted (*solid lines*) numbers of sheep according to year, age (lambs or older), and sex. Predicted numbers are smoothed estimates of the state vector from a model assuming two constant measurement error variances, one for males and a second for females and lambs (table 1, model 5). Sex ratio at birth is assumed to be constant. *Circles*, lambs; *triangles*, females; *squares*, males. Bars indicate 95% confidence intervals.

cluded in the fitting. A model with a time-dependent survival had the lowest AIC value, but in line with the analysis of the individual-based data alone (table 1), a simpler model in which male lamb survival covaried with a measure of winter severity, the NAO index, and population size provided a similar fit to the data and is more parsimonious (table 3, model 26). However, including the in-

teraction between the covariates did not improve model fit significantly (table 3). Survival values and estimates of population size from model 26 correlated well with the estimate from the MRR data and the counts ($R^2 = 0.80$ and 0.79 , respectively). The performance of the integrated approach in estimating hidden parameters was also investigated by simulating time series of population counts

Table 3: Modeling age-independent fecundity parameters, F_i (models 17–23), and male lamb survival parameters, ϕ_1^m (models 24–28), using the joint likelihood in equation (5) but without the relevant individual-based information

Model	Notation	L_{joint}	n_p	AIC
Fecundity:				
17	$F(t)$	233.24	41	548.48
18	$F(T)$	256.17	25	562.33
19	$F(N \times P)$	250.63	27	555.26
20	$F(N + P)$	250.64	26	553.28
21	$F(N)$	251.56	25	553.11
22	$F(P)$	255.86	25	561.71
23	$F(.)$	256.17	24	560.34
First-year survival of males:				
24 ^a	$\phi_1^m(t)$	224.49	53	554.98
25	$\phi_1^m(N \times P)$	240.38	39	558.75
26 ^a	$\phi_1^m(N + P)$	240.39	38	556.78
27	$\phi_1^m(N)$	243.10	37	560.21
28	$\phi_1^m(.)$	244.79	36	561.58

Note: N = North Atlantic Oscillation index, P = population size; other definitions as in table 2. Note that values of L_{joint} and Akaike Information Criterion (AIC) are not directly comparable to those of table 2.

^a Equally supported best models.

using the parameter estimates from the selected model and a range of values for ρ . In all cases, the estimated values of ρ were close to the one used in the simulated time series (see appendix).

Objective 3: Estimating Population Size

Estimates (SE) of total population size in years 1998, 1999, and 2000 obtained by the integrated analysis without the support of census observations for these years were 1,478 (53), 894 (33), and 1,159 (42), respectively. These values are comparable with those obtained from model 5 using the complete time series (1,557, 928, and 1,200, respectively). More importantly, we successfully identified the population crash that occurred in the winter of 1998–1999. Finally, we used the state-space approach to forecast the population size in 2005, a datum that was not included in the analyses. By considering the information available up to 2004 and a range of possible NAO values for 2005, we calculated 95% confidence intervals of the state and observation forecasts for the total number of sheep in 2005 (fig. 3). The observed number of 1,362 sheep in 2005 was within the 95% confidence limits of the observation prediction made by the model (fig. 3). A similar procedure can be used to forecast long-term population responses under different scenarios of climate and/or population changes.

Discussion

State-space models provide a framework for the simultaneous analysis of information on demographic rates and population size (Buckland et al. 2004). This unifying framework allows us to explicitly model process and measurement errors in the population counts and to estimate hidden demographic parameters (Besbeas et al. 2002, 2003; Thomas et al. 2005). Zeng et al. (1998) used a state-space modeling approach based on maximum likelihood to study density-dependent dynamics with univariate ecological time series. Recently, Thomas et al. (2005) have shown how separate demographic subprocesses can be incorporated into the state-space modeling framework for the study of complex dynamics using a Bayesian statistical framework (see also Buckland et al. 2004). Despite its potential, the state-space framework has not yet seen widespread use by population ecologists, and its performance has never been tested with real cases of known outcome. Here we illustrated how state-space models fitted by maximum likelihood can be extended to the simultaneous analysis of multivariate counts. Moreover, we used this approach to estimate unmeasured biological parameters that cannot be accessible otherwise, and we have empirically evaluated the use of this approach on a range of realistic biological applications. The extension to multivariate counts allowed us to model separately the measurement variances associated with each observed time series and greatly improved the power of the state-space modeling approach. For example, the measurement variances were modeled together with the sex ratio at birth, a demographic parameter that we included in the transition model but which has not been measured previously. We found that the variance of measurement errors in the time series of females was similar to that of lambs but significantly larger than that associated with males. This result is likely to reflect the behavior of different types of animals, since females and lambs segregate from males at the time of the census (Ruckstuhl and Neuhaus 2002; Clutton-Brock and Pemberton 2004), or the fact that it is harder to separate lambs and adult females during the population census. Results also indicated a skewed female sex ratio at birth in the whole island. For the Village Bay sector, the probability of giving birth to a male lamb has been positively but weakly associated with population density (Lindström et al. 2002). Our results suggest that such an association does not hold for the whole island of Hirta and that, at the population level, the annual variability of the sex ratio parameter was small. This, coupled with the higher survival of females, predicts a population composition more and more biased toward females, whereas the observed values suggest a parallel dynamic between the two sexes (fig. 1). It is possible that the linear models used

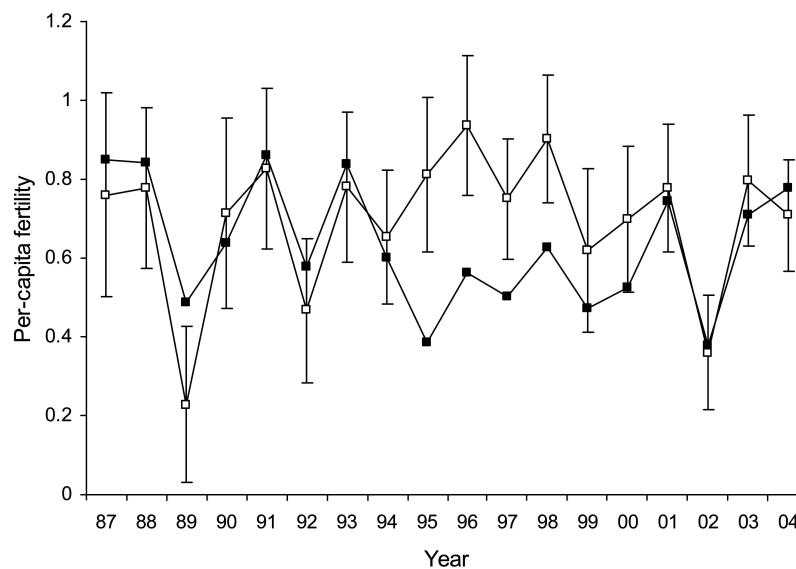


Figure 2: Time-dependent values of per capita fecundity. *Filled squares*, observed values (from individual-based data alone); *open squares*, estimates from the model selected in the joint analysis (model 17) in which individual data on fecundity were omitted. Bars indicate 95% confidence intervals.

here to describe the variation in survival and fertility are not sufficiently complex to fully capture the highly dynamic character of the population, despite a generally good match between observed and predicted numbers.

Inference based on a joint likelihood results in parameter estimates that can be viewed as the best compromise between matching insight from population censuses and individual-based data. In this respect, measurement variances can reflect, in part, disagreement between the two types of data. A disagreement may be due to biased data or inappropriate model structure, for example, not incorporating other components of the dynamics as immigration or spatial heterogeneity; the observation variance can consequently be used to guide model construction. However, the Hirta population is closed, and the count method has been standardized since 1985. Furthermore, in some years (1986–1988, 1991, and 1997) the population was counted more than once within a limited period (2 months), when mortality was negligible. Although these multiple counts refer to the aggregate population only and are not sufficient to provide direct estimates of $\sigma_{r_i}^2$ for the whole period, they can be used to assess the variance of the measurement error for the total count for those years. Thus, the average standard deviation of the measurement error for $y_1 + y_2 + y_3$ calculated from these data is 66. The corresponding standard deviation estimated using the state-space model (model 5) is 147. The two values are similar but not directly comparable because the latter incorporates a lack of fit of the model—that is, a mismatch between counts and individual-based

data—and it is calculated on the entire time series. A mismatch may reflect the inadequacy of the model—that is, important processes have not been included—and/or small differences in the dynamics of Village Bay, the source of the individual-based data, and the whole island. This could be due to movement of animals in response to high density or to differences in the age structure between different parts of the island (Coulson et al. 1999). Nonetheless, the number of sheep in Village Bay is highly correlated with the total island population size ($R^2 = 0.96$), and the effect of such spatial heterogeneity should therefore be small.

The estimation of hidden demographic parameters by state-space modeling offers great potential in ecological studies. However, the interplay of process and observation variances in state-space modeling may be important. Likewise, the variance in observation error or in those parameters that are estimated only through the integrated approach may absorb a part of the lack of fit between counts and the transition model. This will be more pronounced if parameters are fully time dependent. We empirically assessed this possibility by removing detailed data on individual fecundity or survival and comparing the estimated parameters with those from the analysis of the individual-based data alone. The extension to models in which parameters were assumed to be fully time dependent without the support of MRR data was made possible because of the multivariate nature of the counts. For fecundity, for example, it is interesting to note that the agreement between observed and predicted counts from model 17 was

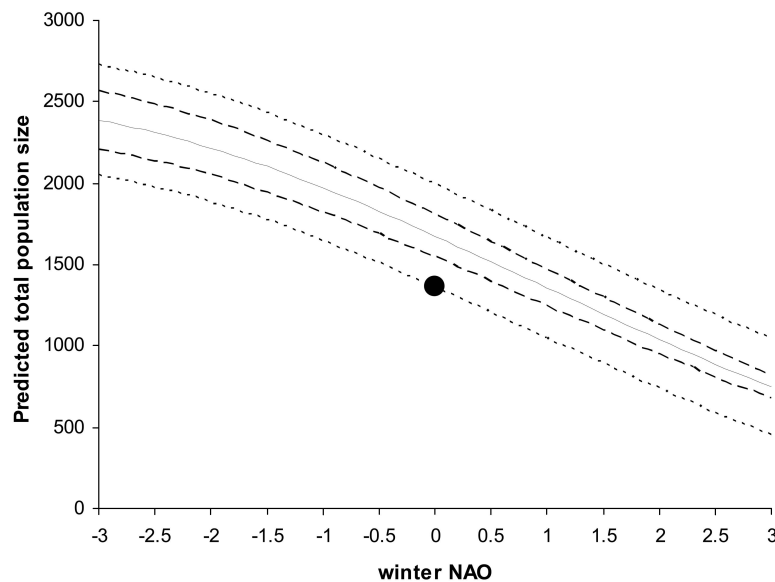


Figure 3: Predicted total population size in 2005 for a range of winter N values. Dotted lines indicate the 95% confidence intervals of predicted values for true population size, and dashed lines indicate the 95% confidence intervals of predicted values for observed population size. Circle shows the observed value for 2005 at the corresponding N value (0.12), which was not used to fit the data.

improved compared with model 5 while at the same time the agreement between observed and estimated fecundity values deteriorated. In fact, model 17 provided the best agreement between observed and predicted population size. Indeed, the discrepancy between the two sets of fecundity estimates from model 5 was higher during the period 1995–1998 (fig. 2), when the mismatch between predictions from the individual-based data and counts was also most evident (fig. 1). This suggests that parameters estimated in the joint likelihood only can, in part, absorb multiple sources of disagreement between individual-based data and counts. Nevertheless, with the exception of the period 1995–1998, the estimated and observed values of fecundity were in general agreement. Thus, we believe that the state-space approach represents a powerful method to provide estimates of hidden parameters. For example, we have been able to detect the influence of ecological conditions in fecundity and survival processes without detailed data on reproduction, and the results were in agreement with previous work (Catchpole et al. 2000; Stenseth et al. 2004). Our analysis also empirically shows that any identifiability problems of the integrated approach depend on the type of information available. Models with age-dependent fecundity were parameter redundant. This is because fecundity is derived by the single value of the total number of lambs; age-specific values could be combined in arbitrarily many ways to obtain the same total breeding output. Additional information on mother age

in count data would have made it possible to estimate the corresponding age-dependent fecundity values.

Soay Sheep, State-Space Modeling, and Wild Population Monitoring

Previous studies on Soay sheep population dynamics have used information from either population counts (Grenfell et al. 1998; Stenseth et al. 2004; Berryman and Lima 2006) or individual-based information (Catchpole et al. 2000, 2008; Coulson et al. 2001, 2008). An analytical framework that unifies these two types of information provides consensual estimates of demographic parameters based on both types of data and permits new biological insights in this well-studied system. In particular, we were able to estimate, for the first time, the variance associated with the error in the counts, critical information required in order to infer biological processes from count data (Grenfell et al. 1998; Stenseth et al. 2004) or to help with use of the Soay sheep data to test new analytical methods (Catchpole et al. 2000, 2008; Coulson et al. 2001, 2008; Berryman and Lima 2006). A second consequence that followed from the integrated approach is the estimation and modeling of the lamb sex ratio at the island scale, a parameter that cannot be measured in the field—since male and female lambs cannot be distinguished during the whole island census—but that has important population and evolutionary dynamic consequences (Lindström et al.

2002; Orzack 2002; Skalski et al. 2005). We have also incorporated, for the first time, the effect of weather, population abundance, and age on female fertility into a population model and provided a valid short-term forecast of population size.

The potential and limitations of the integrated approach highlighted here are particularly relevant to the design of long-term population studies. In some cases, detailed information based on mark-release-recapture procedures could be too expensive or too difficult to collect. For example, individuals of a particular age (i.e., juvenile) or in a particular state (i.e., nonbreeder) might not be detectable, and the corresponding age or state parameter might not be directly estimated. Monitoring programs on colonial birds, for instance, are typically conducted on breeding grounds where only breeders are detectable (Wooller et al. 1992). We have shown that, providing detailed counts are available, these problems may be overcome by using a joint analysis. For example, wildlife managers interested in estimating time-dependent fecundity in systems in which individual breeding success cannot be directly measured should ensure separate censuses of young and adult animals.

Acknowledgments

We thank the National Trust for Scotland and the Scottish Natural Heritage for permission to work on St. Kilda, the Royal Artillery for logistical support, and the Natural Environment Research Council and the Wellcome Trust for providing financial support. We thank J. Pemberton, J. Pilkington, and I. Stevenson for providing help and access to the Soay sheep data and for the many contributions to the project. We thank L. Kruuk for helpful comments on the manuscript. We are also grateful to the many volunteers involved in Soay sheep data collection. G.T. was supported by a grant from the Biotechnology and Biological Sciences Research Council (BBS/B/01219).

Literature Cited

- Berryman, A., and M. Lima. 2006. Deciphering the effects of climate on animal populations: diagnostic analysis provides new interpretation of Soay sheep dynamics. *American Naturalist* 168:784–795.
- Besbeas, P., and S. Freeman. 2007. Methods for joint inference from panel survey and demographic data. *Ecology* 87:1138–1145.
- Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547.
- Besbeas, P., J.-D. Lebreton, and B. J. T. Morgan. 2003. The efficient integration of abundance and demographic data. *Applied Statistics* 52:95–102.
- Brooks, S. P., R. King, and B. J. T. Morgan. 2004. A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* 27:515–529.
- Buckland, S. T., K. B. Newman, L. Thomas, and N. B. Koesters. 2004. State-space models for the dynamics of wild animal populations. *Ecological Modelling* 171:157–175.
- Burnham, K. P. 1993. A theory of combined analysis of ring recovery and recapture data. Pages 199–213 in J.-D. Lebreton and P. M. North, eds. *Marked individuals in the study of bird population*. Birkhäuser, Basel.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and inference: a practical information-theoretic approach*. 2nd ed. Springer, New York.
- Cappuccino, N., and P. W. Price. 1995. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, CA.
- Catchpole, E. A., S. N. Freeman, B. J. T. Morgan, and M. P. Harris. 1998. Integrated recovery/recapture data analysis. *Biometrics* 54:33–46.
- Catchpole, E. A., B. J. T. Morgan, J. N. Coulson, T. N. Freeman, and S. D. Albon. 2000. Factors influencing Soay sheep survival. *Applied Statistics* 49:453–472.
- Catchpole, E. A., B. J. T. Morgan, and G. Tavecchia. 2008. A new method for analyzing discrete life-history data with missing covariate values. *Journal of the Royal Statistical Society B* 70:445–460.
- Chatfield, C. 2004. *The analysis of time series: an introduction*. Chapman & Hall, London.
- Clark, J. S., and O. N. Bjørnstad. 2004. Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology* 85:3140–3150.
- Clutton-Brock, J. 1999. *The natural history of domesticated mammals*. Cambridge University Press, Cambridge.
- Clutton-Brock, T. H., and J. M. Pemberton. 2004. *Soay sheep: dynamics and selection in an island population*. Cambridge University Press, Cambridge.
- Coulson, T., S. D. Albon, G. Pilkington, and T. H. Clutton-Brock. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. *Journal of Animal Ecology* 68:658–671.
- Coulson, T., E. J. Milner-Gulland, and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society B: Biological Sciences* 267:1771–1779.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather and population crashes in Soay sheep. *Science* 292:1528–1531.
- Coulson, T., T. H. G. Ezard, F. Pelletier, G. Tavecchia, N. Stenseth, D. Z. Childs, J. C. Pilkington, et al. 2008. Estimating the functional form for the density dependence from life history data. *Ecology* 89:1661–1674.
- de Valpine, P., and A. Hastings. 2002. Fitting population models incorporating process noise and observation error. *Ecological Monographs* 72:57–76.
- Grenfell, B. T., K. Wilson, B. F. Finkenstädt, T. N. Coulson, S. Murray, S. D. Albon, J. M. Pemberton, T. H. Clutton-Brock, and M. J. Crawley. 1998. Noise and determinism in synchronized sheep dynamics. *Nature* 394:674–677.
- Harvey, A. C. 1989. *Forecasting, structural time series models and the Kalman filter*. Cambridge University Press, Cambridge.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation

- and relationships to regional temperature and precipitation. *Science* 269:676–679.
- Jones, O. R., M. J. Crawley, J. G. Pilkington, and J. M. Pemberton. 2005. Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. *Proceedings of the Royal Society B: Biological Sciences* 272:2619–2625.
- Lindström, J., T. Coulson, L. E. B. Kruuk, M. C. Forchhammer, D. W. Coltman, and T. H. Clutton-Brock. 2002. Sex-ratio variation in Soay sheep. *Behavioral Ecology and Sociobiology* 53:25–30.
- Meyer, R., and R. B. Millar. 1999. BUGS in Bayesian stock assessments. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1078–1086.
- Millar, R. B., and R. Meyer. 2000. Bayesian state-space modeling of age-structured data: fitting a model is just the beginning. *Canadian Journal of Fisheries and Aquatic Sciences* 57:43–50.
- Morgan, B. J. T. 2000. *Applied stochastic modelling*. Arnold, London.
- Newman, K. B. 1998. State-space modeling of animal movement and mortality with application to salmon 54:1290–1314.
- Newman, K. B., S. T. Buckland, S. T. Lindley, L. Thomas, and C. Fernandez. 2006. Hidden process models for animal population dynamics. *Ecological Applications* 16:74–86.
- Orzack, S. H. 2002. Using sex ratios: the past and the future. Pages 383–398 *in* I. C. W. Hardy, ed. *Sex ratios: concepts and research methods*. Cambridge University Press, Cambridge.
- Ruckstuhl, K. E., and P. Neuhaus. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* 77:77–96.
- Skalski, J. R., K. E. Ryding, and J. J. Millspaugh. 2005. *Wildlife demography: analysis of sex, age and count data*. Elsevier, London.
- Stenseth, N. C., K.-S. Chan, G. Tavecchia, T. Coulson, A. Mysterud, T. Clutton-Brock, and B. T. Grenfell. 2004. Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. *Proceedings of the Royal Society B: Biological Sciences* 271:1985–1993.
- Tavecchia, G., T. Coulson, B. J. T. Morgan, J. M. Pemberton, J. C. Pilkington, F. M. D. Gulland, and T. H. Clutton-Brock. 2005. Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology* 74:201–213.
- Thomas, L., S. T. Buckland, K. B. Newman, and J. Harwood. 2005. A unified framework for modelling wildlife population dynamics. *Australian and New Zealand Journal of Statistics* 47:19–34.
- Wang, G. 2007. On the latent estimation of nonlinear population dynamics using Bayesian and non-Bayesian state-space models. *Ecological Modelling* 200:521–528.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(suppl.):120–129.
- Wooller, R. D., J. S. Bradley, and J. P. Croxall. 1992. Long-term population studies of seabirds. *Trends in Ecology & Evolution* 7: 111–114.
- Zeng, Z., R. M. Nowierski, M. L. Taper, B. Dennis, and W. P. Kemp. 1998. Complex population dynamics in the real world: modeling the influence of the time-varying parameters and time lags. *Ecology* 79:2193–2209.

Associate Editor: Wolf M. Mooij
Editor: Donald L. DeAngelis