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Migratory connectivity in the context of differential migration

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Understanding how breeding populations are spatially and temporarily associated with one another over the annual cycle has important implications for population dynamics. Migratory connectivity typically assumes that populations mix randomly; yet, in many species and populations, sex-, age- or other subgroups migrate separately, and/or spend the non-breeding period separated from each other—a phenomenon coined differential migration. These subgroups likely experience varying environmental conditions, which may carry-over to affect body condition, reproductive success and survival. We argue that environmental or habitat changes can have disproportional effects on a population's demographic rates under differential migration compared to random mixing. Depending on the relative contribution of each of these subgroups to population growth, environmental perturbations may be buffered (under-proportional) or amplified (over-proportional). Thus, differential migration may result in differential mortality and carry-over effects that can have concomitant consequences for dynamics and resilience of the populations. Recognizing the role of differential migration in migratory connectivity and its consequences on population dynamics can assist in developing conservation actions that are tailored to the most influential demographic group(s) and the times and places where they are at peril.

1. Introduction

Many migratory populations have experienced massive declines over the past years mainly as a consequence of the single or combined effects of habitat loss and deterioration, climate change, erection of barriers and sensory pollution [1–4]. Their conservation requires understanding migratory connectivity, i.e. how breeding populations are spatially and temporarily associated with one another over the annual cycle—during breeding, migration and the non-breeding season [5–7]. The connectivity patterns have important implications for short-term population dynamics as well as long-term trends.

Migratory connectivity is quantified along a continuum from low interpopulation spread and complete segregation of different breeding populations (strong connectivity) to high interpopulation spread and thorough mixing of individuals from different breeding populations (weak connectivity) [6,8]. Under the original definition of migratory connectivity [6], the entire migratory period is overlooked including in how far individuals from one breeding populations may migrate at different times or use different routes and stopover sites, suggesting that migratory connectivity is not purely a breeding to non-breeding phenomenon. Including the migration period in the definition of migratory connectivity is vital for many species and populations especially those in which sex-, age- or other subgroups migrate separately, and/or spend the non-breeding period separately from each other—a phenomenon coined differential migration [9]. Due to this segregation, subgroups likely experience varying environmental conditions *en route* and at the non-breeding sites.

species		consequence
	male **semi-collared flycatchers** (*Ficedula semitorquata*) migrate earlier than females	early migrants might encounter harsher environmental conditions and food shortage upon arrival at the breeding sites, resulting in higher mortality [10]
sex	female **Nathusius's pipistrelle** (*Pipistrellus nathusii*) leave the breeding areas earlier than males	males and females spend the greater part of the annual cycle in separate locations experiencing different conditions on local and regional scales [25]
	a larger proportion of female **European blackbirds** (*Turdus merula*) are more likely to be migratory compared to males	migratory individuals show higher over-winter survival than complete resident individuals [16]
	moose (*Alces alces*) juveniles migrate longer distances than adults	different migration strategies result in age-specific wintering sites exposing various age-classes to different environments [17]
age	juvenile, female and subordinate **European robins** (*Erithacus rubecula*) migrate longer distances	different age-, sex- and dominance-classes are latitudinally segregates during the non-breeding period [18]
	in **Dolly Varden trout** (*Salvelinus malma*) probability of migration decreases with increasing age	migratory individuals suffer higher mortality [22]

Figure 1. Examples of differential migration from throughout the animal kingdom and its consequences for population dynamics as mediated via migratory connectivity. (Photo credits from top: Martins Briedis, Viesturs Vintulis, Edgars Smislovs, Agris Krusts, Ainārs Mankus, LoveToTakePhotos (pixabay.com).).

Exposure to different environments may carry-over to influence individual physical condition potentially leading to group-specific *en route* mortality [10], spring arrival times [11] or reproductive success [12]. More importantly, if global and climate change alter habitats at varying rates and magnitudes, these segregated subgroups will be affected to different degrees.

We argue in the following that environmental or habitat changes can have disproportional effects on a population's demographic rates under migratory segregation compared to random mixing. Depending on the relative contribution of each subgroup to population growth, negative effects caused by environmental perturbations may be buffered (under-proportional) or amplified (over-proportional). Thus, differential migration resulting in differential mortality and carry-over effects can have concomitant consequences for the dynamics of migratory populations.

2. Differential migration

Differential migration is a widespread phenomenon in the animal kingdom and can take many forms, from differences in the timing of migration to differences in migration routes: subgroups may segregate during relatively short periods, during migration [10,13–15], during non-breeding residency [16,17] or for most of the year [18,19] (figure 1). Similarly, the spatial scales of segregation may vary from local segregation such as the use of microhabitats [20], to regional (several tens to a few hundreds of kilometres) when different stopover or wintering sites are used [16,18], to continental, when subgroups use entirely different flyways [21].

Probably, the most common segregation is between sex- and age-groups but other segregations, e.g. between dominants/subordinates and breeders/non-breeders may also occur (figure 1). In sexual segregation, males precede females (protandry), females precede males (protogeny), females use other habitats than males or migrate via different stopover sites to different non-breeding sites. Similarly, differential migration by age means that juveniles differ in migration timing from adults and/or use different flyways to different non-breeding sites [13,17,22,23]. Dominance status may force subordinates to undertake longer migrations [18,24] or reside in suboptimal non-breeding habitats [20]. In partially migratory populations and short-distance migrants, migratory behaviour is often female skewed with a larger proportion of females being migratory [24], leaving the breeding grounds earlier [25] or travelling longer distances compared to males [18].

These examples illustrate how the two core components of migratory connectivity—spatial and temporal site use across the annual cycle—can be essentially different for distinct groups of individuals within the same core population.

3. Cascading consequences of differential migration on migratory connectivity

Patterns of migratory connectivity can shape population dynamics on local and range-wide scales [26,27]. Strongly connected migratory populations are thought to be more vulnerable to environmental changes as all individuals cluster at certain places and times, and changes on any of those would affect the entire population. By contrast, weak migratory
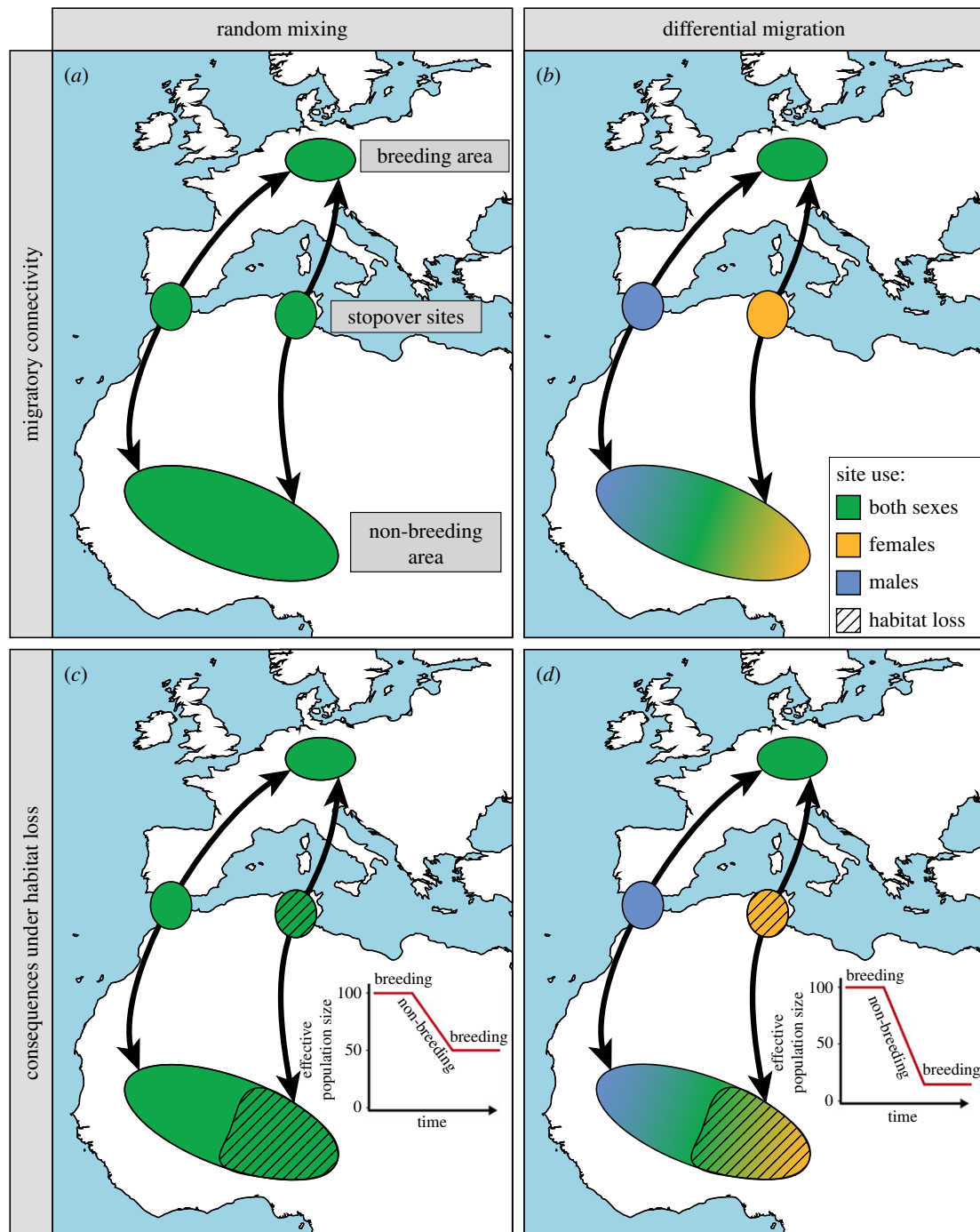
Figure 2. Schematic of (spatial) migratory connectivity in a hypothetical species under (a) random mixing of individuals and (b) sex-specific differential migration. When males and females mix randomly during migration and non-breeding residency, the consequences of habitat loss on population dynamics will be less severe (c) than under differential migration where exclusively one demographic group is affected (d).

connectivity is thought to buffer negative consequences of environmental perturbations, adverse weather or food short-age on specific sites and times as only part of a breeding population experiences these conditions [28].

Under differential migration, connectivity patterns are stronger within groups (e.g. within sex or age classes) than between groups, leading to demography-specific vulnerability across the annual cycle (figure 2). Conse-quently, environmental perturbations may have under- or over-proportional effects on population dynamics if a specific demographic group is concerned, i.e. effects are much larger or smaller than what would be expected under random mixing of individuals. For instance, if

males and females migrate differentially and only females suffer a high mortality, the population's sex ratio will become male-biased and its vital rates plummet even though more than half of the individuals had returned [29]. Male-biased sex ratios are particularly problematic in small populations causing local population declines [30]. By contrast, differential migration may also prevent major consequences of massive (local) habitat alterations if a demographically less significant group is affected. For instance, if young of a long-lived species experience higher mortality for a restricted period, this might show only in short-term population dynamics, but not in the long-term population trajectory [31].

4. Conservation implications

The widespread application of tracking devices over the past decade(s) has yielded a wealth of information on individual migration routes and schedules, and increasingly provides the possibility to determine the degree of migratory connectivity. As mounting individual tags requires the handling of individual animals, their sex and age (or other characteristics) are usually also recorded or determined retrospectively. Although we are not aware of an explicit analysis of differential migration, migratory connectivity and its link to population trends, the data to explore such links are certainly there and will continue to be accumulated [32–34].

Thus, (re-)analysing existing individual migration data with regard to differential migration is a first step in understanding demography-specific connectivity [15]. However, we also need to analyse the contribution of demographic groups to population vital rates (e.g. fecundity and seasonal survival probability) which could then be used to develop full annual cycle population models [35,36] to identify the places and times at which specific demographic groups are most at peril. Conservation and management actions could then be tailored to these places and times and targeted at the most influential demographic groups.

Thus, we call for recognizing the role of differential migration in migratory connectivity as well as its potential consequences for population trends and the implications these may have for conserving and managing migratory populations.

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