

IPM²: Towards better understanding and forecasting of population dynamics

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1 Summary

Dynamic population models?

2 Models of population dynamics typically aim to predict demographic rates in relation to environmental variation. However, they rarely include the diversity of individual responses facing these environmental pressures. When resources become scarce, the performance of low-quality individuals is often the first to suffer. Here, we develop a new model ("IPM²") that is the combination of an integrated population (IPM_{pop}) and an integral projection model (IPM_{ind}). The novel IPM² allows including interaction between environmental and individual variables in models of population dynamics as well as forecasting population size and trait distribution accurately. We illustrated this applying all three models to a population of barn swallows. We also studied bias and precision of ~~all three models~~ using three simulated scenarios with ~~no, a homogeneous, and a heterogeneous~~ environmental influence across individual traits on individual survival and reproduction. When the individual responses to environmental variation were heterogeneous, only IPM² was able to predict unbiased population dynamics according to heterogeneous individual performance.

17 Word count=158 and maxi is 150

(I included a few suggestions to remove some words.)

¹⁸ Introduction

¹⁹ Animal and plant populations are governed by ~~deterministic~~ and stochastic effects ^{both}
²⁰ (Leirs *et al.*, 1997; Bjørnstad *et al.*, 1999; Lande *et al.*, 2003). Yet, populations
²¹ consist of individuals that are unique and hence each individual may respond differ-
²² entially to competition or environmental conditions (Coulson, 2004). For instance,
²³ poor environmental conditions affected the survival of inexperienced but not of ex-
²⁴ perienced breeders of blue petrels (*Halobaena caerulea*, Barbraud & Weimerskirch
²⁵ 2005). In addition, plastic responses may vary among individuals. For exam-
²⁶ ple, the individual phenological responses to climate change are heterogeneous in
²⁷ great tits (*Parus major*) because some individuals were more plastic than others
²⁸ (Nussey *et al.*, 2005). Thus, predicting population dynamics requires knowledge
²⁹ about interactions between individual behaviour ^{and} competition and environmen-
³⁰ tal changes (Lavergne *et al.*, 2010) but common models of population dynamics do
³¹ not allow accounting ^{recent} for these interactions, despite ~~a very active~~ development of
³² analytical methods to understand and predict population dynamics from empirical
³³ data ~~in the recent past~~ (e.g. Caswell 2001; Williams *et al.* 2002; Lande *et al.* 2003;
³⁴ Royle & Dorazio 2008)

³⁵ To account for these interactions, here we focus on analytical methods that es-
³⁶ timate demographic rates and include them in a population model, thus ~~that make~~ ^{making}
³⁷ an explicit link between the level of individuals and the level of the population.
³⁸ A first class of models is known as integrated population model (IPM_{pop}, Besbeas
³⁹ *et al.* 2002; Schaub & Abadi 2011), where count data are jointly analysed with
⁴⁰ one or more demographic datasets (typically capture-recapture and productivity
⁴¹ data). The link between the individual and the population level is provided by a

matrix projection model. Estimates of age- and stage-specific demographic rates and of population growth rates are obtained from these models, allowing to understand the contribution of each demographic rate to population dynamics (Schaub *et al.*, 2012, 2013). The main advantage of this joint analysis of several datasets is that information about demographic processes contained in the count data is exploited, resulting in increased precision of the estimates and the ability to estimate demographic parameters for which no explicit data have been collected (Besbeas *et al.*, 2002; Tavecchia *et al.*, 2009). In the context of geographically open populations, immigration is a relevant demographic process in many populations (Lieury *et al.*, 2016; Szostek *et al.*, 2014; Schaub *et al.*, 2013) that can be estimated using IPM_{pop} (Abadi *et al.*, 2010). A limitation of current IPM_{pop} is that they assume all individuals in a given age- or stage-class are identical. Individually different responses to changes in the environment or competition and their effects on population dynamics cannot therefore be studied.

A second class of models is the integral projection models (IPM_{ind}). Here the focus is on individual demographic performances and on how they affect population dynamics. A population is therefore described by the distribution of one or several individual continuous traits (Easterling *et al.*, 2000; Rees *et al.*, 2014; Ellner *et al.*, 2016). Usually four types of individual data are used: survival and reproduction data allow the estimation of the influence of individual traits on survival and reproductive rates. With inheritance data we estimate how individual traits are inherited from parents to offspring and with transition data we estimate the change in these traits over time. If environmental data or population density are included as well, IPM_{ind} allow an understanding of how environmental conditions or competition influence the development and inheritance of individ-

67 ual traits, and how in turn these traits affect individual survival and reproductive
68 performance under these environmental pressures (Ozgul *et al.*, 2010; Plard *et al.*,
69 2014). A main advantage of IPM_{ind} is therefore that one can study the interaction
70 of individual traits and environmental changes affecting demography. A main
71 limitation of current IPM_{ind} is that data at the population level are not included. Ac-
72 cordingly, the accuracy of population projections based solely on individual data
73 has been questioned (Ghosh *et al.*, 2012). For example, population predictions can
74 be biased if demographic processes for which no data are available are ignored.

75 Here, we develop a new class of model that represents the combination of an
76 IPM_{pop} and an IPM_{ind}: the integrated integral projection model (IPM²). We show
77 that our new model enjoys the advantages of both underlying individual analytical frame-
78 works while at the same time it overcomes their individual weaknesses. The IPM²
79 enables us to study the mechanisms that operate at the individual level and shape
80 the population dynamics while keeping population predictions close to observed
81 population size, even when individual responses to environmental variation are
82 heterogeneous.

83 Material and Methods

84 To illustrate the difference between models and also as a basis for the simulation
85 (see Appendix S1 and Table S1), we consider a hypothetical population of an hypothetical
86 passerine bird species with two age classes: fully grown nestlings (juveniles) and
87 adults. First year (juvenile) survival differs from adult survival, first breeding
88 occurs at age one, and reproductive performance is invariant to age. All individuals
89 are assigned to one heritable, continuous individual trait that is constant with age.
time invariant.

90 In addition, an environmental variable is created. Depending on the scenarios (see
91 below
92 later), the demographic rates may or may not be affected by the individual trait,
93 ~~by~~ the environmental variable or by an interaction between the two. We assume ~~no~~
94 ~~that~~ density dependence ~~is absent~~. We describe the female part of the population
and adopt a model for a post-breeding census.

95 In the following, we denote matrices in capital bold, vectors in bold lowercase,
96 functions ~~in the form~~ ^{as} ~~F()~~ and constants by capital letters. Parameters of a function
97 ~~F~~ are given by the intercept i_F and the ~~slopes~~ ^{Coefficients of (1)} linked to the environmental variable
98 b_F , ~~to~~ the individual trait c_F and ~~to~~ their interaction d_F . We first introduce the
99 integrated population model (IPM_{pop}) ~~then~~ ^{and} the integral projection model (IPM_{ind}),
100 and finally ~~then~~ develop the new model.

I would suggest changing the
Section headings!

Models What is an Integrated Population Model (IPM_{pop})?

101 We define a population model that includes demographic stochasticity and envi-
102 ronmental variation as

$$N_{t+1}^A \sim \text{Bin}(S_t^A, N_t^A) + \text{Bin}(S_t^J, N_t^J) \quad (1)$$

$$N_{t+1}^J \sim \text{Pois}(R_t * N_{t+1}^A)$$

S_t^J

in year t

104 where the number of juveniles in year t is N_t^J ~~and~~, the number of adults N_t^A ,
105 juvenile survival is S_t^J , adult survival S_t^A and reproductive output is R_t . One or
106 several demographic rates can be functions of environmental covariate(s) (Table
107 1). However, within an age class all individuals are assumed to be identical. The
108 population model is the process model of a state-space model that we link to the

¹⁰⁹ count data (C_t^1).

$$C_t^1 \sim Pois(N_t^A) \quad (2)$$

¹¹⁰ Three data sets are used for the integrated population model: annual number
¹¹¹ of breeding females (count data: $C1$), age-specific survival data and data
¹¹² on reproduction. The annual demographic rates are estimated from the survival
¹¹³ and reproductive data, for which we use binomial and Poisson regression models,
¹¹⁴ respectively. The joint ^A analysis requires the ~~X~~ formulation of the joint likelihood
¹¹⁵ which is the product of the single data likelihoods, i.e. of the state-space, binomial
¹¹⁶ and Poisson regression models. For more details about constructing integrated
¹¹⁷ population models, see Besbeas *et al.* (2002) and Schaub & Abadi (2011).

Same:

^{Models} ¹¹⁸ What is an Integral Projection Model (IPM_{ind})~~X~~

¹¹⁹ In an IPM_{ind}, a population is not described by a single number representing its
¹²⁰ size but ^{instead} by a frequency distribution of one or several individual traits (Table 1).
¹²¹ Moreover, demographic rates are not only age- or stage-specific, but in addition
¹²² depend on continuous individual traits (z). For the sake of simplicity, we here
¹²³ consider z to be a single, fixed continuous individual trait ^{In More Complex models} ~~but~~ it could be replaced
¹²⁴ by several continuous and time-dependent traits, ^{which} and may represent body mass,
¹²⁵ laying date or degree of parasitism, for instance. Three datasets (survival, re-
¹²⁶ productive and inheritance) are used to parameterize a simple IPM_{ind} modeling
¹²⁷ the influence of the fixed continuous trait on individual survival and reproductive
¹²⁸ success. The inheritance of this fixed trait from parents to nestlings is estimated
¹²⁹ from the inheritance data.

perhaps $\$z \wedge \{\prime\}$, if you like it better.

130 IPM_{ind} are implemented in practice using the midpoints rule as a numerical
 131 integration method (see e.g. section 8.3.3 in Kéry & Royle 2016). The continuous
 132 trait z is divided into M bins and the bin-value midpoints $\mathbf{z} = [Z_1 Z_2 \dots Z_M]$ are
 133 the medians of these trait classes. IPM_{ind} use similar matrix projection models as
 134 IPM_{pop} but each age class is subdivided into a ~~very~~ large number of trait classes.

135 Diagonal matrices with survival (\mathbf{S}) and reproductive rates (\mathbf{R}) of individuals
 136 in each trait class are constructed based on the available data. Nestlings inherit
 137 a value of the individual trait depending on the maternal trait. This process is
 138 described by the inheritance matrix (\mathbf{I}). Each entry of \mathbf{I} is the probability for
 139 the nestling of a mother with trait z inheriting trait z' . The distribution of all
 140 individuals of a given age a is described by the vector \mathbf{n}^a of length M (number of
 141 artificial trait classes), and the change of this distribution over time is calculated
 142 based on \mathbf{S} , \mathbf{R} and \mathbf{I} .

as here ↴

$$\mathbf{n}_{t+1}^{a+1} = \mathbf{S}_t^a \mathbf{n}_t^{a'}, \quad a \geq 1 \quad (3)$$

$$\mathbf{n}_{t+1}^1 = \sum_{a>1} \mathbf{IR}_t \mathbf{n}_{t+1}^{a'}$$

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

144 The individual trait and the environmental variable influence survival and re-
 145 production in our hypothetical population. Nestlings inherit a trait depending
 146 on the maternal trait but not on the birth environment. Intercepts and slopes
 147 for survival and reproductive rates ($S^J(z, t)$, $S^A(z, t)$ and $R(z, t)$) are estimated
 148 independently ~~from each other~~ from the survival and the reproductive data. The
 149 diagonal vector of \mathbf{S}_t^a is estimated with $S^J(z, t)$ if $a = 1$ and with $S^A(z, t)$ other-

¹⁵⁰ wise. In our hypothetical example, we assume linear functions, but others could
¹⁵¹ be chosen as well.

$$\text{logit}(S^J(z, t)) = i_S + b_S * e_t + c_S * \mathbf{z} + d_S * e_t * \mathbf{z} \quad (4)$$

$$\text{logit}(S^A(z, t)) = i_S + i_{a,S} + b_S * e_t + c_S * \mathbf{z} + d_S * e_t * \mathbf{z} \quad (5)$$

$$\log(R(z, t)) = i_R + b_R * e_t + c_R * \mathbf{z} + d_R * e_t * \mathbf{z} \quad (6)$$

$$I \sim \mathcal{N}(\mu_I(z), \sigma_I) \quad (7)$$

$$\mu_I(z) = i_I + c_I * \mathbf{z} \quad (8)$$

¹⁵² where $i_{a,S}$ is the age effect (adult vs. juvenile) in annual survival. For more details
¹⁵³ ~~about~~^{of} integral projection models, see Easterling *et al.* (2000); Coulson (2012); Rees
¹⁵⁴ *et al.* (2014) and Ellner *et al.* (2016).

¹⁵⁵ Combining IPM_{pop} and IPM_{ind} into IPM²

¹⁵⁶ In our new IPM² (Fig. 1), we combine IPM_{ind} and IPM_{pop}. As in IPM_{ind}, the
¹⁵⁷ population is described by the distribution of one or several individual traits.
¹⁵⁸ Thus, the population development is the same as the one described for IPM_{ind}
¹⁵⁹ (Table 1). The population size can also be summarized for each age/stage class by
¹⁶⁰ integration over individual trait distributions. This offers the possibility to include
¹⁶¹ count data in the model in addition to the datasets used for IPM_{ind}. In contrast
¹⁶² to an IPM_{ind}, the different datasets are now analysed jointly as in an IPM_{pop}. A
¹⁶³ state-space model whose state process is given by eq (4) is used for the integration
¹⁶⁴ of the different datasets. The count data consists ~~X~~ of the number of counted female

165 adults and can include the distribution of their individual trait in each year. The
166 observation process of the state-space model includes therefore the fit between the
167 size of the adult population $\sum_{a>1} n_t^a$ and the count data y_t .

$$\text{population size : } \sum_z y_{z,t} \sim \mathcal{P}\left(\sum_{z,a>1} n_{z,t}^a\right) \quad (9)$$

168 If the count data also include information about the individual trait (count data C2
169 or C3, see below), the observation process also ~~link~~^{links} the observed to the predicted
170 distributions ~~of~~ of the individual trait in each year:

$$\text{distribution of trait : } y_t \sim \text{Density}\left(\sum_{a>1} n_t^a\right) \quad (10)$$

171 The *Density()* function gives the probability for observed and predicted dis-
172 tributions ~~of~~ being the same independently ~~of~~ of population size (fig. S2).
173 We used ~~the~~ Bayesian framework for the analysis because of its ease to propa-
174 gate uncertainty from each dataset to demographic and population growth rates.
175 The likelihoods of the four datasets are multiplied to get a joint likelihood on which
176 inference ~~from the model~~ is based.

177 Simulation study

Fig. or fig?

178 To compare the performance of IPM² with IPM_{pop} and IPM_{ind}, we simulated data
179 from our hypothetical population (see fig. S1). The simulation is described in
180 detail in Appendix S1 (see Fig. S1). We assume that the sampled data are not
181 subject to imperfect detection. This simplifies the calculations, but is not a gen-
182 eral assumption of the models, as we will show in the empirical example. Three

Not sure what is meant by "is not a general assumption..." ?

10

Don't use this double negative here.

Do you mean (which one)?

- We assume the sampled data are subject to imperfect detection. OR,
- We assume perfect detection of the sampled data.

↑ probably this one, I think!

183 different scenarios were included in which demographic rates were influenced by
184 an individual trait only (I), by the additive effects of an environmental trend and
185 an individual trait (II) or by the interactive effect between an environmental trend
186 and an individual trait (III). We simulated 500 populations (replicas) over 20 years
187 under each of these ~~three~~ scenarios and sampled individuals to yield survival, reproduction,
188 inheritance and count datasets. To analyse ~~which amount~~ ^{the degree} of additional
189 information ~~X~~ is needed at the population level to correctly predict population dynamics,
190 three different types of count datasets were simulated; *C1*: contained the
191 counts of females only without any measures of the individual trait; *C2*: contained
192 the counts of females as well as categorical information about the individual trait
193 of each counted female (e.g., in the form of short, medium or tall female size); *C3*:
194 contained the counts of females and exact measure of the individual trait
195 of each counted female. The percentage of females sampled to get the survival,
196 reproductive and the count data did not influence the results and was thus set to
197 50%. Inheritance data are often the most challenging ~~data type~~ to gather in the
198 field. Hence, we investigated the influence of the percentage of inheritance data
199 sampled in our simulation analysis and reported the results for 20% and 2% *switch order?*

200 **Analysis.** Each sampled population was analyzed with 5 different models:

annual numbers

- 201 • IPM_{pop} using the ~~number~~ of surviving individuals ~~each year~~ from the survival *dataset*, the ~~number~~ of recruits per female ~~each year~~ from the reproduction dataset and the ~~X~~ number of females counted each year from *C1*.
- 204 • IPM_{ind} using the survival, reproduction and inheritance dataset including the individual trait.
- 206 • IPM^2_{C1} , IPM^2_{C2} and IPM^2_{C3} using count data (either *C1*, *C2* or *C3*) in

normalized?

207 addition to the datasets that are used for IPM_{ind} .

208 We scaled individual trait ~~as well as~~ the environmental trend to improve convergence. We ~~fitted~~ the models in a Bayesian framework using program NIMBLE (NIMBLE Development Team, 2016) run from R (R Core Team, 2014). We chose diffuse prior distributions for all parameters and generated ~~three~~ chains of length 50,000, ~~using~~ the first 25,000 ~~as~~ *samples* ~~for an additional 10 years~~ *to follow 10 years* and compared these predictions with the truth in the simulated data. ~~An~~ Assessment of the predictive abilities of the models is important for judging their suitability to predict consequences of future environmental changes.

218 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 of the first ten years with the true demographic rates. Second, we compared the predicted demographic rates of the ~~the~~ following years with the true *ones*. Finally, we compared the bias ($posterior\ mean - truth$) and precision (using mean squared errors $MSE = bias^2 + variance$) of estimators of the slopes of each function used to derive the demographic rates using IPM_{ind} and the three IPM^2 .

225 Application to barn swallows

226 The barn swallow (*Hirundo rustica*) is a short-lived, double breeding 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.

230 The laying date has a strong impact on the reproductive output; later first broods
231 yield lower annual reproductive output (Grüebler & Naef-Daenzer, 2008). More-
232 over, fledglings from an early brood have longer life expectancy than fledglings
233 from late broods (Saino *et al.*, 2012). The annual dynamics of the laying-date
234 distribution is described using five functions:

235 • **A**nnual number of successful clutches and **n**umber of fledglings per
236 successful clutch of a pair according to the laying date of the first clutch
237 ($N = 2605$ pairs).

238 • **A**nnual survival according to individual age (< 1 year old or older), sex
239 and laying date of the first clutch ($N = 12222$ individuals). Barn swallows
240 were subject to imperfect detection, hence, we used capture-mark-recapture
241 models to estimate the recapture probability and the annual survival based
242 on previous analysis of these populations (Schaub *et al.*, 2015).

243 • ~~Ne~~**T**ransition between successive annual laying dates of first clutches (using
244 $N = 1053$ duos of successive laying date of first clutches). In contrast to the
245 simulation study, ~~we here~~ ^{here we} include ~~a~~ a transition function, because laying date
246 ~~is not a fixed individual trait~~ *can vary by individual!*

247 • ~~the~~**I**nheritance: laying date of first clutches according to birth laying date
248 ($N = 192$ filiations) and whether the bird ~~as a nestling~~ was born into a first
249 or a second (including also the rare third broods) brood.

250 We used data sampled in 12 populations located throughout Switzerland from
251 1997 to 2004 (see Schaub & von Hirschheydt 2009; Schaub *et al.* 2015; Grüebler
252 *et al.* 2010 for more details) to estimate the intercept and slopes of these functions.

taken

253 Variation among populations was taking into account by including ~~an effect of~~ a
254 site-specific environmental variable. We used spring precipitations (~~sum across~~
255 March to June) as an index of the environmental conditions influencing the avail-
256 ability of resources at each site. Using an IPM^2_{C3} and an IPM_{ind} , we tested the
257 main and interaction effects of individual laying date and spring precipitation on
258 the five functions. Using an IPM_{pop} , we investigated the influence of spring precip-
259 itation only on annual survival, annual number of successful clutches and number
260 of fledglings per successful clutch. Priors and MCMC settings were set identically
261 to ~~the ones~~ *those from* the simulation study. For each model, we conducted vari-
262 able selection iteratively ~~by use of~~ *using* 95% credible intervals (CRI). If the CRI of the
263 interaction term included zero, we removed it, refitted the model with the main
264 effects only and then repeated this for the main effects of individual laying date
265 and spring precipitation in the different functions.

266 As count data, we summed the number of breeding pairs in four (out of the
267 12) populations that were surveyed *every year* ~~annually~~ from 1997 to 2003. To estimate the
268 average demographic rates for the global Swiss population, we used the average of
269 spring precipitation over sites. The Swiss population was geographically open and
270 thus emigration and immigration ~~has~~ *must* be addressed. Emigration was already
271 accounted for, because we used capture-recapture data ~~with~~ *from* which apparent sur-
272 vival, the probability of surviving and staying in the population, was estimated.
273 Immigration was estimated when possible (using IPM_{pop} and IPM^2_{C3}) ~~with~~ *using* the
274 assumption that the distribution of laying dates among immigrants was the same
275 as the distribution of laying dates of residents.

276 We estimated the demographic rates of the Swiss population from 1997 to 2004
277 under each model (IPM_{pop} , IPM_{ind} and IPM^2_{C3}). Finally, we used the three models

²⁷⁸ to forecast the population development of the barn swallows from 2005 to 2015
²⁷⁹ across Switzerland. We compared these predictions with the annual population
²⁸⁰ index of barn swallows compiled from bird monitoring data sampled at 267 1km²
²⁸¹ plots across Switzerland (Sattler *et al.*, 2016).

²⁸² Results

²⁸³ In most cases, the three models IPM²_{C3}, IPM²_{C2} and IPM²_{C1} yielded very similar
²⁸⁴ estimates that were very close to true values, so we report the results ~~for the three~~
²⁸⁵ ~~of them~~ together. *X for those three models*

²⁸⁶ Estimation of demographic rates

²⁸⁷ In scenarios I and II, the ~~agreement of~~ estimates between all models and true simulated values *from*
²⁸⁸ *agreed quite well.* ~~was particularly good~~ (Fig. 2). Generally, the novel IPM² produced
²⁸⁹ more precise estimates than ~~the two~~ "simple" IPMs. *Either* 95% intervals of population
²⁹⁰ growth rate were 83% and 67% larger in IPM_{pop} than in IPM² and 33% and 42%
²⁹¹ larger in IPM_{ind} than in IPM². *Averaged* over the 10 first years of scenarios I and
²⁹² II, respectively.

²⁹³ In scenario III, the environmental pressure was ~~stronger on~~ individuals with a
²⁹⁴ large ~~than a small~~ trait value, which results in a faster adaptation ~~of the former~~
²⁹⁵ *Changer in* ~~changing~~ environmental conditions. Estimates of demographic rates from the
²⁹⁶ IPM_{pop} were biased in most years (Fig. 2). IPM_{ind} over-estimated all demographic
²⁹⁷ rates (mean of juvenile and adult survival and reproduction were 17%, 1% and 30%
²⁹⁸ higher than true values, on average) *as well as* population growth rate (4% higher than
²⁹⁹ true values, on average) at the end of the 10 first years. Moreover 95% intervals of

hyphen

Fig.

300 annual demographic rates were particularly large showing that IPM_{ind} converged
301 far from true values in some ~~of~~ simulations (fig. 2). These errors were caused
302 by the non-linearity of the reproductive function, ~~that~~ which induced an increase ~~of the~~
303 mean reproduction and ~~of the size of the~~ number of? individuals recruited in the population
304 over time. The average individual trait value of adults predicted under IPM_{ind}
305 could be 10 times higher than truth ~~at the end of the first~~ after 10 years. This never
306 ~~occurred~~ happened under IPM². Estimates of demographic rates under IPM² were similar
307 to true values.

308 Population forecasting

Fig.

309 The demographic rates and population growth rate could reliably be predicted
310 by all models under scenarios I and II (fig. 3). In scenario III, however, only
~~IPM² produced accurate predictions.~~
311 ~~predictions under IPM² were accurate.~~ IPM_{pop} underestimated most demographic
312 rates and consequently also population growth, the latter ~~up to~~ as much as 64% in the final
313 predicted year. By contrast, IPM_{ind} overestimated most demographic rates and
314 hence population growth rate, the latter ~~up to~~ as much as 106% in the final year.

315 Parameters of survival and reproductive functions

Fig.

316 Mean estimates of the intercept and slope parameters influencing demographic
317 rates were accurate and similar in IPM_{ind} and the three IPM² (fig. S3). In all
318 scenarios, standard deviations of the slopes of the survival and the reproductive
319 functions were higher in IPM_{ind} than in IPM², resulting in higher MSE in IPM_{ind}.
320 Thus, estimates were more precise using IPM².

321 Parameters of the inheritance function

322 The estimates of the slope of the inheritance function were slightly underestimated
323 but more precise using IPM² than IPM_{ind} in all scenarios, ~~and~~ particularly ~~in~~ sce-
324 nario III (Fig. 4, on average in this scenario, the slope values were differing from
325 the true value by 11% and 3% using IPM² and IPM_{ind}, respectively).

326 When only 2% of the mother-offspring filiations were sampled to estimate the
327 inheritance function, the benefit in terms of precision from the IPM² compared to
328 the IPM_{ind} was even larger (Fig. 4). Among the three models of IPM², IPM²_{C3} and
329 IPM²_{C2} produced slightly more precise estimates than IPM²_{C1} (Fig. 4).

330 Population dynamics of Swiss barn swallows

331 We found a significant negative influence of spring precipitation on annual survival
332 of barn swallows (slope: -0.10^{95%} CRI:[-0.16;-0.03]) but not on reproductive rates
333 when the data were analysed with the IPM_{pop} (Table S2). However, using IPM²,
334 we found that demographic rates were also influenced by individual laying date
335 of the first clutch. Individual laying date influenced negatively annual survival
336 (slope:-0.15^{95%}[-0.23;-0.07], Table S2), the annual number of successful clutches and
337 the number of fledglings per successful clutch (Figs. S4 and S5). Successive annual
338 laying dates of first clutches were positively correlated and positively related to
339 precipitation (Fig. S6). First year laying date was not influenced by maternal laying
340 date ([-0.16;0.16]) but was delayed in years with high precipitation (Fig. S7). The
341 results from IPM_{ind} were similar to those under an IPM² (Table S2), except ~~that~~
342 ^{for} 95% CRI ~~of~~ the effect of precipitation on first year laying date and on annual
343 survival included 0 ([-0.03;0.22] and [-0.08;0.07], respectively, Table S2) and were

³⁴⁴ thus removed from the model. The annual demographic rates based on the three
³⁴⁵ models were similar in most years (Fig. S8). Immigration rate estimated under
³⁴⁶ IPM_{pop} and IPM² was substantial (Table S2). → do you mean significant?
³⁴⁷ The predictions of the population index of barn swallows during the 12 years
³⁴⁸ following the study period were similar from IPM² and IPM_{pop} (Fig. 5), but very
³⁴⁹ different from IPM_{ind}. The predictions from IPM² and IPM_{pop} were remarkably
³⁵⁰ similar to the population index estimated from independent monitoring birds data.
³⁵¹ The predictions of IPM² including individual laying date were slightly better than
³⁵² the ones of IPM_{pop} (predictions from IPM² vs. IPM_{pop} explained 46% vs. 44% of
³⁵³ the variation in the Swiss national index, respectively). IPM_{ind} was unsuccessful
³⁵⁴ for prediction and explained only 9% of the variation.

³⁵⁵ Discussion

³⁵⁶ We developed a population model that can estimate heterogeneous individual de-
³⁵⁷ mographic responses in a changing environment and predict the resulting popula-
³⁵⁸ tion dynamics. This integrated integral projection model (IPM²) is a combination
³⁵⁹ of the existing integral projection and integrated population models and shares the
³⁶⁰ key benefits of each of them. Basically, the new model can either be regarded as
³⁶¹ an extension of an integral projection model that includes count data ~~also~~ ~~in addition~~,
³⁶² or as an extension of an integrated population model that considers individual
³⁶³ traits by ~~including additional information about the link of individuals traits on~~ ^{This}
³⁶⁴ ^{linking them to} demographic rates and their inheritance. Key benefits are that the influence of
³⁶⁵ individual traits on population dynamics can be assessed, ~~that~~ parameter esti-
³⁶⁶ mates become more precise, ~~that~~ population dynamics can be estimated including

³⁶⁷ demographic processes for which no explicit data have been collected, and that ~~less~~

³⁶⁸ a smaller amount of the difficult to gather affiliation data needs to be collected.

³⁶⁹ The model yielded accurate population predictions even if the individuals react

³⁷⁰ differentially to environmental changes. *with individual heterogeneity to environmental factors.*

³⁷¹ The simulation study showed that the count data without information about

³⁷² the individual traits (IPM^2_{C1}) is enough to obtain accurate population predictions,

³⁷³ unless inheritance data are particularly scarce. In this case it is preferable to

³⁷⁴ include a rough measure (small, medium, large) of each counted individual using

³⁷⁵ IPM^2_{C2} . Thus, the count data that need to be included generally do not require

³⁷⁶ additional capture of individuals.

³⁷⁷ Model assumptions

³⁷⁸ Here we used a very simple and specific life cycle model with a single trait and a

³⁷⁹ single environmental covariate, but in principle IPM^2 can be adapted to any life

³⁸⁰ cycle by adapting the model structure and by adding several traits or functions

³⁸¹ *otherwise* (linear or ~~not~~) as used in other IPM_{ind} (Ellner *et al.*, 2016). Influence of density as

³⁸² well as intra- or inter-species competition can also easily be included in an IPM^2 .

³⁸³ In our simple IPM^2 , we did not include demographic stochasticity but assumed

³⁸⁴ that individual heterogeneity in demographic performance was shaped by individ-

³⁸⁵ ual traits only as usually done in IPM_{ind} . In IPM_{pop} , all individuals in a given age-

³⁸⁶ or stage-class are assumed to be identical and, annual heterogeneity in individ-

³⁸⁷ ual performance is created ~~by~~ *only through* demographic stochasticity ~~by~~. Both demographic

³⁸⁸ stochasticity and individual heterogeneity linked to identified or unidentified indi-

³⁸⁹ vidual traits are expected to influence population dynamics (Cam *et al.*, 2016). It

(which is typically difficult to collect)

(which is typically difficult to collect).

390 is an asset of the new IPM² that demographic stochasticity as well as other sources
391 of individual heterogeneity can easily be included (Coulson, 2012).

392 The joint likelihood of the IPM² is formed as a product of the single-data likeli-
393 hoods and therefore requires the assumption of independence among datasets. The
394 violation of this assumption can affect parameter estimates (Besbeas *et al.*, 2009),
395 but the impact is often non-existent or irrelevant (Abadi *et al.*, 2010; Schaub *et al.*,
396 2015). In the case of our new model, we have not explicitly explored the effects
397 of the violation of the independence assumption, but we note that our simulated
398 data are dependent to some degree because we simulated the data collection to
399 mimic a real field study. Since the performance of the estimators was good, we
400 think that the violation of this assumption is not a serious issue for the specific
401 models that we have used. However, more research should evaluate this issue in
402 the future and possibly develop more general models that can handle dependent
403 datasets.

404 The reproductive function linking reproductive success to individual trait was
405 non-linear in the simulations, increasing exponentially with the individual trait.
406 This has strongly contributed to the highly-biased predictions of IPM_{ind}. Individual
407 heterogeneity can influence population dynamics two-fold twice as much when the functions
408 are non-linear, relative to the linear case. Nevertheless, this assumption was justified because repro-
409 ductive output is often modeled with a log link in empirical analyses. Moreover, in
410 some species of plants or oviparous animals, it is common that reproductive out-
411 put increases exponentially with individual size. For instance (Dauer & Jongejans,
412 2013; Miller *et al.*, 2012; Vindenes, 2014).

414 Application to barn swallow

415 Forecasting of the size of the Swiss population of barn swallows under IPM² and
416 IPM_{pop} was very similar to the independent population index estimated from mon-
417 itoring data. The main reason why IPM_{ind} was unsuccessful for forecasting is that
418 this model did not include immigration. This result shows that barn swallow popu-
419 lation dynamics ~~was~~ ^{Wese} strongly driven by the effect of spring precipitation on annual
420 survival and by immigration.

421 The benefit of using IPM² instead of IPM_{pop} can be found in our better under-
422 standing of the mechanisms linking spring precipitation to demographic rates of
423 the barn swallow. The IPM_{pop} only evidenced that there ~~was~~ ^{indicated} a negative effect of
424 spring precipitation on annual survival. However the IPM² allowed us understand-
425 ing that spring precipitation influenced negatively directly and indirectly annual
426 survival. High spring precipitation had an indirect negative effect on individual
427 survival because it also led to delay individual laying date of the first clutch. The
428 IPM² showed that this phenological delay influenced negatively individual sur-
429 vival ~~but also~~ ^{as well as} reproductive outputs. The latter is a well-known result in most
430 birds (Perrins, 1970) but cannot be included in an IPM_{pop}. ^{shown} ~~included~~ ^{had a negative effect on}

431 Population forecasting in a changing environment needs IPM²

432 When ~~ever~~ ^{Covariables} individual traits affect demographic rates with interacting environmen-
433 tal co-variables (as in scenario III), only IPM² produced adequate predictions.
434 This was to be expected, because IPM_{pop} ~~do~~ ^{does} not include individual traits and be-
435 cause IPM_{ind} ~~do~~ ^{does} not make the link between predictions ~~at~~ ^{between} the population level and
436 observed data.

(maybe ignore these, if
IPM_{ind} is meant to be plural)
²¹

(maybe ignore)

437 When individual demographic rates are influenced linearly and homogeneously
438 by annual environmental variables, IPM_{pop} gives accurate estimates and predictions
439 of population size (Johnson *et al.*, 2010; Abadi *et al.*, 2017). However, the influence
440 of any environmental variable is often followed by a heterogeneous individual
441 adaptive or plastic response that will influence demographic rates. For instance,
442 individual laying date is often a plastic trait that responds to environmental
443 changes and has repercussions on reproductive success, as shown in our barn swallow population and in many other bird populations (Charmantier & Gienapp, 2014). Understanding how individual traits shape demography and population dynamics, cannot be performed using an IPM_{pop} while it is needed to improve our understanding of the evolution of quantitative traits.

448 In this direction, IPM_{ind} are very useful to address various questions in ecological evolutionary dynamics (Coulson *et al.*, 2010; Smallegange & Coulson, 2013) at equilibrium or in a constant environment. However, when using an IPM_{ind} to predict population dynamics over successive years in a variable environment, one might check that the distribution of individual traits (see also detecting individual eviction, Williams *et al.* 2012) as well as population size remain close to what is observed in the data. IPM² corrected for the former possible bias by slightly underestimating the slope of the inheritance function in our simulation analysis. For the latter bias or when working in open populations, IPM² allows estimating demographic processes for which not much data are available. For instance, IPM² allowed us to include immigration in the population models for the barn swallows (Abadi *et al.*, 2010). Moreover, IPM² helps to get better estimates of the inheritance function when the inheritance data are scarce. Finally, as a general benefit, modeling demographic rates in the same framework together with count

natural inclusion of
~~the~~

- ⁴⁶² data allows including easily spatial or temporal covariations between survival and
⁴⁶³ reproductive rates, for instance and investigate their influence on population dy-
⁴⁶⁴ namics (Elderd & Miller, 2016; Koons *et al.*, 2016).

⁴⁶⁵ Conclusion

- ⁴⁶⁶ Responses to environmental pressures can vary among individuals and are the main
⁴⁶⁷ drivers of pattern of eco-evolutionary dynamics. To forecast population dynamics,
⁴⁶⁸ we need to understand the individual drivers of populations and thus to include
⁴⁶⁹ individual responses to their environment while following the entire population.
⁴⁷⁰ As a consequence, combining data both at the individual and at the population
⁴⁷¹ level which is done in the new IPM² will help our predictions ~~X~~ become more
⁴⁷² accurate, and thus more powerful in science and more relevant in management.

⁴⁷³ Acknowledgments

- ⁴⁷⁴ We are grateful to all the volunteers and colleagues that have helped in collecting the
⁴⁷⁵ data in the 12 monitored barn swallow populations of the 267 monitoring plots. We
^{also} ~~thank~~
⁴⁷⁶ ~~thanks~~ Marc Kéry and Jan von Rönn for helpful discussion on a previous version of the
⁴⁷⁷ manuscript.

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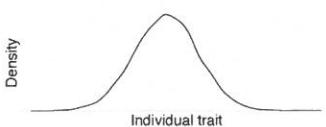
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⁶¹⁴ **Table 1:** Comparison between IPM_{pop}, IPM² and IPM_{ind}.

	IPM _{pop}	IPM ²	IPM _{ind}
Population size	N_t^A, N_t^J		 <p style="text-align: center;">Density Individual trait</p>
Model	$\begin{pmatrix} R_t * S_t^J & R_t * S_t^A \\ S_t^J & S_t^A \end{pmatrix}$	$\begin{pmatrix} I * R_t * S_t^J & I * R_t * S_t^A \\ S_t^J & S_t^A \end{pmatrix}$	
Demographic rates	$\text{logit}(S^J(t)) = i_S + b_S * e_t$ $\text{logit}(S^A(t)) = i_S + i_S^a + b_S * e_t$ $\log(R(t)) = i_R + b_R * e_t$	$\text{logit}(S^J(z, t)) = i_S + b_S * e_t + c_S * z$ $\text{logit}(S^A(z, t)) = i_S + i_S^a + b_S * e_t + c_S * z$ $\log(R(z, t)) = i_R + b_R * e_t + c_R * z$ $I \sim \mathcal{N}(\mu_I = i_I + c_I * z, \sigma_I)$	
Covariates	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 predictions close to reality Can estimate latent demographic processes More accurate estimates	Eco-evolutionary dynamics Include individual mechanisms Can predict population dynamics including heterogeneous individual responses in a changing environment	

615 Figure captions

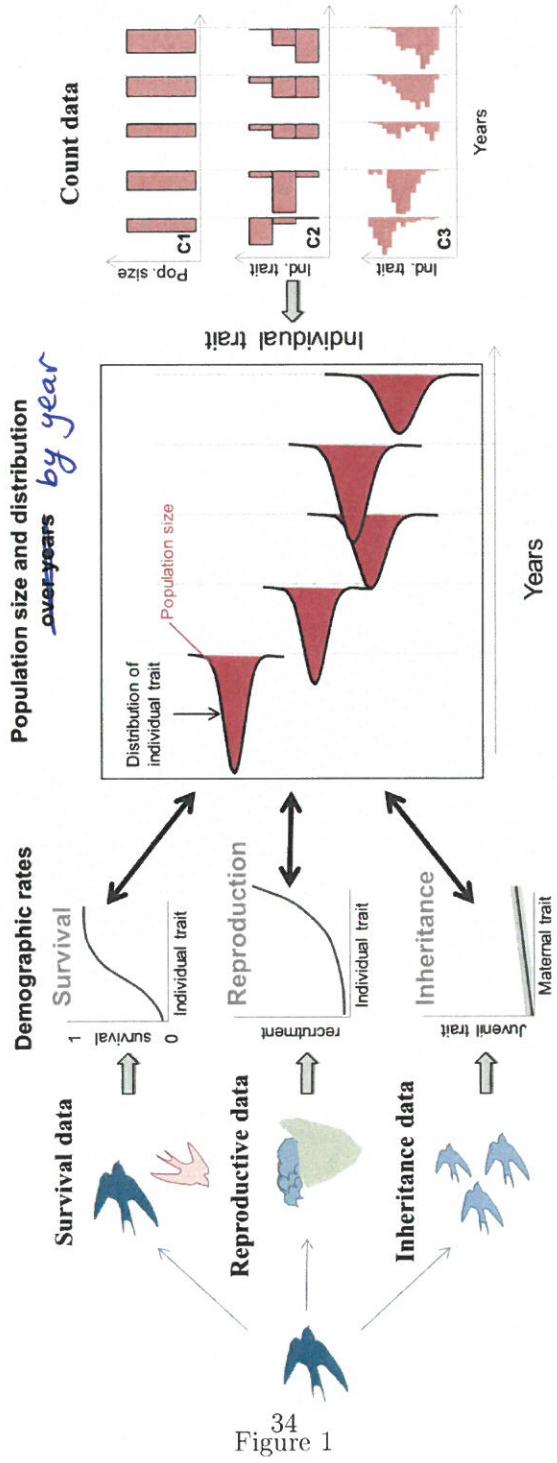
singular, again...?

- 616 **Figure 1:** Conceptual overview of an IPM² describing the dynamics of the distribution of a continuous fixed individual trait (such as wing length) in a population.
- 617 The survival (Sdata), reproductive (Rdata) and inheritance (Idata) datasets are
- 618 used to estimate the influence of the individual trait on demographic rates. These
- 619 estimates are also influenced by the fit between the predicted population size and
- 620 its distribution each year and the count dataset. C1 includes only counts, C2 in-
- 621 cludes counts and a classification of the individual trait of each counted individual,
- 622 and C3 includes counts and the precise value of the individual trait of each ~~counted~~
- 623 individual. C1, C2 or C3 are used to fit an IPM²_{C1}, an IPM²_{C2} or an IPM²_{C3},
- 624 respectively.
- 625
- 626 **Figure 2:** Estimates of demographic rates and population growth rates during
- 627 years 7 to 10 under scenarios I (including only an effect of the individual trait)
- 628 and II (including additive effects of the individual and environmental covariables)
- 629 and during the 10 first years for scenario III (including interactive effects of the
- 630 individual and environmental covariables) using the ~~five~~ different models: IPM²_{C3},
- 631 IPM²_{C2}, IPM²_{C1}, IPM_{ind} and IPM_{pop} (~~in this order~~ from left to right). Averages
- 632 (points) and 95% ~~interval~~ (vertical lines) of posterior means from 500 simulations
- 633 are ~~represented~~. Averages and 95% intervals of the true demographic rates esti-
- 634 mated over 500 sampled populations are ~~represented~~ using a dashed black line and
- 635 a grey rectangle, respectively.
- 636
- 637 **Figure 3:** Forecasting of demographic rates and population growth rates during
- 638 the years 11 to 20 under the three scenarios using the ~~three~~ different models: IPM²_{C3},
- IPM_{ind} and IPM_{pop} (~~in this order~~ from left to right). Averages (points) and 95%

639 intervals (vertical lines) of posterior means from 500 simulations are ~~represented~~
640 *shown*
641 IPM²_{C1} and IPM²_{C2} are not ~~presented~~ because they gave the same results as
642 IPM²_{C3}. Averages and 95% intervals of the true demographic rates estimated over
643 500 sampled populations are ~~represented~~ using a dashed black line and a grey
rectangle, respectively.

644 **Figure 4:** Comparison of bias and mean squared errors (MSE) of the slope of the
645 inheritance function estimated under the three different scenarios when 20% or 2%
646 of the filiation data were collected. Boxplots of estimators from IPM_{ind} and IPM²
647 are ~~in~~ *shown* grey and white respectively. IPM²_{C3}, IPM²_{C2} and IPM²_{C1} are ~~presented~~
648 in white, *ordered* in white ~~in this order~~ from the left to the right.

649 **Figure 5:** Predictions of the Swiss barn swallow population index and their 95%
650 credible intervals from 2004 to 2015 using model IPM²_{C3} (solid red lines), IPM_{pop}
651 (dashed blue lines) and IPM_{ind} (dotted green lines). Models were *fitted* using data
652 collected ~~by~~ *from* 12 populations in Switzerland from 1997 to 2003. The 95% *confidence*
653 interval of the Swiss population index estimated from independent monitoring *bird*
654 data is *represented* in grey.



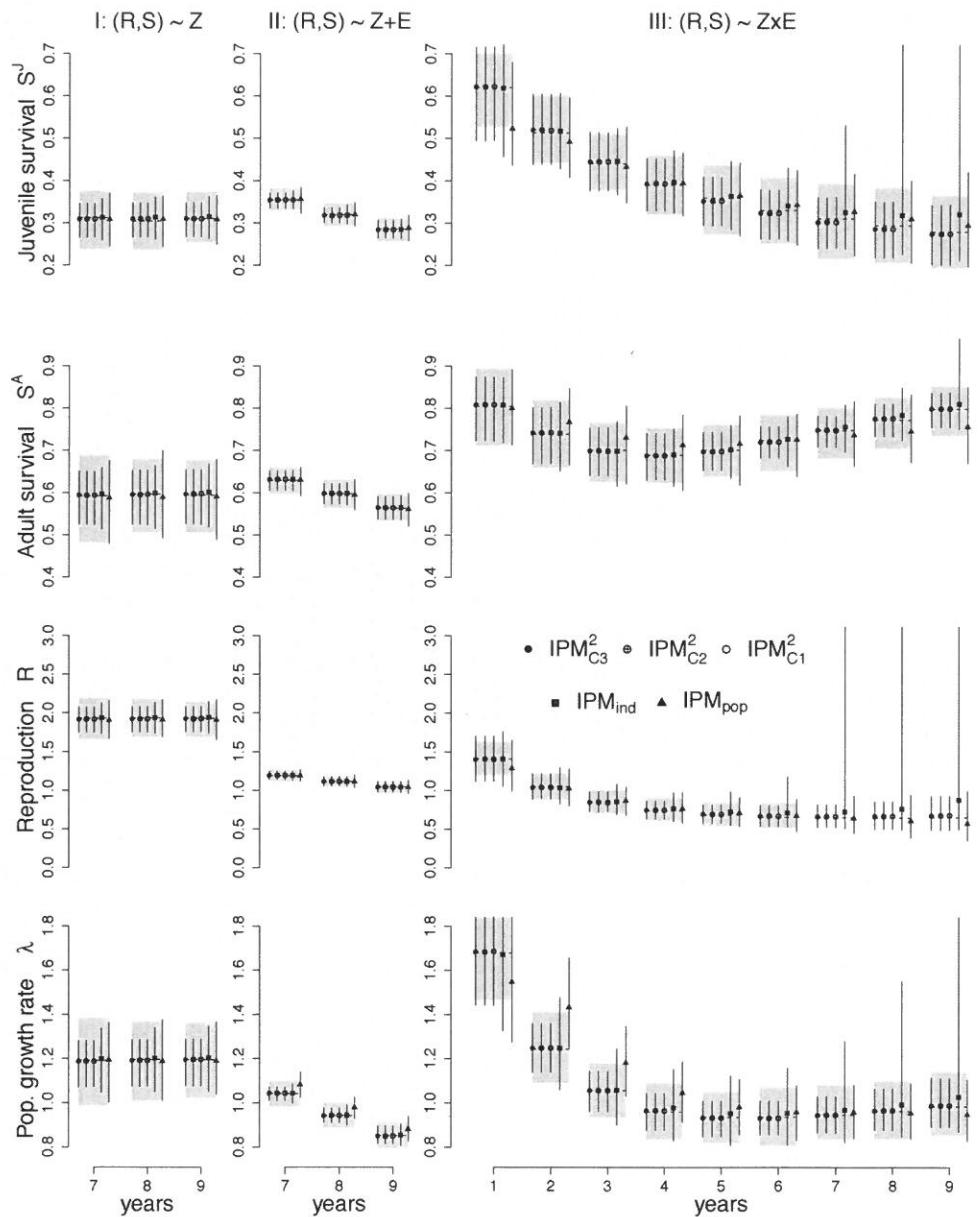


Figure 2

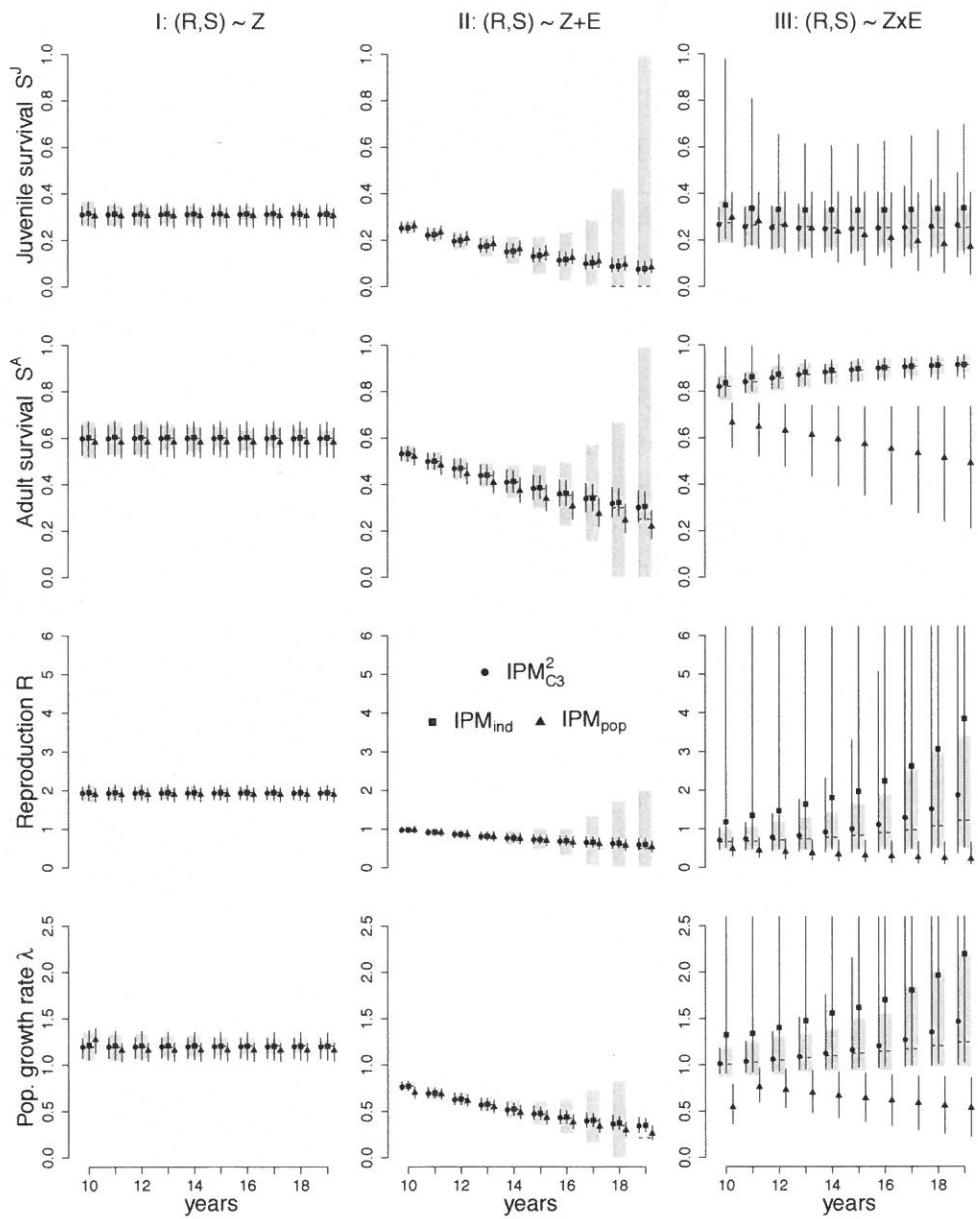


Figure 3

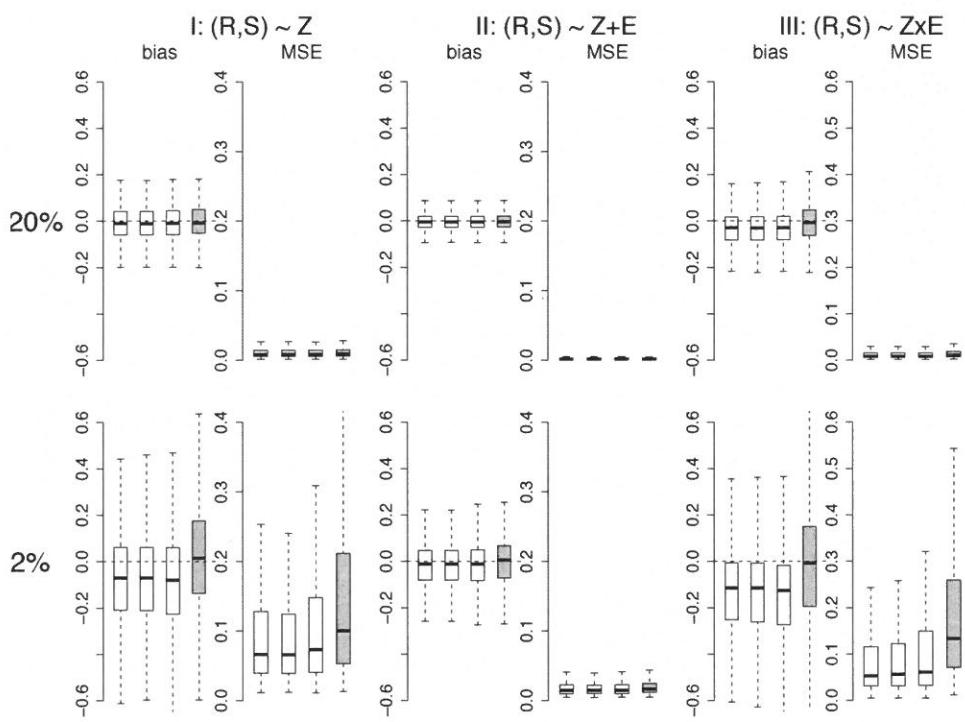


Figure 4

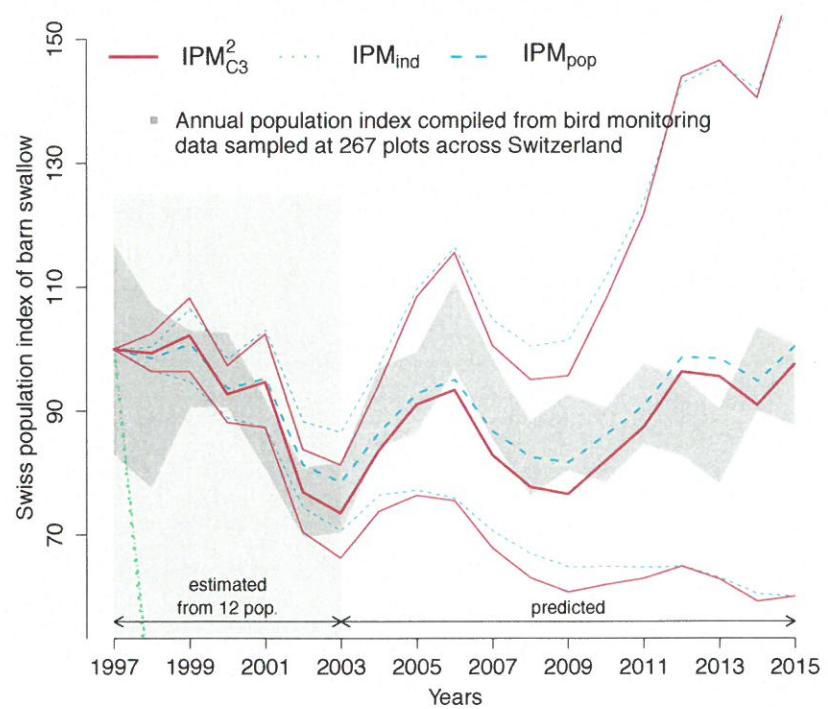


Figure 5

655 Supplementary information

656 Appendix S1: Simulation study

657 Three different scenarios were used to simulate populations:

- (I) Survival and reproductive rates are influenced by an individual trait (z), but not by an environmental trend.

$$\text{logit}(S^J(z, t))_I = i_S + c_S * z \quad (11)$$

$$\text{logit}(S^A(z, t))_I = i_S + i_S^a + c_S * z$$

$$\log(R(z, t))_I = i_R + c_R * z$$

- (II) The individual trait and the environmental trend have additive effects on survival and reproductive rates.

$$\text{logit}(S^J(z, t))_{II} = i_S + c_S * z + b_S * e_t \quad (12)$$

$$\text{logit}(S^A(z, t))_{II} = i_S + i_S^a + c_S * z + b_S * e_t$$

$$\log(R(z, t))_{II} = i_R + c_R * z + b_R * e_t$$

- (III) The individual trait and the environmental trend have interactive effects on survival and reproductive rates.

$$\text{logit}(S^J(z, t))_{III} = i_S + c_S * z + b_S * e_t + d_S * z * e_t \quad (13)$$

$$\text{logit}(S^A(z, t))_{III} = i_S + i_S^a + c_S * z + b_S * e_t + d_S * z * e_t$$

$$\log(R(z, t))_{III} = i_R + c_R * z + b_R * e_t + d_R * z * e_t$$

These values

658 The values used for each parameter are shown in Table S1. They are typical
659 for a short-lived species.

Table S1: Parameters used to simulate the different populations under the three
different scenarios. The same inheritance function was used in all scenarios.
each scenario.

	Inheritance			i	c	σ_I^2						
	0	0.3	1									
	I			II			III					
Survival	i	i_a	c	i	i_a	c	b	i	i_a	c	b	d
Reproduction	-1	1	0.5	0.5	1	0.5	-0.18	1	1	0.5	-0.55	0.25
	0.5		0.17	0.6		0.17	-0.08	0.7		0.15	-0.5	0.15

To mimic a data collection that would have taken place in the field, we sampled simulated some females from the created population. The sampling process worked in the following way: during the first year, a proportion p_{rs} of the female adults were 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 has been collected by observations. Because we only had a limited number of tracking material, a proportion p_i of these female chicks were marked. In addition, random searches allowed a proportion p_{rs} of new female chicks (for which we did not know the mother) each year to be found and marked. The individual traits of all females were measured without error when they were marked. Independently, an annual survey during the breeding period allowed counting a proportion p_C of the breeding females. For this survey data, we simulated three cases: C1: contains the number of counted females only without measures of the individual trait, C2: contains the number of counted females as well as categorical information about the individual

trait of each counted female (small, medium or tall). C3: contains the number of counted females and exact information about the individual trait of each counted female.

and
~~simulated~~ *partially linked*

Finally, we obtained four datasets: partially linked:

- Survival dataset: *annual* survival data of each marked female ~~in each year~~, *including* their individual trait and their age.
- Reproduction dataset: *annual* reproductive success of a surviving marked female ~~females, in~~ in relation to year and individual trait.
- Inheritance dataset: nestling trait according to year and maternal trait, including all the nestlings belonging to a clutch that have been marked and measured and produced by ~~a~~ marked female~~s~~.
- Count dataset: *annual* number of sampled breeding females ~~in each year~~ (for C1, C2, and C3), *including* the distribution of the individual trait (C2: one of three trait classes for each counted female; C3: exact measurement of each counted female).

We used an initial population size of 100 adult females ~~for year 0 in all scenarios~~ *in each scenario*.

The ~~above defined~~ survival, reproductive and inheritance functions (Table S1) were performed 500 simulations of... *progress over* used to simulate the ~~life~~ fate of each individual ~~during~~ over 20 years. For each scenario, we simulated 500 times the population and the data collection. We fitted the different population models ~~to~~ to the first 10 years *of data* to obtain estimates of the different function parameters and demographic rates. We then forecast the demographic rates and population size for the ~~following~~ next 10 years and compared the predictions with the true simulated demographic rates and population sizes.

Each sampled population was analyzed with ~~the~~ different models. The specific datasets that each model uses are summarized below. *using five*
~~used~~ *used by each model are?*

- IPM_{pop} *needed three annual* datasets: a) the number of surviving females *each year* from the survival dataset, b) the *number of recruits per female each year* from the reproduction dataset and c) the *number of females counted each year* ($C1$).

- IPM_{ind} *needed three annual* datasets: a) the *number of surviving females each year* from the survival dataset, including the information about the female trait, b) the *number of recruits per female each year* including the information about the female trait and c) the inheritance dataset.

- $IPM^2_{C1}, IPM^2_{C2}, IPM^2_{C3}$ ~~all~~ *needed four* datasets. All needed the ~~the~~ *same* datasets as the IPM_{ind} , and in addition one count dataset (either $C1, C2$ or $C3$).

mid-points

We used 50 *mid points* to describe the distribution of the individual trait in IPM_{ind} and IPM^2 . Individual as well as environmental covariates were scaled to facilitate convergence. We used normal distributions with mean 0 and variance 10^2 as priors for regression slopes and intercept and uniform distributions over the interval $[0,100]$ as priors for the standard deviations of the inheritance function (Kéry & Schaub, 2012). The parameter values of the simulated populations were used as initial values. To avoid any influence of initial population distribution in first year on the results of IPM^2 and IPM_{ind} , we used the true distribution to initialize *values for the first year*. The initial population distribution must be a continuous distribution and should not be directly estimated as a "histogram" using the data approximated using a histogram of

gaps

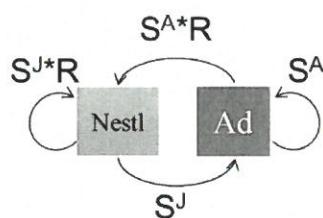
to avoid having ~~holes~~ in the distribution due to individual sampling. Convergence
~~was assessed~~
of all chains has been checked using the Gelman and Rubin convergence diagnostic
($R < 1.5$, Gelman & Rubin 1992).

Table S2: Parameter estimates from the IPM_{pop} , IPM^2 and IPM_{ind} of the functions describing the demography of the 12 barn swallow populations from Switzerland. Means, standard deviations and 95% credible intervals of each parameter are presented. The parameters that were not selected under IPM^2_{C3} were also removed when using IPM_{ind} or IPM_{pop} and are not presented here. *a*: intercepts $i_{S_{age}}$ and $i_{S_{sex}}$: additional *intercepts* for adult and female survival, respectively, $i_{I_{age}}$: correction for age as first-year individuals often lay eggs later than adults, and $i_{I_{clutch}}$: correction for individuals born in a second clutch). *b*: slope linked to environmental covariate, *c*: slope linked to individual trait, σ : standard deviation.

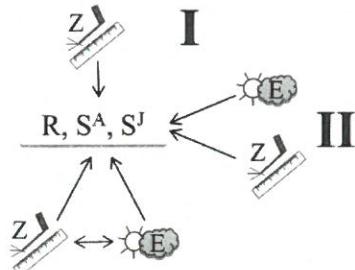
ok.

	IPM _{pop}				IPM ²				IPM _{ind}			
	mean	sd	2.5%	97.5%	mean	sd	2.5%	97.5%	mean	sd	2.5%	97.5%
Survival												
i_S	-3.62	0.15	-3.86	-3.22	-3.65	0.13	-3.87	-3.32	-3.69	0.11	-3.92	-3.47
i_{Sage}	2.99	0.16	2.57	3.26	2.97	0.14	2.64	3.22	3.02	0.13	2.77	3.27
i_{Ssex}	0.41	0.07	0.27	0.55	0.41	0.08	0.26	0.56	0.39	0.08	0.24	0.54
c_S	Not assessable				-0.15	0.04	-0.23	-0.07	-0.13	0.04	-0.21	-0.05
b_S	-0.10	0.03	-0.16	-0.03	-0.07	0.03	-0.14	-0.01	removed		-0.08	0.07
Recapture												
i_{p^O}	-1.35	1.01	-3.40	0.71	-1.38	1.09	-3.81	0.70	-1.15	1.30	-3.83	1.39
i_{p^A}	1.75	0.28	1.23	2.31	1.81	0.26	1.31	2.32	1.73	0.26	1.23	2.24
σ_p	2.16	0.86	1.11	4.36	2.21	0.90	1.15	4.46	2.23	0.95	1.13	4.74
σ_{site}	2.19	0.68	1.25	3.85	2.22	0.69	1.26	3.88	2.20	0.69	1.24	3.89
Number of successful clutches												
i_R	0.36	0.02	0.32	0.39	0.34	0.02	0.31	0.37	0.34	0.02	0.31	0.37
c_R	Not assessable				-0.22	0.02	-0.25	-0.18	-0.22	0.02	-0.25	-0.18
Number of fledglings/successful clutch												
i_F	4.04	0.02	4.00	4.08	4.03	0.02	3.99	4.06	4.03	0.02	3.99	4.06
c_S	Not assessable				-0.24	0.02	-0.28	-0.20	-0.24	0.02	-0.28	-0.20
σ_F	0.94	0.01	0.92	0.97	0.91	0.01	0.89	0.94	0.91	0.01	0.89	0.94
Transitions between annual first laying dates												
i_T	Not assessable				-0.60	0.02	-0.64	-0.56	-0.60	0.02	-0.64	-0.56
c_T					0.19	0.02	0.15	0.23	0.19	0.02	0.15	0.23
b_T					0.16	0.02	0.12	0.19	0.16	0.02	0.12	0.19
σ_T					0.62	0.01	0.60	0.65	0.62	0.01	0.60	0.65
Inheritance												
a_I	Not assessable				0.58	0.08	0.42	0.74	0.51	0.08	0.35	0.67
i_{Iage}					-0.83	0.15	-1.12	-0.53	-0.79	0.15	-1.08	-0.50
$i_{Iclutch}$					-0.30	0.16	-0.61	0.00	-0.29	0.16	-0.60	0.02
b_I					0.13	0.06	0.01	0.26	removed		-0.03	0.22
σ_I					0.90	0.05	0.81	0.99	0.90	0.05	0.82	1.00
Immigration	7.58	1.20	4.71	9.67	8.03	1.12	5.49	10.07	Not assessable			

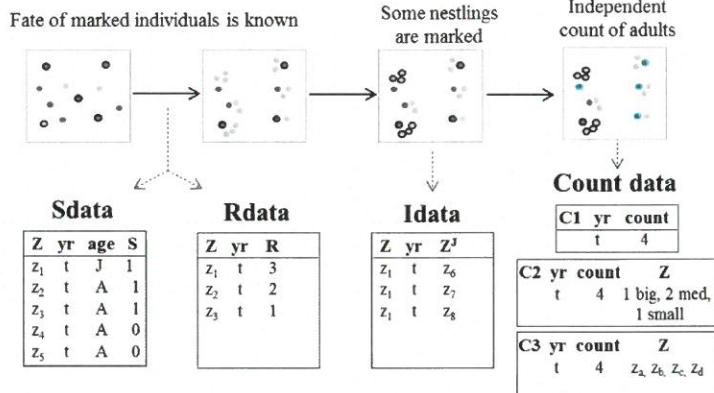
Population



3 scenarios



Sampling: each year



Analysis: 5 models

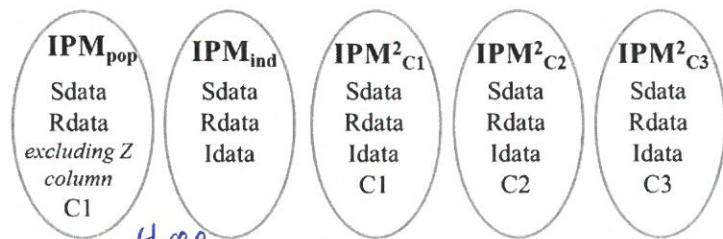
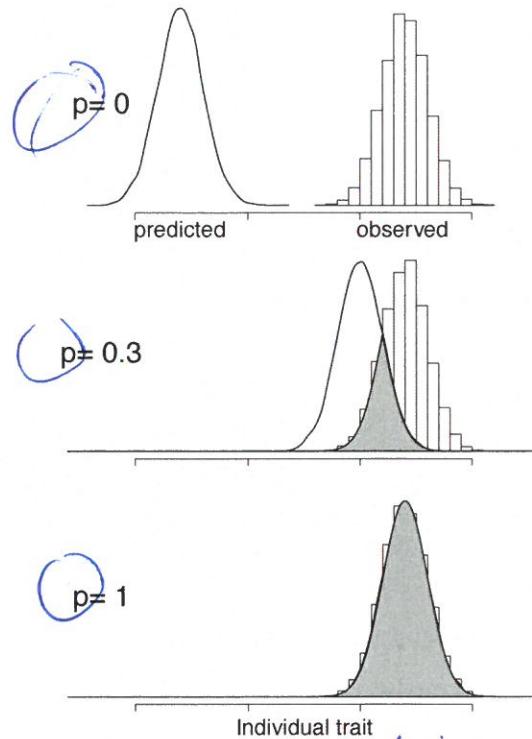


Figure S1: Description of the simulation of the dataset ~~used~~. The populations were simulated under ~~3~~ different scenarios. I: demographic rates are influenced by the individual trait (Z) ~~only~~ (S^J : Juvenile survival, S^A : adult survival and R : reproduction), II: demographic rates are influenced by additive effects of an environmental trend (E) and the individual trait, III: demographic rates are influenced by interactive effects of an environmental trend and the individual trait. Among the females constituting the population, some are marked with ~~a~~ permanent tag that can be easily recovered (e.g. GPS collars). The survival and reproduction of these females are known each year. Some nestlings are also captured and marked. Finally, an independent count of breeding females ~~takes place~~. This sampling allows getting four different datasets that are used to analyze these simulated data with ~~5~~ different models. Sdata: Survival data, Rdata: Reproductive data, Idata: Inheritance data.

produces

five

the



What is "p" here?

Got it..

Figure S2: Illustration of the Density function that gives the probability that the predicted distribution equals the observed distribution. In practice, this function scales the two distributions such that they can be interpreted as probability density functions. It calculates the area where the two distributions are ~~superimposed on each other~~ showing overlap. If the observed and predicted distributions are identical, the function returns $p=1$ and if the two distributions are completely different, the function returns $p=0$.

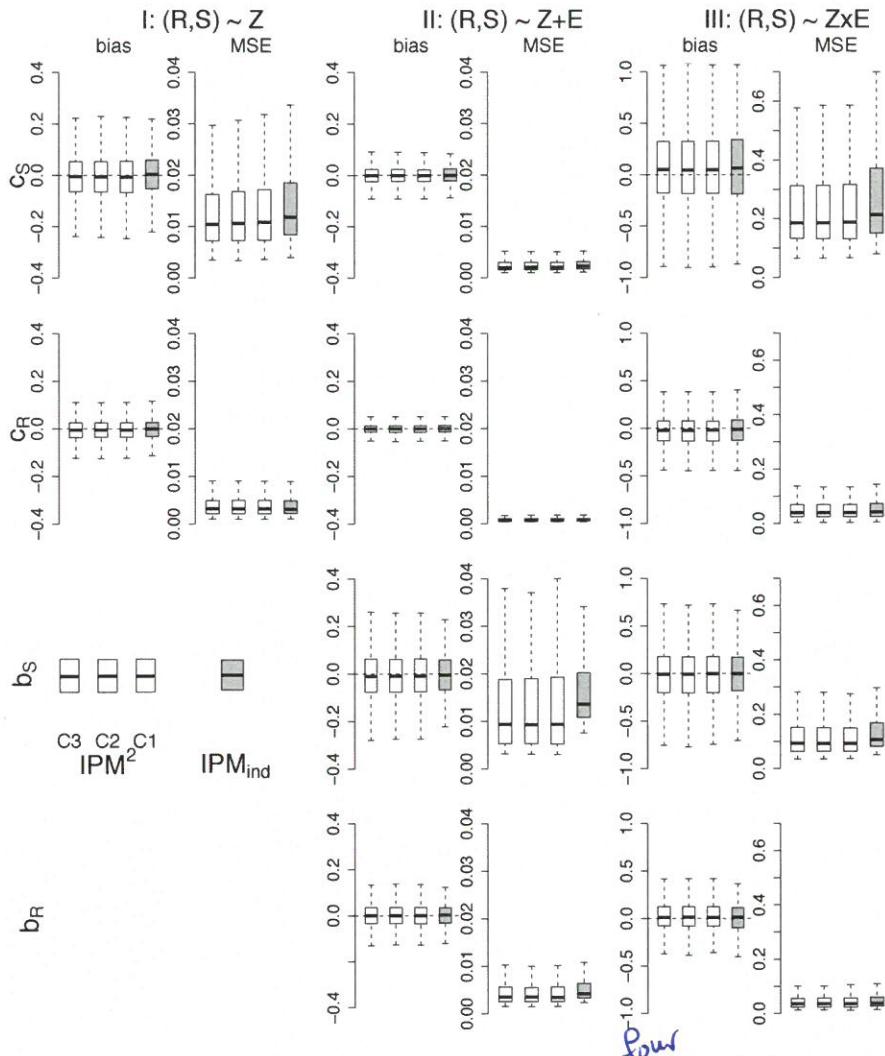


Figure S3: Comparison of bias and mean squared errors (MSE) of the slopes of the survival and reproductive functions estimated from different models under the three different scenarios. Boxplots of estimators from IPM_{ind} and IPM^2 are in grey and white respectively. IPM^2_{C3} , IPM^2_{C2} and IPM^2_{C1} are presented in this order from the left to the right. c_S and c_R are the slopes linking individual trait to the survival (S) and the reproduction (R) functions, respectively. b_S and b_R are the slopes linking the environmental trend to the survival and the reproductive functions, respectively.

shown from

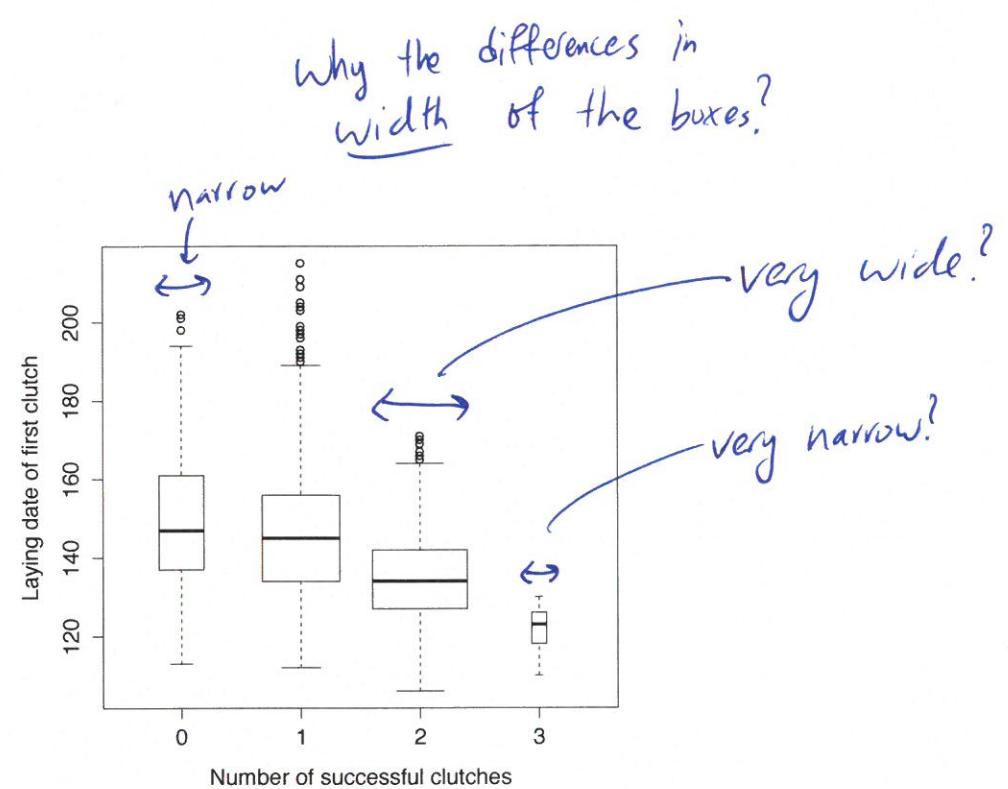


Figure S4: Influence of laying date of the first clutch on the number of successful clutches produced during a breeding season.

Same question:
width of the boxes
 is not the same. why?
 represent the # of data points, perhaps?

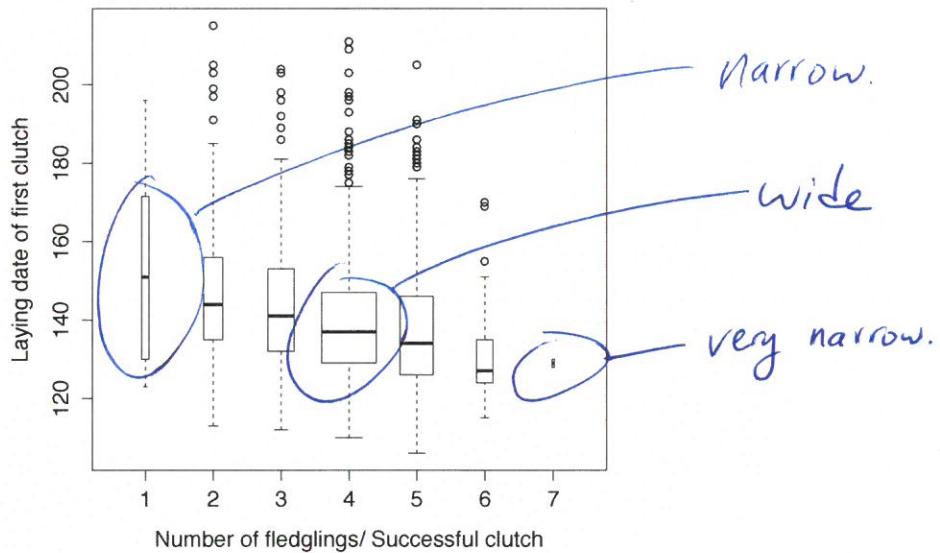


Figure S5: Influence of laying date of the first clutch on the mean number of fledglings (round to the closest integer) per successful clutch.

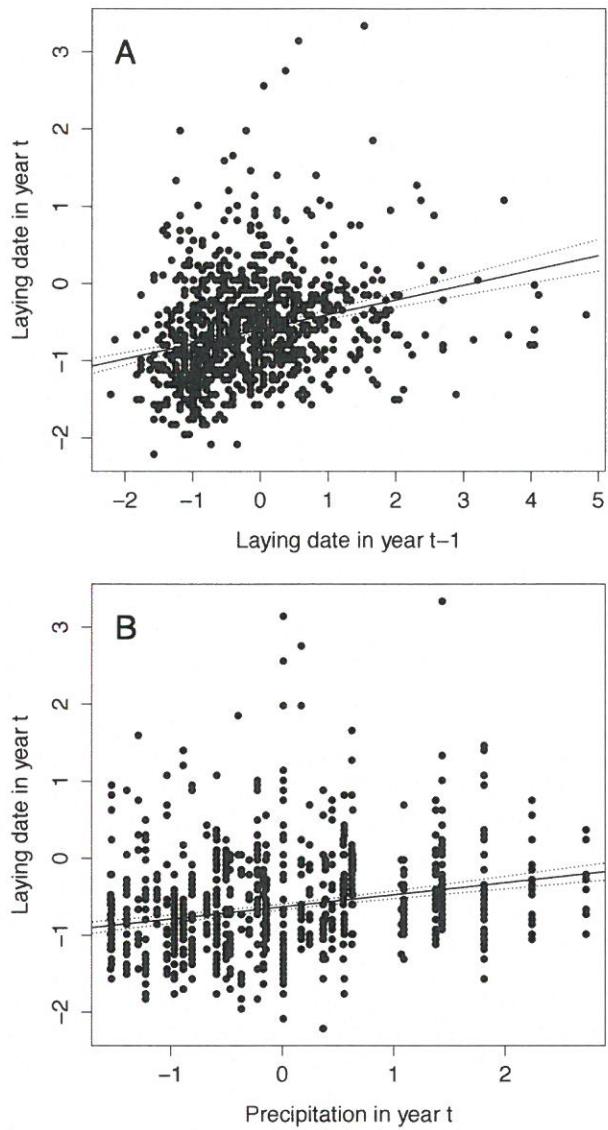


Figure S6: Transitions between annual first laying dates. Influence of laying date of the first clutch laid in year $t-1$ (A) and of precipitation in year t (B) on the laying date of the first clutch ~~laid~~ in year t . The relationships predicted from IPM² are presented with their 95% credible interval.

a

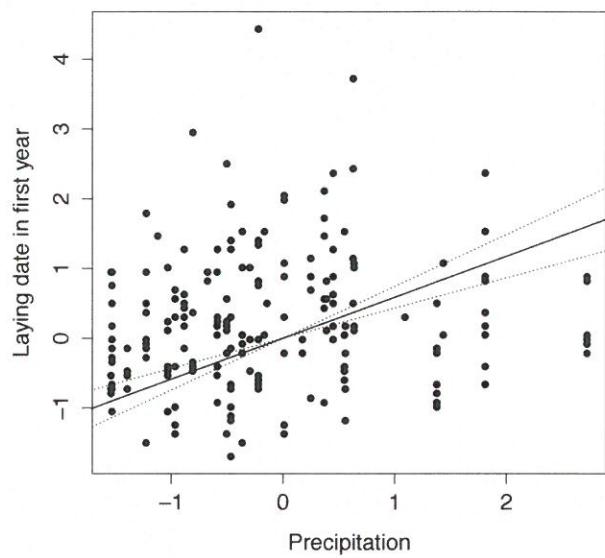
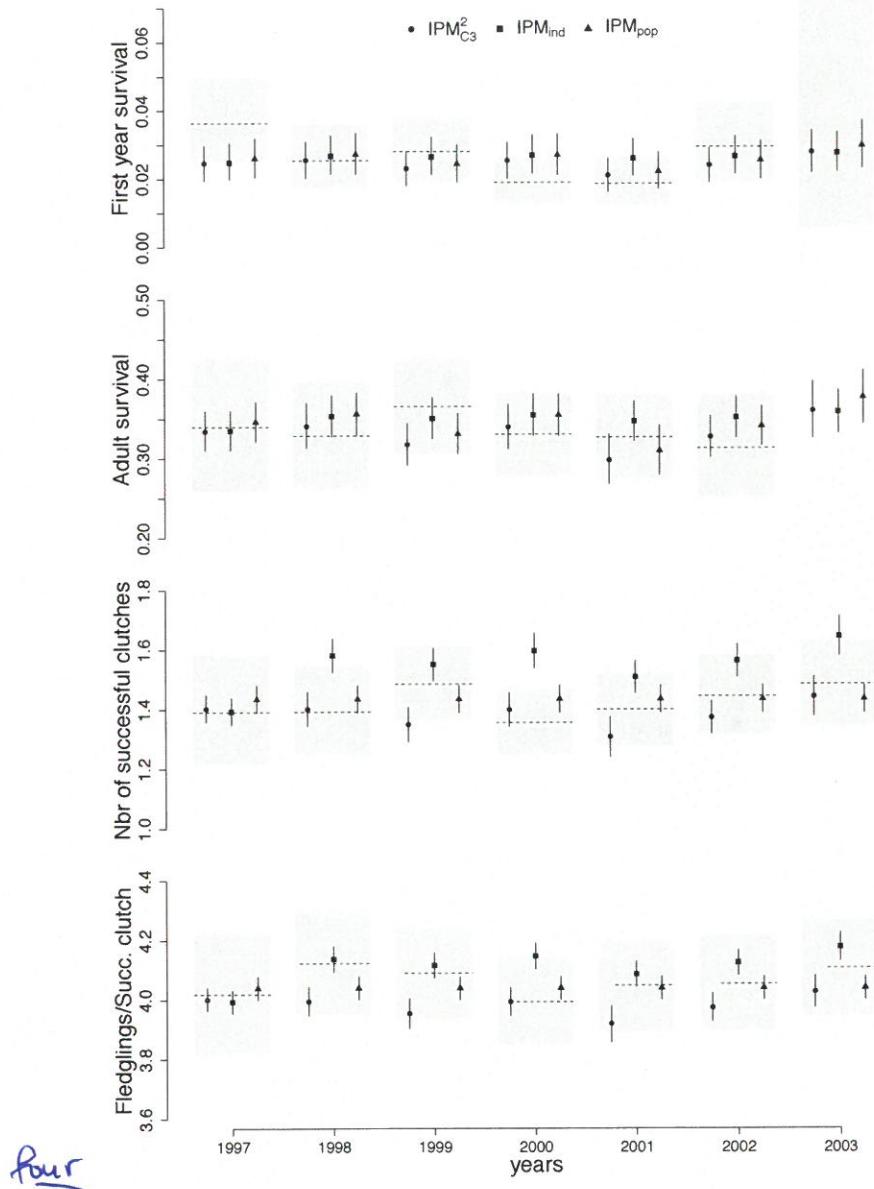


Figure S7: Inheritance of first laying dates. Nestling laying date of the first clutch in the first year was not influenced by maternal laying date, but was influenced by annual spring precipitation. The relationship predicted from IPM² is ~~presented~~ ^{shown} with its 95% credible interval.

a



four
 Figure S8: Estimates of the demographic rates of the Swiss barn swallow population under different models. Mean and 95% credible intervals estimated from $\text{IPM}_{\text{C}3}^2$, IPM_{pop} and IPM_{ind} are presented with points and vertical lines, respectively. Mean ~~and 95% credible interval of yearly variation in demographic rates estimated using a model including an effect of year as a factor~~ are represented using a dashed black line and a grey rectangle each year.

Shown

annual

an annual effect

Appendix S2: Code.R