

A hierarchical population model for the estimation of latent prey abundance and demographic rates of a nomadic predator

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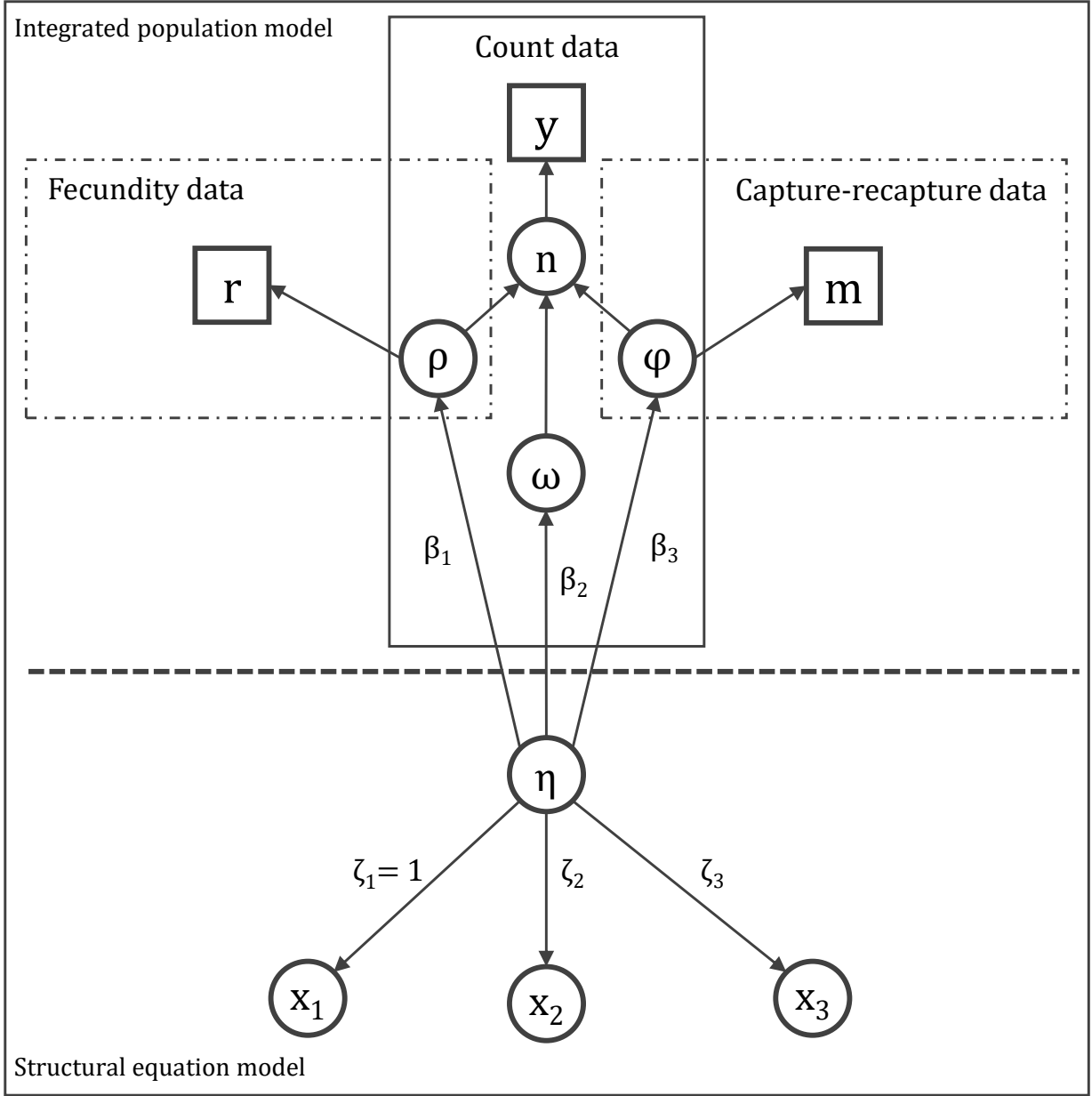


Figure 1. A conceptual figure demonstrating how the survival (ϕ), recruitment (ρ), and immigration (ω) parameters of an integrated population model (top; Kéry & Schaub 2012, Schaub & Kéry 2022) might be linked to a latent environmental variable (η) composed of three measured environmental covariates (x_1 , x_2 , and x_3) estimated using a structural equation model.

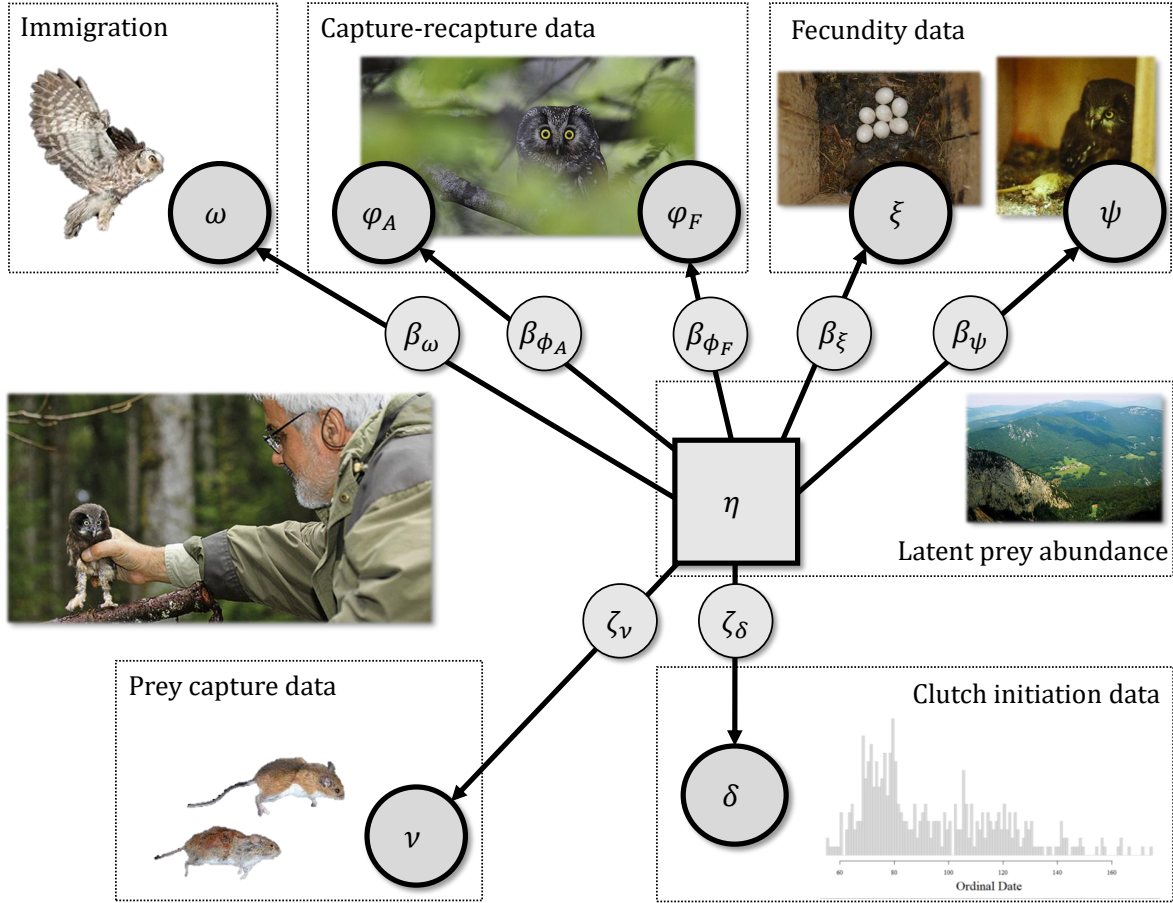


Figure 2. A conceptual figure demonstrating the modelled relationships between the mean number of *Apodemus* mouse and vole (Arvicolinae) remains discovered in nest boxes following breeding (ν), mean laying date (δ), latent breeding conditions (η ; i.e., rodent abundance), and the demographic parameters clutch size (ξ), the probability that each egg fledges (ψ), adult survival (ϕ_A), fledgling survival to adulthood (ϕ_F), and the expected number of immigrants (ω) for Tengmalm's owls breeding in the Jura Mountains in northwestern Switzerland and eastern France (1990-2020).

Abstract

1. Linking the demographic parameters underlying population change to environmental conditions is a central goal of population demography. However, multicollinearity among processes in ecological studies can complicate parameter estimation and inference.
2. We sought to demonstrate the use of structural equation modelling, a technique for estimating hypothesized causal pathways among collinear observed and unobserved variables, in the context of integrated population models.
3. We monitored a population of Tengmalm's owls (*Aegolius funereus*) breeding in the Jura Mountains of northwestern Switzerland and eastern France for 31 years (1990-2020) and collected data on captured prey items. We use concepts central to structural equation models (i.e., latent variables) and integrated population models to estimate the effects of latent prey abundance on Tengmalm's owl demographic parameters.
4. We observed strong positive effects of latent prey abundance during time t on clutch size, fledging probability, and immigration rates into the breeding population, and strong effects of positive changes in latent prey abundance from time t to $t + 1$ on first-year and adult survival. We also observed long-term declines in immigration into the study area.
5. Our work provides a straightforward example of incorporating concepts central to structural equation models (e.g., latent variables) to model environmental processes underlying demographic rates in integrated population models, and has interesting implications for metapopulation ecology of Tengmalm's owl populations in Europe.

Key words: *Aegolius funereus*, hierarchical model, immigration, integrated population model, latent variables, resource availability, structural equation model, Tengmalm's owl

Introduction

Accurately assessing the relationships among environmental conditions and demographic parameters is essential for successful conservation ecology (Koons *et al.* 2022), as well as an understanding of eco-evolutionary processes and population dynamics (Stearns 1992). A substantial challenge researchers face when estimating these relationships is multicollinearity (Legendre & Legendre 1998, Graham 2003). When two or more covariates are collinear (e.g., $|r| > 0.7$), this can affect the reliability and constancy of regression parameter estimates across a range of modeling frameworks, and increase the uncertainty of predictions (Graham 2003, Cade 2015). Accounting for multicollinearity is challenging, and often leads to exclusion of measured covariates from analyses, or use of model selection techniques to estimate which of the correlated covariates is ‘best.’

Notably, covariates are often collinear due to underlying latent ecological processes. For instance, climate oscillations may affect both temperature and precipitation (Bunkers *et al.* 1996), or different correlated measurements of morphometric traits may all be related to the size of an individual (Cubaynes *et al.* 2012). In these instances, it is possible to parameterize hierarchical models in a way that estimates the ‘latent’ underlying process governing changes in multiple observed covariates. Hierarchical models have been growing in popularity in ecology for decades (Royle & Dorazio 2008), where integrated population models (IPM; Besbeas *et al.* 2002, Abadi *et al.* 2010, Schaub & Kéry 2022) and structural equation models (SEM; Grace *et al.* 2010, Cubaynes *et al.* 2012) are specific classes of hierarchical models. Integrated population models

allow researchers to jointly analyse capture-reencounter, count, fecundity, and other data to estimate relationships among environmental covariates, demographic parameters, and population growth rates. Further, structural equation models (Cubaynes *et al.* 2012) and other similar hierarchical models (Gimenez *et al.* 2012) can function to limit the effects of multicollinearity on inference by treating multicollinearity among covariates as a result of latent processes (Graham 2003, Grace 2006). However, despite the ubiquity of multicollinearity in population ecology and demography datasets, these approaches are rarely, if ever, implemented jointly (e.g., Figure 1). Thus, in this study we use a long-term mark-recapture, population count, and fecundity dataset on Tengmalm's owls (*Aegolius funereus*) breeding in the Jura Mountains of northwestern Switzerland and eastern France (1990-2020), as well as data collected on prey remains recovered from nest boxes and natural cavities following breeding, to demonstrate the utility of linking concepts central to structural equation (Grace *et al.* 2010, Cubaynes *et al.* 2012) and integrated population models (Besbeas *et al.* 2002, Schaub & Kéry 2022) in a hierarchical population modeling framework.

Tengmalm's (also 'boreal') owls are small, circumpolar predators that breed in dense coniferous forests across North America and Eurasia. In the northern part of their range, various demographic parameters have been closely linked to vole (Arvicolinae) population dynamics (see Korpimäki & Hakkarainen 2012 for an excellent overview), while in central Europe it has been demonstrated that the abundance of *Apodemus* mice is an important additional driver of reproductive success (Zárybnická *et al.* 2013; 2015a;c). When rodent prey levels are low, breeding Tengmalm's owls turn to alternative prey, (e.g., *Sorex* shrews and small passerine birds), which has been associated with reductions in reproductive success (Kouba *et al.* 2020a) and post-fledging survival (Kouba *et al.* 2023; 2024). While adult males are territorial (Hakkarainen

et al. 2002), females are nomadic, and natal and breeding dispersal are substantial (Korpimäki *et al.* 1987, Korpimäki & Lagerstrom 1988).

The nomadic nature of predators involved in many predator-prey cycles complicates the collection of individual longitudinal data, as individuals often leave the study area and immigration and emigration are important components of population dynamics (Millon *et al.* 2019). Fortunately, integrated population models can be parameterized to resolve this issue (Abadi *et al.* 2010), albeit with additional assumptions (Riecke *et al.* 2019, Paquet *et al.* 2021, Plard *et al.* 2021). Further, many long-term demographic studies lack joint detailed long-term monitoring data for the population dynamics of prey or forage resources, and often instead rely on indices of environmental condition or habitat quality. In this study we use two correlated ($r = -0.79$) indices of latent prey abundance: nest initiation dates, and remnants of rodents captured by individual pairs of Tengmalm's owls recovered from the nest box after breeding. We note that the mean number of rodents captured by each breeding pair of Tengmalm's owls is an imperfect metric of prey abundance. Parental experience (Korpimäki 1988a, Laaksonen *et al.* 2002), the number of nestlings, weather conditions, territory quality (Korpimäki 1988b, Hakkarainen *et al.* 2003), and inter- and intra-specific competition (Lack 1946) undoubtedly influence prey capture rates. Further, prey captures occur after nest initiation, thus using prey captures to model nest initiation is chronologically inappropriate. However, these metrics should both serve as reliable indices of latent prey abundance, as owls initiate nests earlier during years of high rodent abundance (Korpimäki & Hakkarainen 1991, Zárbynická *et al.* 2015c, Korpimäki 2020), and of course owls can capture more prey when more prey are available. We demonstrate strong effects of latent prey abundance on demographic rates, and discuss future research to better understand population dynamics of Tengmalm's owls and other species using hierarchical models.

Materials and methods

Data collection

We monitored Tengmalm's owls breeding in nest boxes and natural cavities in the Jura Mountains (800-1600m elevation; 46.08°N, 6.05°E) of northwestern Switzerland and eastern France from 1990-2020. Approximately 200 potential nest sites were monitored per year. We monitored nests, recorded nest initiation date (i.e., laying date of the first egg), clutch size and the number of fledged offspring, and ringed nestlings. We ringed and recaptured breeding females while monitoring nests (Ravussin *et al.* 2001a;b; 2015; 2018). After the young fledged, the nest contents were collected and sorted, where prey number (specifically mice, *Apodemus* spp., and voles, Arvicolinae) and type were identified to the lowest possible taxonomic level (Ravussin *et al.* 2016). Data collection was ethically approved by the Bundersamt für Umwelt in Switzerland, and by the Centre de Recherches sur la Biologie des Populations d'Oiseaux in France.

Latent prey abundance, prey captures, and nesting phenology model components

We developed a simple structural equation model (Grace *et al.* 2010, Cubaynes *et al.* 2012) to model latent prey abundance as a function of the number of rodent prey remnants collected from each nest and timing of breeding (Figure 2), where we hypothesized that as prey abundance increased, prey captures would increase and laying date would occur earlier in the year. Thus, we modelled latent prey abundance in each year (η_t) as arising from a normal distribution with a mean of 0 and variance (σ_η^2),

$$\eta_t \sim \text{normal}(0, \sigma_\eta^2), \tag{1}$$

$$\sigma_\eta \sim \text{gamma}(1, 1).$$

108 We then modelled the total number of rodent remains ($x_{j,t}$) recovered from each nesting cavity (j)
 109 following breeding during each year (t) as a function of latent prey abundance,

$$\begin{aligned} x_{j,t} &\sim \text{Poisson}(\nu_t), \\ \log(\nu_t) &= \alpha_\nu + \zeta_\nu \eta_t, \\ \alpha_\nu &\sim \text{normal}(3, 10), \end{aligned} \tag{2}$$

110 where α_ν is the mean number of rodent remains recovered from nest boxes during an average
 111 year, and ζ_ν is the effect of latent prey abundance on rodent remains. We fixed $\zeta_\nu = 1$ for
 112 parameter identifiability (Grace *et al.* 2010). This ensures that years with greater numbers of
 113 rodent remains in nest cavities correspond to positive values of latent prey abundance (η), and
 114 provides a scale to the latent variable, such that η has the same scale as $\ln(\nu)$. We modelled mean
 115 nest initiation date during each year (δ_t) as a function of latent prey abundance as well, where the
 116 initiation date of each nest during each year ($d_{j,t}$) was,

$$\begin{aligned} d_{j,t} &\sim \text{normal}(\delta_t, \sigma_\delta^2), \\ \delta_t &= \alpha_\delta + \zeta_\delta \eta_t, \\ \alpha_\delta &\sim \text{normal}(100, 10), \\ \zeta_\delta &\sim \text{normal}(0, 100), \end{aligned} \tag{3}$$

117 where α_δ is the mean ordinal nest initiation date, and ζ_δ is the effect of latent prey abundance on
 118 initiation date. Thus, our model treated annual variation in prey abundance as an unobserved
 119 latent variable that was linked to our observations of prey remains and timing of breeding, given
 120 our expectation that increased latent prey abundance would be associated with increased captures

121 of mice and voles by breeding pairs, and earlier breeding attempts.

122 **Population model components**

123 We built a female-only population model with three age-classes; adults (A), second-years (S),
 124 and fledged juveniles (F). We specified Poisson priors for the initial population sizes of
 125 second-years and adults based on previous (1985-1989) field research at the study site,

$$\begin{aligned} S_1 &\sim \text{Poisson}(15), \\ A_1 &\sim \text{Poisson}(15), \end{aligned} \tag{4}$$

126 We modelled changes in the population from year to year given the number of individuals (N),
 127 adult (ϕ_A) and first-year (ϕ_F) apparent survival probabilities, the number of fledged juvenile
 128 females (F) given clutch size (ξ), fledgling sex ratio ($\pi = 0.5$) and the probability of each egg
 129 becoming a fledgling (ψ), and the number of immigrants in each year (I_t),

$$\begin{aligned} N_{t+1} &= A_{t+1} + S_{t+1} + I_t, \\ F_t &\sim \text{Poisson}(N_t \times \xi_t \times \psi_t \times \pi), \\ A_{t+1} &\sim \text{binomial}(N_t, \phi_{A,t}), \\ S_{t+1} &\sim \text{binomial}(F_t, \phi_{F,t}), \\ I_t &\sim \text{Poisson}(\omega_t). \end{aligned} \tag{5}$$

130 We derived population growth rate (λ_t) as $\lambda_t = \frac{N_{t+1}}{N_t}$. The counts of numbers of nests (y_t) were
 131 assumed to arise from a Poisson distribution around the true population size, $y_t \sim \text{Poisson}(N_t)$.
 132 We modelled all demographic parameters as functions of annual variation in latent prey
 133 abundance (η) experienced by nesting Tengmalm's owls prior to the breeding season. First-year

134 and adult survival were modelled as a function of the change in latent prey abundance from
 135 marking to the next capture occasion (i.e., the change in prey abundance during the survival
 136 interval) and random temporal variation (ϵ_ϕ),

$$\begin{aligned}\text{logit}(\phi_{F,t}) &= \alpha_{\phi_F} + \beta_{\phi_F} \times (\eta_{t+1} - \eta_t) + \epsilon_{\phi,t}, \\ \text{logit}(\phi_{A,t}) &= \alpha_{\phi_A} + \beta_{\phi_A} \times (\eta_{t+1} - \eta_t) + \epsilon_{\phi,t}, \\ \alpha_\phi &\sim \text{normal}(0, 2.25), \\ \beta_\phi &\sim \text{normal}(0, 10), \\ \epsilon_\phi &\sim \text{normal}(0, \sigma_\phi^2), \\ \sigma_\phi &\sim \text{gamma}(1, 1)\end{aligned}\tag{6}$$

137 where α_ϕ is the age-class specific intercept (i.e., survival given average prey abundance), and β_ϕ
 138 is the effect of changes in latent prey abundance on survival estimated separately for each
 139 age-class. Similarly, we modelled clutch size (ξ) and the probability of each egg producing a
 140 fledgling (ψ) as a function of latent prey abundance during the breeding season (η_t), and random

141 temporal variation (ϵ),

$$\begin{aligned}
 \log(\xi_t) &= \alpha_\xi + \beta_\xi \times \eta_t + \epsilon_{\xi,t}, \\
 \text{logit}(\psi_t) &= \alpha_\psi + \beta_\psi \times \eta_t + \epsilon_{\psi,t}, \\
 \alpha_\xi &\sim \text{normal}(1.5, 10), \\
 \alpha_\psi &\sim \text{normal}(0, 2.25), \\
 \beta_\xi &\sim \text{normal}(0, 100), \\
 \beta_\psi &\sim \text{normal}(0, 100).
 \end{aligned} \tag{7}$$

142 Annual random effects for both parameters were modeled in the same way as for apparent
 143 survival. We modelled the expected number of immigrants in each year (ω_t) as a function of latent
 144 prey abundance during the breeding season of immigration (η_{t+1}), a long-term trend (κ_ω) given
 145 broad long-term declines of Tengmalm's owls in Europe (Kouba *et al.* 2020a), and random
 146 temporal variation ($\epsilon_{\omega,t}$) given the same priors as other parameters (e.g., Φ),

$$\begin{aligned}
 \log(\omega_t) &= \alpha_\omega + \beta_\omega \times \eta_{t+1} + \kappa_\omega \times t + \epsilon_{\omega,t}, \\
 \alpha_\omega &\sim \text{normal}(0, 100), \\
 \kappa_\omega &\sim \text{normal}(0, 10), \\
 \beta_\omega &\sim \text{normal}(0, 10).
 \end{aligned} \tag{8}$$

147 If the clutch size was observed (c_i), we modelled it as a function of mean annual clutch size, and
 148 we modelled the number of fledged nestlings in each nest (n_i) as a function of clutch size (ξ_t) and

149 the probability of each egg hatching and fledging (ψ_t),

$$c_{i,t} \sim \text{Poisson}(\xi_t), \quad (9)$$

$$n_{i,t} \sim \text{Poisson}(\xi_t \times \psi_t).$$

150 We modelled annual age-specific (a) recapture probability (p_t) as a function of random temporal
151 variation modelled using the same priors as all other parameters (e.g., Φ),

$$\text{logit}(p_{a,t}) = \alpha_{p_a} + \epsilon_{p,t}. \quad (10)$$

152 In order for an individual to be detected in a nest box or natural cavity at the study site, it must
153 survive (ϕ) and be recaptured in a nest box or natural cavity by researchers (p). Thus, we
154 modelled the cell probabilities (Z) of the age-specific capture-recapture m-arrays (Lebreton *et al.*
155 1992), where i is the year of release, and j is the year of recapture, as a function of first-year and
156 adult survival and age-specific probabilities of detection (p) and non-detection (q). For the adults,
157 cell probabilities were,

$$q_{A,t} = (1 - p_{A,t})$$

$$z_{i,j,A} = \begin{cases} \phi_{A,i} \times p_{A,j}, & \text{if } i = j \\ \prod_{k=i}^j \phi_{A,k} \times \prod_{k=i}^{j-1} q_{A,k} \times p_{A,j}, & \text{if } i < j < T + 1 \\ 0, & \text{if } i > j \\ 1 - \sum_{k=1}^T z_{i,k,A}, & \text{if } j = T + 1 \end{cases} \quad (11)$$

158 The cell probabilities for fledglings shared substantial structure with the adult m-array with the
 159 exception of the main diagonal, which was specific to demographic parameters for fledglings and
 160 second-years, and the inclusion of a sex ratio parameter ($\pi = 0.5$), as marked juveniles were of
 161 unknown sex,

$$q_{S,t} = (1 - p_{S,t})$$

$$z_{i,j,F} = \begin{cases} \phi_{F,i} \times p_{S,j} \times \pi, & \text{if } i = j \\ \phi_{F,i} \times (q_{S,i}) \times \phi_{A,i+1} \times p_{A,j} \times \pi, & \text{if } i = j - 1 < T + 1 \\ (\phi_{F,i}) \times q_{S,i} \times \left(\prod_{k=i+1}^j \phi_{A,k} \right) \times \left(\prod_{k=i+1}^{j-1} q_{A,k} \right) \times (p_{A,j}) \times \pi, & \text{if } i < j - 1 < T + 1 \\ 0, & \text{if } i > j \\ 1 - \sum_{k=1}^T z_{i,k,F}, & \text{if } j = T + 1 \end{cases} \quad (12)$$

162 We provide definitions of demographic parameters in Table 1, and definitions of regression
 163 parameters in the text. We conducted analyses in R 4.4.1 (R Core Team 2024) and JAGS
 164 (Plummer 2003) using the `jagsUI` package (Kellner 2016). We sampled four MCMC chains for
 165 250,000 iterations. We discarded the first 100,000 iterations and retained every 25th saved
 166 iteration. We ensured posterior distributions had \hat{R} values < 1.03 (Brooks and Gelman 1998), and
 167 visually inspected trace plots for convergence (Kéry & Schaub 2012). In the following text,
 168 tables, and figures, we report medians of posterior distributions, Bayesian credible intervals, and
 169 v , the proportion of the posterior distribution on the same side of zero as the mean.

Simulation

To ensure that parameters were identifiable, we constructed a simulation following the model used to analyze the Tengmalm owl data. We first simulated random variation in latent prey abundance, $\eta \sim \text{normal}(0, 1)$. Similar to our observed data, we then simulated prey capture (x) and nest-initiation date (d) data as a function of latent prey abundance (eqs. 2 & 3). We subsequently simulated annual variation in clutch size (ξ ; eq. 7), the probability of each egg becoming a fledgling (ψ ; eq. 7), and fledgling (ϕ_F ; eq. 6) and adult (ϕ_A ; eq. 6) survival. We initiated populations at a similar size as the real population, and simulated populations forward in time following the population model we describe previously in the text (eq. 5). We modeled the data using models almost identical to those described in the text, where we removed some random effects to reduce the number of iteration required to obtain convergence. We simulated 250 datasets spanning 25 years. Once simulated, we formatted the capture-recapture data in m-arrays and used multistate m-array models described in Schaub & Kéry (2022) to analyze the data. We sampled four MCMC chains for 25,000 iterations. We discarded the first 15,000 iterations and retained every 10th saved iteration. We ensured posterior distributions had \hat{R} values < 1.2 (Brooks and Gelman 1998), and visually inspected trace plots for convergence (Kéry & Schaub 2012). In the results, we report the mean difference between simulated parameter values and medians of posterior distributions, as well as coverage, or the proportion of true parameter values contained within the 95% Bayesian credible intervals. Model code containing further details is archived at Dryad.

Results

Over the 31 years of the study, we monitored 539 nesting attempts. We marked and released 1,548 juveniles of unknown sex and ringed 336 breeding females, of which 58 individuals were recaptured in a later year. The contents of 200 nests were collected, and 13,607 prey items were identified to the lowest possible taxonomic level. Mean nest initiation date varied by over a month as a function of latent prey abundance ($\zeta_\delta = -16.1$; $v = 1$), and the number of rodent remnants collected from nesting sites increased by nearly an order of magnitude during the ‘best’ years (Figure 3). Population growth rate was lowest following major declines in latent prey abundance, and highest during years of increased prey abundance (Figure 3). We observed long-term declines in the total number of adults (Figure 4), and some evidence for long-term declines in the number of immigrants ($\kappa_\omega = -0.207$; $v = 0.867$) into the study area. We observed positive effects of latent prey abundance on clutch size ($\beta_\xi = 0.320$; $v = 1$), hatching and fledging success ($\beta_\psi = 1.382$; $v = 1$), and the number of immigrants into the population ($\beta_\omega = 1.276$; $v = 0.999$, Figures 5 and 6). During survival intervals with increasing prey abundance, we observed strong increases in both apparent adult survival ($\beta_{\phi_A} = 1.356$; $v = 1$), and apparent survival from fledging to adulthood ($\beta_{\phi_F} = 1.032$; $v = 1$; Table 2).

Simulation results

Two hundred and twelve of 250 simulations adequately converged ($\hat{R} < 1.2$) for assessing parameter constancy and coverage. In parentheses we report the average difference between the medians of posterior distributions and the data generating parameter value across converged simulations, as well as parameter coverage (cov.). We adequately recovered simulated parameter values for rodent remains (0.047; cov. = 0.977), nest initiation date (-0.959; cov. = 0.986), clutch

size (0.009; cov. = 0.981), the probability of each egg becoming a fledgling (0.090; cov. = 0.972), fledgling survival to adulthood (0.144; cov. = 0.939), adult survival (0.165; cov. = 0.954), and immigration (-0.352; cov. = 0.907). Similarly, we adequately recovered estimates of the effects of latent prey abundance for clutch size (0.001; cov. = 0.944), the probability of each egg becoming a fledgling (0.014; cov. = 0.954), fledgling survival to adulthood (0.180; cov. = 0.917), adult survival (0.154; cov. = 0.949), and immigration (-0.057; cov. = 0.972, Figure 7).

Discussion

Although we did not directly measure prey abundance in this study (e.g., Korpimäki 2020, Kouba *et al.* 2020a), we were able to use concepts central to structural equation modeling (Grace *et al.* 2010, Cubaynes *et al.* 2012) to reconstruct latent prey abundance from measured indicators of rodent abundance (i.e., prey captures and nest initiation dates). We subsequently observed strong relationships between latent prey abundance and adult survival, juvenile survival, clutch size, hatching and fledging probability, and the number of immigrants into the population. Notably, clutch size nearly doubled and the probability of eggs becoming fledglings quadrupled during years with high rodent abundance relative to years with low rodent abundance (Figures 5 and 6). We also observed strong evidence that declining prey populations led to declines in female survival, presumably due to increased emigration.

Relationships between latent prey abundance and demographic parameters

Previous research has demonstrated strong linkages between Tengmalm's owl fecundity and rodent abundance (Korpimäki & Hakkarainen 2012, Kouba *et al.* 2020a). During years of high vole abundance in northern Europe, or high vole or *Apodemus* mice abundance in central Europe, Tengmalm's owls initiate nests earlier (Korpimäki 1987, Zárýbnická *et al.* 2015c), increase clutch

size (Zárybnická *et al.* 2015c, Kouba *et al.* 2020a), and produce a large number of fledglings relative to clutch size (Zárybnická *et al.* 2015c). Beyond reduced food availability for juveniles, depressed populations of *Apodemus* mice and other rodents can also indirectly lead to reduced fecundity in Tengmalm's owls, where nest predation by pine martens (*Martes martes*) increases as rodent populations decrease (Zárybnická *et al.* 2015b).

For resident male and juvenile Tengmalm's owls, survival increases with increasing prey abundance (Hakkarainen *et al.* 2002, Kouba *et al.* 2023; 2024). Here we observed similar patterns for both breeding adult and fledgling females as prey abundance increased during the survival interval (Fig. 5). We attribute this to two primary mechanisms. First, apparent survival is the product of true survival and site fidelity. As natal and adult dispersal are common following major vole and *Apodemus* mouse irruption events (Korpimäki 1987), emigration (or lack thereof) from the study site presumably caused much of the observed changes in apparent survival. Second, increased reproductive allocation in the form of increased clutch size and number of nestlings (Fig. 4) may be energetically taxing for breeding females during years of high latent prey abundance, potentially lowering true survival. Thus, we expect that changes in apparent survival for adults following 'boom' years may be due to both simultaneous increases in emigration and declines in true survival. Additionally, Hipkiss & Hörnfeldt (2004) noted major changes in sex ratio of offspring as a function of vole abundance, where the constant, even sex ratio employed in this analysis may be inadequate. However, other studies did not record an effect of changing prey abundance on Tengmalm's owl brood sex ratios (e.g., Kouba *et al.* 2020b).

Model assumptions and inference

Recent research (e.g., Riecke *et al.* 2019, Paquet *et al.* 2021, Schaub & Kéry 2022) has demonstrated that parameters in integrated population models that are not directly informed by

data can be exceptionally sensitive to model assumption violations. This can be particularly problematic for estimates of immigration (Paquet *et al.* 2021), and we note that these issues often extend to parameters that are informed by few data (Plard *et al.* 2021). Thus, although our estimates of immigration were ecologically feasible based on previous research, we suggest that the posterior distributions of the immigration process be interpreted as weakly identifiable. In particular, variation in immigration may potentially be driven by model assumption violations and unmodelled variation in other parameters given the sparse nature of the capture-recapture data used in this analysis, and the lack of data to directly inform estimates of immigration.

Tengmalm's owl metapopulation dynamics

While Tengmalm's owl populations are generally more stable in central Europe relative to northern Europe (Korpimäki 1986, Kouba *et al.* 2020a), we observed substantial fluctuation in the number of breeding females around a long-term declining trend (Figure 3). Strikingly, we observed a positive correlation ($r = 0.36$) between breeding indices of Tengmalm's owls in our study area and estimates from excellent long-term studies in Finland some 1500 km to the north (Supplementary Figure 1; Korpimäki & Hakkarainen 2012, Korpimäki 2020). Vole population synchrony occurs at large scales in central Europe (Lambin *et al.* 2006, Fay *et al.* 2020), and other studies (Korpimäki 1988a) have demonstrated strong linkages between breeding probability and rodent abundance. Variation in reproductive effort (i.e., breeding probability) and dispersal has the potential to affect estimates of population stochasticity (e.g., Korpimäki 1986) at broad scales. We strongly encourage continued research into the large-scale spatial drivers of variation in vital rates of Tengmalm's and other nomadic owl species to decompose the effects of life-history trade-offs, breeding probability and movement on estimates of population trends, where joint analysis of multiple demographic datasets across Europe may lead to further insight into

metapopulation dynamics.

On the joint use of structural equation and integrated population models

As the use and development of hierarchical models in ecology continues to progress, we see strong potential for the joint use of concepts central to integrated population models (Schaub & Kéry 2022) and structural equation models (Grace *et al.* 2010). Unlike excellent studies elsewhere (e.g., Korpimäki & Hakkarainen 2012, Korpimäki 2020), in this study we did not possess direct long-term data on prey availability. However, we were able to use our knowledge of the literature to reconstruct this parameter as a function of timing of breeding and prey captures and model demographic parameters as a function of this important ecological driver.

Predictive models will require estimating long-term changes in both demographic parameters and underlying changes in environmental conditions. The modeling approach described herein provides a framework to simultaneously model both processes. While not explored here, the ability to model causal relationships among covariates (e.g., Grace 2006, Gimenez *et al.* 2012, van de Pol & Brouwer 2021) has critically important implications for conservation decision making when using population models. For example, rapid increases in a North American blue-winged teal population led to both more relaxed hunting regulations, and density-dependent fecundity (Riecke *et al.* 2022), affecting population growth rate via multiple mechanisms.

Furthermore, in this paper we constrain relationships among variables to be linear, or linear given link functions. In other more complex systems researchers might employ quadratic relationships (e.g., Cubaynes *et al.* 2012) or generalized additive models to fit more complex functions to relationships between covariates and demographic parameters. We hope that this simple example serves as motivation for others facing challenges associated with

multicollinearity when modeling demographic parameters, where we feel that these exceptional tools (Grace *et al.* 2010) have great merit, but are substantially underused in demographic models.

Author Contributions

Pierre-Alain Ravussin led long term data collection efforts in Switzerland, with critical assistance from Ludovic Longchamp and Daniel Trolliet. Thomas V. Riecke led the writing of the manuscript and analysis, with important contributions from Daniel Gibson and Michael Schaub. All authors contributed to manuscript revisions, and approved the article for publication.

Conflict of Interest

The authors have no conflict of interest to declare.

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Data Availability Statement

Data and R script for the integrated population model as well as supporting simulations will be made available at Dryad.

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Tables

Table 1. Parameter notation and definitions for time-varying demographic parameters in an integrated population model for Tengmalm's owls (*Aegolius funereus*) breeding in the Jura Mountains of northwestern Switzerland and eastern France (1990-2020).

θ	Definition
ϕ_A	Probability that an adult female survives and does not emigrate
ϕ_F	Probability that a fledgling female survives and does not emigrate
ξ	Clutch size
ψ	Probability that an egg becomes a fledgling
p	Probability that a marked individual is detected in the study area
ω	Expected number of immigrants into the population during a year
ν	Expected number of rodent remains recovered from nesting cavities
δ	Expected nest initiation date
η	Latent prey abundance
A	Number of adult females
S	Number of 'second-year' or one-year-old females
F	Number of fledged juvenile females
I	Number of immigrant females

Table 2. Medians, lower and upper 95% Bayesian credible intervals (CrI), and v , (the proportion of the posterior distribution on the same side of zero as the median), for the effects of regression parameters (β , κ) on clutch size (ξ), fledging probability for each egg laid (ψ), fledgling survival to adulthood (ϕ_F), adult survival (ϕ_A), and immigration rate (ω), and relationships (ζ) between observed metrics of breeding conditions (brood initiation [δ] and number of prey remains [ν]) and latent rodent abundance of Tengmalm's owls breeding in the Jura Mountains of northwestern Switzerland and eastern France (1990-2020).

Parameter (θ)	Median	2.5% CrI	97.5% CrI	v	Prior
β_ξ	0.320	0.246	0.395	1	$\mathcal{N}(0, \sigma^2 = 10)$
β_ψ	1.369	1.016	1.799	1	$\mathcal{N}(0, \sigma^2 = 10)$
β_{ϕ_F}	1.032	0.424	1.777	1	$\mathcal{N}(0, \sigma^2 = 10)$
β_{ϕ_A}	1.356	0.770	2.122	1	$\mathcal{N}(0, \sigma^2 = 10)$
β_ω	1.276	0.493	2.777	0.999	$\mathcal{N}(0, \sigma^2 = 10)$
κ_ω	-0.207	-0.554	0.219	0.867	$\mathcal{N}(0, \sigma^2 = 10)$
ζ_ν	1	-	-	-	1
ζ_δ	-16.129	-19.708	-12.667	1	$\mathcal{N}(0, \sigma^2 = 100)$

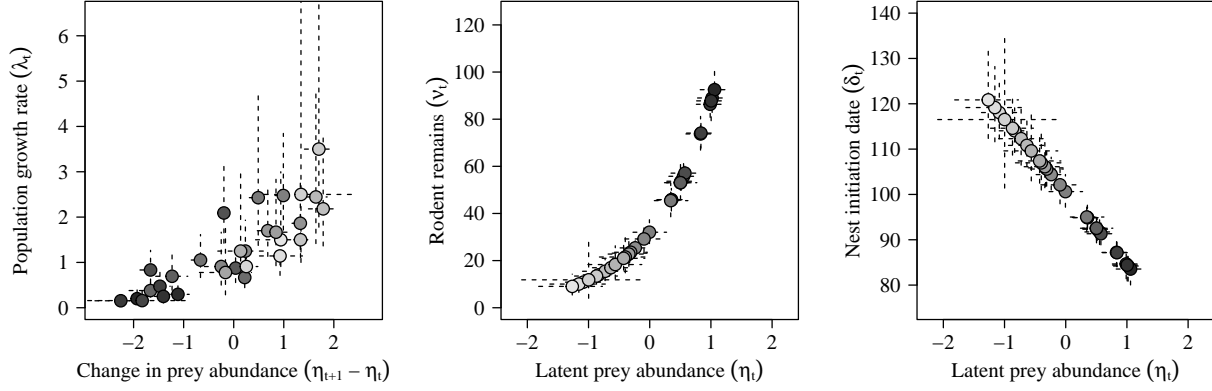
456 **Figures**

Figure 3. Scatterplots of population growth rate (λ), the mean number of rodents remains recovered from nesting cavities (ν), and mean nest initiation date (δ) regressed against the change in latent prey abundance from one breeding season to the next ($\eta_{t+1} - \eta_t$) or latent prey abundance during the breeding season (η_t) for Tengmalm's owls breeding in the Jura Mountains in northwestern Switzerland and eastern France (1990-2020). Note that darker points are representative of years with increased latent prey abundance.

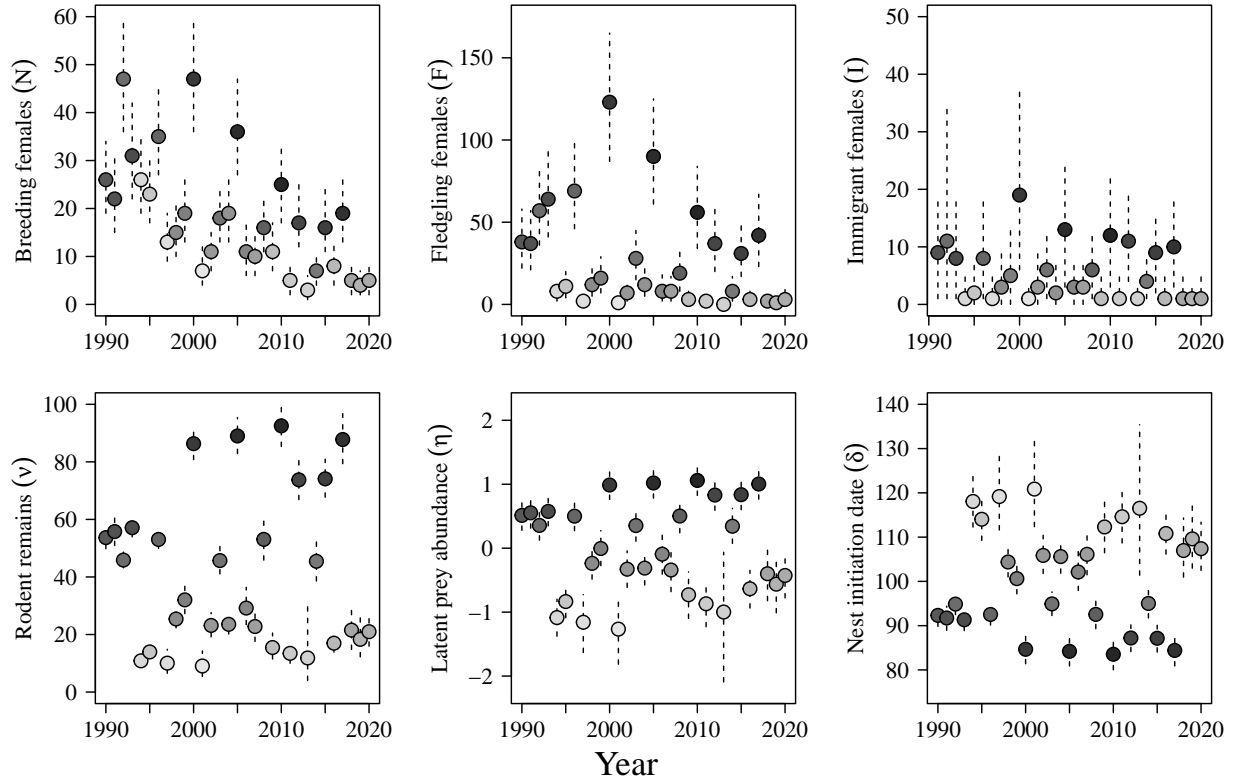


Figure 4. Medians (points) and 95% Bayesian credible intervals (dashed lines) for estimates of the number of breeding females (N; upper left), fledgling females (F; upper center), immigrant females (I; upper right), rodent remains recovered at nests following breeding (ν), latent prey abundance (η), and nest initiation date (δ) for Tengmalm's owls breeding in the Jura Mountains in north-western Switzerland and eastern France (1990-2020). Note that darker points are representative of years with increased latent prey abundance.

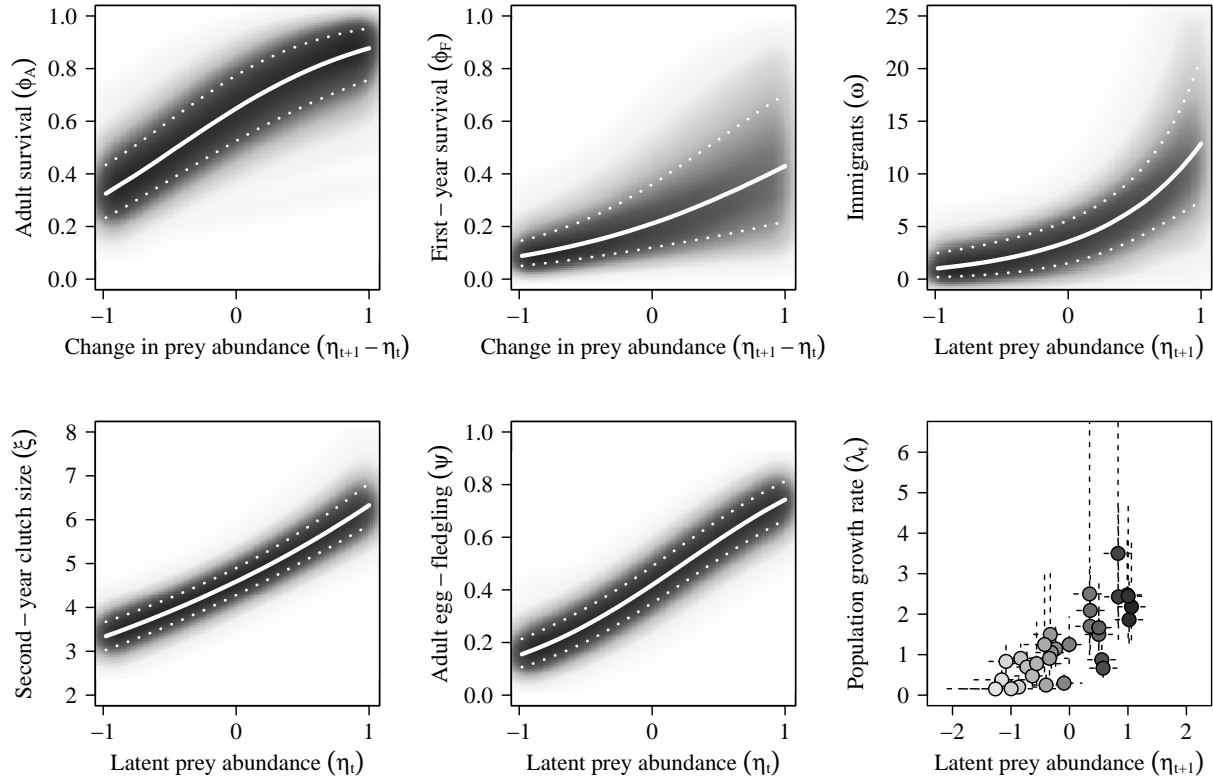


Figure 5. Medians (solid white lines), 85% Bayesian credible intervals (dashed white lines), and posterior densities (grey shading) of the relationships between adult survival (ϕ_A ; upper left), fledgling survival to adulthood (ϕ_F ; upper center), the expected number of immigrants into the adult cohort (ω ; upper right), clutch size (ξ ; lower left), the probability of each egg becoming a fledged juvenile (ψ ; lower center), and population growth rate (lower right) regressed against latent prey abundance in year t or $t + 1$ for Tengmalm's owls breeding in the Jura Mountains in north-western Switzerland and eastern France (1990-2020).

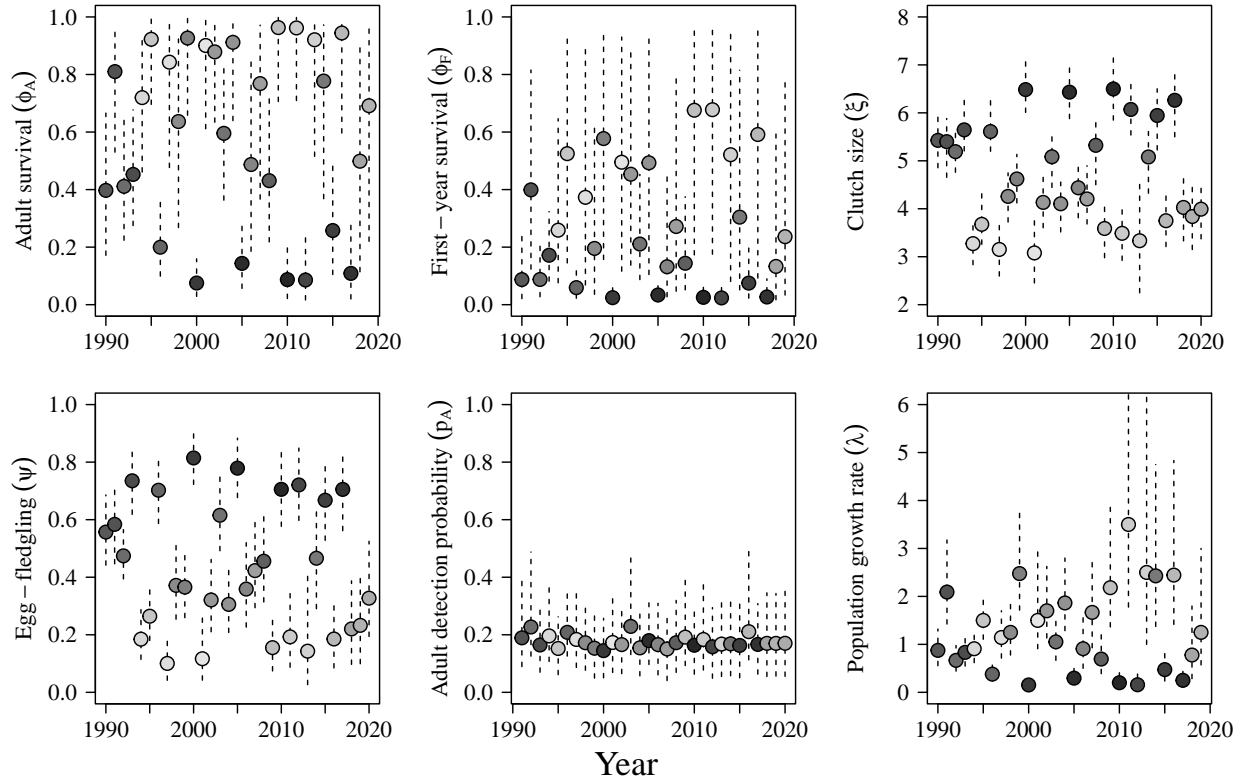


Figure 6. Medians (points) and 95% Bayesian credible intervals (dashed lines) for estimates of adult survival (ϕ_A ; upper left), first-year survival (ϕ_F ; upper center), clutch size (ξ ; upper right), the probability of each egg becoming a fledged juvenile (ψ ; lower left), adult detection probability (p_A ; lower center), and population growth rate (λ ; lower right) for Tengmalm's owls breeding in the Jura Mountains of northwestern Switzerland and eastern France (1990-2020). Note that darker points are representative of years with increased latent prey abundance.

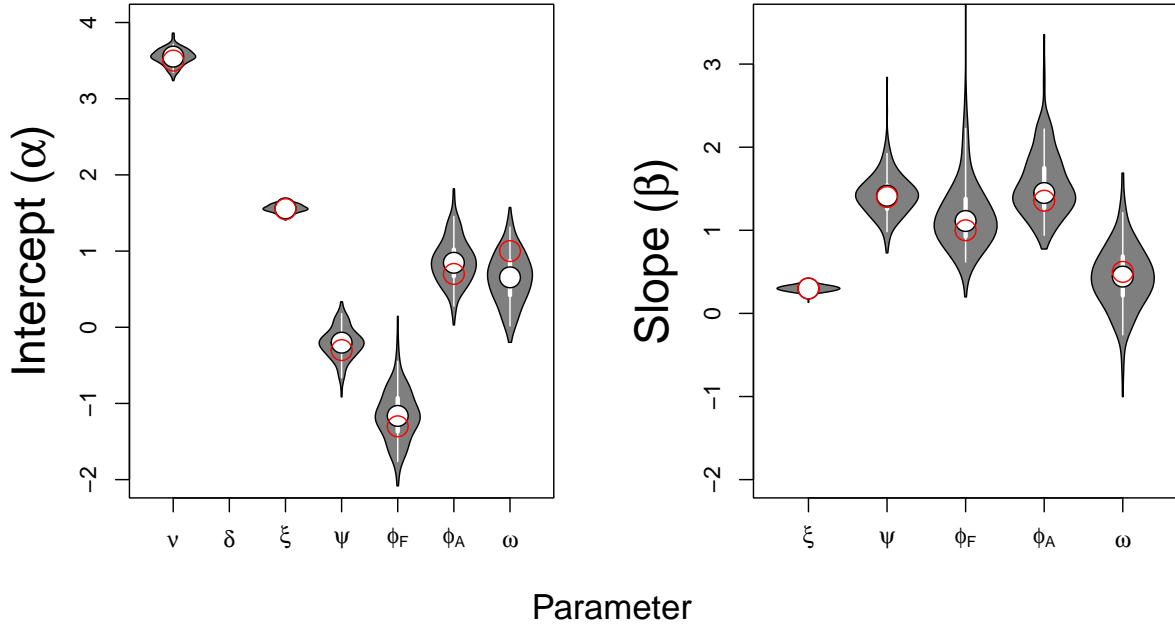


Figure 7. Violin plots of median estimates from integrated population models of intercepts (α) and effect (β) of latent prey abundance for rodent remains (ν), nest initiation date (δ), clutch size (ξ), egg-to-fledging probability (ψ), fledgling survival to adulthood (ϕ_F), adult survival (ϕ_A), and immigration (ω) from 250 simulations of Tengmalm owl populations across 25 years.