Integrated population models: powerful methods to embed individual processes in population dynamics models

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Abstract. Population dynamics models have long assumed that populations are composed of a restricted number of groups, where individuals in each group have identical demographic rates and where all groups are similarly affected by density-dependent and -independent effects. However, individuals usually vary tremendously in performance and in their sensitivity to environmental conditions or resource limitation, such that individual contributions to population growth will be highly variable. Recent efforts to integrate individual processes in population models open up new opportunities for the study of eco-evolutionary processes, such as the density-dependent influence of environmental conditions on the evolution of morphological, behavioral, and life-history traits. We review recent advances that demonstrate how including individual mechanisms in models of population dynamics contributes to a better understanding of the drivers of population dynamics within the framework of integrated population models (IPMs). IPMs allow for the integration in a single inferential framework of different data types as well as variable population structure including sex, social group, or territory, all of which can be formulated to include individual-level processes. Through a series of examples, we first show how IPMs can be beneficial for getting more accurate estimates of demographic traits than classic matrix population models by including basic population structure and their influence on population dynamics. Second, the integration of individual- and population-level data allows estimating density-dependent effects along with their inherent uncertainty by directly using the population structure and size to feedback on demography. Third, we show how IPMs can be used to study the influence of the dynamics of continuous individual traits and individual quality on population dynamics. We conclude by discussing the benefits and limitations of IPMs for integrating data at different spatial, temporal, and organismal levels to build more mechanistic models of population dynamics.

Key words: data integration for population models special feature; density-dependence; eco-evolutionary feedback; heterogeneity; individual quality; integral projection model; integrated population model; population model; structured population.

INTRODUCTION

A unifying goal of most studies in population dynamics is to achieve a mechanistic understanding of population change over time. This requires scaling up from the individual to the population level (Łomnicki 1978, Johnson et al. 1986, Bjørnstad and Hansen 1994). Scaling is typically done by classifying individuals according to their values of one or a small number of traits, for example, age, sex, size (Uchmanski 1985, Caswell 2001, Ellner et al. 2016). Demographic rates are estimated from the fates of individuals that share the same trait values, and trait-specific demographic rates are used to model the dynamics of such a group-structured population. Population dynamics then depend on the demographic rates and on the population structure, that is, on the number of individuals sharing a given trait (Koons et al. 2005).

Individual differences in survival and reproductive performance are due to temporal variation in the environment and individual heterogeneity, in addition to demographic stochasticity. Individual heterogeneity includes all differences in individual traits (e.g., age, sex, body mass, unobserved [i.e., latent] quality, habitat

inhabited) that influence demographic performance (see Gimenez et al. 2018 for a review of individual heterogeneity in the context of capture–recapture models). Because individual heterogeneity translates into demographic heterogeneity, population size is affected by the frequency of individual traits in a population, and population dynamics is affected by trait dynamics (Fig. 1; Vaupel and Yashin 1985, Metz and Diekmann 1986, Benton et al. 2006). Owing to the continuing feedbacks between the individual and the population levels in variable environments, a mechanistic understanding of population dynamics requires the inclusion of individual heterogeneity in population models and of the variable sensitivity of different individuals to density-dependent and -independent effects (Schoener 2011, Smallegange and Coulson 2013; Fig. 2).

Integrated population models (which henceforward we abbreviate as 'IPMs', while we always write out "integral projection models," one of several contenders to the same acronym) offer great opportunities to study the influence of individual heterogeneity on population dynamics because they formally combine data from both the individual level (e.g., capture–recapture and productivity data) and the population level (e.g., population counts) (Besbeas et al. 2002, Schaub and Abadi 2011). IPMs are defined as state-space models, where the Markovian state model typically is a demographic model characterized by a stage-structured model that predicts population size at a given point of time based on the population size at the previous point of time and the demographic rates. Demographic rates may include survival, reproduction, immigration and emigration in addition to transition if the structure of the population changes as individuals get older, for instance (see Kéry and Schaub 2012 for a monograph on IPM with simple code). In this article, our aim was to illustrate how integrating data collected at individual and population scales can contribute to a deeper understanding and more accurate prediction of population dynamics and a fuller appraisal of the role of individual heterogeneity in population dynamics than when these data are used independently.

Using an IPM, information about all the demographic rates operating in a study population can be extracted from several independent data sources at the population and the individual scales in a coherent way (Saunders et al., 2019). The model predictions and their fit to the different data depend on the accuracy of the demographic model. For instance, immigration virtually always contributes to population growth in open populations (Sandercock and Beissinger 2002). If the demographic model does not include immigration or another demographic process, overestimates of either survival or fecundity will result from the misspecified model.

Until now, most IPMs have assumed that demographic rates of all individuals vary with some categorical attributes, often called stages, such as age, sex, or reproductive status (Péron et al. 2012, Schaub et al. 2013, Weegman et al. 2016, Cleasby et al. 2017). In this classic case, the demographic model of the IPM is an age/stage-structured projection model (matrix models, Caswell 2001) typically including a low number of stages
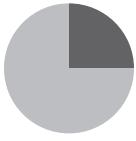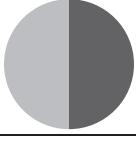

Influence of environment on demographic rates of groups 1 and 2	Environment 1 $S1 = 0.3$ $S2 = 0.5$ $R1 = 0.2$ $R2 = 1.0$	Environment 2 $S1 = 0.3$ $S2 = 0.5$ $R1 = 0.0$ $R2 = 0.5$
	$\bar{S} = 0.450$ $\bar{R} = 0.800$ $\lambda = 1.250$	$\bar{S} = 0.450$ $\bar{R} = 0.375$ $\lambda = 0.825$
	$\bar{S} = 0.400$ $\bar{R} = 0.600$ $\lambda = 1.000$	$\bar{S} = 0.400$ $\bar{R} = 0.250$ $\lambda = 0.650$

Fig. 1. Influence of population structure and environment on population dynamics. In this example, a population is composed of two different groups of individuals with different survival ($S1$ and $S2$) and reproductive success ($R1$ and $R2$). Reproductive success of the two groups is differentially sensitive to environmental changes. The resulting population-level survival, reproductive rates, and population growth rates are weighted averages across both groups and are shown for four different combinations of two population structures and two environments.
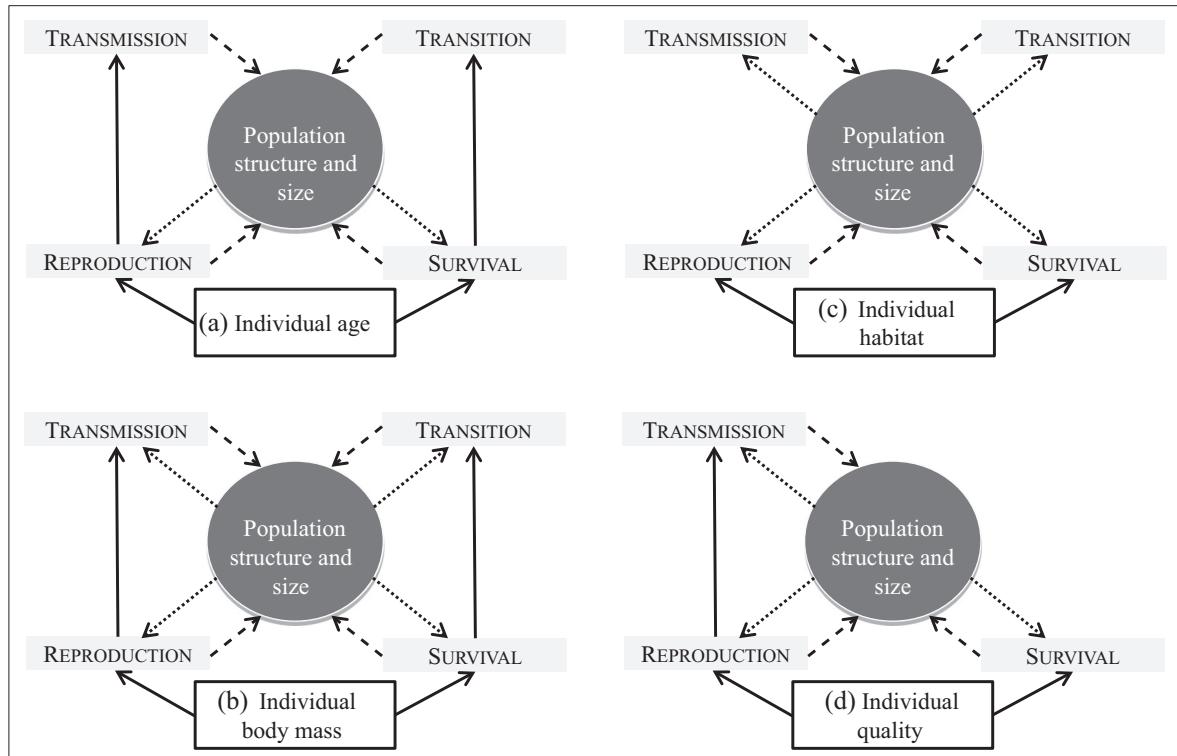
Fig. 2. Conceptual model of the feedback, through demographic rates, between the population and an individual characterized by four different traits (a, age; b, body mass; c, habitat; d, quality). Along trajectories, individual traits influence the individual survival probability and reproduction. If an individual survives, its trait may change (Transition, e.g., aging). If offspring are born, they may inherit individual traits influenced by the parents (Transmission). The individual demographic performance may be influenced by individual traits (solid arrows) and by density-dependent and density-independent effects (dotted arrows). The fates of all individuals based on each demographic performance alter the population structure and size (dashed arrows). Depending on the individual trait considered, transition and transmission may not be influenced by the individual trait (the colonization of a new habitat or breeding site may be independent of the one occupied in the previous year) or may not be influenced by density-dependent and/or independent effects (transition between age only depends on the previous age).

that are known to influence demographic rates and hence population dynamics (Coulson et al. 2001). In the first part of this article, we review the benefits of using such classical IPM combining data at the individual and population scales vs. classical stage-structured projection models, and outline the striking questions that could be investigated using such classical IPMs.

One of the key benefits of IPMs is the ability to estimate the complete population structure explicitly, including unobserved states, which then can be used as a covariate of demographic rates. As with density dependence, the population size or structure can have a feedback loop on demographic rates (Fig. 2). In a second part of the article, we illustrate the flexibility of the state-space model within the IPM, offering the opportunity to investigate the influence of feedback loops of population size and structure on population dynamics explicitly.

In the third part of the article, we show that IPMs can be extended to include different sources of individual heterogeneity, which then allows empirical investigation of their consequences for population dynamics. Classical

IPMs using a categorical characterization of individual heterogeneity necessarily assume that the demographic performance of all individuals in the same stage is identical. This can be a restrictive assumption, because the demographic performance may differ among individuals within the same categorical stage (Vaupel et al. 1979, Huston et al. 1988). Some studies have included demographic stochasticity, which captures a part of the effects of individual heterogeneity (Besbeas et al. 2002, 2009, Schaub and Abadi 2011). However, although models that include demographic and environmental stochasticity often closely fit observed variation in population size (Véran and Lebreton 2008, Schaub et al. 2012), demographic stochasticity is *not* the cause of individual heterogeneity and consequently the understanding of population dynamics remains incomplete in such models. In the third part of the article, we show how the demographic model of the IPM can be adapted to model a population structured by individual heterogeneity, including continuous individual traits or latent quality. If individual heterogeneity can be described by a continuous individual trait such as body mass or size, an IPM

can be formulated using an integral projection model (Easterling et al. 2000, Ellner et al. 2016), which is a more general demographic model than the older matrix projection models. We will abbreviate this type of model as IPM². If individual heterogeneity can be described by a latent variable (Link et al. 2002, Hamel et al. 2018), random effects or mixture models can be included in the demographic model of the IPM.

We conclude that the use of IPMs in eco-evolutionary studies should provide major benefits. First, IPMs can yield accurate estimates of the relationships between individual traits and demographic rates if transmission of these individual traits can be described. Second, combining data from the population and the individual level allows the explicit inclusion of eco-evolutionary feedback between individual traits, and population size and structure.

CLASSICAL IPMs STRUCTURED BY AGE, SEX, AND REPRODUCTIVE STATE

Transitions between age/stage and variability of age/stage-specific demographic rates

The use of age- or stage-structured population models is common in IPMs (Fieberg et al. 2010, Lee et al. 2015, Taylor and Udevitz 2015, Hatter et al. 2017). They can be used to add information on the population structure by including age- or stage-structured count data. Besides estimates of stage-specific demographic rates, population size estimates become available for all stages, allowing new insights into population structure and its changes over time. The first insight is the estimation of stage-specific demographic rates for which no explicit data have been collected. By combining data on different stages of an amphibian species (egg, metamorph, and adult), Duarte et al. (2017) showed that survival from the egg to the metamorph stage and from the metamorph to the adult stage, respectively, and fecundity, could all be estimated separately in an IPM. However, one associated drawback with the additional parameters that can be estimated only from IPMs is that they are usually estimated with low precision and possibly also with bias. Their estimation depends on the accuracy of the state model to describe the population and is often directly influenced by the variability in the count data that cannot be explained by other estimated parameters. The second advantage of including age-structure in IPMs is a better understanding of the sources of variation in demographic rates. Indeed, some age-dependent demographic rates are more variable than others and hence more sensitive to environmental variation and resource limitation (Gaillard et al. 2000, Bonenfant et al. 2009). For instance, the influence of the environment on the demographic rates of emperor penguins (*Aptenodytes forsteri*) in the Antarctic was studied using an IPM (Abadi et al. 2017). Weather variation during the nestling period was found to affect first-year

survival, and identification of this link would not have been possible without an IPM (Abadi et al. 2017). Finally, accounting for the dynamics of the proportion of each age class in the population facilitates prediction of average variation in annual survival, reproductive, and dispersal rates (Coulson et al. 2001; see Mosnier et al. 2015 for an example using an IPM).

Sex-specific demographic rates, sex ratio, and mating systems

Most population models are female-based and assume that male density does not influence female reproductive success (Caswell and Weeks 1986, Lindström and Kokko 1998). The main reason for this choice is often that male demographic rates are more difficult to estimate. However, males and females may have different life-history strategies and thus different demographic rates (Caswell and Weeks 1986, Rankin and Kokko 2007, Véran and Beissinger 2009). To date, only a handful of published IPMs have included a sex structure (Tavecchia et al. 2009, Fieberg et al. 2010, Péron et al. 2012, Cleasby et al. 2017) allowing estimation of the dynamics of each sex separately and its influence on population dynamics.

IPMs could further be used to investigate the influence of mate availability on population dynamics. To date, IPMs have rarely included the operational sex ratio in an explicit manner, although this parameter can have an important impact on population dynamics (Carmona-Isunza et al. 2017). Operational sex ratio varies in relation to mating system. In polygynous species, the female is often the limiting sex (Le Boeuf 1974, Clutton-Brock 1988), whereas in monogamous species, strictly speaking, individuals forming pairs are not available anymore to breed (Kokko and Jennions 2003). IPMs explicitly control for mate availability at the population level. They could also be expanded to include mating functions in order to investigate the dynamics of mate choice and its impact on population dynamics. Mating functions giving the breeding probability of males and females based on their phenotypic traits have been adapted to population models (Schindler et al. 2013, 2015). Finally, IPMs also allow testing for the influence of intrasexual selection on the dynamics at the individual level. Male–male competition is the chief driver of intrasexual selection (Cox and Le Boeuf 1977) and its intensity is often linked to the number of males in a group (Clutton-Brock et al. 1980). Explicitly including two-sex dynamics in an IPM could lay the groundwork for studies of intrasexual competition.

Reproductive state and the influence of the nonbreeder part of the population

In many species, mature individuals may not reproduce every year, such that a population is composed of breeders and nonbreeders. The nonbreeding part of a

population is a key component for a comprehensive understanding of population dynamics and heterogeneity of demographic rates, especially in long-lived species (Newton 1998, Sandercock et al. 2000, Lee et al. 2017). Nonbreeders may play an important role for density-dependent regulation when nonbreeding results from habitat saturation (Rodenhouse et al. 1997) and they can stabilize the dynamics of a population by buffering the breeding population size (Penteriani et al. 2011). Yet, estimating the size of the nonbreeding segment of a population may be very hard. IPMs that explicitly include nonbreeders can provide important insights for this population segment. McCrea et al. (2010) developed an IPM that distinguished breeders and nonbreeders in a great cormorant (*Phalacrocorax carbo*) population. Their capture–recapture survey allowed them to determine the breeding state of each individual at resighting. The population count, however, included just the number of occupied nests, and thus the number of nonbreeders was unknown. Through the integration of these two types of data the estimation of the number of nonbreeders became possible. The ability to estimate structured population size offers the possibility to study the ways in which the nonbreeding component of the population affects the dynamics of the whole population and how this contributes to population regulation.

Using IPM to Detect Feedback Loops of Population Size and Structure on Demographic Rates

In the first part of this review, we have emphasized how IPMs can include the demographic rates of different groups of individuals and their variable sensitivity to environmental conditions. In this section, we illustrate how IPMs can be used when population structure and size have a feedback loop that impacts demographic rates, in a similar way as density dependence. One of the key benefits of IPMs is the ability to estimate the population structure explicitly, including hidden states, which then can be used as a covariate of demographic rates.

The influence of group size and structure on population dynamics of social species

Population dynamics of social species strongly depends on the size and the structure of groups (Alexander 1974), because they affect individual fitness through survivorship and reproductive success (Armitage and Schwartz 2000, Lardy et al. 2015). For instance, living in groups may enhance survival through predator avoidance (Moran 1984, Wrona and Dixon 1991) and improve the reproductive success of breeders through the alloparental care by helpers (Salomon and Lubin 2007, Hatchwell 2009). Finally, group size and structure strongly influence dispersal and the probability to establish as a successful breeder (Koenig et al. 1992). Thus, the population dynamics of many species that are

temporarily or permanently social also depends on the dynamics of group size and structure.

IPMs open up the possibility to link the levels of the individual, the group, and the population, but so far IPMs have not been used for this purpose. To demonstrate how IPMs can include the influence of the population structure on demographic rates in a straightforward way, we developed an IPM for a population of Alpine marmots (*Marmota marmota*), a cooperatively breeding species; see Appendix S1 for details on population and models. Marmots are socially monogamous and live in family groups composed of a dominant pair and subordinates (Allainé et al. 2000). Subordinates are typically young males and females that are relatives of the dominant couple often old pups, sisters or brothers. Pup winter survival increases with an increasing number of male subordinates (called helpers) because of social thermoregulation during hibernation (Arnold 1988). Because males have a larger effect on population dynamics than females, our IPM combines data on males at multiple levels: (1) population level: annual number of dominant males and of helpers (16 yr), (2) family group level: annual number of helpers and annual litter size at emergence (334 litters), and (3) individual level: capture–recapture data of males (571 individuals) including their age, their state (dominant vs. helper) and their family group. Our IPM is a classical IPM including two reproductive states (dominant vs. helper) and three age classes (1 yr, 2 yr, >2 yr). The population is thus structured according to four stages: the dominant individuals (>2 yr), and the helpers of different ages (1 yr, 2 yr, >2 yr). In addition, the IPM included a possible feedback loop of the population stage-structure: the number of helpers per dominant, on two demographic rates: first-year survival and transition probability from helper to dominant. The effect of the number of helpers per dominant was introduced twice in the IPM: in the demographic model and in the multistate capture–mark–recapture model. In the demographic model of our IPM, the mean first-year survival and the mean probability of becoming dominant were linked to the mean number of helpers per dominant. The mean number of helpers was directly derived from the predicted population stage-structure (informed partly from the count data) creating the loop between population structure and demographic rates. In the multistate capture–mark–recapture model (informed from the individual capture history data), these two parameters mediated the influence of the observed number of helpers (family group data) an individual has spent the winter with on the individual survival probability and the probability to become dominant. Thus the effect of the number of helpers per dominant was estimated using information gathered from data at the three different levels (see Appendix S1 for a detailed description of the model and Data S1 for the associated code to fit the model in BUGS software).

The IPM estimated population size and structure with high precision (Fig. 3; compare the predicted black line

to the observed open dots). As expected, the model showed a significant positive effect of the number of helpers per family on first-year survival (mean = 0.45, 95% credible interval [CRI] = [0.24;0.72]) and a negative effect of the number of helpers per family on the transition probability from helper to dominant (mean = −0.23, 95% CRI = [−0.50;0.04]). This suggested that the probability of becoming dominant tended to decrease in large families. If the data at the population level are excluded, predictions of population size become highly uncertain to the point of being practically useless (Fig. 3A, B, blue lines). As the 95% CRI of population size was bounded by 0, its mean was overestimated by this second model excluding population data. Moreover the estimate of the population structure was biased. Too many subordinates become dominants (Fig. 3D, blue lines) who reproduce. This resulted in a predicted population size increasing at a much higher rate than the observed population. We also compared the results of the IPM to the results of a third model excluding the family group data about annual number of helpers in each family. In this model, the capture–mark–recapture data are fitted using individual demographic rates that are not influenced by family-specific number of helpers anymore, but by the mean number of helpers per dominant in the population. In this model, the parameters of the relationships between the number of helpers and the demographic rates can no longer be estimated (Appendix S1: Table S1). Owing to the inclusion of population data (Fig. 3A, B, red lines) estimates of population size and structure were similar to the ones of the IPM, but first-year survival was underestimated and its variation was independent of the number of helpers per family in this third model excluding family data (Fig. 3C, red lines). In conclusion, the IPM combining data at the three levels of individual, family group, and population was the only model able to predict accurately variation in population size that agreed with the inherent dynamics of the population structure.

The power of IPM to detect stage-specific density-dependence processes

Density dependence is *the* key concept to understand population regulation (Turchin 1995, Hixon et al. 2002). Although density dependence has been investigated in numerous studies, properly diagnosing it in the field is far from an easy task. A typical analysis would regress estimates of demographic rates on population counts. However, if the population size estimate is subject to counting errors (which arguably it *always* is), the strength of density dependence will be overestimated (Lebreton and Gimenez 2013). State-space models offer an improvement by accounting for some types of observation errors, but may suffer from serious identifiability problems (Knape 2008, Lebreton and Gimenez 2013). Abadi et al. (2012) developed an IPM that included links between demographic rates and the estimated
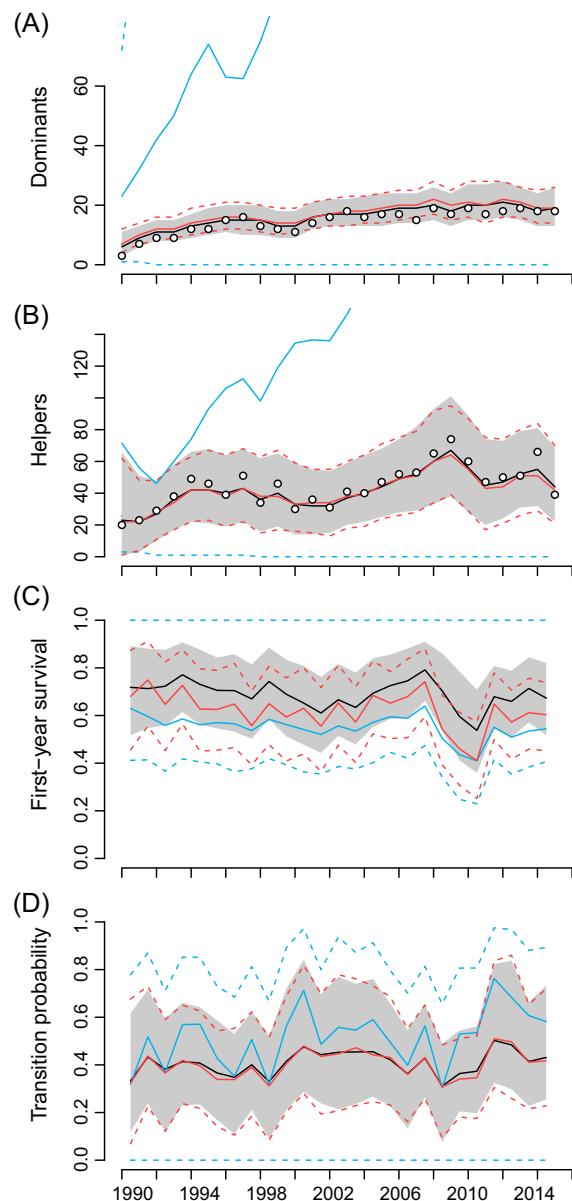

Fig. 3. Estimated number of dominant (A) and subordinate (B, helpers) Alpine marmot males, estimated annual first-year survival (C) and estimated transition probability of a helper of becoming a dominant male (D) from 1990 to 2015 using different population models. IPM: black and gray shade; model excluding family data about specific annual number of helpers per family: red lines; model excluding the observed annual counts: blue lines. Averages and 95% credible intervals of posterior means are shown. Open dots: observed counts.

population size. A negative feedback of the population size on the demographic rates is built directly into the demographic model, by using the population size estimates as a covariate in relationships with demographic rates. The power to detect density dependence is actually increased.

This mechanistic approach can be further extended to obtain more detailed insights into density dependence. For a given population size, the strength of density dependence could differ depending on the age structure of the population. On the one hand, we would expect that both younger and older (i.e., senescent) individuals are more sensitive to resource limitation and affected by density dependence than prime-aged individuals (Coulson et al. 2001, Bonenfant et al. 2009). On the other hand, rather than total population size, the size of critical age groups may affect the strength of density effects on demographic rates. Indeed, prime-aged individuals may be more competitive than younger (and older) individuals and may induce a stronger negative effect on demographic performance. Until now, only a few studies have managed to quantify the relative contribution of different age-classes to density dependence. Gamelon et al. (2016) developed an IPM for great tits (*Parus major*) and showed that density dependence on demographic rates was higher for younger than for older individuals and that the number of young females had a stronger effect on population regulation than did the number of old females. Similarly, we expect that the relative contribution of different individuals to density dependence varies with individual heterogeneity (individual size, quality or rank…).

Influence of density-dependence and individual heterogeneity on individual movements

The movement of individuals between populations, including dispersal or partial migration, may depend on the density in the departure population, on the density in the arrival population (Matthysen 2005, Chapman et al. 2011), or on individual attributes (Clobert et al. 2009). IPMs that include estimates of population size and population structure are therefore particularly suited to yield insights into the linkage between individual movement and population density.

When demographic and count data from several connected populations are available, IPMs can be formulated to include dispersal between sites as a function of the density of the departure or arrival site, exactly analogous to metapopulation models (Hanski 1998). For example, Péron et al. (2010) used an IPM to study dispersal in a metapopulation of black-headed gulls (*Chroicocephalus ridibundus*). Dispersal probabilities were modeled in relation to colony size and individual age. They found that juveniles dispersed mainly from large to small colonies, whereas the opposite pattern was observed in adults.

The study of immigration in open populations amounts to the study of settlement decisions of dispersing individuals. One major advantage of IPMs is that the number of immigrants can be estimated in this situation (Abadi et al. 2010, Schaub and Fletcher 2015) in the absence of explicit data. The estimated number of immigrants can then be correlated with the size of the total

population or of just some population segment, in order to investigate how immigration contributes to population fluctuations and regulation (Schaub et al. 2013). For example, immigrants were attracted by local recruits in the common tern (*Sterna hirundo*; Szostek et al. 2014) and by the presence of breeders in the spoonbill (*Platalea leucorodia*; Tenan et al. 2017).

Until now, very few studies have attempted to assess the source–sink status of populations in an entire metapopulation system (Furrer and Pasinelli 2016 for a review; Weegman et al. 2016 have an example using an IPM). IPMs allow the estimation of all demographic rates, including immigration and emigration rates; hence, they would seem highly suited to investigate source–sink dynamics (see also Heinrichs et al. 2018, Millsap 2018). Although ad hoc analysis had allowed estimating immigration and emigration in source–sink populations (Peery et al. 2006), IPMs offer an integrated framework where all demographic rates are estimated along with their uncertainty, given the demographic model and all data available.

New Extensions of IPMs to Populations Structured by Continuous Individual Trait and Unmeasured Individual Heterogeneity

Most current IPMs assume independence and similarity of individuals within an age or stage class, and this assumption may often be violated (Johnson et al. 1986). For example, when some individuals within a given age or stage class achieve higher reproductive success and/or have higher survival probability than others (Cam et al. 2002, Hamel et al. 2009, Chambert et al. 2013, Fay et al. 2018), the distribution of individual contributions to population growth can become highly skewed. To investigate the influence of individual heterogeneity on population dynamics, it is necessary to characterize the different sources of the variability. Typically, a part of the variability in individual performance can be explained by variation in continuous individual traits, such as size in plants (for instance, rosette area in a monocarpic perennial, *Onopordum illyricum*, Ellner and Rees 2006), body mass/body length in mammals and fishes (Coulson et al. 2010, Vindenes and Langangen 2015), or birth/laying date in mammals and birds (Plard et al. 2015). Given the long-lasting effects of conditions experienced during early life on adult performance, cohort effects have also been recognized as crucial to predict individual performance in many species (Kruuk et al. 1999, Lindström 1999). Modeling the change over time in the frequency distribution of one or several of these measured continuous traits is a first approach to assess the influence of variable individual performance on population dynamics. However, one trait is rarely enough to characterize individual quality; instead, it may be necessary to measure positive covariation between different individual life-history traits that are jointly linked to fitness (Vaupel et al. 1979, Lailvaux

and Kasumovic 2010, Wilson and Nussey 2010, Fay et al. 2018). A second approach is thus the adoption of latent variables such as individual groups or random effects, because individual quality can rarely be measured directly (Link et al. 2002, Hamel et al. 2018).

Up to now, researchers have typically studied the stable distribution of individual quality and much less its dynamics. Despite the obvious impact of individual heterogeneity on population dynamics, there are several reasons for why it has remained a challenge to demonstrate empirically how individual heterogeneity shapes population dynamics. First, identifying the sources of differences in individual demographic performance can be a challenge (Cam et al. 2013). If these sources are unknown, it is difficult to construct meaningful population models. Second and most importantly, the impact of individual heterogeneity on demographic performance is often modulated by the environment (Wall and Begon 1987, Pelletier et al. 2012, Wood and Brodie 2016). For instance, we expect high-quality individuals to be less affected by resource limitation than those of poor quality (Lescroël et al. 2010). Thus, even if the distribution of individual quality remains stable in a population, the distribution of demographic performance can vary (Fig. 1, environmental effect). Third, advantageous individual traits under some environmental conditions may be selected. As individuals get older, selective disappearance of certain traits can consequently change the distribution of demographic performance (Kendall et al. 2011, Fig. 1 population structure effect). Finally, if traits have a genetic or another cultural or parental transmissible component, the distribution of demographic performance will evolve. In contrast, if individual differences are generated solely by environmental effects, the trait distribution of the offspring will be independent of that in the parents. Thus, whether individual differences have a genetic basis or not (as, e.g., cohort effects) should be reflected by population models, and both are expected to be influenced by environmental condition (Fig. 2, Metcalf and Pavard 2007).

Combining data at the individual and the population level and including individual heterogeneity in IPM offer new avenues to model the complex interactions between individual heterogeneity and density-dependent and-independent effect to understand how the dynamics of individual heterogeneity influence population dynamics.

Including continuous traits in IPMs

The first population models that included the influence of individual continuous traits were physiologically structured population models derived from differential equations (Metz and Diekmann 1986, De Roos 1997). In these models, the dynamics of individual body size, survival, reproduction and growth are explicitly linked with resource availability, population density, and distribution. These models have mainly been applied to fish populations and shown continuous interactions between individual body size, individual performance, resource availability, and population dynamics (Persson and De Roos 2006).

Later, matrix models were extended to integral projection models where a population is no longer classified by discrete stages, but by a distribution of individuals according to one or multiple continuous traits (Easterling et al. 2000, Ellner et al. 2016). This trait distribution may change over time as a response to growth, survival, and reproductive and inheritance functions. Growth functions describe how a trait changes within an individual as it gets older, and inheritance functions describe how a trait is transmitted (i.e., inherited) from parents to offspring. The power of these models for dealing with eco-evolutionary questions has been emphasized (Smallegange and Coulson 2013). Such models can improve our understanding of the impact of environmental change on population dynamics, and continuous trait can respond plastically or evolutionarily (e.g., Ozgul et al. 2010, Plard et al. 2014).

However, a major limitation of existing integral projection models is that they are formulated for data collected at the individual level only, and not for data collected at the population level (e.g., time-series of population surveys). Inference about population dynamics is based exclusively on the transition probability, which is estimated at the individual level only, and not at the population level. The scaling up to the population level is therefore purely model-based, and even small sampling variability (e.g., catching some particular individuals or individuals in particular habitats) may result in large biases of predictions at the population level (Ghosh et al. 2012). One obvious solution would therefore appear to be a joint analysis of data from the individual and the population level. Recently, Plard et al. (2019) developed an IPM whose demographic model was an integral projection (this model is abbreviated by IPM²) instead of an age/stage-structured projection model. Their model estimated the temporal dynamics of the distribution of continuous traits in a population as well as the demographic rates and the population growth rate, and achieved greater accuracy than either simpler models (i.e., a classical integrated population model using an age-structured projection model or an integral projection model). Because the dynamics of the trait distribution is a function of the environment, accounting for individual processes increases the predictive power of the model. Moreover, at the individual level, parameters linking the trait with survival, reproduction, growth and inheritance are estimated with greater precision. The IPM² modeling framework was applied to model the dynamics of the distribution of laying dates in Swiss barn swallows (*Hirundo rustica*, Plard et al. (2019)). A key result was that they were able to include in the IPM² individual mechanisms (laying date) that influenced individual survival and reproduction, and, thus population dynamics. For instance, reproductive success declined in

years with high precipitation because egg laying was delayed. The integral projection model, where the information from population counts cannot be exploited, was unable to predict population size accurately because of the model's inability to estimate immigration. Moreover, confidence intervals of the parameter linking individual laying date to survival were much wider than in the IPM[2]. Based on the integral projection model, one would have concluded that survival was unrelated to laying date. By contrast, the application of a classical IPM that ignored the relationship between individual laying date and demographic rates would have prevented a mechanistic understanding of the variation of the demographic rates because we would have remained ignorant about why reproductive success was lower in years with high precipitation. Only the combination of the modeling of continuous individual traits and of both individual and population scale input data yielded the full breadth of the inferences.

Advantages of IPMs to study the influence of unmeasured individual heterogeneity on population dynamics

In principle, it is straightforward to extend the IPM[2] framework to describe the dynamics of multiple continuous traits simultaneously (Plard et al. 2015, Vindenes and Langangen 2015). However, in practice, the multivariate aspects of individual quality cannot be modeled with the required number of traits with current computer performance; based on our experience, with typical desktop computers no more than two or three continuous traits are possible. There is mounting empirical evidence for heterogeneity in individual quality that cannot be described by a single measurable trait (Cam et al. 2016). To describe such multivariate heterogeneity, either models with individual random effects or finite mixture models are used (or a combination of the two, Gimenez et al. 2018, Hamel et al. 2017, 2018). Random effects models normally assume that individual quality follows a Gaussian distribution with a variance that is estimated from the data (other distributions such as the t are also possible). In contrast, finite mixture models assume that a population can be split into a known (small, i.e., usually two or three) number of groups, each of different quality, and that every member of a group has exactly the same value of a survival and/or reproductive rate. In between them, infinite mixture models (e.g., Dorazio et al. 2008, Johnson and Sinclair 2017) employ Dirichlet process priors and assume the finite number of groups is unknown and must be estimated.

All other things equal, individual quality is expressed by the positive correlation between successive reproduction and/or reproduction and survival, such that a high-quality individual has both high survival and high reproductive performance. Multistate capture–recapture models including groups of different qualities (using finite mixtures) or a distribution of individual quality (using random effects) can be used to study individual quality investigating the covariation between survival and reproductive success (Link et al. 2002, Souchay et al. 2014, Fay et al. 2018). Finite mixture models or random effects can similarly be embedded into an IPM to investigate covariation of reproduction and survival simultaneously. One advantage of using an IPM for this purpose is the freedom to model a large number of possible reproductive outcomes, whereas multistate models are in practice restricted to a finite and usually smallish number of discrete stages. In an IPM, reproductive outcomes can be the combination of different biological functions, such as pregnancy rate and twinning rate, or nest success combined with the probability of laying a replacement clutch, hatching success, and fledgling success. All these processes can be included and modeled in an IPM if this is needed and suitable data are available, and one can investigate in which of these components heterogeneity in quality is most prevailing. Reproductive outcomes can also be modeled with alternative statistical distribution such as zero inflated models reflecting the distribution of the number of offspring or fledglings produced, for instance. IPMs appear therefore particularly suited for species whose reproductive success is highly variable among individuals due to large clutch or litter sizes or due to several reproductive events per year (Clutton-Brock 1988, Santidrián-Tomillo et al. 2009).

To show how unmeasured individual heterogeneity can be included in an IPM to get a better understanding of the life-history strategies existing in a study population and their impact on population dynamics, we developed here an IPM using finite mixtures. Specifically, we used the Swiss barn swallow population as an illustrative example and we study the joint influence of density dependence and individual heterogeneity in unmeasured individual quality on its dynamics (see Appendix S2 for details on population and model and Data S1). We used a finite mixture model with two groups and investigated the differences of survival and reproductive performance between these groups. Two groups of heterogeneity were chosen because we expected individual performance to be strongly dependent on whether a successful second brood was raised. In addition, we included possible group-specific, density-dependent effects on reproductive success. Swallows belonging to the larger group (mean = 88%, 95% CRI = [81%; 93%] of all individuals) were of higher quality and had higher reproductive success in most years due to a higher number of successful clutches raised on average (mean = 1.33, 95% CRI = [1.07;1.69]; Fig. 4). The number of successful clutches decreased with increasing density (effect of density: mean = −0.46 95% CRI = [−0.86; −0.21]) in both groups but there was some evidence that the strength of this density-dependent effect was stronger in the low-quality than in the high-quality individuals (difference between density-dependent effects in the two groups: mean = 0.03, 95% CRI = [−0.04; 0.10], Fig. 4). Survival and the number of fledglings per successful brood were identical in both groups (Appendix S2: Table S1). In an

alternative analysis excluding population count data, we failed to achieve Markov chain Monte Carlo (MCMC) convergence, even when running four times more iterations (100,000) than for the IPM.

Thus, IPMs provide a powerful modeling framework to estimate the influence of density-dependent effects and individual heterogeneity on population dynamics simultaneously. Density-dependent effects are expected to affect differently groups of different quality with poor-quality individuals being more affected by a stronger competition for resources than higher-quality individuals.

CONCLUSIONS AND PERSPECTIVES

Advantages of integrated population models combining data at the population and the individual levels

We have shown that IPMs are powerful inferential tools in an eco-evolutionary context, because they allow the analysis of data at the individual, the group, and the population levels simultaneously to study the dynamics of population either structured by age or stage classes
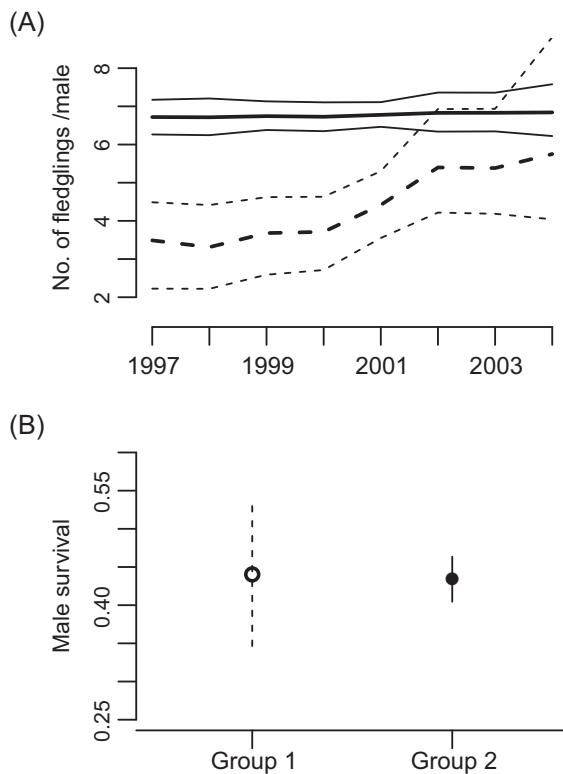
(A)

(B)

FIG. 4. Estimates of reproductive success (A, total number of fledglings per male during the breeding season) and survival (B) of two groups (solid and dashed lines) of males of different quality in the Swiss barn swallow population from 1997 to 2004. An IPM including a finite mixture model with a density-dependent effect on reproduction was used. Posterior means and 95% credible intervals are shown.

(using a stage-structured projection model to define the demographic model of the IPM) or structured by continuous individual traits (using an integral projection model to define the demographic model of the IPM). The advantages of IPMs over either stage-structured or integral projection models are twofold. First, IPMs oftentimes offer estimates of demographic rates for which no data are available (Besbeas et al. 2002, Tavecchia et al. 2009, Abadi et al. 2017, Duarte et al. 2017), and also more accurate estimates of parameters influencing demographic rates (Plard et al. 2019). Second and perhaps more importantly, IPMs explicitly model the dynamics of the population structure and the interactions between the population and the individual level (McCrea et al. 2010, Péron et al. 2010). Thus, we believe that IPMs are the modeling framework of choice to investigate the influence of density-dependent effects on the performance of different groups of individuals (Gamelon et al. 2016). Moreover, it is straightforward to use IPMs for the study of transient population dynamics and thus to get insights into the demographic and structural drivers of the realized, rather than only the asymptotic population growth rates (Koons et al. 2016).

Some limitations of using an IPM to study individual processes

IPMs require more and qualitatively different data than either matrix or integral projection models, namely, population count or index data in addition to data on individual demographic rates. However, population monitoring is usually conducted to get index of population data, using a wide variety of data collection (direct observations, transects, count of feces, hair, or animal tracks, genetic analyses, etc.). Thus we think that the requirement of count data is not a serious limitation. Another potential limitation may be seen in the requirement of IPMs for the different data set to be independent, which is almost never true in wild populations. For instance, some individuals that appear in the capture–recapture data set will also occur in the reproductive data and often also in the count data. Ideally, the different data sets should be sampled using a different protocol each. On the other hand, simulation studies done so far have shown that partial dependence between data sets does not seem to influence estimates much, as long as sampling protocols are not biased toward a restricted sample of individuals (Schaub and Fletcher 2015, Plard et al. 2019). A more important potential limitation is that the demographic parameters for which no explicit data have been collected are usually estimated with low precision. Their estimation may be biased if unknown mechanisms (excluded from the state model) generate uncertainty and/or variability in the count data. In order to avoid erroneous conclusions, whenever possible one should avoid estimating more than one parameter for which no explicit data are available (Besbeas and Morgan 2014). But, any demographic process that is

known to influence the dynamics of the studied population (such as immigration for open-population that influence count data) must be included in the demographic model. In addition, goodness-of-fit of all component models in an IPM should be conducted (Besbeas and Morgan 2014, Conn et al. 2018). Another challenge, albeit one that is shared with ALL of parametric statistical models, is that the estimated population structure does depend on how the model is defined. Model selection not only for the inclusion of covariates, but also for the basic demographic model structure, is important in principle, but the latter is not straightforward in such complex hierarchical models (Hooten and Hobbs 2015). For example, a model with two age classes or two groups of different quality may show different stage dynamics than a model with four age classes or quality groups for the same population.

Finally, although including individual heterogeneity in population models allows the study of the influence of the evolution of some continuous traits on population dynamics, a first step before building such population models is to get accurate models of trait heritability (Janeiro et al. 2017) and transmission. Traits may be inherited though genetic inheritance or nongenetic inheritance including maternal effects, epigenetics, or environmental effects (Bonduriansky and Day 2009, Danchin et al. 2011). The relative contributions of these different transmission pathways are still unknown and arbitrary assumptions about trait transmission using a common mean value, a parent–offspring regression, or a genetic model are used in dynamic models (Childs et al. 2016, Coulson et al. 2017, Janeiro et al. 2017). Although these different assumptions about trait transmission can have a large impact on population dynamics (Plard et al. 2016), they are typically chosen arbitrarily according to data availability instead of biological reasons in population models.

Conclusions

IPMs readily allow for integration of the dynamics and modeling of different sources of heterogeneity. The study of the mechanisms of transmission and generation of individual heterogeneity is an active area of research and a matter of current debate (Bonduriansky and Day 2009, Cam et al. 2013, Janeiro et al. 2017, Jouvet et al. 2018). We need to disentangle the relative roles of genetic effects, parental fixed effects, parental condition, and environmental effects on the transmission of measured and unmeasured individual heterogeneity. The ability of IPMs to estimate parameters with improved precision will be useful in this endeavor. IPMs might be able to link more distant levels of biological organization, from genes to communities (Lahoz-Monfort et al. 2017), interspecific competition (Péron and Koons 2012), and predator–prey interactions. A deeper mechanistic understanding of the population dynamics ultimately depends on physiological and genetic levels. Physiological and genetic data could be integrated in IPMs to study direct physiological impacts of density-dependent effects, the evolution of continuous traits (Coulson et al. 2017) and speciation (Peter et al. 2010). We foresee further developments and extensions of integrated population models to improve our knowledge in this very active field at the interface between statistics, population, and eco-evolutionary biology.

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SUPPORTING INFORMATION