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1 **Estimating the strength of density dependence** 2 **in the presence of observation errors using** 3 **integrated population models**

4

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Running head: Assessing density-dependence

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Summary

1. Assessing the strength of density-dependence is crucial to understand population dynamics, but its estimation is difficult. Because estimates of population size and demographic parameters usually include errors due to imperfect detection, estimations of the strength of density-dependence will be biased if obtained with conventional methods which in addition lack statistical power to detect density-dependence.
2. We propose a Bayesian integrated population model that combines different sources of demographic information (capture-recapture, population counts, and data on reproductive success) into a single model to study density-dependence. The model allows assessing the effect of density both on the population growth rate and on the demographic parameters while accounting for imperfect detection. We studied the performance of this model by simulation and illustrate its use with a case study on red-backed shrikes *Lanius collurio*.
3. Our simulation results showed that the strength of density-dependence is identifiable and estimated with good precision. The strength of density-dependence was estimated with higher precision when the integrated population model was used than when a conventional regression model, which ignores the observation error, was applied. As expected, the conventional regression model tended to overestimate density-dependence at the population and to underestimate density-dependence at the demographic level. The analysis of the red-backed shrike data revealed negative density-dependence at the population level most likely mediated by a density-dependent decline in adult survival.

1 4. This work highlights the potential of integrated population models in assessing density-
2 dependence and its practical application in population studies.

3 **Key-words:** Bayesian; demographic parameters; density-dependence; integrated population
4 model; *Lanius collurio*; observation error; population growth rate; population size; simulation
5

1 **Introduction**

2 Factors that regulate population size are broadly classified into density-independent (stochastic)
3 and density-dependent (deterministic) factors (Williams, Nichols & Conroy 2002, page 136).
4 Density-independent factors (e.g. weather) affect all individuals in a population in the same way
5 regardless of population density. In contrast, the effects of density-dependent factors intensify as
6 the population density increases. Depending on their effect, they can be differentiated as negative
7 and positive density-dependent processes. Negative effects of density-dependence occur if a
8 demographic rate decreases as density increases, whereas positive effects occur when both
9 increase (Sinclair & Pech 1996). Intraspecific competition for resources (e.g. food, nest site) and
10 predation are the main drivers of negative density-dependence (Newton 1998; Gunnarsson *et al.*
11 2006), whereas a low chance to find mates at low population density is a typical mechanism
12 resulting in positive, or inverse, density-dependence (Allee effect) (Sæther, Ringsby & Røskaft
13 1996; Courchamp, Clutton-Brock & Grenfell 1999; Morris 2002). The two mechanisms can
14 operate within the same population at different periods of time, depending on current density
15 (Courchamp *et al.* 1999).

16 In order to understand better how populations are regulated, the effect of density on
17 different age or stage classes should be quantified. Knowledge of density-dependence is also
18 crucial in practical applications such as conservation or harvest regulations (Hanski, Foley &
19 Hassell 1996; Sinclair & Pech 1996; Drake 2005). Many studies have used long-term time series
20 data to estimate the strength of density-dependence (Dennis & Taper 1994; Lande, Engen &
21 Sæther 2003). The main principle is to study whether there is a negative relationship between
22 population growth rate and population size. An important limitation of this approach is that it
23 needs the assumption of a population census, i.e., a complete enumeration without errors in the
24 counts. If an observation error is present and not accounted for, it inflates the type I error and

1 misleadingly indicates the presence of density-dependence (Shenk, White & Burnham 1998;
2 Freckleton *et al.* 2006; Knappe 2008; Lebreton 2009). More recently, state-space models have been
3 used to reduce or remove bias in parameters or functional forms of density relationships resulting
4 from observation error (de Valpine & Hastings 2002; Jamieson & Brooks 2004; Dennis *et al.*
5 2006). However, estimates are unbiased only if the observation error is relatively small (Knappe
6 2008). A further limitation is that the analysis of population counts only reveals the effect of
7 density at the population level and, consequently, the demographic mechanisms causing density-
8 dependence remain unknown.

9 Some studies have used long-term data to assess the impact of density on demographic
10 parameters by regressing estimates of demographic parameters on population counts (Coulson,
11 Milner-Gulland & Clutton-Brock 2000; Sæther *et al.* 2000; Barker, Fletcher & Scofield 2002;
12 Paradis *et al.* 2002; Barbraud & Weimerskirch 2003; Tavecchia *et al.* 2007). To get unbiased
13 estimates of the strength of density-dependence this approach requires estimates of demographic
14 rates and population counts that are not subject to observation errors. If there are observation
15 errors (either on the demographic rates and/or on the population counts), the test for density-
16 dependence will suffer from a lack of statistical power (Lebreton 2009). Recently, Schofield,
17 Barker & MacKenzie (2009) applied the Jolly-Seber model to mark-recapture data to estimate the
18 strength of density-dependence on survival. Using this model, estimates of survival and of
19 population sizes are obtained while accounting for imperfect detection, and thus the power to
20 detect density-dependence is maximized.

21 Despite the development of different methods for studying density-dependence, there are
22 currently no approaches to assess the effect of density on all demographic parameters
23 simultaneously while accounting for observation error. This is a drawback because the full

1 demographic mechanisms of density-dependent population regulation cannot rigorously be
2 studied.

3 Here we propose the use of a Bayesian integrated population model to study density-
4 dependence in a coherent fashion. Integrated population models combine different sources of
5 demographic data into a single model and provide estimates of all demographic parameters and
6 population size with improved precision and that are free of observation error (Besbeas *et al.* 2002;
7 Brooks, King & Morgan 2004; Schaub *et al.* 2007; Abadi *et al.* 2010a). Parameters that are
8 unidentifiable from a single source can be estimated with these models [e.g. fecundity (Besbeas *et*
9 *al.* 2002); immigration rate (Abadi *et al.* 2010b)]. These models also are very appealing and
10 powerful when the sample size is small (Abadi *et al.* 2010a). So far, integrated population models
11 have been successfully used to estimate key demographic parameters from single-site
12 demographic data (Brooks *et al.* 2004; Schaub *et al.* 2007; King *et al.* 2008; Véran & Lebreton
13 2008; Reynolds *et al.* 2009; Abadi *et al.* 2010b) as well as from multi-site data (Borysiewicz *et al.*
14 2009; Péron *et al.* 2010; McCrea *et al.* 2010) and their performance has been investigated using
15 simulations (Besbeas, Borysiewicz & Morgan 2009; Abadi *et al.* 2010a).

16 The model we propose for studying density-dependence potentially has several advantages.
17 Firstly, because integrated population models involve the use of state-space models for the
18 population counts, it is possible to assess density-dependence based on estimates of population
19 indices corrected for random observation errors rather than on the population counts including
20 errors, which avoids the confounding effect of observation errors. Secondly, because demographic
21 parameters (e.g. age-specific survival, fecundity) are estimated, it allows a test of density-
22 dependence for them, and thus the demographic mechanisms of density-dependent population
23 regulation can be identified. It also allows assessing density-dependence at the population level
24 using the derived population growth rate. Thirdly, combined analysis of demographic data results

1 in improved precision of estimates, which is expected to increase the statistical power to detect
2 density-dependence.

3 We conducted simulations to examine the performance of integrated population model in
4 estimating the strength of density-dependence under different magnitudes of observation error. We
5 illustrate the method using a data set on a population of red-backed shrikes *Lanius collurio*.
6 Previous studies have shown that the studied shrike population is regulated by density at the level
7 of the population (Pasinelli *et al.* 2011), but that neither survival nor fecundity were a function of
8 local density (Schaub, Jakober & Stauber in press). The latter study was performed with
9 conventional methods which are expected to have lower power than the integrated analysis. Our
10 objective here was to evaluate whether density-dependence at the level of the demographic rates
11 could be identified using the new proposed model.

12

13 **Methods**

14 We present first the integrated population model to estimate the strength of density-dependence,
15 and then describe the simulation set up and the procedure to generate the data sets. Finally, we
16 describe the case study and how the model is implemented in the Bayesian framework. We were
17 motivated by a short-lived bird species from which we sampled capture-recapture and reproductive
18 success data, as well as annual population counts. However, the estimation of density-dependence
19 using the integrated population model is not restricted to this life history type and these data sets,
20 other life histories and data sets could also be modelled by adaptations of the underlying
21 population and observation models.

22 *Modelling density-dependence in the integrated population model*

23 Integrated population models first require the formulation of the likelihood for the available
24 demographic data sets. Detailed discussion of this likelihood formulation is provided in Abadi *et*

1 *al.* (2010a). In summary, we used the standard Cormack-Jolly-Seber model (CJS; Lebreton *et al.*
2 1992) for the capture-recapture data. We assumed the number of individual encounter histories
3 summarized in the \mathbf{m} -array (\mathbf{m}) follows a multinomial distribution with parameters that are
4 functions of age-specific apparent survival (ϕ_{jv}, ϕ_{ad}) and recapture probabilities (\mathbf{p}). ϕ_{jv} denotes
5 the probability that a newborn individual survives and becomes a yearling (1 year old) and ϕ_{ad}
6 denotes the survival probability of yearlings and adults (older than 1 year). We denoted the
7 likelihood for this model by $L_{cr}(\mathbf{m} | \phi_{jv}, \phi_{ad}, \mathbf{p})$. For the data on reproductive output, we assumed
8 that the number of offspring produced per female (\mathbf{J}) is Poisson distributed whose parameter is the
9 product of fecundity (f) and the number of females recorded to produce young (\mathbf{R}). Fecundity (i.e.
10 the number of newborns per adult females) of both yearlings and adults is assumed to be the same.
11 The likelihood for this model is denoted by $L_{rp}(\mathbf{J}, \mathbf{R} | f)$.

12 To describe the population counts we use a state-space model, which consists of a process
13 and an observation model (Besbeas *et al.* 2002). The process model describes the evolution of the
14 underlying population sizes over time, thus it determines the link between the demographic rates
15 and population size. Let $N_{1,t}$ denote the number of 1 year old individuals in year t , $N_{2+,t}$ denote the
16 number of individuals older than 1 year in year t , and $N_t = N_{1,t} + N_{2+,t}$, denote the total population
17 size in year t . We assume that $N_{1,t+1}$ is generated by a Poisson process, as $N_{1,t+1}$ only takes a value
18 between 0 (if no recruitment occurs) and ∞ (if recruitment is massive). The parameter of the
19 Poisson process is the product of fecundity, juvenile survival and population size in year t . The sex
20 ratio of newborn is assumed to be even and therefore we divide f by 2, and thus,

$$21 \quad N_{1,t+1} \sim \text{Po}\left(N_t \left(\frac{f_t}{2}\right) \phi_{jv,t}\right) \quad \text{eqn 1.}$$

1 We further assume that $N_{2+,t+1}$ is generated by a Binomial process, as $N_{2+,t+1}$ only takes a value
 2 between 0 (if no individual survives) and the total population size a year before (if all survive).

3 Thus,

$$4 \quad N_{2+,t+1} \sim \text{Bin}(N_t, \phi_{ad,t}) \quad \text{eqn 2.}$$

5 The observation model links the population counts (i.e. the number of detected and counted
 6 female breeders, denoted by y_t) to the latent population sizes (N_t). We then assume

$$7 \quad y_t \sim N(N_t, \sigma_y^2) \quad \text{eqn 3}$$

8 where the variance σ_y^2 quantifies the observation error. The likelihood for the state-space model is

9 given by the product of the likelihood of the process and observation models, $L_{\text{sy}}(N | \phi_{jv}, \phi_{ad}, f)$

10 $\times L_{\text{ob}}(y | N, \sigma_y^2)$. The likelihood of the complete integrated population model is obtained as the

11 product of the likelihoods of all three data sources under the assumption of independence, as

$$12 \quad L_{\text{joint}}(\mathbf{m}, \mathbf{J}, \mathbf{R}, \mathbf{y} | \phi_{jv}, \phi_{ad}, f, \mathbf{p}, N, \sigma_y^2) = L_{\text{cr}}(\mathbf{m} | \phi_{jv}, \phi_{ad}, \mathbf{p}) \times L_{\text{rp}}(\mathbf{J}, \mathbf{R} | f) \\ 13 \quad \times L_{\text{ob}}(y | N, \sigma_y^2) \times L_{\text{sy}}(N | \phi_{jv}, \phi_{ad}, f) \quad \text{eqn 4.}$$

14 A simulation study by Abadi *et al.* (2010a) that combined and analyzed completely dependent data
 15 of capture-recapture, population counts, and reproductive success showed that the violation of the
 16 independence assumption only had a negligible effect on the precision of parameter estimates. We
 17 assume that this is true also in the present study.

18 All demographic parameters and population sizes appear in the likelihood of the integrated
 19 models as shown in eqn 4. This offers the possibility to model density-dependence of the
 20 demographic rates within a single model. We modelled the recapture probability with a random
 21 year parameter and assessed the effect of density on both survival probabilities and fecundity,

$$22 \quad \text{logit}(\phi_{jv,t}) = \beta_0 + \beta_1 N_t^* + \varepsilon_{\phi_{jv,t}} \quad \varepsilon_{\phi_{jv,t}} \sim N(0, \sigma_{\phi_{jv}}^2) \quad \text{eqn 5}$$

1 $\text{logit}(\phi_{ad,t}) = \beta_2 + \beta_3 N_t^* + \varepsilon_{\phi_{ad,t}} \quad \varepsilon_{\phi_{ad,t}} \sim N(0, \sigma_{\phi_{ad}}^2)$ eqn 6

2 $\log(f_t) = \beta_4 + \beta_5 N_t^* + \varepsilon_{f_t} \quad \varepsilon_{f_t} \sim N(0, \sigma_{f_t}^2)$ eqn 7

3 where N_t^* is the standardized population size (i.e., $N_t^* = \frac{N_t - \text{mean}(N_t)}{\text{sd}(N_t)}$), $N_t = N_{1,t} + N_{2+,t}$ is the

4 population size in year t , and the σ^2 are the temporal variances of the demographic parameters as

5 well as of recapture probability. The goal is to estimate the regression coefficients (α , β) and the

6 magnitude of temporal variability (σ^2). The slope coefficients (β_1 , β_3 , β_5) estimate the strength of

7 density-dependence on juvenile survival, adult survival and fecundity, respectively. For the

8 recapture probability, which is a nuisance parameter, we assumed a random year effect, thus

9 $\text{logit}(p_t) = \alpha + \varepsilon_{p_t}$ with $\varepsilon_{p_t} \sim N(0, \sigma_p^2)$.

10 We also estimated the strength of density-dependence on the population growth rate (i.e. at

11 the level of the population). This was done by first calculating the population growth rate ($\lambda_t =$

12 N_{t+1}/N_t), and then regressing the growth rate on population size as

13 $\log(\lambda_t) = \beta_6 + \beta_7 N_t^* + \varepsilon_{\lambda_t} \quad \varepsilon_{\lambda_t} \sim N(0, \sigma_{\lambda_t}^2)$ eqn 8.

14 We calculated this regression outside the integrated population model, because we did not want to

15 induce any constraints on the density-dependence at the population level, since density-

16 dependence at the population level is always the result of density-dependent variation of

17 demographic rates.

18 We also estimated the strength of density-dependence, ignoring the observation error, by

19 regressing demographic rates estimated with single data analysis (i.e. survival probabilities from

20 capture-recapture data estimated with the CJS model, and fecundity estimated from data on

21 reproductive success with a Poisson regression model) on standardised population counts. The

22 relationships between demographic parameters and population counts were similar with eqns 5-8,

1 but here we used the population counts y_t^* rather than N_t^* and the population growth rate was
 2 calculated as $\lambda_{\text{obs},t} = y_{t+1}/y_t$ and modelled as a function of y_t^* .

3 *Simulation study*

4 Using simulations we evaluated the identifiability of the estimates of the strength of density-
 5 dependence (β) and assessed their precision at varying levels of observation error under the
 6 integrated population model developed above. We also evaluated the effect of ignoring the
 7 observation error on the estimates of density-dependence obtained by regressing demographic
 8 rates on population counts.

9

10 *A. Individual-based simulation of the data*

11 The way we conducted simulations is analogous to that described in Abadi *et al.* (2010a). It
 12 consists of creating a population by simulating fates of individuals, sampling demographic data
 13 from this population, and analyzing these data with the developed integrated population model.
 14 These steps are repeated several times and point estimates stored, serving the base to evaluate the
 15 performance of the model.

16 To create the population, we mimic a short-lived bird species and the development of the
 17 population sizes from one year to another is described by eqns 1 and 2. We specified the
 18 relationship between demographic parameters and the actual population size in year t as

$$19 \quad \text{logit}(\phi_{jv,t}) = 0 - 0.05N_t + \varepsilon_{\phi_{jv,t}} \quad \varepsilon_{\phi_{jv,t}} \sim N(0, (0.15)^2) \quad \text{eqn 9}$$

$$20 \quad \text{logit}(\phi_{ad,t}) = 1.735 - 0.02N_t + \varepsilon_{\phi_{ad,t}} \quad \varepsilon_{\phi_{ad,t}} \sim N(0, (0.20)^2) \quad \text{eqn 10}$$

$$21 \quad \log(f_t) = 1.386 - 0.01N_t + \varepsilon_{f_t} \quad \varepsilon_{f_t} \sim N(0, (0.10)^2) \quad \text{eqn 11}$$

22 If the population size (N) increases by 10 individuals, the slope coefficients can be interpreted as
 23 the expected change in juvenile survival odds ratio to be $\exp(-0.5)$; in adult survival odds ratio to

1 be $\exp(-0.2)$; and in fecundity to be $\exp(-0.1)$, indicating a negative effect of density on
2 demographic parameters. The simulation parameters in eqns 9-11 were chosen in such a way that
3 they result in reasonable demographic rates for a short lived bird species at the population size of
4 about 50.

5 Next, we created the life history of individuals in the population for 20 years. To start the
6 creation of the population, we set the initial population size at 40 individuals. We then specified
7 the actual probabilities of survival and fecundity applying eqns 9-11 under consideration of the
8 actual population size. For each individual alive in the population it was then simulated whether it
9 survived for another year, how many juveniles it produced, and how many of the juveniles
10 survived. The sum of the number of yearlings and surviving adults gives then the population size
11 in the following year, and we specified the demographic rates for this following year. This was
12 repeated for 20 years. Information about the state of an individual (dead, alive, in which age group
13 it is given alive) and the number of offspring it has produced were stored. To avoid transition
14 effects of the initial conditions we only used the last 10 years of the simulated data sets.

15 Once we created the population, the next step was to sample individuals for the different
16 studies. We independently selected 1000 individuals at random from the population to be available
17 for capture-recapture and reproductive success data sampling. To create the capture-recapture
18 histories and reproductive success data based on individuals subject to each study, we set the
19 initial capture probability at 0.90 and 0.50 for juveniles and adults (1 year and older), respectively,
20 and the recapture probability at 0.50. The probability to detect and record reproductive success
21 was set at 0.90. All these capture/recapture and detection probabilities were assumed to be
22 constant across time. To create the population counts in each year, we used a binomial distribution
23 with parameters actual population size in the given year (N_t) and detection probability (P_s). The
24 detection probability was assumed to be constant over time. We considered two scenarios, one

1 with detection probabilities of female breeders of 0.50, and one with 0.90. The lower detection
2 probability corresponds to a large observation error in the population counts. This is because the
3 variance of binomial sampling (i.e. $NP_s(1-P_s)$) is largest with $P_s=0.50$. Our sampling procedures
4 did not result in completely independent data sets as some individuals that were involved in either
5 capture-recapture or reproductive success data sampling also had a chance to be included in the
6 population counts. We simulated 500 data sets and analyzed them using the proposed integrated
7 population models.

8

9 *B. Case study*

10 We used 26 years of demographic data of red-backed shrikes collected from 1981-2006 in south-
11 western Germany near Göppingen (48°39'N, 9°47'E) to illustrate the method. The red-backed
12 shrike is a medium-sized (~30g) migratory passerine living in agricultural landscapes during the
13 breeding season (Glutz von Blotzheim & Bauer 1993). The study area has a size of about 18 km²
14 and mostly consists of meadows and pastures with interspersed orchards and hedgerows (for a
15 more detailed description see Jakober & Stauber 1987). During numerous visits we localised each
16 year the nests of nearly all breeding pairs, recorded the number of fledglings of each nest (n =
17 3580 fledglings from 1242 nests) and ringed the nestlings at an age of about 8 days (n = 3598).
18 Territorial adults were caught with clap or mist nets and ringed with individual colour rings (n =
19 513 females). Each spring we visited the study area almost daily to resight colour-marked
20 individuals. The population size varied between 35 and 71 observed breeding pairs, the mean size
21 was about 50 pairs. For the analysis we assumed an even sex ratio and only considered capture-
22 recapture data of females. The goal was to estimate the strength of density-dependence at the
23 population level and of the demographic rates to assess 1) whether the population is regulated by
24 density, and 2) if so, through which demographic mechanisms.

1 Because the studied red-backed shrike population is geographically open, we had to extend
 2 the integrated population model to include immigration (Abadi et al. 2010b). Therefore, we
 3 modified the state-space model (eqns 1-3) as follows: the number of 1 year old individuals $N_{1,t+1}$
 4 followed a Poisson process with

$$5 \quad N_{1,t+1} \sim \text{Po}\left(N_t \left(\frac{f_t}{2}\right) \phi_{jv,t}\right) \quad \text{eqn 12}$$

6 The number of immigrants $N_{im,t+1}$ was modelled with a Poisson distribution as

$$7 \quad N_{im,t+1} : \text{Po}(N_t \omega_t) \quad \text{eqn 13}$$

8 where the immigration rate ω_t is defined as the number of female immigrants of age 1 year or
 9 older in year $t+1$ per breeding females in the previous year N_t .

10 The number of at least 2 years old surviving individuals followed a binomial process with

$$11 \quad N_{ad,t+1} \sim \text{Bin}(N_t, \phi_{ad,t}) \quad \text{eqn 14}$$

12 The total number of individuals in year t is given by $N_t = N_{1,t} + N_{ad,t} + N_{im,t}$.

13 For the observation equation, we assumed a normal distribution, hence y_t the annual number of
 14 counted breeding females in year t distributed as a $N(N_t, \sigma_y^2)$.

15 To estimate the strength of density-dependence on the demographic parameters as well as
 16 the population growth rate, we fitted the models specified in eqns 5-8. We also modelled
 17 immigration rate with a random year parameter, but did not impose density-dependence on it.
 18 Further, the recapture probability (p) was modelled time-dependent where time was treated as
 19 random. Beside the model that includes density dependence for the demographic parameters, we
 20 also fitted a model without density-dependence (i.e. $\beta_1 = \beta_3 = \beta_5 = 0$ in eqns 5-7), in order to get
 21 unconstrained annual estimates of the demographic parameters.

22 *C. Bayesian analysis of the model*

1 All the models were fitted within the Bayesian framework, specifying non-informative priors in
2 order to reflect limited knowledge about the parameters. Specifically, we assigned a $N(0, 100)$
3 distribution on the regression coefficients (α and β). A $N(100, 100)$ distribution truncated to
4 positive values was assigned for age specific initial population sizes, and a $U(0, 10)$ distribution
5 for the temporal standard deviations of demographic parameters. To assess convergence of the
6 Markov chain Monte Carlo (MCMC) algorithm to the stationary distribution, we randomly chose a
7 single simulated data set and run three chains, each with different initial values, of 20000 iterations
8 with a burn-in of 15000 iterations. The \hat{R} (Brooks & Gelman 1998) values were less than 1.1 for
9 all parameters, suggesting convergence. We therefore run a single chain of 30000 MCMC
10 iterations with a burn-in of 20000 thinning every 10th observation in order to compute the posterior
11 summary statistics. Using this setting, the analysis of one data set took approximately 50 minutes
12 (on a 3.3 GHz processor, 2 GB RAM PC). For the case study, we first run three chains of 20000
13 iterations with a burn-in of 10000 to check whether convergence was reached. Since convergence
14 was obtained (all the \hat{R} values < 1.02), we run a single chain of length 100000, discarded the first
15 50000 as burn-in and thinned every 10th observation. The run time to analyse the red-backed shrike
16 data set was approximately 5 days (on a 3.3 GHz processor, 2 GB RAM PC). The posterior
17 summary statistics were then computed based on 5000 samples. We used the R software version
18 2.9.1 (R Development Core Team 2008) to simulate the data and the analyses were done using the
19 WinBUGS software calling it from R through the package R2WinBUGS (Sturtz, Ligges &
20 Gelman 2005). The R and WinBUGS codes for the density-dependence model of the red-backed
21 shrike data are provided in Appendix S1 in Supporting Information.

22

23 **Results**

1 *Simulation study*

2 Our simulation study clearly showed that the strength of density-dependence in the demographic
3 rates as well as in the population growth rate was identifiable with the integrated population model
4 regardless of the magnitudes of observation error we considered, indicated by smooth posterior
5 densities with a clear peak (Figs 1 & 2). If the parameters were not identifiable, we would have
6 expected a posterior density that is similar to the specified prior distribution (Gimenez, Morgan &
7 Brooks 2009). The widths of the posterior distributions resulting from the integrated population
8 model were narrower when the observation error was small compared to when it was large. This
9 indicates that the precision of the density-dependence estimator declines with increasing
10 observation error of the population counts. In general, the strength of density-dependence was
11 estimated with more precision at the population level than at the demographic level, indicated by a
12 narrow width of the posterior distributions (Figs 1 & 2).

13 Estimates of the strength of density-dependence obtained from the integrated population
14 model were generally more precise compared to that of the regression analysis. This was
15 particularly evident for adult survival (Figs 1 & 2). As expected, the estimates of strength of
16 density-dependence in the demographic parameters were slightly shifted towards zero when the
17 observation error was large and not accounted for. However, this effect was not very strong. The
18 model which ignores the observation error yielded stronger and slightly less precise estimates of
19 density-dependence at the population level in comparison to the integrated population model (Figs
20 1 & 2).

21 *Case study*

22 Since there is no established goodness-of-fit test of the complete integrated population model
23 available, we tested the goodness-of-fit just for the capture-recapture model using contingency
24 tables (Pradel et al. 2005) via program U-CARE (Choquet *et al.* 2009): there was no sign of lack

1 of fit ($\chi^2_{59} = 42.75, P = 0.94$). Based on the integrated population model without density-
2 dependence, the annual estimates of age-specific survival, fecundity and population growth rate
3 tended to decline with increasing population size in red-backed shrikes (Fig. 3), suggesting
4 density-dependence in these demographic parameters and at the population level. We then
5 explicitly estimated the strength of density-dependence in the demographic parameters and in the
6 population growth rate using the integrated population model with density-dependence. The
7 estimated linear relationships between demographic rates as well as population growth rate (on the
8 transformed scale) and population size are shown in Fig. 3. The posterior distributions of the
9 strength of density-dependence were wide for juvenile survival and fecundity, and more pointed
10 for adult survival and population growth. As expected, the posterior means of the strengths of
11 density-dependence were negative in all parameters (Fig. 4). The posterior probability that the
12 estimated effect of density were negative was high for population growth (0.960), followed by
13 adult survival (0.792), fecundity (0.598) and juvenile survival (0.559). Thus, there was clear
14 evidence of a density-dependent population regulation at the level of the population that was more
15 likely due to adult survival, than due to juvenile survival or fecundity.

16

17 **Discussion**

18 Density-dependence is an important ecological concept and understanding how it operates is
19 crucial in conservation, harvesting and for accurate demographic projections (Sinclair & Pech
20 1996, Lande et al. 2003). In this paper we provide a framework for studying density-dependence
21 using a Bayesian integrated population model. A key advantage of this unifying framework is that
22 it allows estimating strength of density-dependence both at the demographic and population level
23 while accounting for observation error and, consequently, the demographic mechanism causing
24 density-dependent population regulation can be identified. In contrast, most existing techniques for

1 testing density-dependence rely on time series data and do not account for observation error, or
2 focus either on the effect of density on population growth rate or on a single demographic
3 parameter only.

4 Using simulations, we showed that integrated population models provide estimates of the
5 effect of population size on demographic parameters as well as on population growth rate with
6 good precision. The parameters estimating the strength of density-dependence were identifiable
7 with our model regardless of the magnitudes of observation error we considered. As expected, the
8 estimates were slightly more precise when the observation error was small than large. Our
9 simulation study also highlight that ignoring observation error had differential impact on the
10 estimators of the strength of density-dependence at the population than at the demographic level.
11 The conventional regression model tended to estimate stronger density-dependence at the
12 population than at the demographic level. These results are in agreement with previous findings
13 (e.g. Shenk *et al.* 1998; Freckleton *et al.* 2006; Lebreton 2009).

14 We also illustrated the application of the method using demographic data from a
15 geographically open red-backed shrike population. We found strong support of density-
16 dependence for the population growth rate. Of the considered demographic parameters, only adult
17 survival was likely to be regulated by density-dependence, while juvenile survival and fecundity
18 were hardly impacted by breeding density. Using the same data analysed with regression analyses
19 with population counts uncorrected for observation error, Schaub *et al.* (in press) did not find
20 support of density-dependence for survival and fecundity. With the application of the integrated
21 population model the power to detect density-dependence increases (see simulations), which is the
22 reason why we now found support of density-dependence operating on adult survival. One may
23 wonder how there can be strong density-dependence for population growth and only relatively
24 weak density-dependence for the demographic rates. First, even if density-dependence for the

1 demographic rates is weak, all demographic rates work jointly, and thus the effect at the
2 population level magnifies. Second, the red-backed shrike population is geographically open, and
3 immigration is substantial (mean (sd): 0.545 (0.036)). It is well possible that immigration is
4 regulated by density, i.e., few individuals immigrate in years where the number of survivors and
5 local recruits is high, and vice-versa. Yet, immigration is a parameter in our integrated population
6 model that is estimated without having explicit data (Abadi *et al.* 2010), and for such parameters it
7 appears that the strength of density-dependence cannot be estimated (i.e., it is not an identifiable
8 parameter of the model). To evaluate for which demographic parameter density-dependence is
9 important, we computed the probability that the strength of density-dependence is negative and use
10 this as a testing criterion. Alternatively, one could also apply model selection for the same
11 purpose. The set of models could then include models that impose density-dependence in some
12 demographic parameters only. Yet, model selection in Bayesian hierarchical models is not an easy
13 task (Link & Barker 2006; Millar 2009).

14 In our simulation as well as in the case study we expressed density in terms of population
15 size. Since the study area associated with the red-backed shrike population remained the same over
16 time, the use of population size as a measure of density was justified. However, it is important to
17 note that the influence of density on biological processes can be overlooked due to an
18 inappropriate measure of density (Williams *et al.* 2002; Barker *et al.* 2002). Moreover, the main
19 driving force for density-dependence is often competition for resources and not space. Ideally, one
20 would therefore model the strength of density-dependence not with population size, but with the
21 available resources per individual. Our model could be extended in this way if an estimate of
22 resource availability could be obtained.

23 The goals of our simulation were mainly on the assessment of the identifiability of the
24 estimates of strength of density-dependence and on the evaluation of the effect of observation

1 error. We specified a short study period (i.e., 10 years), thus conditions where the estimation of
2 density-dependence were difficult. Yet, the model was able to estimate density-dependence with
3 good precision in this set-up. We could further examine the performance of the model in different
4 directions. For instance, we could set up a simulation varying the strength of density-dependence
5 and also the length of the study period. The ability to detect density-dependence often increases
6 with long time series data (Brook and Bradshaw 2006). In our simulation study, we focused on the
7 common kind of observation error (i.e. non-detection or false-negative error). One might further
8 evaluate the performance of the model considering other kinds of observation error such as false-
9 positive errors occur.

10 The integrated population model is very flexible to include different shapes of density-
11 dependence. Here we used the density-dependence model of the Ricker type for population growth
12 rate (Dennis & Taper 1994), but specifying other density-dependence models which are discussed
13 in the literature (e.g. Dennis & Taper 1994; Jamieson & Brooks 2004) is straightforward.
14 Moreover, some studies have shown that the effect can be non-linear in the parameters (Paradis *et al.*
15 *2002*; Saether & Engen 2002; Tavecchia *et al.* 2007). The integrated population model could
16 also be extended to assess non-linear density-dependence, for instance by using penalized splines
17 (Gimenez *et al.* 2006). In the present study, we looked at the direct effect of density but it is
18 possible that density-dependence can affect demographic parameters and population growth rate
19 with time lag (Paradis *et al.* 2002). Our model can easily be extended to study delayed density-
20 dependence.

21 Overall, our model provides an improved statistical tool over current methods for
22 estimating density-dependence. We believe it has great potential in conservation, management and
23 ecology.

24

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5

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3

1 **Supporting Information**

2 The following supporting information is available for this article online.

3 **Appendix S1.** R and WinBUGS codes including red-backed shrike data to fit the density-
4 dependence models.

5

1 **Figure Captions**

2
3 Fig. 1. Density plots of 500 estimated posterior means of strength of density-dependence on

4 juvenile survival (ϕ_{jv}), adult survival (ϕ_{ad}), fecundity (f) and population growth rate (λ)

5 obtained from integrated population model (blue), and from single data analysis ignoring

6 observation error (red) when the observation error for population count data was large (probability

7 to detect female breeders = 0.50). Dotted, vertical lines are the means of the estimated posterior

8 means of the strength of density-dependence over 500 simulations.

9
10 Fig. 2. Density plots of 500 estimated posterior means of strength of density-dependence on

11 juvenile survival (ϕ_{jv}), adult survival (ϕ_{ad}), fecundity (f) and population growth rate (λ)

12 obtained from integrated population models (blue), and from single data analysis ignoring

13 observation error (red) when the observation error for population count data was small (probability

14 to detect female breeders = 0.90). Dotted, vertical lines are the means of the estimated posterior

15 means of the strength of density-dependence over 500 simulations.

16
17 Fig. 3. Annual variation in demographic rates and population growth rate against standardized

18 population size in the studied red-backed shrike population. Posterior means (open circles) with

19 95% credible intervals (vertical line) obtained from an integrated population model without

20 density-dependence, along with the estimated linear relationship between demographic parameters

21 as well as population growth rate and standardized population size obtained from an integrated

22 population model with density-dependence.

23

1 Fig. 4. Posterior distributions of the estimated strength of density-dependence on juvenile survival
2 (blue), adult survival (brown), fecundity (black) and population growth rate (red) in studied red-
3 backed shrike population.
4