

NEWS AND VIEWS

PERSPECTIVE

Unravelling migratory connections: the next level

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Migration is widespread among birds, and the strength of the link between the breeding and wintering grounds, migratory connectivity, influences many ecological and evolutionary processes. Despite its importance, migratory connectivity is poorly estimated for most species. Traditionally, visual observations and bird ringing have been used to monitor migration, but these methods require more effort for relatively little return. Genetic markers and stable isotope signatures have increasingly been used to study connectivity. Each approach has its distinct strengths and weaknesses, and as is often the case, a combination may yield the most insight. In this issue of *Molecular Ecology*, Rundel and colleagues (2013) present a novel Bayesian statistical framework in which genetics and stable isotope data can be combined to improve the assignment of individuals to different winter or breeding regions. The development of such new statistical methods combined with the increasing number and ease of access of isotopic and genetic data sets will greatly enhance our understanding of migratory connectivity. Add to this the developments of miniature devices to track movements of individuals, and the field is destined to make major progression in the decades to come.

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Migratory connectivity describes the associations between breeding sites, stopovers and wintering grounds of groups of individuals (Webster *et al.* 2002; Ambrosini *et al.* 2009). Strong connectivity implies that individuals share similar breeding, stopover and wintering grounds (Fig. 1a), whereas in the case of low connectivity, these areas differ and may be shared with birds from other populations (Fig. 1b). The strength of the link can have important consequences for a variety of ecological and evolutionary

processes through ‘carry-over’ effects (Marra *et al.* 1998). For example, individuals inhabiting a high-quality wintering ground may have higher overwinter survival, migrate earlier and mate with other high-quality partners on the breeding grounds. Connectivity may thus influence the strength and direction of natural and sexual selection within breeding populations, but can also drive macro-evolutionary processes such as speciation (Bearhop *et al.* 2005; Ruegg 2008). Unravelling migratory connectivity is also important for guiding conservation decisions (Norris *et al.* 2004; Sheehy *et al.* 2010; Fraser *et al.* 2013) and monitoring the spread of diseases like avian influenza.

Despite its importance, migratory connectivity has only been described in detail for relatively few species. Observational studies and bird ringing have provided many important insights but are inefficient in terms of time spent per recovery. For example, of the more than 40 million birds ringed in Britain and Ireland through to 2012, <0.05% were recovered (Robinson & Clark 2013). Over the last few decades, genetic markers and stable isotope signatures have been increasingly used to measure migratory connectivity (Kelly *et al.* 2005; Inger & Bearhop 2008). For example, one may want to assign individuals caught at their wintering grounds to their breeding population (and *vice versa*). The genotype of an individual can be used to probabilistically assign it to a breeding population based on genetic similarity. Stable isotope ratios systematically vary across ecosystems and geographical regions (e.g. Bowen 2010) and are incorporated in growing tissue, for example feathers. A feather collected at the wintering ground but moulted at the breeding ground can thus be used to estimate where the bird bred. These ‘intrinsic’ markers do not require the recapture of an individual and they do not degenerate over time. Stable isotope and genetic analyses are relatively cheap, and samples are relatively easy to obtain by collecting feathers at bird ringing station or through already existing collections in, for example, museums (Smith *et al.* 2003). However, there are some important considerations. The accuracy of the genetic assignment approach relies on the level of genetic differentiation between the breeding populations and requires a thorough knowledge of the spatial genetic structure of the species. This constraint is weakening by the increased use of next-generation sequencing (largely due to decreasing costs), which provides researchers with many markers facilitating detection of weak population differentiation. Stable isotope signatures require similar knowledge about their spatial distribution, which is often obtained indirectly through environmental samples like rainwater. Stable isotope ratios can be affected by various factors such as diet, which may considerably increase variance if, for example, food resources vary on a small geographical scale.

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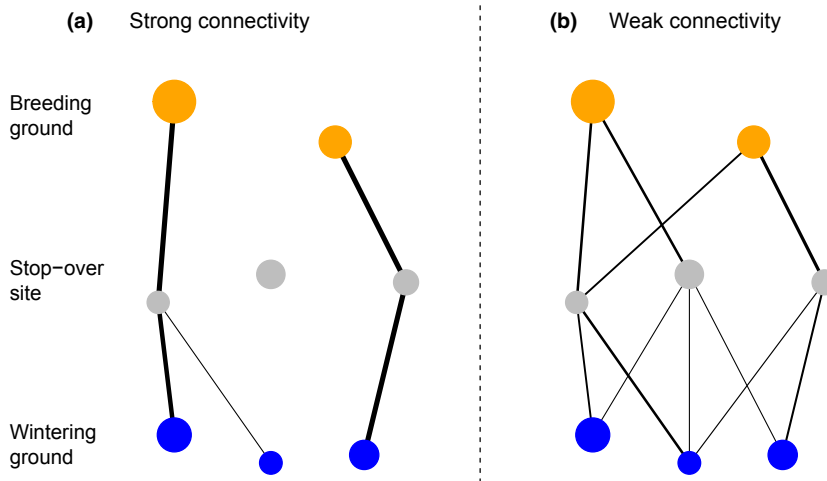


Fig. 1 Migratory connectivity measures how closely individuals of migratory species spatially cluster throughout the annual cycle. (a) Strong connectivity implies that most individuals from the same breeding population (orange) use the same stopover sites (grey) and winter (blue) together, whereas for (b) weak connectivity, this is not the case and, for example, the individuals spread across various stopover and wintering locations. The sizes of the circles represent geographical area, and the thicknesses of the lines represent the relative number of migrants.

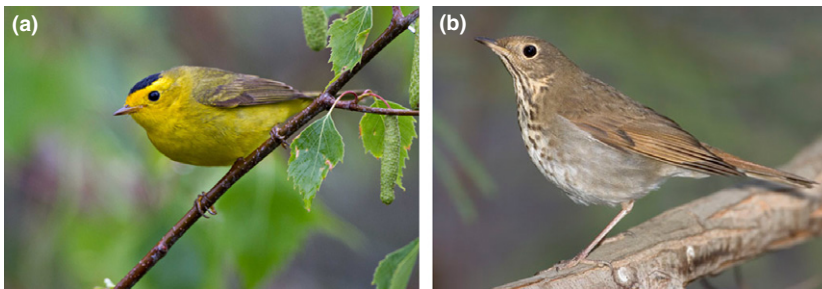


Fig. 2 (a) Wilson's warbler and (b) hermit thrush (photograph credits: Thor Veen and Mark Chappell).

Either approach can be used in isolation, but given they both rely on a probabilistic assignment and have different strengths and weaknesses, combining them is most powerful (e.g. Kelly *et al.* 2005; Boulet *et al.* 2006). In this issue, Rundel and colleagues describe a Bayesian statistical framework that integrates data from both approaches and empirically test it using data from Wilson's warblers (*Wilsonia pusilla*: Fig. 2a) and hermit thrushes (*Catharus guttatus*: Fig. 2b). In the first step, known hydrogen stable isotopes values from precipitation and genetic data are used to derive posterior probability surfaces across the breeding range using methods built on work by Wunder (2010) and Wasser *et al.* (2004).

This allows them to calculate a probability that an individual's unique genotype and stable isotope signatures originate from a certain location. These probabilities can be calculated across the breeding range and plotted, and the most likely region(s) of breeding origin of an individual can be estimated, resulting in a more robust statistical link between winter and breeding grounds.

Rundel and colleagues subsequently combine the probabilities of the two markers. Using genetic and stable isotope data from Wilson's warblers and hermit thrushes from their breeding grounds, the authors apply several cross-validation methods and show that the combined assignment greatly reduces the error associated with the predicted breeding ranges compared with either genetic or stable isotope data alone. Their results also indicate that the two data types cannot be simply treated as equally important in inferring breeding origin, but different relative weights need to

be applied to optimize the assignments. Assignment methods heavily depend on the quality of the reference data, and especially for the genetic data, extensive geographical coverage of breeding ranges is desirable.

The authors make an important contribution to the field by developing a general Bayesian framework to incorporate different data types and make it available as an R package (*isoscater*). The method is versatile and can be expanded to other data types, such as species-distribution models. Combining different data types is, however, not new (e.g. Kelly *et al.* 2005; Hobson *et al.* 2012; van Wilgenburg & Hobson 2011; and especially Chabot *et al.* 2012) and it would have been very useful to have a comparison of the performance of the new and the earlier methods by applying them to the exact same data sets.

The next step is to focus on improving our knowledge of population genetic structure and spatial distribution of stable isotopes (so-called isoscapes) of the focal species. This will require an intensive effort to collect samples for genetic and stable isotope analyses across a large geographical. For the isoscapes, the data required are more generally applicable (i.e. not species specific) and good resources are available (Bowen *et al.* 2012). Calibration of this method using animal tissues, such as feathers, with a known growth location is desired (see Hobson *et al.* 2012). It is good news that a considerable amount of data needed to estimate migratory connectivity has already been gathered (see <http://www.migratoryconnectivityproject.org> for recent studies). The challenge is now to bring it all together, make it easily accessible, and locate and fill the

gaps in our knowledge. Online data repositories such as Dryad (www.datadryad.org) for many different data types or Movebank (www.movebank.org) for animal tracking data provide a solution for data storage (alongside other benefits: Whitlock 2011) and have grown rapidly in recent years. Alongside encouraging authors to submit data of new publications to these repositories, it would be very useful to archive the raw data of previously published papers to get the most comprehensive data set possible.

Indirect markers have provided many new insights into migratory connectivity but are currently still often imprecise if used in isolation. Combining different markers as shown by Rundel *et al.* (2013) in this issue of *Molecular Ecology* will greatly improve the accuracy of estimating the strength of migratory connectivity. The ease of collecting a feather without the need of recapture makes intrinsic marker very suitable to measure migratory connectivity on a large geographical scale, but it is of limited use to track individual migratory routes. Fortunately, rapidly advancing technological developments allow individuals of a wide range of species to be tracked using, for example 'geolocators', devices that store the dark and light patterns to infer geographical location or GPS-based systems. These techniques provide data revealing novel migratory behaviour and connectivity (e.g. Egevang *et al.* 2010; Delmore *et al.* 2012; Fraser *et al.* 2012) and furthermore can be used to ground truth the much cheaper intrinsic marker methods. Using combinations of intrinsic markers, together with ambitious programs like the Icarus initiative (<http://icarusinitiative.org/>), which aims to track individual organisms with high precision using the International Space Station, shows the very exciting future for the study of migration and migratory connectivity.

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