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

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Running head: Contribution of immigration to population dynamics

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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
90 size over time are due to birth and mortality events across the whole species distribution. When 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

95 site, entering the unsuitable matrix, completing the dispersal process by successfully
immigrating and 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
100 dispersal results also in gene flow, transfer of pathogens, modification of local genetic
diversity, and the 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
105 suffering strongly from reduced genetic diversity (*e.g.* Åkesson *et al.*, 2016).

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
110 community occupying the mainland (MacArthur & Wilson, 1967), then, by analogy in
studies 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
115 recolonisation and can also prevent extinction according to the level of connectivity between
the focal patch and the 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

120 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
125 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
(McPeck & 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
130 and may be more relevant to explain the diversity of situations encountered (Sæther *et al.*,
1999; Matthysen, Adriaensen, & Dhondt, 2001; Schaub, von Hirschheydt, & Gruebler,
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
135 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*
140 *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

145 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 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
150 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 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.*
155 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
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
160 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
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
165 populations (Williams, Nichols, & Conroy, 2002). Population studies disregarding spatial
demographic processes assume, *inter alia*, that immigration and emigration have a marginal
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

170 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
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
175 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 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
180 in different contexts of landscape fragmentation, either natural or anthropogenically induced
(Connor, Faeth, & Simberloff, 1983; Pulliam, 1988; Nichols & Pollock, 1990; Stacey &
Taper, 1992; 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
185 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 including spatial processes and that goes beyond the restricted case of
metapopulation *sensu stricto* (Hanski, 1999). Such a framework ought to be of paramount
190 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
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,
195 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
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
200 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 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
205 outline emerging avenues of research in both theoretical and applied ecology concerning
spatial demographic processes.

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

210 (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 $t-1$
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
215 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 components:

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

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

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

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

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

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
225 immigration (Runge *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
230 total number of 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:

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

235 where F_t stands for floaters (*i.e.* non-breeders) and B_t 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
240 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):

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

245 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

250 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
255 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).

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 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-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 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 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 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
335 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 genotype sampling through a variable number of loci, may conspire to produce
340 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 Switzerland (Kormann *et al.*, 2012), there is a substantial risk that the frequency
345 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 polymorphism is likely to reduce some of the constraints in accurately
350 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 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
375 born 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
390 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
395 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-
400 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

405 (*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
410 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
415 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),
420 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
425 studied using multi-state capture-recapture models (Arnason, 1973; Spendelov *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

430 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
445 to immigration, provided that 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
450 precision of the estimates contributing 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
455 that this population was a sink with a very 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
460 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;
465 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
470 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,
475 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).

480 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 usually required due to the manner in which most IPMs compute the joint likelihood. Using
485 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
490 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:
495 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.

500

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
505 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
510 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,
515 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, & Olf, 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.
520 *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
525 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.

530 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, & 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
535 to 8 taxonomic orders were available with the $\log(\text{study area/body mass})$. We found no effect of the $\log(\text{study area/body mass})$ 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
540 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 $\log(\text{study area/body mass})$. As expected, we found a negative relationship,
545 though only marginally significant, between the $\log(\text{study area/body mass})$ 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
550 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.

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 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.

(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 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

600 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 al.*, 2014], barn swallow [*Hirundo rustica*;
Schaub, von Hirschheydt, & Gruebler, 2015]). In the red-backed shrike, demography was
605 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 other case due to
immigration (van Oosten *et al.*, 2015). In a cross-continental study conducted on the wood
610 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 visual
inspection of the time-series of immigration rate suggested demographic traits other than
615 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.

Much rarer are applications of IPMs focusing on mammals. A recent paper, however,
620 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 rate declined as population size increased, mainly because the same number of

625 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 species, including the meadow vole in the seminal study.
630 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
635 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
640 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.

645 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

650 (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. caeruleus*). Interestingly, whereas they found that local recruitment was indeed higher in isolated patches
655 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 commonplace. Populations located at species range margin, and characterised by researchers
660 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
665 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
670 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

675 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
680 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?

685 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
690 stability of the population 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
695 years, with lowered local 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 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 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 may be limited by the production and prospecting activities of emigrants from source 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 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 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
725 consideration here is whether immigrants come 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
730 populations to culling at rather large spatial scales, 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 ($\lambda_m = 0.84-0.89$),
cougar densities show high resilience to harvest because of immigration from surrounding
735 areas and remain stable over five years (Robinson *et al.*, 2008). 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
740 through lethal management (Dalerum, Shults, & Kunkel, 2008; Oliver *et 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).

745 There is more to compensatory immigration than numbers: while numbers may be
equalised 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).
750 Such changes in population structure might alter population growth rate on the long-term and
induce undesired 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-
755 biased, the dispersing sex being typically male in mammals and female in birds. Whether
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;
760 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).

765 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
770 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
775 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
780 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,
785 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
790 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
795 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
800 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
805 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
810 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
815 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
820 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.

835 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 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).

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 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).

875 **(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
880 these connections may vary in intensity through time (McPeck 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
885 attention. Complex patterns 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
890 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
895 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
900 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
905 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
910 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
915 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

920 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.

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IX. SUPPORTING INFORMATION

1290 **Alternative methods to estimate immigration: Data, analyses & assumptions**

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

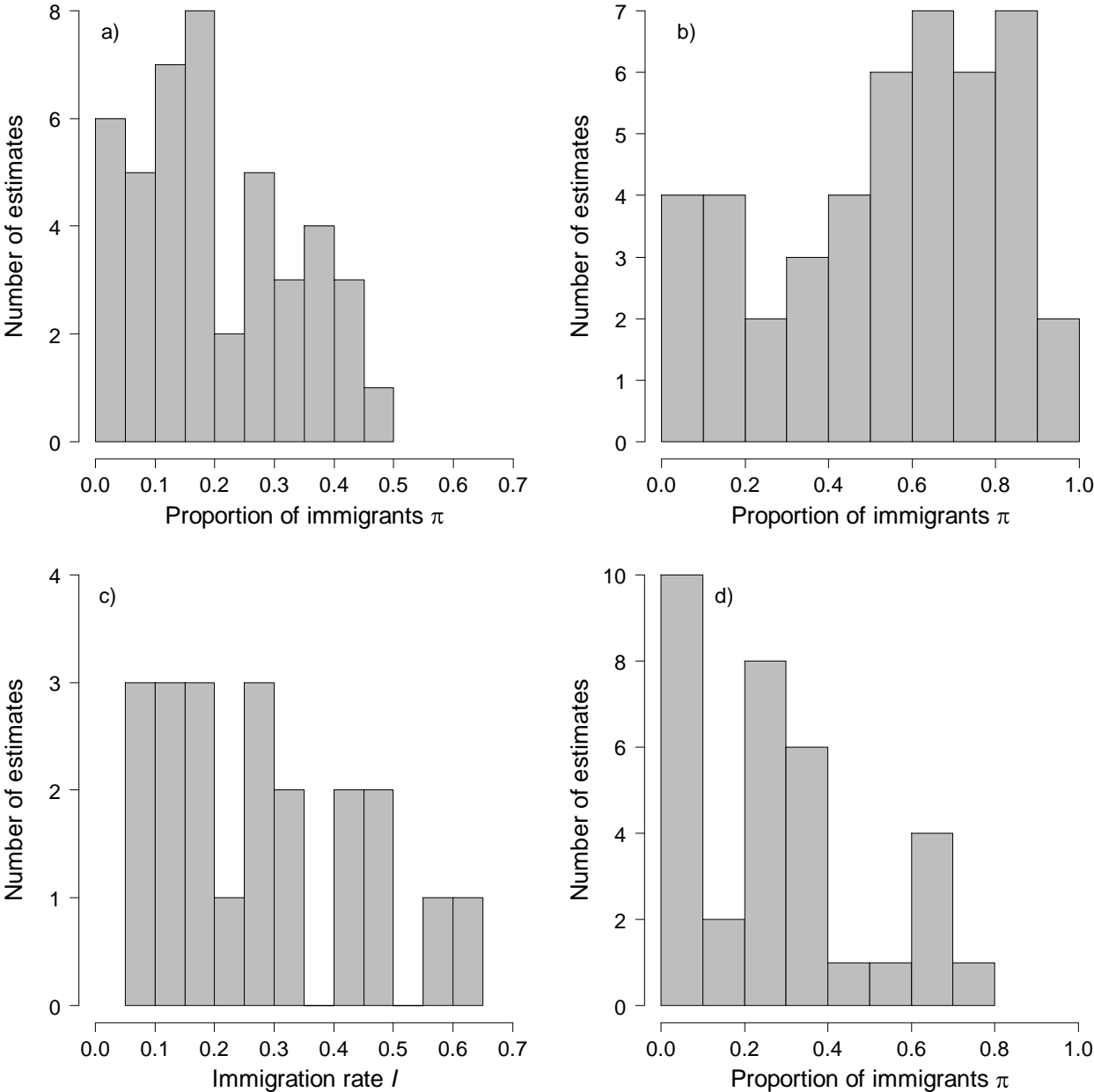
Figure S2: Trend in publications with quantitative estimates of immigration for birds and mammals between 1983 and June 2017.

1295 **Online Supplementary Material:**

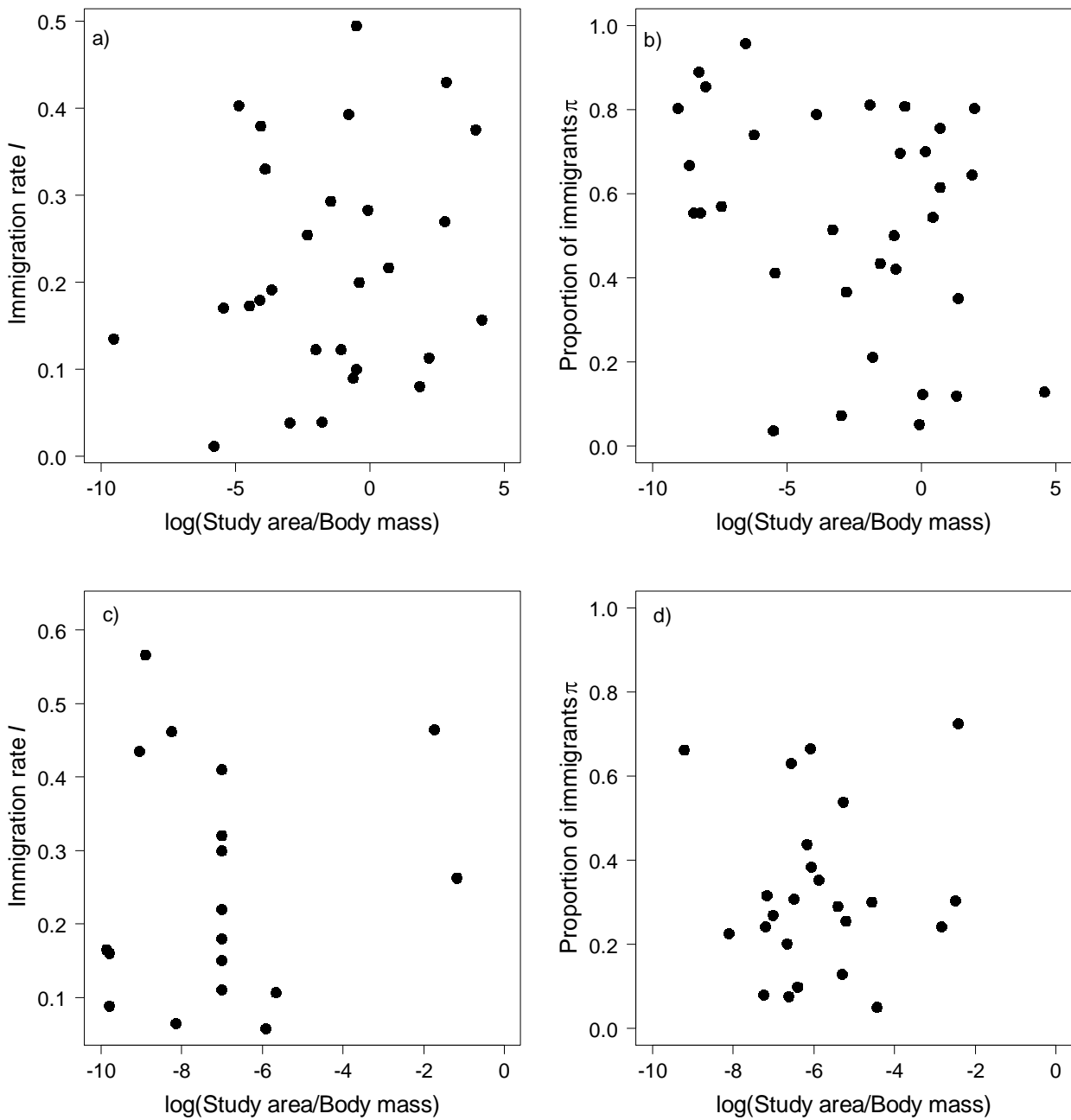
Excel file with parameter values for immigration rate and proportion of immigrant among new recruits extracted from the literature review on birds and mammals.

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

1300 (upper panels) and mammals (lower panels).



1305 **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).

