Quantifying the contribution of immigration to population dynamics: a review of methods, evidences and perspectives in birds and mammals

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ABSTRACT

The demography of a population is often reduced to the apparent (or local) survival of individuals and their realised fecundity within a study area defined according to logistical constraints rather than landscape features. Such demographics are then used to infer whether a local population contributes positively to population dynamics across a wider landscape context. Such a simplistic approach ignores a fundamental process underpinning population dynamics, dispersal. Indeed, it has long been accepted that immigration contributed by dispersers that emigrated from neighbouring populations may strongly influence the net growth of a local population. To date however, we lack a clear picture of how widely the immigration rate varies both among- and within-populations, in relation to extrinsic and intrinsic ecological conditions, even for the best studied avian and mammalian populations. This empirical knowledge gap precludes the emergence of a sound conceptual framework that ought to inform conservation and population ecology. This review, conducted on both birds and mammals, has thus three complementary objectives. First, we describe and evaluate the relative merits of methods used to quantify immigration and how they relate to widely applicable metrics. We identify two simple and unifying metrics to measure immigration: the immigration rate i_t defined as the ratio of the number of immigrants present in the population at time $t+1$ and the total population size in year t, and π_t, the proportion of immigrants among new recruits (*i.e.* new breeders). Two recently-developed methods are likely to provide the most valuable data on immigration in the near future: individual parentage (rather than population) assignments based on genetic sampling, and spatially-explicit integrated population models combining multiple sources of demographic data (survival, fecundity and population counts). Second, we report on a systematic literature review of studies providing a quantitative measure of immigration. Although the diversity of methods employed precluded detailed analyses, it appears that the number of immigrants exceeds locally-born individuals in recruitment for most

avian populations (median $\pi_t = 0.57$, $N = 37$), a figure twofold higher than estimated for mammalian populations (0.26, $N = 33$). Third, recent and truly quantitative studies revealed that immigration can be the main driver of the temporal variation in population growth rates, across a wide array of demographic and spatial contexts. To what extent immigration acts as a regulatory process has however been only rarely considered to date and deserves more attention. Overall, it is likely that most populations benefit from immigrants without being necessarily sink populations. Furthermore, we suggest quantitatively estimating immigration should be core to future demographic studies and plead for more empirical evidence about the ways immigration interacts with local demographic processes to shape population dynamics. Finally, we discuss how to tackle spatial population dynamics by exploring, beyond the classical source-sink framework, the extent to which populations exchange individuals according to the spatial scale and the type of population distribution throughout the landscape.

Key words: Balanced Exchange Hypothesis, Dispersal, Demography, Immigration rate, Integrated Population Models, Metapopulation, Parentage Assignment, Source-Sink,

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I. INTRODUCTION

Ecologists define a population as *a group of organisms of the same species occupying a particular space at a particular time* (Krebs, 2001). On a global scale, changes in population size over time are due to birth and mortality events across the whole species distribution. When

90 considering smaller spatial scales however, there is accumulated evidence that species are often not uniformly distributed but rather occur in a set of patchy populations separated by a more-or-less unsuitable habitat matrix. These local populations are connected to some degree to each other by dispersing individuals, often the young, emigrating from their natal site, entering the unsuitable matrix, completing the dispersal process by successfully immigrating and

95 reproducing in another population. Accounting for the way animals disperse across space is crucial for understanding both population dynamics and genetics through time (Gaines & McClenaghan, 1980; Pulliam, 1988; Hanski, 1999; Clobert *et al.*, 2001, 2009; Bonte *et al.*, 2012). Indeed, in addition to its direct effect on local population size, successful dispersal results also in gene flow, transfer of pathogens, modification of local genetic diversity, and the

100 alteration of adaptations to local conditions (Blondel *et al.*, 1993; Julliard, Perret, & Blondel, 1996; Keller *et al.*, 2001; Lambin, Aars, & Piertney, 2001; Postma & van Noordwijk, 2005; Loveridge *et al.*, 2007; Cornuault *et al.*, 2012; Genton *et al.*, 2015; Tringali & Bowman, 2015). Immigrants can also provide genetic rescue to small populations suffering strongly from reduced genetic diversity (*e.g.* Åkesson *et al.*, 2016).

105 Spatial processes have been increasingly taken into consideration in ecological studies over the last 50 years, partly because of the growing awareness that natural habitats are becoming increasingly fragmented. Immigration was first incorporated into the theory of island biogeography as the process responsible for colonisation of islands by species from the community occupying the mainland (MacArthur & Wilson, 1967), then, by analogy in studies

110 of populations experiencing extinction-recolonisation dynamics in fragmented landscapes as part of the metapopulation theory (Levins, 1969; Hanski, 1999). In this framework, local populations can vary in size but are small enough to be sensitive to stochasticity and subject to extinction over ecological timescales. Immigration allows for recolonisation and can also prevent extinction according to the level of connectivity between the focal patch and the

115 network of patches that constitutes the metapopulation (Hanski, 2001). When populations are large enough such that they are largely immune from stochasticity, and therefore to extinction, it remains that variation in habitat quality can alter the resulting balance between mortality and fecundity and thus create sink or source populations (Pulliam, 1988; Stacey & Taper, 1992). By definition, sink populations have a negative demographic balance and rely on immigration

from adjacent sources for their long-term persistence. The source-sink concept is often invoked in conservation biology, although assessment of its occurrence is rarely performed rigorously (Runge, Runge, & Nichols, 2006; Furrer & Pasinelli, 2016). Some spatial populations are said to function according to the balanced exchange framework that proposes that populations can simultaneously act as a source and a sink, receiving immigrants and sending emigrants from/to neighbouring populations, as a consequence of environmentally-driven individual dispersal decisions (McPeek & Holt, 1992; Doncaster *et al.*, 1997). This framework is free of any assumption regarding spatial and temporal variation in the balance between emigration and immigration and may be more relevant to explain the diversity of situations encountered (Sæther *et al.*, 1999; Matthysen, Adriaensen, & Dhondt, 2001; Schaub, von Hirschheydt, & Grüebler, 2015).

Thus, irrespective of whether local populations are extinction-prone, immigration is surely an ubiquitous and crucial process in population dynamics. Empirical quantification of its prevalence, however, seems to have lagged behind theoretical reasoning. Indeed, it is striking that high-profile seminal studies on avian and mammalian demography, take place on islands where spatial demographic processes, and immigration in particular, can be left out of demographic accounting. For instance, while an insular system such as Mandarte island in Canada makes it possible to detect rare instances of immigration of song sparrows (*Melospiza melodia*), the recovery from recurrent environmental shocks by populations in such semi-isolated conditions is much more reliant on in-situ reproduction than upon the arrival of immigrants compared to less remote islands (Smith *et al.*, 1996; Wilson & Arcese, 2008). Such seminal studies have undoubtedly contributed to improving our understanding of population dynamics of wild animals in general, and of the interactions between environmental variability and demographic processes in particular. However, it has long been known that experimentally preventing individuals from dispersing from crowded areas may exacerbate the

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145   strength of density feedbacks (Krebs, Keller, & Tamarin, 1969). Therefore, whether the
       findings regarding demographic processes at work in insular populations, such as the role of
       over-compensatory density dependence in the high amplitude fluctuations as observed in the
       Soay sheep (*Ovis aries*) population on one island of St Kilda archipelago (Grenfell *et al.*, 1992;
       Coulson *et al.*, 2001), can be extrapolated to populations open to immigration and emigration
150   remains unknown.

       Immigration is one of the three steps composing the dispersal process, the final one
       following emigration and transience. In the large body of literature concerning dispersal (*e.g.*
       Clobert *et al.*, 2012), immigration has been mainly studied from the angles of habitat
       selection, behavioural ecology and the evolution of life history. Until recently, immigration
155   have been only rarely quantified in studies on population dynamics, which focused instead on
       the variation of demographic rates (survival and recruitment) of locally-born individuals in
       response to changes in population density or environmental conditions. However, accounting
       for spatial dynamics in conservation planning is a major challenge for ecologists if they are to
       contribute to halting the loss of biodiversity in a world where natural habitats are increasingly
160   reduced and fragmented (Ceballos, Ehrlich, & Dirzo, 2017). The overriding reason why
       spatial demographic processes have been largely ignored in studies on population dynamics is
       pragmatic and stems from the notorious difficulty with quantifying movements to and from
       populations (Williams, Nichols, & Conroy, 2002). Population studies disregarding spatial
       demographic processes assume, *inter alia*, that immigration and emigration have a marginal
165   impact on population size relative to local demography or that immigration and emigration
       cancel out, something which is rarely verified. However, ignoring the propensity of animals to
       disperse hampers the mechanistic understanding of how local population processes operate
       and can lead to spurious inference about *e.g.* the demographic status −source *vs.* sink− of a

population, a key assessment in conservation planning (Runge *et al.*, 2006), or the way

170 populations demographically respond to environmental variation (Stacey & Taper, 1992).

Answering the enduring questions about the role of immigration in the dynamics of populations requires quantitative estimates of the rate at which it occurs. Over the past decade, there has been advances in demographer's ability to quantitatively measure the relative direct contributions of locally-born *vs.* immigrant individuals to the overall local dynamics. They stem

175 from an increasing number of large-scale and long-term monitoring studies, principally on birds and mammals, together with recent methodological and analytical developments. Immigration has thus been repeatedly identified as a key demographic process in different contexts of landscape fragmentation, either natural or anthropogenically induced (Connor, Faeth, & Simberloff, 1983; Pulliam, 1988; Nichols & Pollock, 1990; Stacey & Taper, 1992;

180 Hanski, 1999; Schaub *et al.*, 2012; Lieury *et al.*, 2016; Robertson *et al.*, 2018).

To date however, we lack a clear picture of how widely the immigration rate varies both among- and within-populations, in relation to extrinsic and intrinsic ecological conditions, even for the best studied avian and mammalian populations. This empirical knowledge gap precludes the emergence of a sound conceptual framework on animal population demography explicitly

185 including spatial processes and that goes beyond the restricted case of metapopulation *sensu stricto* (Hanski, 1999). Such a framework ought to be of paramount importance for the fields of ecology and conservation biology.

Our review thus focusses on the estimation of immigration and on the direct implication of the addition of a number of immigrants to population size *per se*, and deliberately ignores

190 indirect effects of immigration on population dynamics through the alteration of population structure. The first part of this work includes a critical review of how immigration is defined, the range of methods used for measuring it and the analytical frameworks now available for

estimating the contribution of immigration to population dynamics. Next, we systematically review quantitative estimates of immigration rates in birds and mammals. We seek to quantify

195   the extent of variation in immigration across species, verifying whether increased movement ability in birds indeed translates into higher immigration in avian populations compared to mammalian ones and whether estimates of immigration propensity co-vary with the spatial scale of study areas. Third, we assess how varyingly robust quantitative estimates of immigration have improved our understanding of enduring ecological issues in which dispersal

200   play a key role, such as the prevalence of source-sink systems and the identification of regulatory processes at work in local populations, including those harvested. Finally, we outline emerging avenues of research in both theoretical and applied ecology concerning spatial demographic processes.

205   **II. ESTIMATING IMMIGRATION: A CRITICAL REVIEW OF THE MEASURES AND METHODS**

(1) What is immigration?

A population at time t can be envisaged as being composed of three types of individuals: established reproducers (E_t) are individuals that have reproduced in the population in year $t-1$

210   and survived until year t; local recruits (R_t) are individuals that are born in the focal population one or several years ago and that reproduce for the first time in year t in the focal population; and immigrants (I_t) are individuals that are born outside the focal population and that reproduce for the first time in the focal population in year t (*i.e.* non-breeding immigrants are not considered here). The size of the breeding population in year t is the sum of the three

215   components:

$$N_t = E_t + R_t + I_t \ (1)$$

The population growth rate over one time step can then be written as:

$$\lambda_t = \frac{N_{t+1}}{N_t} = \frac{E_{t+1}}{N_t} + \frac{R_{t+1}}{N_t} + \frac{I_{t+1}}{N_t} \quad (2)$$

This expression can be rewritten in terms of demographic rates as:

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$$\lambda_t = \varphi_t + r_t + i_t \quad (3)$$

where φ_t is apparent survival (*i.e.* the probability to survive and not emigrate from the population) of adults, r_t is the *per capita* recruitment rate and i_t is the *per capita* immigration rate. The sum of $\varphi_t + r_t$ is the local rate of replacement that measures the ability of a population to maintain itself based on local demographic processes only, *i.e.* without immigration (Runge

225 *et al.*, 2006).

The immigration rate i_t is here defined as the ratio of the number immigrants present in the population at time *t+1* and the total population size in year *t*. If the immigration rate is included in a demographic population model, it has to be expressed as per unit a time step before. N_t most often refers to the number of breeding individuals but can be expressed as total number of

230 individuals or total number of a given sex. The number of breeding individuals can be much lower than the total population size, and particularly so in species with delayed reproduction and territoriality where individuals queue to access reproduction (*e.g.* van de Pol *et al.*, 2010; Millon *et al.*, 2014). Equation 1 can be modified to explicitly incorporate non-breeders and consider total population size:

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$$N_t = E_t + lB_t + iB_t + lF_t + iF_t \quad (1b)$$

where F_t stands for floaters (*i.e.* non-breeders) and B for individuals that breed for the first time in the population with the prefix l/i indicating their origin (local / immigrant). In avian studies where the survey consists in nest-box monitoring, N_t is the number of occupied nest-boxes. In social group-living species, N_t is typically the size of the group and i_t is then averaged

across the number of groups surveyed (Rollins *et al.*, 2012). The immigration rate i_t is an instantaneous measure of immigration. Immigrants contribute to i in the year they enter the local population only. Afterwards, they will be considered established individuals.

Another often-used metric to quantify immigration, is the proportion of immigrants among new breeders (or recruits):

$$\pi_t^{IM} = \frac{I_t}{R_t + I_t} = \frac{i_t}{r_t + i_t} \quad (4)$$

π_t^{IM} then measures the contribution of immigration to total recruitment. Thus, the immigration rate of a given population can be low, despite the majority of new recruits being composed of immigrants.

(2) How to estimate immigration? Data, assumptions & analyses

We identified four broad types of methods relevant to the quantification of immigration: (1) population or dispersal status assignment, (2) individual parentage assignment, (3) capture-recapture techniques and (4) population models. We provide below a synthetic overview of the most used or promising methods based upon a selection of compelling avian and mammalian studies, including an evaluation of their strengths and limitations, their underlying assumptions, the nature of the data collected and the type of immigration measurement obtained.

(a) Population or dispersal status assignment

Among methods based on the longitudinal survey of marked individuals, one of the simplest way to estimate immigration is to calculate the proportion of unmarked animals among new recruits in an intensively monitored core area, using capture-recapture data and assuming all

offspring born within the study area are marked. It is by far the most common method to quantitatively assess immigration in wild populations (48% of studies, $N = 94$, birds and mammals combined, see section III).

265   This method obviously assumes that all animals born in the study area are marked (*i.e.* capture probability of local recruits is 100%), and therefore, that any unmarked/previously unseen individual recruiting in the population is necessarily an immigrant. The validity of the inferences then relies on the population being monitored in an exhaustive manner, an assumption however seldom tested. We found only one study on long-tailed tits (*Aegithalos* 270 *caudatus*) that checked the dispersal status for 244 unmarked birds. Using genetic parentage analyses, a parental match to the local pedigree was found for 41 of them, the remaining individuals were considered as potential immigrants (83%; Sharp, Simeoni, & Hatchwell, 2008).

      The use of nest-boxes is expected to greatly facilitate the study of immigration as cavity-275 nesting birds usually prefer settling in nest-boxes rather than in natural cavities (Perrins, 1965). This type of data is the basis for the calculation of π in studies of cavity nesting birds, that are over-represented in avian studies. In studies where captures (and recaptures) are only made in nest-boxes and in which the proportion of the population breeding in natural cavities is not negligible, the estimated immigration rate combines both individuals coming from outside the 280 study area and individuals born within the study area but not in nest-boxes. More generally, any individual that was born in a natural cavity in the study population and moved to a nest-box appeared as immigrant, thus the estimated immigration rate has, in a context of nest-box monitoring, a specific meaning. Comparisons of immigration rates among multiple study areas or years would therefore be problematic if there were variations in the proportion of the 285 population breeding in nest-boxes between populations or amongst years according to *e.g.* densities (Abadi *et al.*, 2010b; Schaub *et al.*, 2012; Brommer, Wistbacka, & Selonen, 2017).

In some species, juveniles may disperse before they become trappable, as it was documented for banner-tailed kangaroo rats (*Dipodomys spectabilis*), thus biasing the estimate of π downward (Waser & Hadfield, 2011).

Three other methods have also been used to identify immigrant individuals. First, for some group-living species such as long-lived large mammals and primates, phenotypic variation is sufficiently large, and population size sufficiently small, to identify unambiguously the arrival of new individuals in a social group (Kahlenberg *et al.*, 2008). Second, genetic information (occurrence of a set of alleles) is used to ascertain population membership of individuals or groups of individuals and, as a corollary, can detect individuals that, according to their multilocus genotype are unlikely to be born in the population where they are sampled, *i.e.* they have immigrated. Third, the ratio between natural isotopes of elements in animal tissues measured by mass spectrometry can be used as a marker to locate the likely natal area (Hobson, 2005; Hobson & Norris, 2008). These three methods can provide estimates of immigration, providing some restrictive assumptions and conditions are met (see online appendix for details).

(b) Individual parentage assignment based on kinship

Kinship-based methods, targetted to linking individuals to a kin group rather than to a population, may be more appropriate than population-level methods to estimate meaningful immigration rates (Manel, Gaggiotti, & Waples, 2005). Fundamentally, given a set of pre-defined demographic parameters, one can derive through simulations the expected frequency of occurrence of close kin, such as parent-offspring dyads, for populations either closed to immigration or subject to variable rates of immigration. Such approaches can be used to determine the immigrant or philopatric status of individuals based on their location in relation to that of close kin that, together with ancillary information (*e.g.* age to focus the search of

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parents in older cohorts only, mother's breeding location, etc.), are used to establish likely birth locations. When an individual is in a different location than its parents and/or pre-dispersed siblings, it is parsimonious to infer it has dispersed from its natal site (Peacock & Smith, 1997; Palsbøll, 1999). Where populations are fragmented, this information can be used to detect immigration events (Telfer *et al.*, 2003). Key to the approach is the reliable reconstruction of pedigrees based on (1) a partially sampled pool of potential parents, (2) genotypes characterized from a variable number of typically micro-satellites and single nucleotide polymorphic loci and (3) with varying amount of prior firm knowledge on the relationships between some pairs of individuals (*e.g.* fawn suckling its likely mother but of unknown father or siblings; Pemberton, 2008).

The use of individual parentage (rather than population) assignment methods has seen a rapid rise in recent studies of dispersal and provides estimates of the rate of immigration more similar to those used in classical demographic studies. In water voles (*Arvicola amphibius*), individual parentage approaches increased the estimated rate and spatial scale of intra-metapopulation dispersal between sub-populations by three- and two-fold respectively, compared to an estimation from an intensive capture-recapture sampling with high capture probabilities (73-92%; Telfer *et al.*, 2003). Similarly, three pedigree reconstructions, obtained from three different algorithms running on a 17-year-long dataset of dispersal in banner-tailed kangaroo rats, each revealed widespread pre-capture dispersal by juveniles, at slightly different rates, that, if overlooked would have led to an underestimation of dispersal rate (Waser & Hadfield, 2011). In the marbled murrelet (*Brachyramphus marmoratus*), Peery *et al.* (2008) detected 70 parent–offspring dyads sharing at least one allele at all loci out of 271 individuals, a frequency lower than expected if the population was closed to immigration. Rather, it was consistent with immigration occurring at the rate of 2–6% per year, given a population size of 550-800 individuals.

A recent simulation study, inspired by empirical data with American mink (*Neovison vison*) highlighted how the assumptions made during the pedigree reconstruction process on the prevalence of paternal half-sibling, the differentiation among populations, and the intensity of

340   genotype sampling through a variable number of loci, may conspire to produce false assignments (Melero, Oliver, & Lambin, 2017). The prevalence of errors was particularly high for half-sibling relationships, and not reflected by the assignment probability score provided by the widely-used software COLONY 2.0 (Wang & Santure, 2009). Where this has been overlooked, as was the case for a metapopulation of capercaillie (*Tetrao urogallus*) in

345   Switzerland (Kormann *et al.*, 2012), there is a substantial risk that the frequency of inter-population dispersal has been over-estimated as they included half-sibs. In contrast, estimates of dispersal distances based on brown bear (*Ursus arctos*) mother-offspring dyads alone should not suffer from this bias (Norman & Spong, 2015). The increasing affordability of scoring large numbers of individuals at a larger number of diallelic markers such as single nucleotide

350   polymorphism is likely to reduce some of the constraints in accurately characterising pedigree in the wild, and their use for estimating immigration. The spatial resolution afforded by the method is directly linked to the sampling regime, which is under the control of researchers.

(c) The capture-recapture framework

355   The capture-recapture framework, in its original form, aims at estimating population size N from successive capture sessions gathering individual capture histories (*e.g.* 1010, where '1' denotes the capture of an individual and '0' the absence of capture), assuming the population is demographically closed over the duration of the survey (*i.e.* no gain or loss of individuals, closed population models). Three different approaches −Jolly-Seber, Pradel's temporal

360   symmetry and super-population models− have then been developed to relax the assumption of closure by incorporating additional parameters to model gains and losses of individuals in order

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to estimate variation in population size (Williams *et al.*, 2002; Cooch & White, 2015). These approaches have benefited from extensions allowing the estimation of immigration by taking advantage of ancillary data on local recruitment.

365   O'Hara et al. (2009) developed an extension of the Jolly-Seber model (Jolly, 1965; Seber, 1965), to estimate the number of immigrants in addition to population size. Their model assumes that all locally born individuals in the population are marked, with the consequence that all unmarked individuals are necessarily immigrants. The entry of these unmarked individuals into the population is modelled and thus the timing of immigration is accurately

370   estimated, even if the capture probability of adults is less than one and varies over time. Immigration is expressed as the number of individuals entering the population and the model also allows for different survival of immigrants and established adults. Applied to data of a willow tit (*Parus montanus*) population revealed that the number of immigrants was positively correlated with population size. Due to the restricting assumption that all locally born

375   individuals were marked every year, this model can only be applied to very intensive studies and to our knowledge has not been applied since the seminal study.

The 'reverse-time capture-recapture' model, or temporal symmetry model, developed by Pradel (1996) estimates the probability that an individual alive at time *t* was present in the population at time *t*-1 (or seniority γ), from which the population growth rate and total

380   recruitment rate can be estimated (Nichols *et al.*, 2000). If fecundity data are available, immigration rate can then be inferred from the model including the recruitment parameter (f) by subtracting local recruitment obtained from estimates of fecundity (ρ) and apparent juvenile survival (φ): $i_t = f_t - \rho_t \varphi_{j,t}$. Using this method, Peery et al. (2006) showed that the recruitment in an endangered population of marbled murrelets consisted mainly of immigrants

385   ($\pi = 0.88$).

Capture-recapture models based on a robust design combine live recapture and closed capture models into a single framework (Pollock, 1982; Williams *et al.*, 2002). Again focusing on a single population, a robust design includes capture sessions that occur repeatedly within a breeding season (secondary occasions) during which the population is assumed to be demographically closed, and this is repeated over several periods (primary occasions) between which mortality events can occur. The temporal scale varies with the focal species: in short-lived small mammals, primary and secondary sessions take place over months and days respectively while in birds the setting spans over years and months. The robust design capture-recapture model allows the separation between *in situ* reproduction (*i.e.* local recruits) and immigrants providing that the timing of sampling allows the capture of young individuals (and their identification as such) before dispersal takes place and that the time elapsed between two primary sessions correspond to the period required for young individuals to mature into adult ones (Nichols & Pollock, 1990). Under such conditions, the capture probability of each age class and hence their population sizes can be estimated from repeated sampling within each primary session. When combined with the estimates of age-specific survival probabilities between primary capture occasions, it is then possible to derive the number of immigrants and their contribution to the dynamics of the local population. Besides Nichols's seminal work with meadow voles (*Microtus pennsylvanicus*), capture-recapture data collected according to a robust design have been modelled in banner-tailed kangaroo rats (Wen *et al.*, 2011, 2014). These authors used a super-population formulation (*i.e.* considering N_i as the total number of individuals, marked or not, available for capture during the primary session i, Schwarz & Arnason, 1996) together with ancillary information. Wen et al. (2011) demonstrated that adding genetic population assignment (whether a particular individual was born in the local population) allowed them to disentangle the relative contributions of locally-born and immigrant individuals to population dynamics, an unfeasible inference when using single-age

class data in open population models. Assignment information could originate from other types of data than genetics (*e.g.* isotopic analysis), does not need to be available for all individuals and can be modelled with uncertainty. Similar information brought to a two age-class model further improved parameter estimation and precision (Wen *et al.*, 2014). These two studies confirmed the relatively weak exchanges among populations of kangaroo-rats with immigrants 2.4-5 times less numerous than local recruits, and the latter category showing higher survival.

Several key assumptions, common to all CMR approaches, have to be fulfilled in order to obtain unbiased estimates for immigration and other demographic rates. The capture probabilities should not be affected by the previous capture history (*i.e.* no trap-dependence), nor be different between marked and unmarked individuals (Williams *et al.*, 2002; O'Hara *et al.*, 2009). When these assumptions are met, the combination of recruitment and capture-recapture data from a single location can provide reliable estimates for both immigration rate and proportion of immigrant among new recruits.

Movements of marked individuals among geographically separated populations can be studied using multi-state capture-recapture models (Arnason, 1973; Spendelow *et al.*, 1995; Grosbois & Tavecchia, 2003; Henaux, Bregnballe, & Lebreton, 2007; Lebreton *et al.*, 2009). They potentially allow the quantification of the number of individuals that a particular population has received from the other study populations. However, there are two main issues that render this method challenging for the quantification of immigration. First, it models only the movement of individuals within the study system. The quantification of total immigration remains therefore incomplete unless the study system includes all potential donor populations from where immigrants could originate. This requirement seems to be rarely met. Second, the movement probabilities are specific to the donor sites, while immigration is quantified with respect to the size of the receiving population. Even if emigration and immigration are indeed

435   the two sides of the same process, we are not aware of any study having adopted a specific

formulation for deriving immigration rates.

(d) Population models

This methods requires the combination of multiple sources of data: capture-recapture data to
440   estimate survival, fecundity data as well as counts of the (breeding) population. Here the idea

is to compare the predicted growth rate, obtained from a population model (λ_m) parameterized

with local demographic rates, with the realized population growth rate (λ_r) derived from either

the counts of the population or temporal symmetry models based on capture-recapture data. λ_m

is typically lower than λ_r and the difference is assumed to be due to immigration, provided that

445   demographic rates incorporated into the model were estimated without bias. An estimate of

immigration rate can be obtained by implementing a model parameter corresponding to

immigration which is then adjusted by iterations until $\lambda_m = \lambda_r$. Confidence intervals around

the immigration rate can be obtained from a bootstrap procedure or the delta method (Peery et

al., 2006, Schaub et al. 2006). Their size depends on the precision of the estimates contributing

450   to λ_m and the estimated population size used for λ_r. Peery et al. (2006) found convergent results

regarding immigration rate in a population of marbled murrelets in California by comparing

growth rates obtained from matrix modelling (*i.e.* ignoring immigration) on the one hand and

from a temporal symmetry model and at-sea counts (both including local recruits and

immigrants) on the other hand. This study concluded that this population was a sink with a very

455   low *per capita* fecundity rate (0.04 ± 0.01) though it remained stable owing to a relatively

important immigration rate (0.16 ± 0.06). This figure was much higher than the one estimated

through kinship genetic assignment (0.02-0.06; Peery *et al.*, 2008).

Provided the estimates of the demographic rates are unbiased and the population counts are accurate, this method is likely to genuinely reflect the extent of immigration. This *ad hoc* method, however, does not rely on a model likelihood and thus precludes proper hypothesis testing regarding *e.g.* density-dependent immigration. A more rigorous formulation has been recently proposed with the different data sources being analysed jointly by formulating a common likelihood within an Integrated Population Model (IPM; Besbeas *et al.*, 2002; Besbeas, Lebreton, & Morgan, 2003; Abadi *et al.*, 2010a, 2010b). Information about immigration originates from the population counts that can be extracted because fecundity and capture-recapture data provide information about the remaining demographic processes (apparent survival and local recruitment; Fig. S1). A particular strength of this method is that it ensures an adequate representation of errors of the immigration parameter such that its variability can be studied. IPMs are very flexible in that they can accommodate different types of data such as age-at-death ratios or telemetry data in addition to, or as substitute, for other demographic data (Schaub *et al.*, 2010). The flexibility applies also to the immigration parameter itself, which can be expressed and modelled as a rate (relative to previous population size) or as a flux, *i.e.* the number of immigrating individuals (Schaub & Fletcher, 2015). The age at which immigration occurs cannot be estimated, but is fixed by the way the population model is specified. Because insights into the population structure (*e.g.* proportions of immigrants, local recruits or experienced breeders) are possible, the IPMs allows full flexibility in the quantification of immigration (*e.g.* π can be obtained as a derived parameter) and further interesting analyses can follow (see below).

To avoid bias, demographic parameters and in particular those affected by dispersal (typically apparent juvenile survival), must be estimated at the same spatial scale as that used for estimating population size. Most often, these two types of survey are performed with the very same population, which raises the issue of data independence. Independent data sets are

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usually required due to the manner in which most IPMs compute the joint likelihood. Using simulations, Abadi *et al.* (2010a) showed the violation of this assumption was essentially inconsequential for parameter estimation. A weakness of IPMs is that the immigration parameter is typically quite imprecise (Schaub & Fletcher, 2015; Riecke *et al.*, 2019). The coefficients of variation of immigration range from 0.08 (Schaub et al. 2013) to 0.58 (Lieury et al. 2015) among 16 empirical studies. The low precision could potentially be improved by the inclusion of additional information (*e.g.* genetic population assignment information; Wen *et al.*, 2011), sampling following the robust design (Nichols & Pollock, 1990) or of additional assumptions (*e.g.* analysing the capture-recapture data with the unconditional Jolly-Seber model). A further challenge is that immigration is only unbiased when the rest of the model is correctly specified (Schaub & Fletcher, 2015; Riecke et al. in press in MEE: Integrated population models: model assumptions and inference) which renders goodness of fit testing of each model component of an IPM important. Finally, the current formulations of integrated population models are based on the assumptions of equal survival of immigrants and established adults (Szostek, Schaub, & Becker, 2014), but it is possible to relax this assumption by including additional information.

III. SYSTEMATIC LITERATURE REVIEW

We performed a systematic review of the literature to shed light on both methodological and ecological issues related to the contribution of immigration to the growth of populations. Following the guidelines proposed by Pullin and Stewart (2006), we accessed the two databases *Web of Science* and *BibCNRS*, searching for the topics "immigra*" and "bird*" or "mammal*" with no time restriction. The search took place in June 2017 and a total of 737 references were returned for birds and 231 for mammals. Then, we specifically looked for papers in which the

contribution of immigrants to local population dynamics was quantified thus producing either an immigration rate I or a proportion of immigrants among new recruits π. We were able to extract at least one of these quantitative measures on immigration from 75 studies conducted on 52 bird species, and 19 studies conducted on 17 mammal species (see online appendix for the complete list of studies).

On methodological grounds, the spatial scale at which immigration is assessed is likely to affect the derived measures. We therefore explored the influence of size of the study area, weighted by species' body mass, given the positive allometric relationship between body mass and territory size has been documented in both birds and mammals (Haskell, Ritchie, & Olff, 2002). We predicted that the estimates of immigration should decrease as this ratio increases. The rationale underpinning this prediction was as follows: the larger this ratio, the higher the probability that dispersers bred within the study area, all other things being equal. *In extremis*, there would be no immigration recorded if the studied population covered the whole distribution of the species. Specifically, we used the log-ratio between the size of the study area (km²) and body mass (g). Analyses were run using linear mixed models with arcsine-square-root transformation of the response variables (immigration rate and proportion of immigrants among new recruits) and REML method. To account for the hierarchical structure of the data reflecting multiple observations in some species and phylogenetic links among species, we added the species nested within taxonomic order as a random term. We averaged I and π in cases of sex- and method-specific calculations but kept estimates from several populations (whether or not from the same study). When the same dataset was repeatedly used over time, we only used the estimates from the longest time-series.

In birds, immigration rates (expressed as the number of immigrants divided by the total population size) ranged from 0.012 in the song sparrow on Mandarte island off Canada (Keller *et al.*, 2001) to 0.495 in the red-backed shrike (*Lanius collurio*) in Germany (Schaub, Jakober,

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& Stauber, 2013). I averaged 0.20 ± 0.13 (median = 0.172, N = 44 data from 35 species in 39 studies; Fig. 1a). Twenty-eight observations from 21 different species belonging to 8 taxonomic orders were available with the log(study area/body mass). We found no effect of the log(study area /body mass) on the estimates of I ($\beta = 0.01 \pm 0.01$, $P = 0.22$; Fig. 2a).

The proportion of immigrants among new recruits ranged from 0.037 in the song sparrow on an isolated island to >0.9 in the same species on a less isolated island (Wilson & Arcese, 2008) and in the black-legged kittiwake (*Rissa tridactyla*; Coulson & Coulson, 2008). Over the 45 datasets collected on 29 species in 37 studies, the average proportion of immigrants among new recruits reached 0.53 ± 0.27. In the majority of studies, immigration contributed more than local recruitment to total recruitment of bird populations (median = 0.57; Fig. 1b). Thirty-three observations from 20 different species belonging to 7 taxonomic orders were available with the log(study area/body mass). As expected, we found a negative relationship, though only marginally significant, between the log(study area/body mass) and the proportion of immigrants among new recruits ($\beta = -0.028 \pm 0.014$, $P = 0.067$; Fig. 2b). The larger the number of territories included in the study area, the lower the proportion of immigrants among new recruits was.

In mammals, we gathered 23 estimates of immigration rate covering 10 species from 9 studies. Immigration rates ranged from 0.026 in porcupine males (*Erethizon dorsatum*) to 0.63 in American pika (*Ochotona princeps*, mean $\pm$ SD = 0.26 ± 0.17, median = 0.256, Fig. 1c). No trend in the variation of immigration rate with the log(study area/body mass) was detected ($\beta = -0.006 \pm 0.03$; Fig. 2c). Regarding the proportion of immigrants among recruits, we gathered 33 estimates on 10 mammal species from 11 studies. The averaged proportion of immigrants among recruits was 0.27 ± 0.22 (mean $\pm$ SD, range [0.014-0.725]; Fig. 1d). Again, the relationship between the log(study area/body mass) and the proportion of immigrants among

recruits was not obvious in seven species of two taxonomic orders ($N = 24$, $\beta = 7.7 \times 10^{-4} \pm$ 0.025; Fig. 2d).

Overall, we observed a wide range of variation in I and π for both birds and mammals. The main difference between the two taxonomic classes is the proportion of immigrants among new recruits, which was twice as large in birds compared to mammals (Fig. 1). I was somewhat higher in mammals compared to birds but this difference may only reveal a difference between samples in terms of population turnover. However, the inconsistency of the methods used and in the ways quantitative estimates and explanatory variables are reported precluded more detailed analyses regarding the effects of *e.g.* population size/density, temporal trend or the degree of isolation affect immigration. Addressing questions as basic as whether there is any relationship between the size of study areas and estimates of immigration rate and body mass would benefit from further analyses restricted on data collected and analysed in a consistent way. The growing use of IPM and kinship-based assignment might improve this present paucity of suitable data and we encourage researchers to systematically provide key information on the size of the study area, mean population size (with temporal coefficient of variation), and formal test of temporal trend to facilitate future comparative analyses.

Finally, it is probable we overlooked relevant studies in this literature search and in particular those estimating immigration using genetic data because of a terminological mismatch between demographers and geneticists, the latter frequently employing the terms migration and migrant for immigration and migration. Furthermore, using the terms 'assignment' and/or 'gene flow' would have undoubtedly increased the occurrence of genetic estimates of immigration rate in the dataset, especially in mammals. Nevertheless, it is unlikely we missed numerous genuine estimation of immigration (either I and π) from these types of paper.

580 **IV. TOWARDS A MORE SPATIALLY-EXPLICIT STUDY OF ANIMAL DEMOGRAPHY**

Below, we discuss how quantitative estimates of immigration have improved, or could improve, our knowledge about population dynamics in a variety of demographic contexts. Specifically, we organise this section around three simple structuring questions: 1) to what extent study

585 populations are open to immigration? 2) does immigration regulate population dynamics? and 3) how does immigration co-vary with emigration? We provide compelling examples from the above literature review and beyond for each of these questions before offering some recommendations and suggestions for future research.

590 **(1) To what extent are study populations open to immigration?**

Our review reveals that immigration is an ubiquitous demographic process in avian populations. Deciphering the relative contribution of the different demographic rates (recruitment, adult survival and fecundity) to variation in population growth rate λ, is a long-standing challenge in population ecology (Lack, 1954; Sæther *et al.*, 2016). Above we emphasised that recruitment

595 rates should be further broken down into local recruitment *vs.* immigration rates, and that this can be achieved in a meaningful manner within the statistical framework of IPMs. Focusing on 11 studies using this method (but excluding species monitored in nest-boxes; see above), we found that immigration contributed the most to temporal variation in λ in three cases (California spotted owl [Tempel, Peery, & Gutiérrez, 2014], common tern [*Sterna hirundo*, Szostek *et*

600 *al.*, 2014], barn swallow [*Hirundo rustica*; Schaub, von Hirschheydt, & Grüebler, 2015]). In the red-backed shrike, demography was mainly driven by immigration in females but not males for which variation in local recruitment was the main driver of change (Schaub et al. 2013). In three remnant populations of the northern wheatear (*Oenanthe oenanthe*) in the Netherlands,

the discrepancy in growth rates among populations in one case was due to fecundity and in the

605   other case due to immigration (van Oosten *et al.*, 2015). In a cross-continental study conducted

on the wood thrush (*Hylocichla mustelina*), Rushing *et al.* (2017) found that immigration was

the main demographic component underpinning the variation in λ in four out of 12 sub-

populations (adult survival for five sub-populations, juvenile survival for two, fecundity for

one). For the remaining five studies, the relative contribution was not directly assessed, but

610   visual inspection of the time-series of immigration rate suggested demographic traits other than

immigration might drive temporal variation in λ. While these examples do not constitute a

representative sample of avian populations, they provide strong evidence that variation in

immigration can indeed be the main demographic driver of local populations, and that

demographically-closed populations might be the exceptions rather than the rule.

615   Much rarer are applications of IPMs focusing on mammals. A recent paper, however,

considered the contribution of immigration in the Siberian flying squirrel (*Pteromys volans*) in

two distinct study areas in Finland (Brommer *et al.*, 2017). These authors emphasize the

importance of immigration for driving the fluctuations of population size, contrasting with the

low impact of other demographic traits such as survival and fecundity. Moreover, immigration

620   rate declined as population size increased, mainly because the same number of squirrels were

estimated to immigrate into the focal populations each year. Squirrel monitoring, however, was

achieved in nest-boxes, therefore inference was restricted to the squirrels living in nest boxes

(see above). The Nichols and Pollock (1990) method has been used to estimate the separate

components of recruitment (in situ reproduction *vs.* immigration) with several mammal

625   species, including the meadow vole in the seminal study. In a stable population of brushtail

possums (*Trichosurus vulpecula*) occupying prime habitat in New Zealand approximately three

in four breeding males and one in five breeding females were estimated to be immigrants

(Efford, 1998). Similar estimates were obtained for the same species also in prime habitat in

Australia (Clinchy, Krebs, & Jarman, 2001). Worryingly, the inference that both populations appeared to act a dispersal sink was interpreted as reflecting mortality associated to capture and handling induced stress, emphasising that even robust analytical methods cannot preclude biased inference when the empirical data are contaminated by observational biases (Clinchy *et al.*, 2001). In a replicated CMR experiments contrasting populations of meadow vole occupying (1) corridor-linked fragments, (2) isolated or non-linked fragments, no difference in either component between treatments was evident, nor were significant differences in overall recruitment between the pre- and post-treatment periods (Coffman, Nichols, & Pollock, 2003). The authors ascribed, however, the lack of effect as reflecting an issue of estimator precision and test power rather than a result of biological interest. Altogether, these examples highlight the difficulty to estimate immigration in mammals.

While the degree of isolation could obviously affect the extent of immigration, very few studies presented an explicit measure for this, as done in *sensu stricto* metapopulation studies. In four populations of little owls (*Athene noctua*) of southern Germany and Switzerland, the immigration rate estimated using Pradel's model ranged from 0.09 to 0.27 and its contribution to λ seemed to decrease with increasing spatial extent and isolation of the local populations (Schaub *et al.*, 2006). Note however that this study was based on nest-box monitoring and might therefore suffer from bias in link to the proportion of the population breeding outside nest-boxes (see above). Matthysen et al. (2001) more explicitly explored the effect of forest isolation on local recruitment of great and blue tits (*Parus major* and *P. caereleus*). Interestingly, whereas they found that local recruitment was indeed higher in isolated patches compared to patches embedded within large forests, there was no relationship, among isolated patches, between the degree of isolation (measured as the quantity of forest within a 1-km radius) and the proportion of immigrants π. Moreover, this proportion exceeded 50% in all contexts (and up to 100%), suggesting movements of individuals among patches are

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commonplace. Populations located at species range margin, and characterised by researchers as semi-isolated, experienced immigration. This was the case for the great reed warbler (*Acrocephalus arundinaceus*) in Sweden (Bensch *et al.*, 1998) and two endangered raptors (Bonelli's eagle, *Aquila fasciata* and Egyptian vulture, *Neophron percnopterus*) in France. For the latter two species, immigration occurred at an apparently constant rate and seems to have prevented the populations from collapsing to very low levels. Following efficient conservation actions, local demography appears now to be stable and immigrants further contribute to a slow recovery in both species (Lieury *et al.*, 2015a, 2016).

Immigration can boost the growth of expanding populations to the extent that the recruitment of immigrant overwhelms local recruitment during the exponential growth phase of newly established populations. This has been documented in the early phase of the rapidly growing population of glossy ibis (*Plegadis falcinellus*) in Spain (from 7 to ca. 700 breeding pairs seven years later; Santoro, Green, & Figuerola, 2016) and of Eurasian spoonbills (*Platalea leucorodia*) in Italy (from 17 to 182 in 20 years; Tenan *et al.*, 2017). Another striking example comes from the rapid recovery of the Yelkouan shearwater (*Puffinus yelkouan*) on Zembretta island (Tunisia) that was fuelled by immigration following rat eradication (Bourgeois *et al.*, 2013). The growth of two colonies over three years (8 to 10-fold) was largely attributed to immigration given the low fecundity and the late age at maturity of this species. This result somehow contradicts the belief that seabirds are highly philopatric. Indeed, this general perception might be based upon spatially-restricted capture-recapture study designs. The study of two black-legged kittiwake (*Rissa tridactyla*) colonies actually revealed that immigrants formed 77-96% of the new recruits (Coulson & Coulson, 2008). Overall, there is little doubt immigration is a major driver of population growth rate in a variety of demographic and ecological contexts.

(2) Does immigration regulate population dynamics?

680 If immigration rate was adjusted according to the demographic deficit of recipient populations, it could act in a regulatory fashion, contributing to maintaining the size of populations within some bounds. Immigrants can provide a demographic rescue to populations showing local demographic deficit. The case of a population of eagle owl (*Bubo bubo*) in Switzerland compellingly illustrates such regulatory influence with the observed stability of the population

685 resulting from massive immigration (1.6 yearling immigrant female per pair and per year) balancing the very low survival of adult females (0.61) due to electrocution and collisions (Schaub *et al.*, 2010). Similarly in Kielder Forest (UK), tawny owls experienced a decline in prey density especially during the breeding season that reduced their reproductive rates. Nevertheless, total population size remained roughly stable over 15 years, with lowered local

690 recruitment being precisely compensated for by the doubling of the proportion of immigrants among new recruits (Millon *et al.*, 2014). Immigration was demonstrated to sustain positive population growth rate in all years and subunits through density-dependent immigration in the feral horses (*Equus ferus caballus*) of Sable Island National Park Reserve, Canada (Contasti *et al.*, 2013). In the American pika (*Ochotona princeps*), immigration strongly contributes to

695 population growth rate, by balancing low birth rate of populations located in snowbeds with immigration from more productive meadows in alpine habitats of the USA (Kreuzer & Huntly, 2003).

Clearly, inferring the health of a population from counts only can be misleading and mask the identification of cryptic sinks. Therefore, a mechanistic approach considering the response

700 of demographic rates, including immigration, to environmental change and population size must be preferred to provide insightful inferences for management (Frederiksen *et al.*, 2014). A degree of connectivity of the local population to its surrounding neighbours is not however a guarantee of full compensation through immigration; the number of prospective immigrants

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may be limited by the production and prospecting activities of emigrants from source

705 populations. A population of the endangered California spotted owl (*Strix o. occidentalis*) kept

declining at an annual rate of 3.1% despite relatively high immigration rate (9.7%; Tempel,

Peery, & Gutiérrez, 2014). Low connectivity to a small number source population(s) may limit

the scope for compensation by immigration.

Immigration notoriously contributes to the regulation of harvested populations. The

710 estimation of the level of compensation and by which demographic rate this compensation takes

place, is key to determine sustainable harvest rates (Weinbaum *et al.*, 2013). In addition to any

compensatory responses involving reproduction and survival (Péron, 2013), immigration can

compensate for the impact of hunting in harvested populations. Radio-tracking of the willow

ptarmigan (*Lagopus lagopus*) in Scandinavia revealed non-compensatory mortality whereas

715 annual counts suggest an almost complete compensation (Hörnell-Willebrand, Willebrand, &

Smith, 2014). The most parsimonious explanation for this discrepancy is that immigrants

compensate for losses to harvesting because of spatial heterogeneities in the extent to which

harvesting depletes the pool of potential dispersers. Immigration into local populations may

also directly affect wider populations. A key consideration here is whether immigrants come

720 from a pool of 'surplus' individuals prevented from breeding in their source populations by the

lack of space and territoriality (Jenkins, Watson, & Miller, 1963) or exercise habitat selection

and thus possibly deplete populations at a larger scale (Jenkins *et al.*, 1963; Loveridge *et al.*, 2007). In the red fox (*Vulpes vulpes*), immigration has been identified as the most likely

process involved in the resilience of populations to culling at rather large spatial scales,

725 highlighting the fact that the current harvesting period might be ill-defined to efficiently control

the population (Lieury *et al.*, 2015b). Despite a high hunting pressure imposed on cougar

(*Puma concolor*) within a 1,000-km² game management unit aiming to reduce the growth rate

far below 1 (λ_m = 0.84-0.89), cougar densities show high resilience to harvest because of

immigration from surrounding areas and remain stable over five years (Robinson *et al.*, 2008).

730 That immigration adds to the size of populations has been repeatedly demonstrated within the context of population management, whereby fluxes of individuals compensate for the mortality of local individuals, thus making harvesting sustainable or boosting the growth of recently established or failing populations. In this manner, immigration also counters attempts to reduce population size through lethal management (Dalerum, Shults, & Kunkel, 2008; Oliver *et*

735 *al.*, 2016). Wolverines (*Gulo gulo*) are subject to intensive regulation in Norway whereas it benefits from full protection in adjacent Sweden. This spatial heterogeneity in species regulation entails an important immigration from Sweden to Norway that hinders both conservation and conflict mitigation actions in either side of the border (Gervasi *et al.*, 2015).

There is more to compensatory immigration than numbers: while numbers may be equalised

740 by compensatory immigration, this may nevertheless result in diverging population trajectories because of the nature of immigrants. In the aforementioned study of cougar, a closer inspection revealed a shift in population structure with decreasing female densities but an increase in density of young males, the main dispersing stage (Robinson *et al.*, 2008). Such changes in population structure might alter population growth rate on the long-term and induce undesired

745 side effects, such as increase in infanticide in social species, up to population collapse (Milner, Nilsen, & Andreassen, 2007).

In most species, dispersers are young non-breeding individuals, although other (st)age classes can occasionally move between successive breeding events. Dispersal is often sex-biased, the dispersing sex being typically male in mammals and female in birds. Whether

750 dispersers differ in terms of phenotypic quality compared to residents, either in source or recipient populations, remains an open question. Whereas most studies found lower demographic traits and lifetime reproductive success for immigrants compared to residents of the recipient populations (Julliard *et al.*, 1996; Hansson, Bensch, & Hasselquist, 2004; Millon,

Petty, & Lambin, 2010; Pakanen *et al.*, 2010; Wen *et al.*, 2014), some found the opposite pattern (Altwegg, Ringsby, & Saether, 2000). Moreover, it has been argued, that heritability in dispersal propensity might bias fitness estimates (offspring from immigrants more likely to leave the study area, thus not counted as recruit), such that comparing fitness between dispersers and philopatrics is difficult (Doligez & Pärt, 2008).

Where it is variable and negatively related to density, immigration can act a strong compensatory mechanism buffering local demographic imbalance. Estimates of how immigration rate varies with recipient population density or deficit make it possible to assess whether compensation through dispersal is partial or complete. However, time-varying estimates of immigration rates are rare to date. Nevertheless, Schaub *et al.* (2013) found evidence for a negative feedback of population density on immigration rate in the red-backed shrike. The mechanism underpinning this finding is likely a saturation of available territories in the recipient population with increasing population size coupled with possible competitive advantages of residents over immigrants regarding territory access. The number of immigrants into a Norwegian dipper (*Cinclus cinclus*) population was affected by an interaction of population density and winter weather: immigration was stronger after mild winters but only when the local population density was low (Gamelon *et al.*, 2017). While the negative feedback of population density on immigration rate is naturally expected, sample size may provide only weak statistical power to detect it. For example, Lieury *et al.* (2015a, 2016) failed to detect any density feedback on immigration from populations of two large raptor species with ca. 25 pairs over 16-24 years (to be compared with ca. 55 pairs of shrike monitored over 35 years and 30-120 pairs of dipper over 34 years, see above). In the colonial common tern, Szostek *et al.* (2014) found a positive correlation between the number of immigrants and the number of local recruits but not with colony size (the relationship was actually positive, though not significantly). In a great tit population in the Netherlands, recruitment rates of locally-born birds and immigrants

were both positively correlated to the production of beech mast, the main food resource in winter (Grøtan *et al.*, 2009). Similarly, immigration by little owls in years with peak vole abundance tended to be stronger than in years with low vole abundance (Abadi *et al.*, 2010b).

If prospective immigrant have access to information on variation in population density over a large scale and respond accordingly, immigration can also contribute to population synchrony as shown by a study on barn swallows in Switzerland (Schaub *et al.*, 2015). As a consequence of high natal dispersal, local recruitment in swallow colonies was very low, and was compensated for by high immigration. Immigration requires, of course, the availability of a number of potential immigrants which depends in first place on productivity the year before but also on juvenile survival. If these two demographic rates are synchronised by a large-scale process, it offers the possibility that immigration is also spatially synchronized and hence does contribute to population synchrony, especially if local gaps are filled. This seems to happen in the barn swallow. More quantitative assessments of immigration are however needed to investigate how dispersers redistribute themselves according to spatial variation in density.

(3) How does immigration covary with emigration rate?

Without immigration, this population would have declined… and can therefore be categorized as a sink. This type of statement was repeatedly found in the literature we reviewed, in both birds and mammals. While they reveal the perceived key role immigration is playing in population dynamics, such statements illustrate, however, a common misunderstanding of genuine source-sink dynamics. As advocated by Runge et al.'s (2006), the source-sink status of a focal population cannot be assessed from population growth rates λ derived solely from demographic parameters that are estimated locally. Remarkably, a recent review highlighted that most studies assessing the source-sink status of animal populations focused solely on

processes taking place within local populations, and very few studies actually accounted for emigration and immigration (four and six, respectively, out of 73 studies according to Furrer & Pasinelli, 2016).

Furthermore, the fact that a population receives immigrants does by no means imply this population is a sink (Doncaster *et al.*, 1997). The estimate of local (or apparent) juvenile survival rate indeed includes, in addition to true mortality, individuals permanently emigrating to other populations within a large-scale network. Jointly considering estimates of immigration and emigration rates, based on *e.g.* radio-tracking, joint live and dead recoveries or spatial recapture data (see below), is therefore essential to a relevant assessment of the source-sink status of a population, yet it is rarely achieved. Populations receiving immigrants might however produce an annual number of offspring exceeding mortality losses (pseudo-sink; Watkinson & Sutherland, 1995; Thomas & Kunin, 1999; Hixon, Pacala, & Sandin, 2002). From our literature review, wherever studies are able to quantify the proportion of immigrants among new recruits, it appears that the number of immigrants often exceeds that of local recruits, at least in bird populations (Fig. 1). Rather than assuming that researchers predominantly study sinks, it appears more plausible that the reciprocal exchange of individuals among populations is a widespread demographic process across a large range of species spatial distribution. Therefore we support Doncaster et al.'s conclusions (1997) that most populations probably have reciprocal exchanges of individuals with their neighbours, irrespective of whether those populations occupying discrete patches and holding small populations experience extinction-recolonisation turnover, and thus function as metapopulations *sensu stricto*, or are more continuously distributed across space without discernible local extinctions.

V. RECOMMENDATIONS FOR FUTURE WORK

(1) Using the appropriate terminology and method

Our review revealed that many studies dealing with immigration suffer from a lack of clarity and precision in the terminology used (Herrando-Perez *et al.*, 2012). We identified two key parameters for characterising immigration, the immigration rate *I* and the proportion of immigrants among new recruits π, ideally together. Therefore, we recommend that these two parameters should be properly calculated based on Eq. 4 & 5, and using data from the adequate time periods to ensure results can be used for future comparative and meta-analyses.

While some of the methods we reviewed have delivered a new quantitative estimation of immigration rate, so far immigration rate is often taken as rate aggregated over age classes and deemed time invariant, not least because of the amount of data required to obtain a satisfactory point estimate. However, understanding of intraspecific variation in immigration rate will require estimates of time-varying rates, as with any other demographic rate. We believe two methods are promising in delivering this. Integrated population modelling offers flexibility in the manner immigration rate is specified and other measures of immigration (π) can be obtained as derived parameters. It is currently the most common method used to investigate immigration in birds (15/36 studies since 2010), thus contributing to the rise of quantitative studies of immigration over the last decade (Fig. S2). IPMs can be further improved by incorporating spatial information from capture-recapture data to estimate animal movement and dispersal (Gardner *et al.*, 2010; Royle *et al.*, 2014; Schaub & Royle, 2014; Chandler *et al.*, 2018). In contrast to the classical IPMs that are written for summaries of individuals (*e.g.* number of individuals in an age class), spatially-explicit IPMs proposes an individual-based hierarchical formulation of survival, dispersal and observation processes. Moreover, and most importantly, models specified in continuous space are not restricted to an artificially defined population boundary, thus reducing the spatial scale issue that affects estimates of immigration rate. Immigration and emigration could then be measured at various spatial scales, which would open

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the possibility to compare immigration across studies. The on-going miniaturisation and life lengthening of high-resolution Global Positioning System tags will further improve our ability to track animal movements without any boundary (Kays *et al.*, 2015).

855   Another promising method for quantifying immigration is kinship assignment based on pedigree data. This method is a major progress in the use of genetic material to infer immigration. Contrary to genetic population assignment that only provides immigration estimates averaged over several generations, pedigree-based methods enable one to derive rates that are wholly comparable to classic demographic studies, providing that pedigree can be

860   reconstructed without bias. This method holds promise to yield direct estimates of immigration without necessitating the many years of intensive demographic studies required for specifying IPM, taking advantage of the increasing use of non-invasive genetic sampling for demography (*e.g.* hair, scat).

865   **(2) Answering enduring questions by investigating the factors responsible for spatio-temporal variation in immigration**

Besides a more precise estimation of animal demography that includes estimates for both of immigration and emigration in addition to births and deaths of locally-born individuals, more data are needed to evidence the way populations are connected among each other and how these

870   connections may vary in intensity through time (McPeek and Holt, 1992; Thomas and Kunin, 1999). The balanced exchange hypothesis (Doncaster et al., 1997) posits that local populations receive/send an equal number of immigrants and emigrants, resulting from a dispersal strategy conditioned by environmental cues (*e.g.* conspecific density, conspecific reproductive success). This hypothesis has been rarely tested and deserves more empirical attention. Complex patterns

875   of spatio-temporal variability in habitat quality, such as those observed in farmlands, may

generate a combination of balanced exchanges and source-sink dynamics across the landscape (Diffendorfer, 1998; Tattersall *et al.*, 2004). Investigating the effects of connectivity and temporal variation in habitat quality on the balance between immigration and emigration, beyond the classical source-sink theory and akin to what is currently achieved in the metapopulation context (*e.g.* Sutherland et al., 2014), surely constitutes the major challenge ahead if we are to better inform conservation prioritisation. As population ecologists, our role is also to provide more empirical evidences to practitioners and managers about the way immigration interacts with other demographic processes to shape population dynamics. Is immigration time-varying with magnitude commensurate to variation in recruitment? Is variation synchronised with recruitment, reflecting large scale environmental forcing? If variable, is it limited by the number or connectivity to sources (are they identified?), or is it density-dependent upon recipient population (compensation)? Identifying the origin of successful immigrants might indeed help in designing/protecting efficient habitat networks (Robertson et al., 2018). Answering these questions across a variety of ecological contexts and taxonomic groups is now achievable using relevant and consistent techniques, as identified above.

VI. CONCLUSIONS

(1) We extracted quantitative measures of immigration from 94 studies conducted on birds (75) and mammals (19), and their analysis revealed that the number of immigrants often exceeds the number of locally-born individuals among new recruits in avian populations (median proportion of immigrants of 57%), but less so in mammalian ones (26%).

(2) A diversity of measures and methods have been used to quantify immigration, a notoriously difficult demographic rate to estimate, which somewhat hampers a thorough

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comparison across studies. Truly quantitative methods (such as integrated population modelling) applied to data collected on identified individuals (through marks or genetic analyses) are now available, and together with properly defined measures of immigration, should be used as routine in future demographic studies.

(3) Analyses derived from a comparable set of studies further revealed that immigration can be the main demographic process affecting the temporal variation in population growth rates, but its potential regulatory action is still poorly known. Future studies should quantify how immigration and emigration rates vary over time across different landscapes, spanning highly fragmented to more continuously distributed populations, and different demographic contexts, from small populations showing high turnover to large ones with extinction probability close to zero. We thus advocate applying the modern metapopulation thinking in a wide range of demographic and spatial arrangement contexts, so as to provide the evidence required to maintain spatial processes that are crucial to the viability of populations.

VII. ACKNOWLEDGEMENTS

VIII. REFERENCES

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IX. SUPPORTING INFORMATION

Alternative methods to estimate immigration: Data, analyses & assumptions

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Figure S1: Diagram showing the combination of multiple sources of data allowing the estimation of immigration within an integrated population model.

Figure S2: Trend in publications with quantitative estimates of immigration for birds and mammals between 1983 and June 2017.

1285 **Online Supplementary Material:**

Excel file with parameter values for immigration rate and proportion of immigrant among new recruits extracted from the literature review on birds and mammals.

Figure 1: Distribution of estimates for immigration rate *I* (left panels) and the proportion of immigrants among new recruits π (right panels) drawn from for studies conducted on birds (upper panels) and mammals (lower panels).
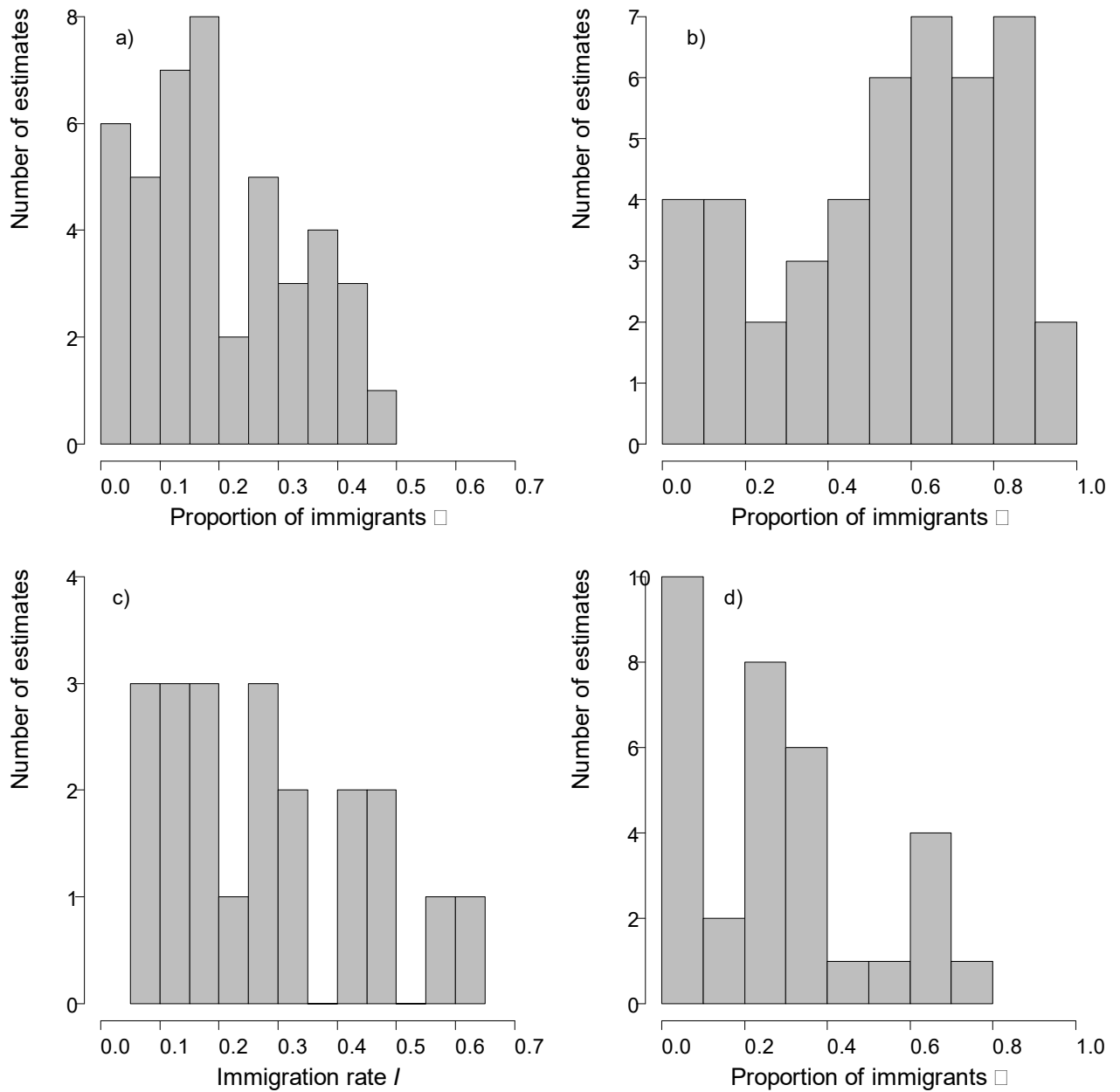
1295 **Figure 2:** Relationships between immigration rate (left panels) or proportion of immigrants among new recruits (right panels) and a biological-relevant measure of the size of the study area (log of the ratio between the size of the study area in km² and species body mass in kg), for birds and mammals (upper and lower panels, respectively).