Ecological Monographs, 0(0), 2019, e01364
© 2019 by the Ecological Society of America

IPM^2: toward better understanding and forecasting of population dynamics

Floriane Plard[1,3] Daniel Turek,[2] Martin U. Grüebler,[1] and Michael Schaub[1]

[1]*Swiss Ornithological Institute, CH-6204 Sempach, Switzerland*
[2]*Department of Mathematics and Statistics, Williams College, 18 Hoxsey Street, Williamstown, Massachusetts 01267 USA*

Citation: Plard F., D. Turek, M. U. Grüebler, and M. Schaub. 2019. IPM^2: toward better understanding and forecasting of population dynamics. Ecological Monographs 00(00): e01364. 10.1002/ecm.1364

Abstract. Dynamic population models typically aim to predict demography and the resulting population dynamics in relation to environmental variation. However, they rarely include the diversity of individual responses to environmental changes, thus hampering our understanding of demographic mechanisms. We develop an integrated integral projection model (IPM^2) that is a combination of an integrated population model (IPM$_{pop}$) and an integral projection model (IPM$_{ind}$). IPM^2 includes interactions between environmental and individual effects on demographic rates and can forecast both population size and individual trait distributions. First, we study the performance of this model using eight simulated scenarios with variable reproductive selective pressures on an individual trait. When the individual trait interacts with the environmental variable and the selective pressure on the individual trait is nonlinear, only IPM^2 produces adequate predictions, because IPM$_{ind}$ does not link predictions between the population level and observed data and because IPM$_{pop}$ does not include the individual trait. Second, we apply IPM^2 to a population of barn swallows. The model accurately predicts trends of the barn swallow population while also providing mechanistic insights. High precipitation negatively influenced population dynamics through delaying laying dates, which lowered reproductive and survival rates. To predict the future of populations, we need to understand their individual drivers and thus include individual responses to their environment while following the entire population. As a consequence, IPM^2 will improve our ability to test ecological and evolutionary hypotheses and improve the accuracy of population forecasting to aid management programs.

Key words: barn swallow; environmental variation; individual plasticity; individual response; integral projection model; integrated population model.

INTRODUCTION

Animal and plant populations are governed by eco-evolutionary dynamics (Carroll et al. 2007, Pelletier et al. 2009). Climate and environmental conditions influence the individuals constituting populations in ways that shape annual distributions of individual phenotypic and life-history traits (such as body mass, body size, or birth date). The annual variations in trait distributions may result either from environmental pressures that positively or negatively select individual characteristics through survival or recruitment, or from plastic responses of individual traits (Gienapp et al. 2008, Boutin and Lane 2014, Crozier and Hutchings 2014, Franks et al. 2014).

The strengths of selective pressures are characterized by selection gradients that vary over space and time. A recent study has reported that environmental variables, such as the amount of precipitation, partly shape the strength of selective pressures through survival and reproduction in all taxa (Siepielski et al. 2017). The increasing mean and variability of environmental variables is thus expected to alter the distribution of individual traits, while simultaneously influencing individual survival, reproduction, trait growth, and trait transmission. Any change in these processes will impact individual performance and population growth rates. For example, the strength of selection for earlier clutch initiation date of House Wrens (*Troglodytes aedon*) has increased with temperatures, while average reproduction has decreased (Bowers et al. 2016). These interactions between individual trait distributions and environmental conditions determine population dynamics (Reed et al. 2012, Campbell and Powers 2015). Benefiting from a longer growing season, yellow-bellied marmots (*Marmota flaviventris*) can reach a larger mean mass before hibernation. At the same time, the strength of fertility selection on mass has increased, resulting in heavy marmots

---

Manuscript received 6 August 2018; revised 23 December 2018; accepted 4 February 2019. Corresponding Editor: Brian D. Inouye.

[3] E-mail: floriane.plard@vogelwarte.ch

having a higher probability of reproduction than light marmots (Ozgul et al. 2010). Thus, population dynamics depend on the distribution of individual traits and on their relationships with individual survival and reproduction.

In the context of climate change, a better understanding of these eco-evolutionary dynamics would improve prediction of population resilience (Visser 2008, Moritz and Agudo 2013). To anticipate how populations will perform, we need to account for variation in environmental variables as well as responses of individual traits to these changes (Dawson et al. 2011). Thus, predicting future population dynamics requires knowledge of interactions between individual traits and environmental pressures (Lavergne et al. 2010). However, common applications of population models do not account for these interactions, despite the recent development of analytical methods to understand and predict population dynamics from empirical data (e.g., Caswell 2001, Williams et al. 2002, Lande et al. 2003, Royle and Dorazio 2008).

Forecasting population dynamics using simple matrix models has been criticized because these methods rely on the observed environment to estimate average demographic rates, which in turn are used to forecast future population dynamics (Crone et al. 2013). These simple models cannot predict eco-evolutionary population dynamics because demographic rates may vary according to changes in selective pressures or in individual responses. A second drawback is that these models may not include demographic processes, such as immigration, that are difficult to estimate (Grøtan et al. 2009, Schaub and Fletcher 2015), or use demographic rates that have been estimated with large uncertainties due to restricted data such as early survival (Pike et al. 2008, Eckhart et al. 2011, Cox et al. 2014). To cope with these two drawbacks, we propose to combine two existing classes of models that can individually resolve these two issues, with the benefit of predicting eco-evolutionary population dynamics with increased confidence.

A first class of models commonly used in population ecology and conservation is known as integrated population models (Besbeas et al. 2002, Schaub and Abadi 2011, Zipkin et al. 2019). We abbreviate this model as $\mathrm{IPM}_{\mathrm{pop}}$ because its main advantage is to use data at the population level, i.e., count data that are jointly analyzed with demographic data (typically capture–recapture and reproduction data). The main feature of this joint analysis of multiple data sets is that it exploits information about demographic processes contained in the count data, resulting in increased precision of estimates and the ability to estimate demographic parameters for which no explicit data have been collected (Besbeas et al. 2002, Tavecchia et al. 2009). A limitation of current $\mathrm{IPM}_{\mathrm{pop}}$ is that they estimate average demographic rates of all individuals of a given age- or stage-class and assume that these individuals are identical. For now, they cannot study the influence of environmental condition on individual traits.

A second class of models is the integral projection model, which we abbreviate as $\mathrm{IPM}_{\mathrm{ind}}$ because its main feature is to use demographic relationships that depend on individual traits. These models focus on the link between individual traits and demographic performances, and on how they affect population dynamics. A population is therefore described by the distribution of one or several individual continuous traits such as body mass, body size, or laying date (Easterling et al. 2000, Rees et al. 2014, Ellner et al. 2016). Survival and reproductive functions link individual traits to individual performance. An inheritance function can include both genetic and non-genetic transmission (Bonduriansky and Day 2009, Coulson et al. 2017) and describes how individual traits are transmitted from parents to offspring. For traits that vary in the course of an individual life, the transition function links individual traits at time $t+1$ to individual traits at time t. If environmental effects are included, a main advantage of $\mathrm{IPM}_{\mathrm{ind}}$ is the ability to investigate the influence of interactions between individual traits and environmental changes on demography (Ozgul et al. 2010, Plard et al. 2014). Thus, these models assume that performance of individuals of a given age or stage class vary with a given set of continuous traits. Estimated demographic rates describe the mean response of each age or stage class according to these traits.

A main limitation of classical $\mathrm{IPM}_{\mathrm{ind}}$ is that data at the population level are not included. As a result, the accuracy of population projections based solely on individual data has been questioned (Ghosh et al. 2012). The use of demographic functions fitted at the individual level to project the population distribution introduces a mismatch of scales and corresponds to an ecological fallacy (Ghosh et al. 2012). For instance, many life-history traits are age dependent, such as laying date decreasing with age at the individual level. If this relationship is extrapolated to the population level, we might wrongly infer that the laying date is under negative selective pressure because individuals that live longer have on average an earlier laying date (for this general issue, see van de Pol and Wright 2009). Some authors have suggested analyzing population data with an $\mathrm{IPM}_{\mathrm{ind}}$, to infer survival and reproductive functions that may have generated the observed data only (Ghosh et al. 2012, White et al. 2016). However, as these models focus on population data only, the ecological fallacy is still possible. White et al. (2016) partially solved this problem by including prior distributions of the individual-level parameters obtained from the literature. Here we go one step further and develop an integrated integral projection model (IPM^2) that combines data at the population and individual levels. Thus, IPM^2 enjoys advantages of both $\mathrm{IPM}_{\mathrm{pop}}$ and $\mathrm{IPM}_{\mathrm{ind}}$ and enables us to study the mechanisms that operate at the individual level and shape the population dynamics while keeping population predictions close to observed population sizes.

We first present results from a simulation study to assess the environmental conditions for which the IPM^2 results in improved predictions relative to the use of either IPM$_{\text{pop}}$ or IPM$_{\text{ind}}$. We compare the relative efficiency of IPM^2 to IPM$_{\text{pop}}$ and IPM$_{\text{ind}}$ in (1) estimating relationships between individual traits, environmental variables and individual performance, (2) population forecasts, and (3) estimating demographic rates for which few data on trait transmission have been collected. Second, we apply these three models to an empirical data set of a Barn Swallow population (*Hirundo rustica*). We show that IPM^2 can reliably estimate relationships between environmental variables, laying dates, individual reproductive success, and survival, as well as forecast population size with accuracy. Conversely, IPM$_{\text{pop}}$ cannot account for the relationships between laying date and individual performance and classical IPM$_{\text{ind}}$ does not accurately predict future population size, as it cannot estimate immigration.

MATERIALS AND METHODS

To illustrate the differences between models and also as a basis for the simulation (see Appendix S1), we consider a hypothetical population of a passerine bird species with two age classes: fully grown nestlings (juveniles) and adults. First year (juvenile) survival differs from adult survival, first breeding occurs at age one, and reproductive performance is invariant with age. All individuals are assigned to one heritable, continuous individual trait that is time invariant. In addition, an environmental variable is created. Depending on the scenarios (see Fig. 3), the demographic rates may be affected by additive or interactive effects of the individual trait and the environmental variable. We assume no density dependence. We describe the female part of the population and adopt a model for a post-breeding census. In the following, we denote matrices in capital bold, vectors in bold lowercase, functions as $F()$ and constants by capital letters. We first introduce the integrated population (IPM$_{\text{pop}}$) and the integral projection (IPM$_{\text{ind}}$) models, and then develop the combined model (IPM^2).

Integrated population models (IPM$_{pop}$)

Integrated population models jointly analyze different data sets to simultaneously estimate trajectories of population size and demographic rates (Besbeas et al. 2002, Schaub and Abadi 2011). This analytical framework relies on a population model as a prior distribution for the annual data at the population level, and combines it with additional data at the individual level to inform demographic parameters such as survival and reproduction. In our simulation study, three data sets are used: annual number of breeding females, age-specific survival data and reproductive data. Taken independently, count data are often an index of the population size over years and survival and reproductive data allow estimation of annual survival and reproductive rates. These data are analyzed within a single model, where the joint likelihood of these three data sets given the estimated demographic parameters comprise the full model likelihood. The construction of an IPM$_{\text{pop}}$ is based on the definition of the population model, the likelihoods for each data set and the joint likelihood.

The population model IPM$_{\text{pop}}$ is defined as a state-space model. The state process model that links the true state of the population with the demographic rates is identical to an annual matrix projection model:

$$\begin{bmatrix} \mathrm{N}^{\mathrm{J}}_{t+1} \\ \mathrm{N}^{\mathrm{A}}_{t+1} \end{bmatrix} = \begin{pmatrix} S^{\mathrm{J}}R & S^{\mathrm{A}}R \\ S^{\mathrm{J}} & S^{\mathrm{A}} \end{pmatrix} \begin{bmatrix} \mathrm{N}^{\mathrm{J}}_{t} \\ \mathrm{N}^{\mathrm{A}}_{t} \end{bmatrix}$$

where in year t the number of juveniles is $\mathrm{N}^{\mathrm{J}}_t$, the number of adults is $\mathrm{N}^{\mathrm{A}}_t$, juvenile survival is S^{J}, adult survival is S^{A} and reproductive output is R. Demographic rates can also be functions of environmental variable(s) (Fig. 1).

Including demographic stochasticity, the population projection over years is given by

$$\begin{aligned} \mathrm{N}^{\mathrm{A}}_{t+1} &\sim \mathrm{Bin}(S^{\mathrm{A}}, \mathrm{N}^{\mathrm{A}}_t) + \mathrm{Bin}(S^{\mathrm{J}}, \mathrm{N}^{\mathrm{J}}_t) \\ \mathrm{N}^{\mathrm{J}}_{t+1} &\sim \mathrm{Pois}(R \times \mathrm{N}^{\mathrm{A}}_{t+1}) \end{aligned}, \tag{1}$$

Within an age class, all individuals are assumed to be identical.

The survival of the individuals is known with certainty in the simulation study. The observed annual survival of a bird i of age a ($a = J$ for juveniles and $a = A$ for adults) is given by

$$\Phi_{i,a} \sim \mathrm{Bern}(S^a), \tag{2}$$

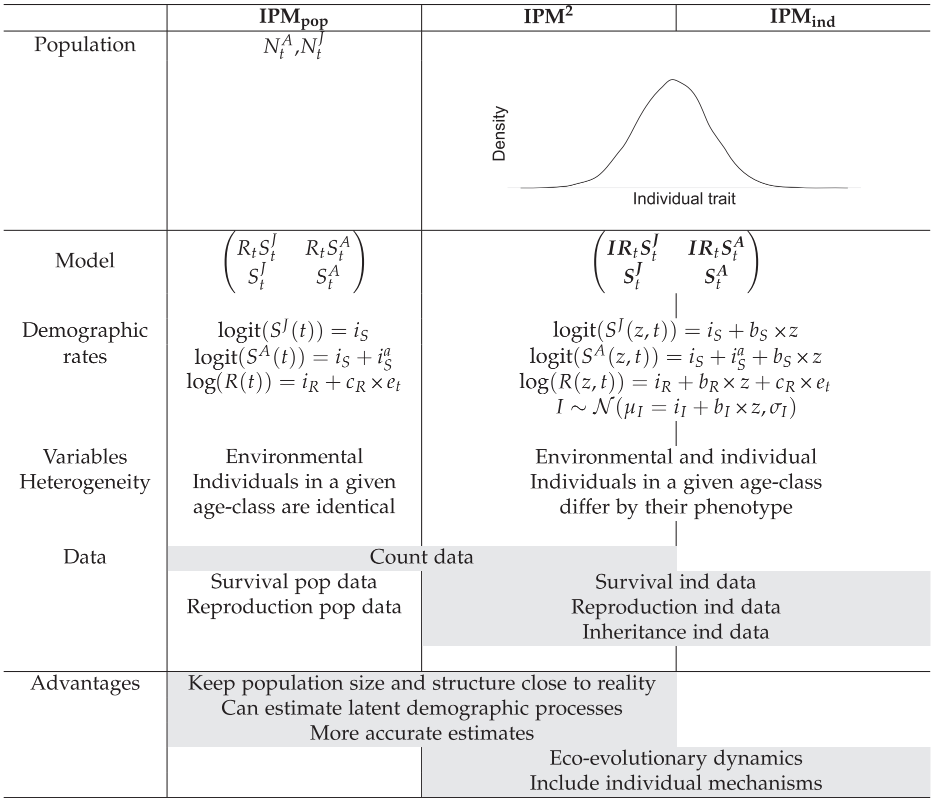
The annual reproductive output (number of fledglings) of bird i of age a is recorded and given by

$$F_{i,a} \sim \mathrm{Pois}(R), \tag{3}$$

The state-space observation model links the predicted true population size to the annual number of observed adult females (count data, C_t) using a Poisson distribution

$$C_t \sim \mathrm{Pois}(\mathrm{N}^{\mathrm{A}}_t). \tag{4}$$

Estimates of age- and stage-specific demographic rates and of population growth rates are obtained from the joint analysis of these data, providing an understanding of the contribution of each demographic rate to the population dynamics (Schaub et al. 2013, Koons et al. 2017). The joint likelihood of the model is the product of the single data likelihoods, in this case, the state-space



	$\mathbf{IPM_{pop}}$	$\mathbf{IPM^2}$	$\mathbf{IPM_{ind}}$
Population	N_t^A, N_t^J		
Model	$\begin{pmatrix} R_tS_t^J & R_tS_t^A \\ S_t^J & S_t^A \end{pmatrix}$	$\begin{pmatrix} \boldsymbol{IR_tS_t^J} & \boldsymbol{IR_tS_t^A} \\ \boldsymbol{S_t^J} & \boldsymbol{S_t^A} \end{pmatrix}$	
Demographic rates	$\text{logit}(S^J(t)) = i_S$ $\text{logit}(S^A(t)) = i_S + i_S^a$ $\log(R(t)) = i_R + c_R \times e_t$	$\text{logit}(S^J(z,t)) = i_S + b_S \times z$ $\text{logit}(S^A(z,t)) = i_S + i_S^a + b_S \times z$ $\log(R(z,t)) = i_R + b_R \times z + c_R \times e_t$ $I \sim \mathcal{N}(\mu_I = i_I + b_I \times z, \sigma_I)$	
Variables	Environmental	Environmental and individual	
Heterogeneity	Individuals in a given age-class are identical	Individuals in a given age-class differ by their phenotype	
Data	Count data		
	Survival pop data Reproduction pop data	Survival ind data Reproduction ind data Inheritance ind data	
Advantages	Keep population size and structure close to reality Can estimate latent demographic processes More accurate estimates		
		Eco-evolutionary dynamics Include individual mechanisms	

FIG. 1. Comparison between integrated population model (IPM_{pop}), integrated integral projection model (IPM^2), and integral projection model (IPM_{ind}). See equations 8–12 for definition of the parameters.

(product of the likelihood of the process L_{Pr} and the observations equations: L_{Ob}), binomial (L_{Bi}) and Poisson (L_{Po}) regression models:

$$L_{\text{IPM}_{\text{pop}}}(C, \Phi, F|\text{N}, S, R) = L_{\text{Ob}}(C|\text{N}) \times L_{\text{Pr}}(\text{N}|S, R) \times L_{\text{Bi}}(\Phi|S) \times L_{\text{Po}}(F|R). \quad (5)$$

This formulation assumes that survival, reproduction and count data are independent.

Integral projection models (IPM_{ind})

IPM_{ind} do not describe a population by a single number representing population size, but rather use frequency distribution ($n_t(a,z)$) of one or more individual traits (z) for individuals of age a at time t. Moreover, demographic rates (Survival, $S()$, Transition, $T()$, Reproduction, $R()$, and inheritance, $I()$) are not exclusively age or stage specific, but are functions of continuous individual traits (z and z' at t and $t+1$, respectively). For simplicity, we model only the female population, but in principle the distribution of both sexes can be included in IPM_{ind} (Schindler et al. 2013). The population size can be summarized for each age/stage class by integrating over individual trait distributions. As for IPM_{pop}, we used two age classes for our hypothetical bird example (for comparison with IPM_{pop}: $a = J$ if $a = 1$ and $a = A$ if $a > 1$). The number of adults ($a > 1$) at time $t+1$ depends on the number of adults and juveniles at time t and their survival and transition rates. As we focus on a post breeding model, the number of juveniles at $t+1$ depends on the number of adults alive at $t+1$ (and not at t) and on reproduction and inheritance. The population model for our passerine bird example is

$$n_{t+1}(a+1, z') = \int dz T(a, z'|z) S(a, z) n_t(a, z), \ a \geq 1$$
$$n_{t+1}(1, z') = \sum_a \int dz I(a, z'|z) R(a, z) n_{t+1}(a, z). \quad (6)$$

For the sake of simplicity of our hypothetical population, we take z to be a single, fixed continuous individual trait (so $T(a, z'|z) = 1$). In more complex models, it could be replaced by several continuous and time-dependent traits, which may represent body mass, body size, or laying date. IPM_{ind} are implemented in practice using the midpoints rule as a numerical integration method (see, e.g., section 8.3.3 in Kéry and Royle 2016). The continuous trait z is divided into M bins and the bin-value midpoints $\boldsymbol{z} = [Z_1 Z_2 \ldots Z_M]$ are the medians of these trait classes. IPM_{ind} use similar matrix projection models as IPM_{pop} but each age class is subdivided into a large number of trait classes. The model for our hypothetical bird population can be rewritten as

$$\begin{aligned} \boldsymbol{n}^{\mathbf{1}}_{t+1} &= \sum_{a>1} \boldsymbol{IRn}^{\boldsymbol{a}'}_{t+1} \\ \boldsymbol{n}^{\boldsymbol{a}+\mathbf{1}}_{t+1} &= \boldsymbol{S}^{\boldsymbol{a}} \boldsymbol{n}^{\boldsymbol{a}'}_{t}, \ a \geq 1 \end{aligned} \tag{7}$$

where $\boldsymbol{n}^{\boldsymbol{a}'}$ is the transpose (column vector) of $\boldsymbol{n}^{\boldsymbol{a}}$.

Diagonal matrices with survival ($\boldsymbol{S}$) and reproductive ($\boldsymbol{R}$) rates of individuals in each trait class are constructed based on the available data. The survival matrices give the probability of survival according to individual trait and age. The reproductive matrix gives the annual number of female nestlings raised by a female according to maternal trait values. Nestlings inherit a value of the individual trait depending on the value of the maternal trait. This process is described by the inheritance matrix (**I**). Each entry of **I** is the probability for the nestling of a mother with trait z inheriting trait z'. The distribution of all individuals of a given age a is described by the vector $\boldsymbol{n}^a$ of length M (number of artificial trait classes). The change of this distribution over time is calculated based on S, R and I.

Only the individual trait (z) influences individual survival while both the individual trait and the environmental variable (e_t) influence reproduction in our hypothetical population. Nestling traits do not depend on the birth environment. Intercepts and slopes for survival rates ($S^{\mathrm{J}}(z)$ and $S^{\mathrm{A}}(z)$) are estimated from the survival data. Independently, parameters of the reproductive function ($R(z, e)$) are estimated from the reproductive data. The diagonal of the matrix $\boldsymbol{S}^{\boldsymbol{a}}$ is estimated with $S^{\mathrm{J}}(z)$ if $a = 1$ and with $S^{\mathrm{A}}(z)$ otherwise. In the simplest scenario, we assume linear and directional selection on the individual trait through reproduction but non-linear functions are used for others scenarios. Parameters of any function ($F()$ for instance) are given by the intercept i_F and the coefficients of the individual trait b_F, the environmental variable c_F, and their interaction d_F:

$$\mathrm{logit}(S^{\mathrm{J}}(z)) = i_S + b_S \times z \tag{8}$$

$$\mathrm{logit}(S^{\mathrm{A}}(z)) = i_S + i^a_S + b_S \times z \tag{9}$$

$$R(z, e) = i_R + b_R \times z + c_R \times e_t + d_R \times e_t \times z \tag{10}$$

$$I \sim \mathcal{N}(\mu_I(z), \sigma^2_I) \tag{11}$$

$$\mu_I(z) = i_I + b_I \times z \tag{12}$$

where i^a_S is the age effect (adult vs. juvenile) in annual survival. The parameters $\mu_I(z)$ and σ_I are the mean and the standard deviation of the inheritance function. Adult and juvenile survival, reproduction, and inheritance are assumed to be independent. Demographic stochasticity is not included in this model, as is typical for $\mathrm{IPM}_{\mathrm{ind}}$, although in principle it could be.

Three data sets (survival, reproduction, and inheritance) are used to model the influence of the fixed continuous trait on individual survival and reproductive success. The observed annual survival of bird i with trait z and age a is

$$\Phi_{i,a,z} \sim \mathrm{Bern}(S^a(z)). \tag{13}$$

The observed number of fledglings in year t of bird i with trait z and age a is

$$F_{i,a,z,t} \sim \mathrm{Pois}(R(z, e_t)). \tag{14}$$

The observed trait Z' of nestling i whose mother had trait Z is given by

$$Z'_i \sim \mathcal{N}(\mu_I(Z_i), \sigma_I). \tag{15}$$

The likelihood of this model is the product of the likelihoods of each data set, i.e., of a binomial regression (modeling survival), a Poisson regression (modeling reproduction) and normal linear regression (L_{No} modeling inheritance)

$$\begin{aligned} &L_{\mathrm{IPM}_{\mathrm{ind}}}(\Phi, F, Z' | \mathrm{I}, S, R) \\ &= L_{\mathrm{Bi}}(\Phi | S, i_S, i^a_S, b_S) \times L_{\mathrm{Po}}(F | R, i_R, b_R, c_R, d_R \times) \\ &\quad L_{\mathrm{No}}(Z' | I, \mu_I, i_I, b_I, \sigma_I). \end{aligned} \tag{16}$$

In contrast to $\mathrm{IPM}_{\mathrm{pop}}$, the three likelihoods do not share any parameters. Maximizing the product of these likelihoods is equivalent to maximizing each of them independently. For more details on integral projection models, see Easterling et al. (2000), Coulson (2012), Rees et al. (2014), Elderd and Miller (2016), and Ellner et al. (2016).

Combining IPM_{pop} and IPM_{ind} into IPM^2

The IPM^2 is a combination of an $\mathrm{IPM}_{\mathrm{ind}}$ and an $\mathrm{IPM}_{\mathrm{pop}}$ (Fig. 2). As in $\mathrm{IPM}_{\mathrm{ind}}$, the population is described by the distribution of one or more individual traits, and as in $\mathrm{IPM}_{\mathrm{pop}}$, multiple data sets including data at the population level are jointly analyzed. Here we jointly analyze count data with the three data sets already used in $\mathrm{IPM}_{\mathrm{ind}}$ (survival, reproduction, and inheritance data sets). The count data consist of the number of adult females and may be supplemented with individual trait data for each female. As in $\mathrm{IPM}_{\mathrm{pop}}$, the construction of an IPM^2 is based on the definition of the population model, the likelihood of each data set and the joint model likelihood. The state-space model process is given in Eq. 7 and does not include demographic stochasticity in our simple example. This assumption could be relaxed. The trait-dependent demographic functions are estimated as in Eqs. 8–12.

The likelihoods of the survival, reproduction and inheritance data sets are the same as described for the $\mathrm{IPM}_{\mathrm{ind}}$ Eqs. 13–15. The likelihood of the state-space model is the product of the likelihood of the predicted

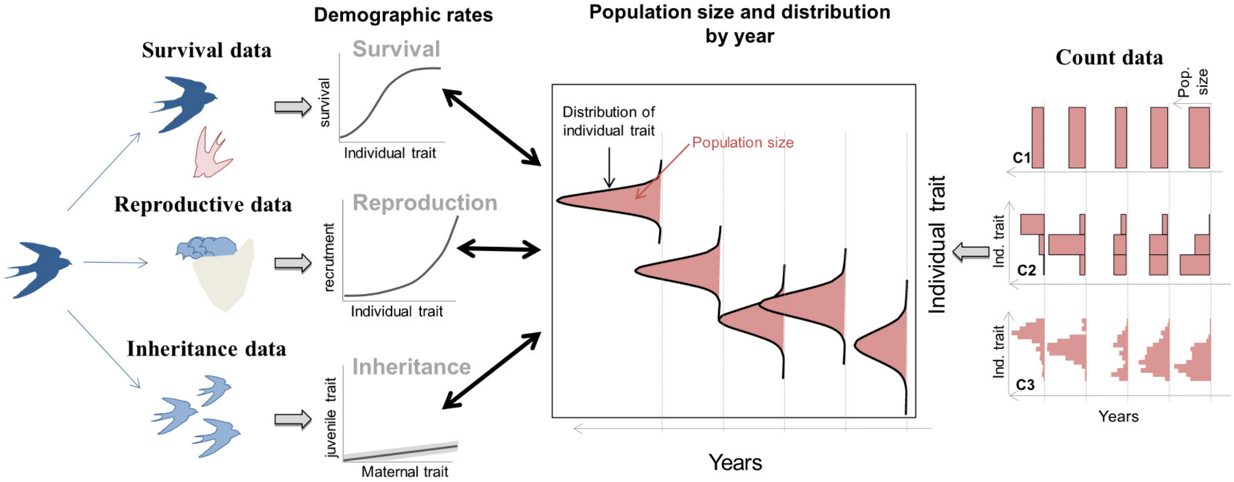


FIG. 2. Conceptual overview of IPM^2 describing the dynamics of the distribution of a continuous fixed individual trait (such as wing length) in a population. The survival, reproductive, and inheritance data sets are used to estimate the influence of the individual trait on demographic rates. These estimates are also influenced by the fit between the annual predicted population size and its distribution and the annual observed counts. C1 includes only counts, C2 includes counts and a classification of the individual trait of each individual, and C3 includes counts and the precise value of the individual trait of each individual.

population size and distribution given the demographic parameters (state model) and the likelihood of the observation model. The observation process of the state-space model includes the likelihood of the observed population size $\sum_z \boldsymbol{C}_{z,t}$ given the estimated true size of the adult population $\sum_{z,a>1} \boldsymbol{n}_t^{\boldsymbol{a}}$

$$\text{population size:} \sum_z \boldsymbol{C}_{z,t} \sim \text{Pois}\left(\sum_{z,a>1} \boldsymbol{n}_{z,t}^{\boldsymbol{a}}\right). \tag{17}$$

If the count data are supplemented with information about the individual trait (count data C2 or C3, see Simulation study section), the observation process includes the likelihood of the annual observed distribution of the individual trait given the predicted distribution

$$\text{distribution of trait: } \boldsymbol{C}_{z,t} \sim \text{Density}\left(\sum_{a>1} \boldsymbol{n}_{z,t}^{\boldsymbol{a}}\right). \tag{18}$$

The Density() function computes the probability that the observed and the predicted distributions are identical, independently of population size (Appendix S2: Fig. S1). The likelihoods of the four data sets are multiplied to form a joint likelihood upon which inference is based (the state-space, binomial, Poisson, and normal regression models)

$$\begin{aligned} L_{\text{IPM}^2} = & L_{\text{Ob}}(\boldsymbol{C}|\boldsymbol{n}) \\ & \times L_{\text{Pr}}(\boldsymbol{n}|S, i_S, i_S^a, b_S, R, i_R, b_R, c_R, d_R, I, \mu_I, i_I, b_I, \sigma_I) \\ & \times L_{\text{Bi}}(\Phi|S, i_S, i_S^a, b_S) \times L_{\text{Po}}(F|R, i_R, b_R, c_R, d_R) \\ & \times L_{\text{No}}(Z'|I, \mu_I, i_I, b_I, \sigma_I). \end{aligned} \tag{19}$$

here, the likelihood of the state-space model shares parameters (intercepts and slopes of the survival, reproductive and inheritance functions) with each of the three other likelihood terms. This formulation assumes that the survival, reproduction, inheritance, and count data are independent. Code for the complete model can be found in the online supporting material: IPM2c3.R. We used a Bayesian framework for the analysis as it facilitates propagating uncertainty from each data set to demographic and population growth rates.

Simulation study

To demonstrate how the influence of an environmental variable on the population trait distribution and the demographic rates can impact population dynamics, we consider different scenarios representing fundamentally different underlying ecological processes. We simulated data from our hypothetical population for eight different scenarios (see Fig. 3). The parameterization of this simulation is described in detail in Appendix S1. We assume perfect detection of the sampled survival data, because the simultaneous estimation of survival and recapture probabilities would require application of a capture–recapture model with individual and time varying variables that is computationally demanding for a simulation study. Moreover, the efficiency of capture–recapture models has been demonstrated repeatedly and is not expected to change when used as part of a joint likelihood. We relax the assumption of perfect detectability in the empirical example on barn swallows.

Eight different scenarios were included that combined four different shapes of selective pressures (I, directional and linear; II, directional and nonlinear; III, disruptive; IV, stabilizing, see Fig. 3) and two different environmental influences on the selective pressures. The environmental variable impacted either (1) the mean reproductive

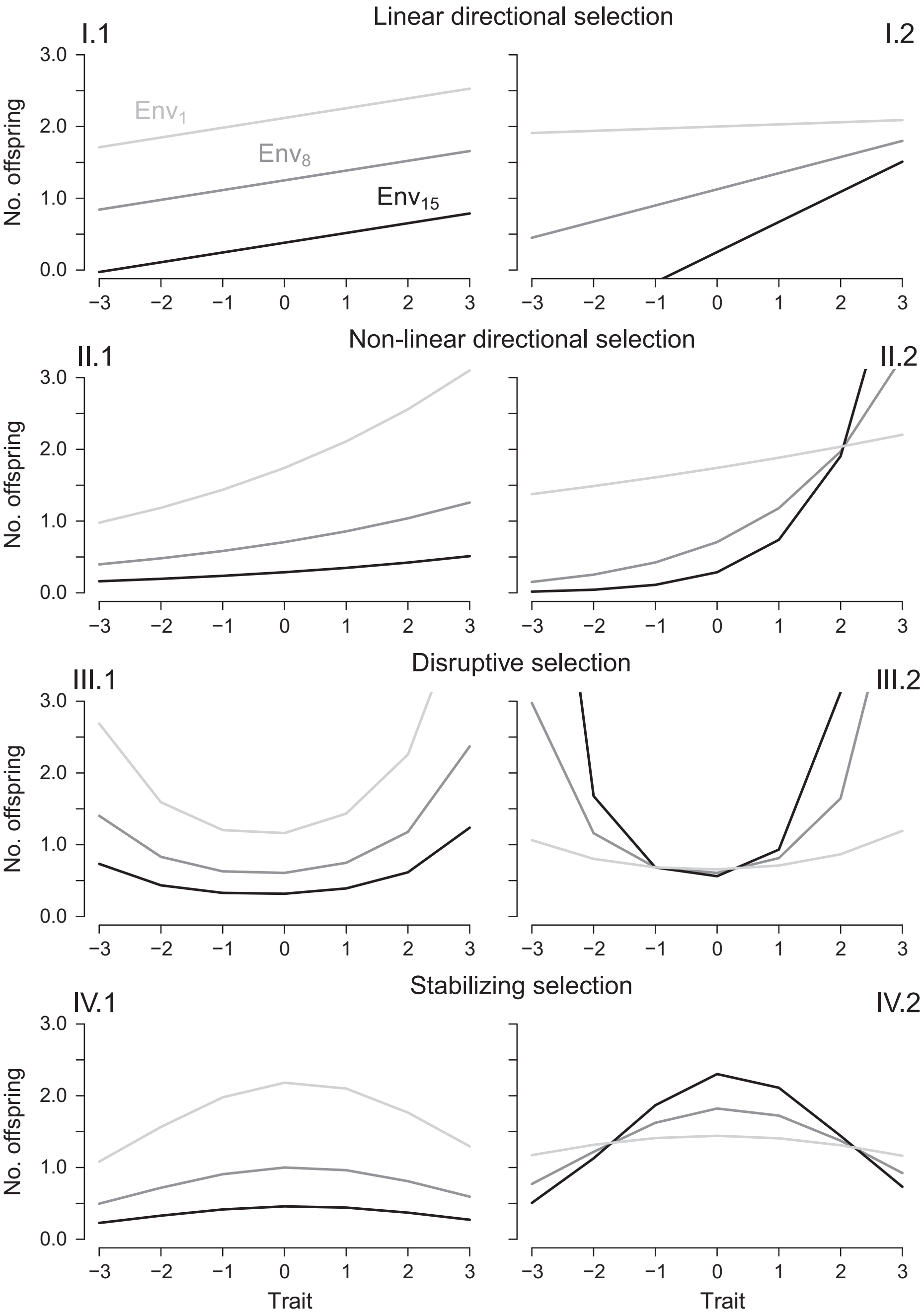


Fig. 3. Fertility selection in the year 1 (light gray), 8 (medium gray), and 15 (dark grey) linking the number of offspring produced and the individual trait in the different scenarios. I–IV.1: The mean number of offspring per individual declines with time (additive effects of the individual trait and the environmental variable). I–IV.2: The strength of the selective pressure increases over time (interactive effects of the individual trait and the environmental variable).

rate by decreasing the intercept of the function only (additive effect of the individual trait and the environmental trend on reproduction) or (2) the strength of the fertility selection on the trait (interactive effect of the individual trait and the environmental variable on reproduction). In our model notation, for example, scenario III.2 includes disruptive fertility selection with a strength (slope) that increased with the environmental variable. To simplify readability of the results, we focus on an environmental variable simulated with a linear trend over time (instead of a more complex environmental variable with stochastic variation), which mimics global environmental change. We have restricted its effect to the reproductive function. To mimic data collection in the field, we randomly sampled females from the simulated populations. During the first year, a proportion p_{rs} of females was marked with permanent tracking marks such as radio- or GPS-tracking, such that once an individual is marked, its state (alive or dead) was known each year. The reproductive success (number of female nestlings) of all marked females was observed. A proportion p_i of female nestlings from the observed broods was also marked. In addition, random searches allowed a proportion p_{rs} of new female nestlings (with unknown mothers) to be found and marked each year. The individual trait of all marked females was measured exactly. Independently, an annual survey during the breeding period counted a proportion p_C of the breeding females. The count data and the survival data are sampled independently from the total populations, so the same data are not used twice. However, some females used for the survival data may also appear in the count data. We verified that changing the probability of capture or the probability of being counted does not affect the results (not shown). To analyze the extent of additional information needed at the population level to correctly predict population dynamics, three different types of count data sets were simulated: C1, the counts of females without any measure of the individual trait; C2, the counts of females as well as categorical information about the individual trait of each counted female (three classes, in the form of small, medium or large individual trait): and C3, the counts of females and an exact measure of the individual trait of each counted female. We used an initial population size of 100 adult females in each scenario. The survival, reproductive and inheritance functions (Appendix S1: Table S1) were used to simulate the course of each individual over 15 yr.

Finally, we obtained four not completely independent data sets:

Survival data.—Annual survival data of each marked female including the individual trait and age.

Reproductive data.—Annual reproductive success of marked females, the individual trait of the female and the year.

Inheritance data.—Individual trait of marked nestlings, individual trait of their marked mothers and year.

Count data.—Annual number of counted breeding females (C1). Data set C2 and C3 also include the distribution of the individual trait (C2, one of three trait classes for each counted female; C3, exact measurement of each counted female).

Each sampled population was analyzed using five different models. The specific data sets used by each model were the following:

- $\mathrm{IPM}_{\mathrm{pop}}$ used three data sets: (a) the annual number of surviving females from the survival data set, (b) the annual number of recruits per female from the reproduction data set, and (c) the annual number of females counted (C1).
- $\mathrm{IPM}_{\mathrm{ind}}$ used three data sets: (a) the survival data set, including the information about the female trait, (b) the reproduction data set including the information about the female trait, and (c) the inheritance data set.
- $\mathrm{IPM}^2_{\mathrm{C1}}$, $\mathrm{IPM}^2_{\mathrm{C2}}$, $\mathrm{IPM}^2_{\mathrm{C3}}$ each used four data sets. Each of them need the same three data sets as the $\mathrm{IPM}_{\mathrm{ind}}$ and in addition one count data set (C1, C2, or C3).

We simulated 500 populations (independent simulations) over 15 yr under each of these eight scenarios, and sampled individuals during the 10 first years to yield survival, reproduction, inheritance and count data sets. We fitted each population model to the first 10 yr of data to obtain estimates of the different function parameters and demographic rates. We then forecasted the demographic rates and population size for the next five years and compared the predictions with the true simulated demographic rates and population sizes. Assessment of the predictive abilities of the models is important for judging their suitability to predict consequences of future environmental changes. The percentage of females sampled was set to prs = 0.4 for survival and reproductive data and pc = 0.5 for count data. Preliminary analyses found that variability in these percentages did not influence the results. However, inheritance data are often the most challenging to gather in the field and we assume that inheritance data was collected from pI = 0.2 of individuals in each scenario. To investigate the impact of the percentage of inheritance data sampled, we also report results when only pI = 0.02 of the inheritance data were sampled for scenario II (the most common scenario).

We used 50 midpoints to describe the distribution of the individual trait in $\mathrm{IPM}_{\mathrm{ind}}$ and IPM^2. Individual as well as environmental variables were scaled to facilitate model convergence. We used normal distributions with mean 0 and variance 10^2 as priors for regression slopes and intercepts and uniform distributions over the interval [0,100] as priors for the standard deviations of the inheritance function (Kéry and Schaub 2012). The parameter values of the simulated populations were used as initial values. To avoid any influence of the population distribution in the first year on the results of IPM^2 and $\mathrm{IPM}_{\mathrm{ind}}$, we used the true distribution to generate initial values for the first year. The initial population distribution must be simulated from a continuous distribution to avoid gaps (zero individual) in the distribution due to variable sampling. We generated three MCMC chains of length 25,000, discarding the first 12,500 samples as burn-in. Convergence of all chains was assessed using the Gelman and Rubin convergence diagnostic ($R < 1.5$; Gelman and Rubin 1992). We fit the models in the Bayesian framework using NIMBLE (NIMBLE Development Team 2016) run from R (R Core Team 2014).

To compare the performance of these five models, we first compared the 95% interval (over the 500 simulations) of posterior means of the demographic rates estimated during the first 10 yr to the true value used for the simulation. Second, we compared the forecasted demographic rates using the following five years with the true demographic rates. Third, we compiled bias (posterior mean − truth) and precision (using mean squared errors $\mathrm{MSE} = \mathrm{bias}^2 + \mathrm{variance}$) of the slopes of each demographic function. We compared their estimates using $\mathrm{IPM}_{\mathrm{ind}}$ and the three IPM^2.

Application to Barn Swallows

The Barn Swallow is a short-lived, double-brooded, and long-distance migratory passerine bird that breeds in Europe in agricultural landscapes (Grüebler et al. 2010). Laying date of the first annual brood was chosen as the individual continuous trait to describe the distribution of females in the population. The laying date has a strong impact on the reproductive output; later first broods yield lower annual reproductive output (Grüebler and Naef-Daenzer 2008). Moreover, fledglings from early broods have longer life expectancy than fledglings from later broods (Saino et al. 2012). The annual dynamics of the laying-date distribution is described using five functions that we have fit to the data:

1) Annual number of successful clutches and number of fledglings per successful clutch of a pair according to the laying date of the first clutch (N = 2,605 pairs). The product of these two functions is the reproductive output. To retain only females in our population model, we divided the reproductive output by two, assuming an even sex ratio. The annual number of successful clutches was modeled with a Poisson distribution and a log link. The number of fledglings was modeled with a normal distribution.
2) Annual survival according to individual age (<1 yr old or older), sex, and laying date of the first clutch (N = 12,222 individuals). Barn Swallows were subject to imperfect detection, hence, we used capture–mark–recapture models to estimate the recapture probability and the annual survival based on a previous analysis of these populations (Schaub et al. 2015).
3) Transition between successive annual laying dates of first clutches (using N = 1,053 duos of successive laying date of first clutches). In contrast to the simulation study, we included a transition function modeled with a normal distribution, because laying date can vary by individual.
4) Inheritance: laying date of first clutches according to birth laying date (N = 192 filiations) and whether the bird was born into a first or a second (including also the rare third broods) brood. The inheritance function has been modeled with a normal distribution.

We assumed no sex difference in inheritance and transition between successive laying dates. We used data sampled in 12 populations located throughout Switzerland from 1997 to 2004 (see Schaub and von Hirschheydt 2009, Grüebler et al. 2010, Schaub et al. 2015 for more details) to estimate intercepts and slopes of these functions. Variation among populations was taken into account by including a site-specific environmental variable. We used site-specific spring precipitation (total from March to June) as an index of the environmental conditions influencing the availability of resources at each site. The most complex models for each function included the interactive effects between individual laying dates and spring precipitation in the $\mathrm{IPM}^2_{\mathrm{C3}}$ and the $\mathrm{IPM}_{\mathrm{ind}}$. If the 95% credible interval of an interaction included 0, we removed it and then repeated this selective test for the main effects of individual laying date and spring precipitation in the different functions. When an $\mathrm{IPM}_{\mathrm{pop}}$ was used, we investigated the influence of spring precipitation on annual survival, annual number of successful clutches and number of fledglings per successful clutch using its 95% credible intervals. We used the $\mathrm{IPM}^2_{\mathrm{C3}}$ rather than an $\mathrm{IPM}^2_{\mathrm{C2}}$ or $\mathrm{IPM}^2_{\mathrm{C1}}$ to illustrate an application on the most complex model.

We used the sum of the number of breeding pairs in four (out of the 12) populations that were surveyed annually from 1997 to 2003 as count data. The swallow populations were geographically open and thus emigration and immigration must be addressed. Emigration is already accounted for using capture–recapture data that yields estimates of apparent survival, the probability of surviving and staying in the population. Immigration was estimated when possible (using $\mathrm{IPM}_{\mathrm{pop}}$ and $\mathrm{IPM}^2_{\mathrm{C3}}$) using the assumption that the distribution of laying dates among immigrants was the same as the distribution of laying dates of residents.

We estimated the demographic rates of the Swiss population from 1997 to 2004 under each model ($\mathrm{IPM}_{\mathrm{pop}}$, $\mathrm{IPM}_{\mathrm{ind}}$ and $\mathrm{IPM}^2_{\mathrm{C3}}$, the code for the three models are presented in the online supporting material). Finally, we used the three models to forecast the population development of the barn swallows from 2005 to 2015 across Switzerland. To estimate and predict the population index for the total Swiss population, we used the average of spring precipitation over the four sites where count data were available. We compared these predictions with an independent annual population index of barn swallows. This independent index was compiled from the Swiss bird monitoring program, which samples abundance data at 267 1-km^2 plots, randomly distributed throughout Switzerland (Sattler et al. 2016).

RESULTS

In most cases, the three models $\mathrm{IPM}^2_{\mathrm{C3}}$, $\mathrm{IPM}^2_{\mathrm{C2}}$ and $\mathrm{IPM}^2_{\mathrm{C1}}$ yielded similar estimates that were very close to true values, so the results for those three models are reported together in the text.

Estimation of demographic rates

Scenarios I: linear directional selection.—Demographic estimates from all models were unbiased for the years with data as well as for the forecasting years, regardless of whether the environment had an additive or interactive effect with the individual trait (Figs. 4A and 5A). In these simple and predictable scenarios, $\mathrm{IPM}_{\mathrm{ind}}$ produced more precise demographic estimates than either the IPM^2 or the $\mathrm{IPM}_{\mathrm{pop}}$ (Figs. 4A and 5A). Mean estimates of intercept and slope parameters influencing demographic rates were accurate and similar in $\mathrm{IPM}_{\mathrm{ind}}$ and the three IPM^2 (Appendix S2: Fig. S2). However, IPM^2 and $\mathrm{IPM}_{\mathrm{ind}}$ produced slightly biased parameter estimates for the reproductive function (Appendix S2: Fig. S2) because identity

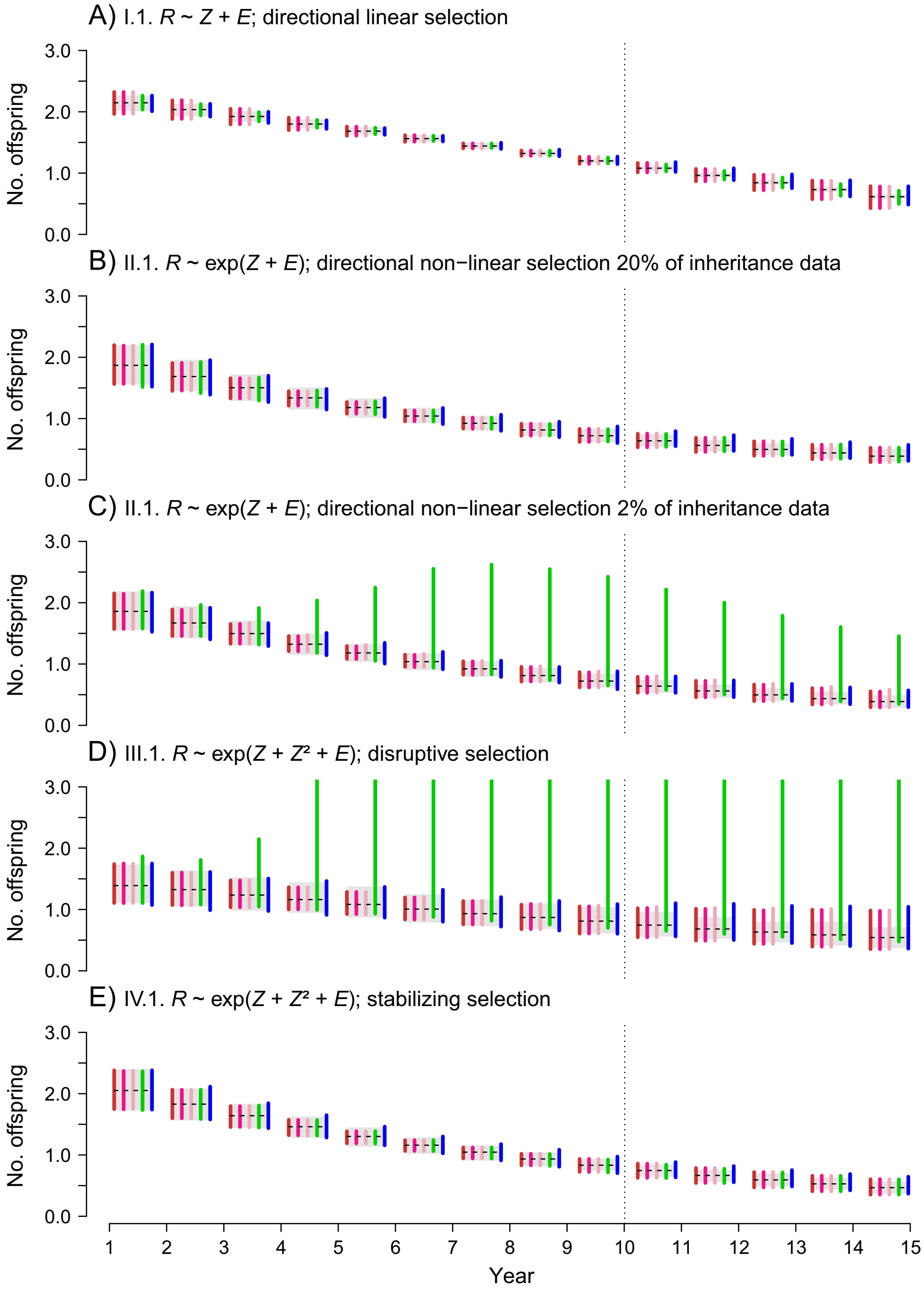


FIG. 4. The 95% confidence intervals of posterior means of estimates of reproductive rates during years 1 to 15 under scenarios I–IV.1 using the five different models: $\mathrm{IPM}^2_{\mathrm{C3}}$ (dark red), $\mathrm{IPM}^2_{\mathrm{C2}}$ (red), $\mathrm{IPM}^2_{\mathrm{C1}}$ (pink), $\mathrm{IPM}_{\mathrm{ind}}$ (green), and $\mathrm{IPM}_{\mathrm{pop}}$ (blue). Until year 10 (vertical dotted lines), reproductive rates were estimated from data collected under each simulation. After year 10, data were excluded and demographic rates were forecast. Averages and 95% intervals of the true demographic rates estimated over 500 sampled populations are shown by horizontal dashed black lines and gray shades, respectively. For scenario II.1, the results are shown when 20% (B) or 2% (C) of the inheritance data have been collected. In A, D, and E, 20% of the inheritance data have been collected. R is the reproductive rate, Z is the individual trait and E the environmental variable.

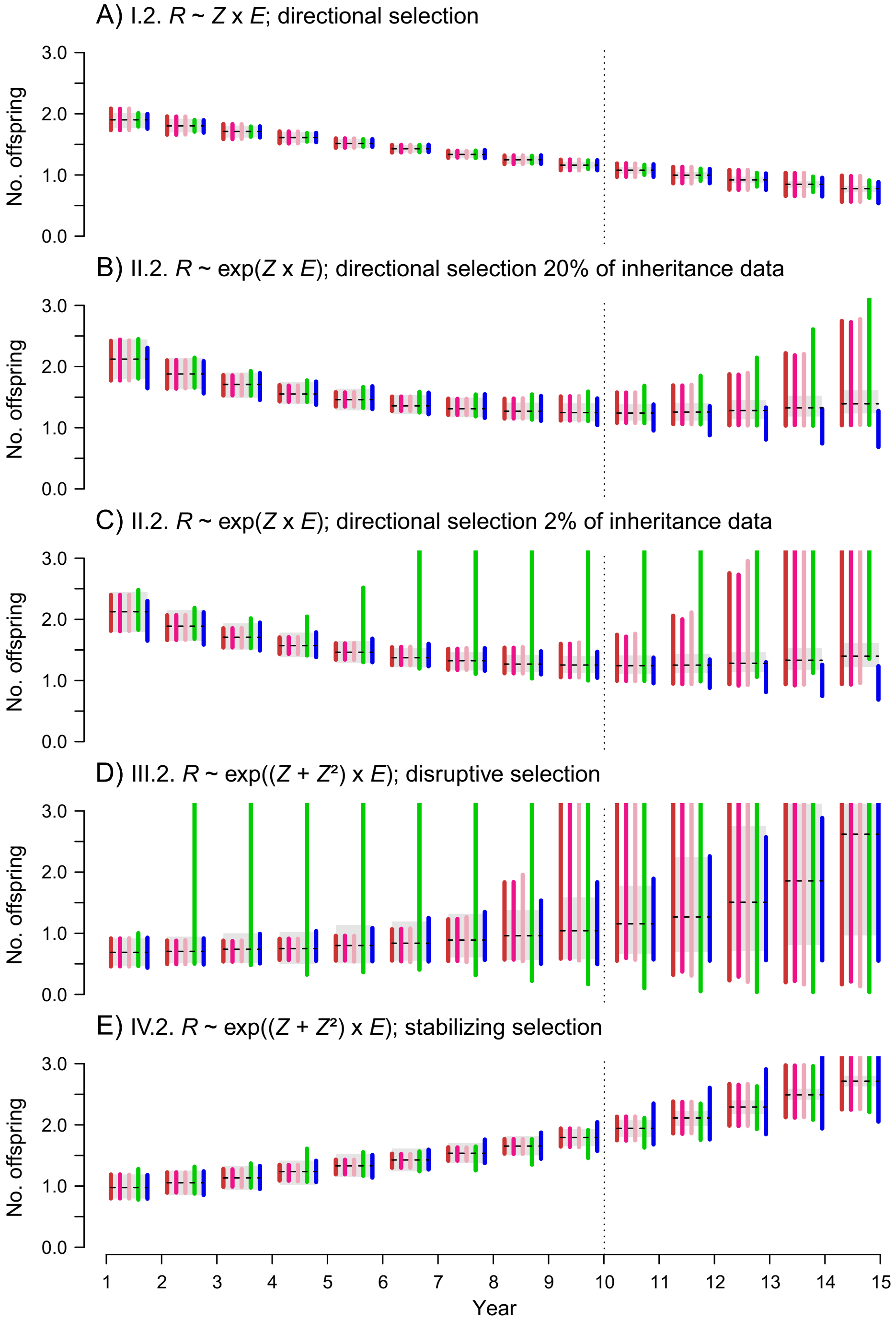


FIG. 5. The 95% confidence intervals of posterior means of estimates of reproductive rates during years 1 to 15 under scenarios I–IV.2 using the five different models: IPM$^2_{C3}$ (dark red), IPM$^2_{C2}$ (red), IPM$^2_{C1}$ (pink), IPM$_{ind}$ (green), and IPM$_{pop}$ (blue). Until year 10 (vertical dotted lines), reproductive rates were estimated from data collected under each simulation. After year 10, data were excluded and demographic rates were forecast. Averages and 95% intervals of the true demographic rates estimated over 500 sampled populations are shown by horizontal dashed black lines and gray shades, respectively. For scenario II.2, the results are shown when 20% (B) or 2% (C) of the inheritance data have been collected. In A, D, and E, 20% of the inheritance data have been collected.

link functions were used and so the linear relationships were truncated below zero.

Scenarios II: non-linear directional selection.—The demographic rates could reliably be estimated by all models when the environment and the individual trait affected reproductive rate in an additive way (scenario II.1, Fig. 4B). When the environment and the individual trait interacted (scenario II.2), estimates of demographic rates of all models were unbiased for the years with data.

However, the demographic rates of $\mathrm{IPM_{pop}}$ were biased in forecasted years (years 10 to 14, Fig. 5B; Appendix S2: Figs. S7 and S9, the reproductive rate as much as 35% in the last year) because $\mathrm{IPM_{pop}}$ could not predict the increase in the mean individual trait. In this second scenario, the environmental pressure was more severe for individuals with a large trait value, which resulted in a faster adaptation to changes in environmental conditions. Uncertainties around forecasted demographic estimates increased at a higher rate using $\mathrm{IPM_{ind}}$ compared to IPM^2. In year 9, the 95% interval of the population growth rate was 47% larger in $\mathrm{IPM_{ind}}$ than in IPM^2. When only 2% of the mother–offspring affiliations were sampled to estimate the inheritance function, the benefit in terms of precision from the IPM^2 compared to the $\mathrm{IPM_{ind}}$ was more pronounced (Figs. 4C and 5C). The estimates of the slope of the inheritance function were slightly underestimated but more accurate using IPM^2 than $\mathrm{IPM_{ind}}$ (Fig. 6).

The mean estimates of most slope parameters were similar and close to true values using $\mathrm{IPM_{ind}}$ or IPM^2 (Appendix S2: Fig. S3). However, IPM^2 tended to under-estimate the negative influence of the environmental trend on the reproductive rate (parameter c_R, Appendix S2: Fig. S3). In most scenarios, standard deviations of the slopes of the survival and the reproductive functions were higher in $\mathrm{IPM_{ind}}$ than in IPM^2, resulting in higher MSE in $\mathrm{IPM_{ind}}$. Thus, estimates were more precise using IPM^2.

Scenarios III: disruptive selection.—Demographic rates were accurately estimated by $\mathrm{IPM_{pop}}$ and IPM^2. However, the high non-linearity of the disruptive selective pressure had the same amplifying effect than in the above scenario for $\mathrm{IPM_{ind}}$. It yielded over-estimated demographic rates in scenarios III.1 and III.2 (Figs. 4D and 5D; Appendix S2: Figs. S6–S9). Uncertainties around estimated demographic rates increased in scenario III.2, when the intensity of the selective pressure on the individual trait increased with time. Even IPM^2 forecasted demographic rates with high uncertainty in this scenario (Fig. 5D, years 10 to 14). Only $\mathrm{IPM_{pop}}$ estimated demographic rates with relatively small uncertainty because it predicted linear trends in the demographic rates, independently of the distribution of the individual trait.

While most estimated parameters (intercepts and slopes of demographic functions) were not different from true values using IPM^2 or $\mathrm{IPM_{ind}}$, IPM^2 tended to over-estimate the strength of the selection on the individual trait through the reproductive rate over time (parameter d_R, Appendix S2: Fig. S4). In scenarios III, MSE were higher using $\mathrm{IPM_{ind}}$ than IPM^2.

Scenarios IV: stabilizing selection.—Under stabilizing selection, all models reliably estimated demographic rates (Figs. 4E and 5E). In scenario IV.2 (Fig. 5E), IPM^2 gave more precise estimates of demographic rates than either $\mathrm{IPM_{ind}}$ or $\mathrm{IPM_{pop}}$, but differences in demographic rate estimates between models were smaller compared to other scenarios. Estimates of the intercept and slope parameters influencing demographic rates were unbiased in $\mathrm{IPM_{ind}}$ and the three IPM^2 (Appendix S2: Fig. S5). However, estimates were more precise using any of the IPM^2 as compared to $\mathrm{IPM_{ind}}$.

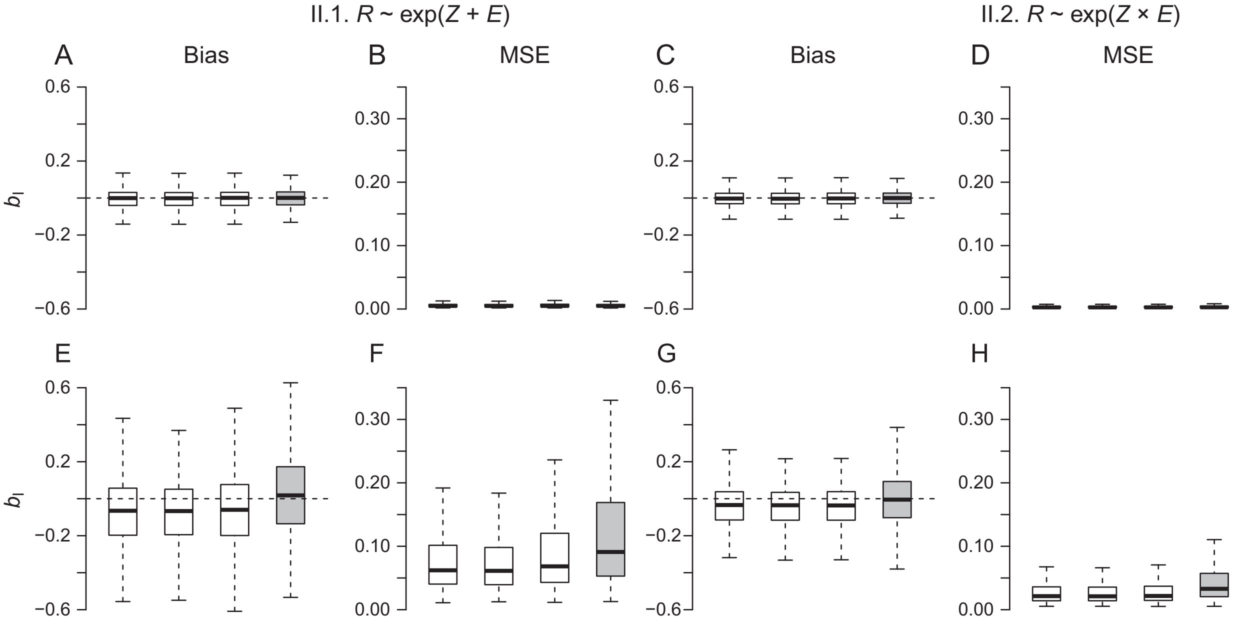


FIG. 6. Comparison of bias and mean squared errors (MSE) of the slope of the inheritance function estimated under the scenarios II.1 and II.2 when 20% (A–D) or 2% (E–H) of the inheritance data were collected. Box plots of estimators from $\mathrm{IPM_{ind}}$ are shown in gray. IPM^2_{C3}, IPM^2_{C2}, and IPM^2_{C1} are shown in white, ordered from the left to the right. Dotted lines show an absence of bias. For box plots, the mid lines show the median, the box edges show the 25% and 75% percentiles and the whiskers showed the 25% and 75% percentile ± 1.5*the interquartile range.

Population dynamics of Swiss barn swallows

We found a significant negative influence of spring precipitation on annual survival of barn swallows (slope, −0.10; 95% CRI (credible interval), [−0.16; −0.03]), but not on reproductive rates when the data were analyzed with the IPM_{pop} (Appendix S3: Table S1). However, using IPM^2 we found that demographic rates were also influenced by the individual laying date of the first clutch. Individual laying date negatively influenced annual survival (slope: −0.15 [−0.23; −0.07], Appendix S3: Table S1), the annual number of successful clutches and the number of fledglings per successful clutch (Appendix S3: Figs. S1 and S2). Successive annual laying dates of first clutches were positively correlated and positively related to precipitation (Appendix S3: Fig. S3). First year laying date was not influenced by parental laying date ([−0.16;0.16]) but was delayed in years with high precipitation (Appendix S3: Fig. S4). The results from IPM_{ind} were similar to those under an IPM^2 (Appendix S3: Table S1), with the exception that the 95% CRI of the effects of precipitation on first year laying date and on annual survival included zero ([−0.03;0.22] and [−0.08;0.07], respectively, Appendix S3: Table S1). Consequently they were removed from the model. The annual demographic rates based on the three models were similar in most years (Appendix S3: Fig. S5). The 95% credible interval of the immigration rate estimated under IPM_{pop} and IPM^2 did not include zero (Appendix S3: Table S1).

Similar population predictions during the 12 yr following the study period were obtained from IPM^2 and IPM_{pop} (Fig. 7), but these predictions differed greatly from those of IPM_{ind}. The predictions from IPM^2 (red) and IPM_{pop} (blue) were remarkably similar to the population index obtained from independent monitoring bird data (gray). The predictions from the IPM^2 including individual laying date were slightly better than those from IPM_{pop} (predictions from IPM^2 and IPM_{pop} explaining 46% and 44%, respectively, of the variation in the Swiss national index). IPM_{ind} was not effective in predicting population index (explaining only 9% of the variation) as it did not include immigration.

Discussion

We developed a population model that can estimate demographic responses in a changing environment and predict the resulting population dynamics. This model has improved forecasting abilities compared to existing models and allowed better understanding of the underlying mechanisms of population dynamics.

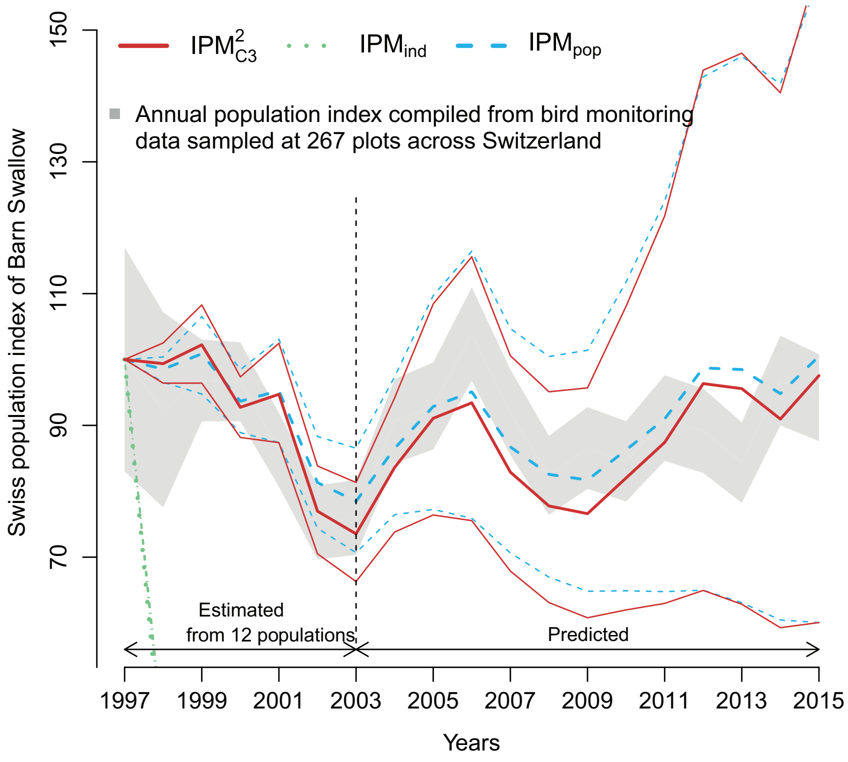


Fig. 7. Predictions of the Swiss Barn Swallow population index and their 95% credible intervals from 2004 to 2015 using model IPM^2_{C3} (solid red lines), IPM_{pop} (dashed blue lines) and IPM_{ind} (dotted green lines). Models were fit using data collected from 12 populations in Switzerland from 1997 to 2003. The 95% confidence interval of the Swiss population index estimated from independent bird monitoring data is shown in gray.

Population forecasting when individual traits evolve

When individual traits affect demographic rates with interacting environmental variables (as in scenario II–III.2), only IPM^2 produced adequate inferences relating the individual trait, the environmental variable and individual performance, and accurate forecasting. This was expected, because IPM_{pop} does not include individual traits and because IPM_{ind} does not use count data.

Our simulation analysis showed that simple population models such as IPM_{pop} give accurate estimates and predictions of population size (see also Johnson et al. 2010, Abadi et al. 2017) when individual demographic rates are influenced linearly and homogeneously by annual environmental variables (scenario I–IV.1). However, the influence of any environmental variable is often followed by a heterogeneous individual response that in turn influences demographic rates. When individuals evolutionarily adapt to their environment and demographic rates do not follow a linear trend, forecasts from IPM_{pop} can be biased (scenario II.2). In the wild, demographic performance is not expected to increase or decrease linearly because it depends on the complex feedback between environmental conditions and individuals traits (Pelletier et al. 2007, 2009). In these scenarios, only models including the interaction between individual traits and environmental variables (IPM_{ind} and IPM^2) were able to account for the eco-evolutionary dynamics of trait distribution and the resulting change in demographic performance (Coulson et al. 2010, Smallegange and Coulson 2013). Thus, in many cases, we expect that simple models such as IPM_{pop} will not be able to forecast long-term population dynamics correctly (Crone et al. 2013).

Even if IPM_{ind} accounts for the interaction between individual traits and environmental variables, the uncertainty of predictions can increase at a higher rate than those of IPM^2 when the selective pressure is nonlinear. While disruptive and stabilizing selection are often quite weak (Kingsolver et al. 2001), selective pressures are often directional but nonlinear, as in scenario II (Siepielski et al. 2009). In some species of plants or oviparous animals, it is common for reproductive output (such as the number of seeds or of eggs) to increase non-linearly with individual size (Miller et al. 2012, Dauer and Jongejans 2013, Vindenes et al. 2014). Thus, the log link function is often used to model reproductive output in relation to individual traits in empirical analyses. Contrary to scenario I, the reproductive function linking reproductive success to the individual trait included a log link in the scenarios II to IV. Thus, reproduction increased exponentially with the individual trait. In the case of IPM_{ind}, reproduction exceeded exponential growth with the trait, contributing to the highly-biased predictions of IPM_{ind}. As an example, if there are no data for the trait distribution, the uncertainty around the trait distribution will create a gently biased trait distribution toward high values, because they are positively and non-linearly selected. In the IPM_{ind}, the individuals with high trait values will produce more offspring (that will inherit a high trait value) than individuals with a low trait value. Over time, the predicted number of individuals with a high trait value will be exponentially over-estimated. Nevertheless, we expect that variable selection gradients over time and space would reduce this exponential growth in the wild. For population analysis and forecasting, this can remain problematic when the reproductive function is modeled using a log link (the commonly used transformation as the number of offspring is positive) or when the uncertainty around the population distribution is high. While IPM_{ind} can produce biased estimates (see also detecting individual eviction, Williams et al. 2012), IPM^2 compensated for the former potential bias by slightly underestimating the slope of the inheritance function.

Individual heterogeneity influences population dynamics twofold when functions are non-linear relative to the linear case (see Plard et al. [2016] for an illustration) as predicted by the Jensen inequality (Ruel and Ayres 1999). Nevertheless, except under the very strong directional selective pressure in the second period of scenario II, the distribution of the phenotypic distribution did not change much. In the wild, quantitative traits rarely change or evolve as fast as expected in the presence of directional selection (Merilä et al. 2001). In IPM_{ind} and IPM^2, this stasis is often manifested in the inheritance function, which reverses the phenotypic effect of selective pressures (Coulson et al. 2017).

Plastic responses of individual traits to environmental variability

The interaction between environmental conditions and individual trait distributions can be stronger in the wild than in our simulation analysis. Environmental conditions might simultaneously influence survival and reproduction, and also inheritance and transition of individual traits. For instance, individual laying date is often a plastic trait that responds to environmental changes and has repercussions on reproductive success (Charmantier and Gienapp 2014). Advancing spring phenology of food resources has been followed by advancing laying dates in many birds in recent years (Gienapp et al. 2008).

Forecasted sizes of the Swiss Barn Swallow population under IPM^2 and IPM_{pop} were very similar to the independent population index derived from monitoring data. This result demonstrates that barn swallow population dynamics were strongly driven by the effect of spring precipitation on annual survival and by immigration. Even if IPM_{pop} can predict the indirect variation in survival and reproductive performance when plastic responses occur, IPM_{pop} cannot provide an understanding of how individual traits shape demography and population dynamics. This understanding is necessary to improve our knowledge of the evolution of quantitative traits. The benefit of using IPM^2 over IPM_{pop} is the improved understanding of the mechanisms linking spring precipitation to demographic rates of the barn swallow. The IPM_{pop} only indicated a direct negative effect of spring precipitation on annual survival. However the IPM^2 shows that spring precipitation directly and indirectly had negative effects on annual survival. High spring precipitation had an indirect negative effect on individual survival by delaying individual laying date of the first clutch. The IPM^2 showed that this phenological delay negatively influenced individual survival as well as reproductive output. The latter is a well-known result in most birds (Perrins 1970) but cannot be included in an IPM_{pop}.

Accuracy of demographic processes for which few data are available

The main reason why IPM_{ind} was unsuccessful for forecasting the size of the Swiss barn swallow population was that this model did not include immigration. Models using data only at the individual level may deliver biased estimates of population dynamics because some demographic rates are not included (such as immigration) (Abadi et al. 2010*b*) or because some demographic rates are estimates with large uncertainties (such as early survival). Thus, IPM_{ind} should not be used in open populations. Only if its value is known a priori can immigration be included in IPM_{ind} (Bruno et al. 2011). Using IPM^2 and including data at the population level (counts) results in estimates of immigration and of other demographic rates with higher accuracy (Tavecchia et al. 2009, Abadi et al. 2017).

Inheritance data that are needed to fit an IPM_{ind} or IPM^2 can be particularly difficult to collect. We showed that when inheritance data are limited, IPM^2 allow forecasting population dynamics with higher accuracy than IPM_{ind}. Nevertheless, we do not suggest that inheritance estimates can be estimated in the absence of any data, because any bias in other parameters will generally result in biased inheritance models. Applications of IPM_{ind} in these cases commonly assumed that the trait distribution at birth follows a normal distribution with a mean common to all newborns and a given variance (Miller et al. 2012, Gonzalez et al. 2013, Zambrano and Salguero-Gomez 2014). Another option is to use information from the literature as prior information to parametrize the inestimable parameters of the model.

Surprisingly, adding data on population size (model IPM^2_{C1}) was enough in all scenarios to improve model predictive abilities; information about traits of the counted individuals was not necessary. Thus, the count data generally would not require additional capture of individuals for assessing individual traits. While it appears that IPM^2 needs more data compared to the two other models, the availability of data should not be a limitation for the application of IPM^2. IPM^2 can be applied to the same data as IPM_{ind}; the only addition is the count data. Ideally, these count data are independent of the demographic data. Count data are available for many monitored populations where transect, monitoring of breeding pairs or families, or indirect indices of population size (i.e., collection of song, feces, or marks) are collected. Moreover, long term individual data sets are increasingly available and will help us to understand better the mechanisms driving population dynamics (Clutton-Brock and Sheldon 2010).

IPM^2 and future developments

The integrated integral projection model (IPM^2) is a combination of the existing integral projection and integrated population models and shares key benefits of each. This model can be regarded as an extension of an integral projection model that also includes count data, or as an extension of an integrated population model that considers individual traits linking them to demographic rates and their inheritance. Using this model, the influence of individual traits on population dynamics can be assessed, parameter estimates become more precise, population dynamics can be estimated including demographic processes for which no explicit data have been collected (see also White et al. 2016), and less inheritance data needs to be collected. The model yielded accurate population predictions even with individually heterogeneous responses to environmental factors. As a general benefit, modeling demographic rates in the same framework (which can also be done with IPM_{ind} or IPM_{pop}) allows natural inclusion of positive or negative covariations (reflecting individual quality or trade-offs, respectively) between survival and reproductive rates, and investigation of their influence on population dynamics (Elderd and Miller 2016, Koons et al. 2016). Here we used a very simple and specific life cycle model with a single trait and a single environmental variable, but in principle IPM^2 can be formulated for any life cycle by adapting the model structure and by adding several traits or functions (linear or otherwise) as used in other IPM_{ind} (Ellner et al. 2016). Influence of density as well as intra- or inter-species competition can also be included in IPM^2. In our simple IPM^2, we did not include demographic stochasticity but assumed that individual heterogeneity in demographic performance was shaped exclusively by individual traits, as is typically done in IPM_{ind}. Both demographic stochasticity and individual heterogeneity linked to identified or unidentified individual traits are expected to influence population dynamics (Cam et al. 2016). It is an asset of IPM^2 that demographic stochasticity as well as other sources of individual heterogeneity can easily be included, in the same way as was implemented for IPM_{ind} (Coulson 2012).

The joint likelihood of the IPM^2 is formed as a product of the single-data likelihoods and therefore requires the assumption of independence between the count, the survival, the reproduction and the inheritance data. Violating this assumption can affect parameter estimates (Besbeas et al. 2009), but the impact is often non-existent or irrelevant (Abadi et al. 2010*a,b*, Schaub and Fletcher 2015). In the present analysis, our simulated data exhibit some dependence as they were simulated to mimic a real field study. Indeed, we sampled the same individuals to obtain reproduction and survival data, so these two data sets were not independent. The strong performance of the resulting inferences suggest that violation of this assumption is not a serious limitation. However, further research should consider the issue of dependence in more details and could develop more general models appropriate for dependent data sets. By combining different data sets, one can also combine a poor quality data set with a good quality data set, although, the bias of some parameter values would perhaps increase relative to the results using only a single data set. When population-level data are biased, estimated values at the individual level may be biased if the individual data are scarce. In this case, one can weight the different data sets to reduce bias (Fletcher et al. 2019). Nevertheless, the main reason why estimates might be biased when combining different data sets is the misspecification of the model, as shown in our simulations. For example, if one demographic rate is missing in the demographic model such as immigration (Abadi et al. 2010*a,b*), or when the shapes of the demographic functions at the individual level are not optimal (e.g., linear instead of log link reproductive function) bias was apparent. We encourage the application of goodness of fit tests on the different data sets (Besbeas and Morgan 2014, Conn et al. 2018) to avoid model misspecification.

Responses to environmental pressures can vary among individuals and are the main drivers of patterns in eco-evolutionary dynamics. To forecast population dynamics we need to understand the individual drivers of populations and thus to include individual responses to their environment, while also following the entire population. Inclusion of different data sets allows for understanding the responses of individuals to environmental changes and their effects on population dynamics. As a consequence, combining data from the individual and population levels as in the IPM^2 will help our predictions become more accurate, and thus more powerful and relevant for ecological research and management.

ACKNOWLEDGMENTS

We are grateful to all the volunteers and colleagues that have helped to collect the demographic and monitoring data on barn swallows. We also thank Marc Kéry, Jan von Rönn, and two anonymous reviewers for their helpful comments on previous versions of the manuscript.

LITERATURE CITED

Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010*a*. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. Ecology 9:7–14.

Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub. 2010*b*. Estimation of immigration rate using integrated population models. Journal of Applied Ecology 47:393–400.

Abadi, F., C. Barbraud, and O. Gimenez. 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. Global Change Biology 23:1353–1359.

Besbeas, P., and B. J. T. Morgan. 2014. Goodness-of-fit of integrated population models using calibrated simulation. Methods in Ecology and Evolution 5:1373–1382.

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 3:540–547.

Besbeas, P. R., S. Borysiewicz, and B. J. T. Morgan. 2009. Completing the ecological jigsaw. Pages 513–539 *in* E. G. Cooch, D. L. Thomson, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Environmental and ecological statistics. Volume 3. Springer-Verlag, New York, New York, USA.

Bonduriansky, R., and T. Day. 2009. Nongenetic inheritance and its evolutionary implications. Annual Review of Ecology, Evolution, and Systematics 40:103–125.

Boutin, S., and J. E. Lane. 2014. Climate change and mammals: evolutionary versus plastic responses. Evolutionary Applications 7:29–41.

Bowers, E. K., J. L. Grindstaff, S. S. Soukup, N. E. Drilling, K. P. Eckerle, S. K. Sakaluk, and C. F. Thompson. 2016. Spring temperatures influence selection on breeding date and the potential for phenological mismatch in a migratory bird. Ecology 97:2880–2891.

Bruno, J. F., S. P. Ellner, I. Vu, K. Kim, and C. D. Harvell. 2011. Impacts of aspergillosis on sea fan coral demography: modeling a moving target. Ecological Monographs 81:123–139.

Cam, E., L. M. Aubry, and M. Authier. 2016. The conundrum of heterogeneities in life history studies. Trends in Ecology & Evolution 31:872–886.

Campbell, D. R., and J. M. Powers. 2015. Natural selection on floral morphology can be influenced by climate. Proceedings of the Royal Society of London B: Biological Sciences 282:20150178.

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. Functional Ecology 21:387–393.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Charmantier, A., and P. Gienapp. 2014. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. Evolutionary Applications 7:15–28.

Clutton-Brock, T. H., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562–573.

Conn, P. B., D. S. Johnson, P. J. Williams, S. Melin, and M. B. Hooten. 2018. A guide to Bayesian model checking for ecologists. Ecological Monographs 88:526–542.

Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in ecology. Oikos 121:1337–1350.

Coulson, T. N., S. Tuljapurkar, and D. Z. Childs. 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. Journal of Animal Ecology 79:1226–1240.

Coulson, T., D. R. MacNulty, D. R. Stahler, B. vonHoldt, R. K. Wayne, and D. W. Smith. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. Science 334:1275–1278.

Coulson, T., B. E. Kendall, J. Barthold, F. Plard, S. Schindler, A. Ozgul, and J.-M. Gaillard. 2017. Modeling adaptive and nonadaptive responses of populations to environmental change. American Naturalist 190:313–336.

Cox, W. A., F. R. Thompson, A. S. Cox, and J. Faaborg. 2014. Post–fledging survival in passerine birds and the value of post–fledging studies to conservation. Journal of Wildlife Management 78:183–193.

Crone, E. E., et al. 2013. Ability of matrix models to explain the past and predict the future of plant populations. Conservation Biology 27:968–978.

Crozier, L. G., and J. A. Hutchings. 2014. Plastic and evolutionary responses to climate change in fish. Evolutionary Applications 7:68–87.

Dauer, J. T., and E. Jongejans. 2013. Elucidating the population dynamics of Japanese knotweed using integral projection models. PLoS Biology 8:e75181.

Dawson, T. P., S. T. Jackson, J. L. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: Biodiversity conservation in a changing climate. Science 332:53–58.

Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. Ecology 81:694–708.

Eckhart, V. M., M. A. Geber, W. F. Morris, E. S. Fabio, P. Tiffin, and D. A. Moeller. 2011. The geography of demography: long-term demographic studies and species distribution models reveal a species border limited by adaptation. American Naturalist 178:S26–S43.

Elderd, B. D., and T. E. X. Miller. 2016. Quantifying demographic uncertainty: Bayesian methods for integral projection models (IPMs). Ecological Monographs 86:125–144.

Ellner, S. P., D. Z. Childs, and M. Rees. 2016. Data-driven modelling of structured populations. A practical guide to integral projection models. Lecture Notes on Mathematical Modelling in the Life Sciences. Springer, Cham, Switzerland.

Fletcher, R. J., T. Hefley, E. P. Robertson, B. Zuckerberg, R. A. McCleery, and R. M. Dorazio. 2019. A practical guide for combining data to model species distribution. Ecology. *In press.*

Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. Evolutionary Applications 7:123–139.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.

Ghosh, S., A. E. Gelfand, and J. S. Clark. 2012. Inference for size demography from point pattern data using integral projection models. Journal of Agricultural, Biological, and Environmental Statistics 17:641–677.

Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and evolution: disantangling environmental and genetic responses. Molecular Ecology 17:167–178.

Gonzalez, E. J., M. Rees, and C. Martorell. 2013. Identifying the demographic processes relevant for species conservation in human-impacted areas: Does the model matter? Oecologia 171:347–356.

Grøtan, V., B.-E. Saether, M. Lillegård, E. J. Solberg, and S. Engen. 2009. Geographical variation in the influence of density dependence and climate on the recruitment of Norwegian moose. Oecologia 161:685–695.

Grüebler, M. U., and B. Naef-Daenzer. 2008. Fitness consequences of pre- and post-fledgling timing decisions in a double-brooded passerine. Ecology 89:2736–2745.

Grüebler, M. U., F. Korner-Nievergelt, and J. von Hirschheydt. 2010. The reproductive benefits of livestock farming in barn swallows *Hirundo rustica*: Quality of nest site or foraging habitat? Journal of Applied Ecology 47:1340–1347.

Johnson, H. E., L. S. Mills, J. D. Wehausen, and T. R. Stephenson. 2010. Combining ground count, telemetry, and mark–resight data to infer population dynamics in an endangered species. Journal of Applied Ecology 47:1083–1093.

Kéry, M., and A. Royle. 2016. Applied hierarchical modeling in ecology. Analysis of distribution, abundance and species richness in R and BUGS. Volume 1. Academic Press.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Burlington, Massachusetts, USA.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. American Naturalist 157:245–261.

Koons, D. N., D. T. Iles, M. Schaub, and H. Caswell. 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. Ecology Letters 19:1023–1031.

Koons, D. N., T. W. Arnold, and M. Schaub. 2017. Estimating the demographic drivers of realized population dynamics. Ecological Applications 27:2102–2115.

Lande, R., S. Engen, and B. E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford, UK.

Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. Annual Review of Ecology, Evolution and Systematics 41:321–350.

Merilä, J., B. C. Sheldon, and L. E. B. Kruuk. 2001. Explaining stasis: microevolutionary studies in natural populations. Genetica 112–113:199–222.

Miller, T. E. X., J. L. Williams, E. Jongejans, R. Brys, and H. Jacquemyn. 2012. Evolutionary demography of iteroparous plants: incorporating non-lethal costs of reproduction into integral projection models. Proceedings of the Royal Society of London B: Biological Sciences 279:2831–2840.

Moritz, C., and R. Agudo. 2013. The future of species under climate change: Resilience or decline? Science 231:504–508.

NIMBLE Development Team. 2019. NIMBLE User Manual. https://doi.org/10.5281/zenodo.1211190. R package manual version 0.7.1. https://r-nimble.org

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

Pelletier, F., T. Clutton-Brock, J. Pemberton, S. Tuljapurkar, and T. Coulson. 2007. The evolutionary demography of ecological change: Linking trait variation and population growth. Science 315:1571–1574.

Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364:1483–1489.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

Pike, D. A., L. Pizzatto, B. A. Pike, and R. Shine. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. Ecology 89:607–611.

Plard, F., J.-M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, C. Warnant, and C. Bonenfant. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. PLoS Biology 12:e1001828.

Plard, F., J.-M. Gaillard, T. Coulson, and S. Tuljapurkar. 2016. Des différences, pourquoi? Transmission, maintenance and effects of phenotypic variance. Journal of Animal Ecology 85:356–370.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Reed, T. E., S. Jenouvrier, and M. E. Visser. 2012. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. Journal of Animal Ecology 82:131–144.

Rees, M., D. Z. Childs, and S. P. Ellner. 2014. Building integral projection models: a user's guide. Journal of Animal Ecology 83:528–545.

Royle, A. J., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology. The analysis of data from populations, metapopulations and communities. Elsevier, Amsterdam, The Netherlands.

Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. Trends in Ecology & Evolution 14:361–366.

Saino, N., M. Romano, R. Ambrosini, D. Rubolini, G. Boncoraglio, M. Caprioli, and A. Romano. 2012. Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching date and phenotypic quality. Journal of Animal Ecology 81:1004–1012.

Sattler, T., P. Knaus, H. Schmid, and N. Strebel. 2016. Etat de l'avifaune en Suisse. Swiss Ornithological Institute, Sempach, Switzerland.

Schaub, M., and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152:S227–S237.

Schaub, M., and D. Fletcher. 2015. Estimating immigration using a Bayesian integrated population model: choice of parametrization and priors. Environmental and Ecological Statistics 22:535–549.

Schaub, M., and J. von Hirschheydt. 2009. Effect of current reproduction on apparent survival, breeding dispersal, and future reproduction in barn swallows assessed by multistate capture-recapture models. Journal of Animal Ecology 78:625–635.

Schaub, M., H. Jakober, and W. Stauber. 2013. Strong contribution of immigration to local population regulation: evidence from a migratory passerine. Ecology 94:1828–1838.

Schaub, M., J. von Hirschheydt, and M. U. Grüebler. 2015. Differential contribution of demographic rate synchrony to population synchrony in barn swallows. Journal of Animal Ecology 84:1530–1541.

Schindler, S., P. Neuhaus, J.-M. Gaillard, and T. Coulson. 2013. The influence of nonrandom mating on population growth. American Naturalist 182:28–41.

Siepielski, A. D., J. D. DiBattista, and S. M. Carlson. 2009. Its about time: the temporal dynamics of phenotypic selection in the wild. Ecology Letters 12:1261–1276.

Siepielski, A. M., et al. 2017. Precipitation drives global variation in natural selection. Science 355:959–962.

Smallegange, I. M., and T. Coulson. 2013. Towards a general, population-level understanding of eco-evolutionary change. Trends in Ecology & Evolution 28:143–148.

Tavecchia, G., P. Besbeas, T. Coulson, B. J. T. Morgan, and T. H. Clutton-Brock. 2009. Estimating population size and hidden demographic parameters with state-space modeling. American Naturalist 173:722–733.

van de Pol, M., and J. Wright. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. Animal Behaviour 77:753–758.

Vindenes, Y., E. Edeline, J. Ohlberger, O. Langangen, I. J. Winfield, N. C. Stenseth, and L. A. Vollestad. 2014. Effects of climate change on trait-based dynamics of a top predator in freshwater ecosystems. American Naturalist 183:243–256.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649–659.

White, J. W., K. J. Nickols, D. Malone, M. H. Carr, R. M. Starr, F. Cordoleani, M. L. Baskett, A. Hastings, and L. W. Botsford. 2016. Fitting state-space integral projection models to size-structured time series data to estimate unknown parameters. Ecological Applications 26:2675–2692.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California, USA.

Williams, J. L., T. E. X. Miller, and S. P. Ellner. 2012. Avoiding unintentional eviction from integral projection models. Ecology 93:2008–2014.

Zambrano, J., and R. Salguero-Gomez. 2014. Forest fragmentation alters the population dynamics of a late-successional tropical tree. Biotropica 46:556–564.

Zipkin, E., B. D. Inouye, and S. R. Beissinger. 2019. Innovations in data integration for modeling populations. Ecology. *In press.*

SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1364/full

DATA AVAILABILITY

The data supporting the results will be archived in Dryad if the manuscript is accepted.