

Timing is crucial for consequences of migratory connectivity

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28 **Abstract**

29 Migratory connectivity – the geographic linkage of individuals and populations across life-cycle stages
30 – can have important consequences, from individual fitness and population dynamics to gene flow,
31 transmission of parasites, and community dynamics. We argue that most consequences not only
32 depend on *which* sites are used, i.e. the spatial dimension of migratory connectivity, but importantly
33 also on *when* these are used.

34 Timing of migration can be characterised by three dimensions - phenology, synchrony, and
35 consistency, and we illustrate their importance for shaping the various consequences of migratory
36 connectivity using examples from throughout the animal kingdom. Exemplarily for one consequence –
37 the transmission of pathogens and parasites – we develop a dynamic network model to demonstrate
38 how changes in migration phenology and synchrony differently affect disease dynamics.

39 Extending the original framework into a spatio-temporal framework can importantly contribute to
40 understanding the links migratory animals make across the globe and the consequences these may
41 have both for the dynamics of migrant populations and the communities they visit throughout their
42 journeys.

Introduction

Billions of animals from various taxa migrate every year in pursuit of improved foraging conditions, safety, and reproductive opportunities (Milner-Gulland et al. 2011). It is widely appreciated that the use of different sites and the conditions experienced have consequences not only for migrant fitness and the dynamics of their populations but also for gene flow, transmission of pathogens and parasites as well as for interactions with the separated communities visited (Bauer and Hoyer 2014, Marra et al. 2010, Webster and Marra 2005). Migratory connectivity describes the “geographic linking of individuals and populations between one life cycle stage and another” (Webster et al. (2002), p. 76). It is a framework that can importantly contribute to answering a range of fundamental and applied questions and therefore, has been enthusiastically embraced by the scientific community. Although predominantly applied in studies of migratory birds, the concept of migratory connectivity is equally applicable to migratory animals of other taxa (e.g. Godley et al. 2010, Miller et al. 2012).

The importance of migratory connectivity is thus generally acknowledged; yet, most studies describe the nature of connectivity but surprisingly few quantitatively link consequences to the degree of migratory connectivity. If we wish to progress the concept towards an explanatory and predictive framework, we need to gain a better understanding of the mechanisms behind the consequences of migratory connectivity and this requires an explicit consideration of time within the migratory connectivity framework: As we show in the following, most consequences not only depend on *which* sites are used, i.e. the spatial dimension of migratory connectivity, but importantly also on *when* these are used.

The consequences of migratory connectivity broadly include those on a) individual fitness and population dynamics, b) gene flow and genetic mixing, c) transmission of parasites, and d) community dynamics and ecosystem function. The first three consequences focus on state and fate of the migrants themselves that result from the conditions experienced at particular sites and times. The last consequence takes another perspective and highlights the effects migrants can have on the structure and dynamics of the communities visited.

All consequences result from the use of specific sites and from the timing of their use as both determine the conditions migrants experience. Although it is widely agreed upon that conditions differ between sites and thus, that fitness and other consequences differ likewise (Norris and Marra 2007), conditions at these sites also change over time and therefore, timing of migration will not only shape the magnitude of these consequences but also their nature.

We suggest that the timing of migration is characterised by three dimensions - phenology, synchrony, and consistency – as variations in each of these may contribute differently to specific consequences of migratory connectivity. Migration **synchrony** describes how wide-spread over time individuals of a population migrate (Fig. 1). At one extreme all individuals migrate at the same time - synchronously (Orell et al. 2007), while at the other, individuals migrate at different times - asynchronously. Specific examples of asynchronous migration include differential migration (Colbeck et al. 2013), where (age-, sex-, or family-)subgroups of a population migrate at different times, or partial migration, where some individuals migrate while others remain resident.

Migration **phenology** describes the timing of migratory steps - arrival, departure and staging times at sites - relative to the phenology of other relevant processes, e.g. the temporal availability of key-resources or presence of biological agents with which migrants interact (Fig. 1). At the two extremes, the migrants' presence on a particular site fully coincides with the peak of resources ('matched') or is completely separated from the availability of resources ('mismatched').

Finally, **consistency** describes how repeatable migration phenology and synchrony are over time - usually over several migrations. Consistency is regarded an individual trait, and variations in the degrees of consistency in a population might be an adaptation to environmental variability (Brodersen et al. 2012). Therefore, consistency is important for understanding evolutionary adaptations between migrants and the populations, species and communities on sites they visit (Alerstam et al. 2003). (Note that consistency also exists in the spatial sense, describing the degree to which migrants return to the same locations for breeding, non-breeding and/or stopping-over in successive migration bouts (also referred to as site fidelity, philopatry, e.g. (Jorgensen et al. 2010)).

In the following, we illustrate the importance of considering timing for the consequences of migratory connectivity using examples from throughout the animal kingdom, and as we focus on ecological time-scales, we primarily consider the roles of phenology and synchrony. Exemplarily for one of these consequences – the transmission of pathogens and parasites – we develop a dynamic network model to demonstrate how changes in phenology and synchrony affect disease dynamics.

We would like to emphasize that we not aim at compiling a comprehensive review of the consequences of migratory connectivity here (for such, see e.g. Boulet and Norris (2006)) but hope to stimulate discussion and research on the effects of changes in migration phenology and synchrony.

Consequences of migratory connectivity shaped by timing

Individual fitness and population dynamics

A variety of factors can affect a migrant's fitness (Fig. 2): Abiotic conditions, e.g. temperature, precipitation, wind, influence energy expenditure during residency (e.g. thermoregulation) and locomotion (e.g. flight); resource availability and abundance of competitors determine how fast migrants can replenish fuel reserves (Stahl et al. 2006, Wittwer et al. 2015), and predators pose mortality risks (Middleton et al. 2013) or spark a range of non-lethal effects (Morrisette et al. 2010).

All of these factors change over time, usually seasonally but often at smaller time-scales, at time-scales similar and thus, relevant, to the visitation of migrants. Therefore, variations in the phenology of migration will lead to the population experiencing on average different resource levels, abundances of competitors and predators ('phenological match/mismatch', Johansson et al. (2015)), and migration synchrony determines the within-population variation with regard to the overall effects of these factors.

If, for instance, resource availability changes as a consequence of natural decay or due to finite resources being exhausted, early migrants would benefit from abundant resources compared to late migrants in an asynchronously migrating population. This is exemplified in a population of Arctic

breeding geese, where individuals that arrived at stop-over locations at the peak of vegetation growth had a higher breeding success (Kölzsch et al. 2015).

Similarly, within-population competition may be alleviated under asynchronous migration while it is fully effective under synchronous migration (Skoglund et al. 2011), e.g. as in the exclusion of competitively inferior individuals from high-quality foraging patches (Beauchamp 2012, Eichhorn et al. 2009). Alternatively, synchronous migration can be beneficial if the joint consumption of a resource increases its quality or productivity, as in the case of grazing by migratory geese on a spring stop-over site (Stahl et al. 2006) or the increased productivity of the African savannah through the temporal grazing of migratory herbivores (Holdo et al. 2007).

The level of predation (incl. hunting) may also change at the time-scale of migrant visitation e.g. as resulting from seasonal hunting permissions or mobile predators. For instance, hunting on spring-migrating geese in Russia is permitted during 10 days of peak migration and individuals migrating outside this 10-day hunting window experience much lower mortality risks (Mooij et al. 1999).

Similarly, late-migrating sandpipers responded to the arrival of predators (peregrine falcons, *Falco peregrinus*) on a common stop-over site with behavioural changes, e.g. increased vigilance, reduced foraging and consequently, reduced migration speed – behaviours that early-migrants failed to show (Hope et al. 2014).

Gene flow and genetic mixing

Migratory connectivity can influence the degree of gene flow between populations – both as a result of spatial or temporal segregation (Bensch et al. 2009, Moussy et al. 2013, Webster and Marra 2005).

Although it is commonly acknowledged that strong (spatial) migratory connectivity can lead to limited or no gene flow, to local adaptations and ultimately, speciation (Bensch et al. 1999, Fraser and Bernatchez 2005), temporal segregation can have the same effects. A prominent example is the European blackcap (*Sylvia atricapilla*), in which site there is no or very little gene flow between two sub-populations despite them mixing at a common breeding site. This is mainly explained by differences in arrival and onset of breeding between these sub-populations that segregates them

temporally and resulted in assortative mating, restricted gene flow and ultimately, phenotypic divergence (Bearhop et al. 2005, Berthold et al. 1992).

Transmission of parasites and disease dynamics

The dynamics of parasites within migratory host populations can be influenced by migratory connectivity (Altizer et al. 2011, Møller and Szep 2011): If individual migrants visit the same sites at the same times, they are thought to encounter the same variety of parasites and prevalence in the population is driven by local (re-)infections, following an SIR/SIS (susceptible-infectious-recovered and immune) dynamics (Hudson et al. 2002). In contrast, if migrants visit different sites or the same sites at different times, they potentially encounter a different diversity and abundance of parasites (Kamiya et al. 2014); once these individuals congregate on a common site, they may harbour, and exchange, a greater variety of parasites (Gaidet et al. 2012).

Considering time explicitly is required for predicting the consequences of migratory connectivity to parasite prevalence and dynamics for several reasons: First, prevalence may vary over time resulting from variations in environmental conditions (Reperant et al. 2010), density (Gaidet et al. 2012) or by the influx of immunologically naïve individuals. Thus, there are periods during which transmission is more likely than in others (Hoye et al. 2011). Secondly, infected individuals need to actually meet susceptible (un-infected) individuals to transmit parasites. However, this might be efficiently prevented when infected and uninfected individuals migrate asynchronously. For instance in Monarch butterflies (*Danaus plexippus*), individuals infected with a protozoon parasite migrate at lower speeds than their healthy conspecifics (Bradley and Altizer 2005). Indeed, such “migratory escape” has been suggested as a mechanism by which migration can actually decrease prevalence as infected, low-performing individuals lag behind their healthy conspecifics and thus, introduce a barrier to the spread of parasites (Altizer et al. 2011, Hall et al. 2014).

To underpin our verbal argumentation on the importance of migration timing for consequences of migratory connectivity, we used a simple dynamic network model to demonstrate how the prevalence

of parasites may change with variations in migration phenology and synchrony (for details on model and scenarios, see Supplementary material S1). Individuals ('nodes') in this network could be linked, migrate and get infected, and all of these characteristics could change over time as a result of dynamics in contact structures, migration and infection dynamics as follows: (1) Links between individuals form and dissolve probabilistically over time while the average number of links per individual in the network is preserved. (2) We considered a simple type of migration, in which individuals migrated from a starting to a destination site at or around a mean migration date. As we assumed the two sites to be distant, no links (and thus, no parasite transmissions) were allowed between individuals at disparate sites. (3) We used a SIS (susceptible-infectious-susceptible) model for infection dynamics (Keeling and Rohani 2008), in which susceptible individuals can get infected with a given probability if they are connected to infected individuals and likewise, infected individuals recover with a probability and re-enter the pool of susceptibles.

We changed migration synchrony by varying the standard deviation around the mean migration date and thus, from completely synchronous to highly asynchronous. We found prevalence to remain at the same level on both starting and destination site in a completely synchronously migrating population. However, if individuals migrated asynchronously, i.e. spread out over time, prevalence gradually decreased at the starting site and gradually increased at the destination and thus, differed considerably for a long period (Fig. 3a-b).

Secondly, we introduced a 20-day period of elevated (environmental) parasite pressure (or increased susceptibility to infections) at one location and varied its onset relative to the timing of migration such that this period was before, coinciding with, or after migration. While prevalence obviously was unaffected when parasite pressure increased *after* migration, prevalence was elevated when this happened before or during migration. These variations in prevalence at the starting location then spilled over to, and influenced, prevalence at the destination (Fig. 3c-d).

Thus, both migration synchrony and phenology importantly shaped (local) disease dynamics (Fig. 3) and prevalence varied widely with alterations in the phenology or synchrony of migration even though the underlying epidemiology was kept constant.

Community dynamics and ecosystem functions

With their movements, migrants connect widely separated and diverse communities and ecosystems, influence their structure and dynamics through a variety of transport and trophic effects (Bauer and Hoyer 2014). Clearly, migratory connectivity describes which communities and ecosystems are linked by migratory movements but the phenology and synchrony of visitation are also profoundly important to assessing the influence migrants can have on these communities.

The timing of migration relative to resident phenology is fundamental to the strength and direction of migrant-resident interactions (Yang and Rudolf 2010) and can influence key-features of communities (Nakazawa and Doi 2012). For instance, migrants can only be important pollinators if their visits coincide with peak flowering, e.g. Lesser long-nosed bats (*Leptonycteris yerbabuenae*) that time migration to coincide with peak flowering in the cacti-populations along their way (Fleming 2004). Similarly, if parasite prevalence shows a marked seasonal dynamics, transmission may be restricted to sites where high prevalence and migrant visitation coincide (Hoyer et al. 2011)(see above).

Effects of migrants on communities also depend on the synchrony of migration. For instance, the simultaneous input of nutrients can constitute resource pulses, which can profoundly alter demographic rates and abundances of interacting populations, with cascading effects that may persist long after the pulse is extinguished (Holt 2008). Also asynchrony in migration can have attendant consequences for communities and ecosystems, e.g. in partially migratory freshwater fish the proportion of the population migrating determines, via various intermediate steps, the transition between alternative stable states in the lake ecosystem (Brodersen et al. 2008).

Conclusions

Migratory connectivity is an important framework that describes the links migrants make between different parts of the world. Its implications are far-reaching and can be immense: the dynamics, conservation and management of migratory populations and species, the effects of potential habitat and climatic changes (Bauer et al. 2008), structure and dynamics of separated communities (Bauer and

Hoye 2014), and the spread of parasites, including those with zoonotic potential (Altizer et al. 2011).

In addition to the exclusive consideration of spatial links in its original definition, we have shown here that all potential consequences of migratory connectivity can depend on the timing of migration –its phenology and synchrony.

Migration phenology has long been acknowledged as vital for our understanding of the migrants’ population dynamics – numerous studies have shown its importance for individual fitness, population demographic rates as well as for the transmission of parasites and the interactions with resident communities. An individual’s phenology results from using cues that trigger migration (Bauer et al. 2011, McNamara et al. 2011) and other life-history processes and is the result of adaptations to (local) conditions, to the variability in these conditions, and to interactions with other species (Reed et al. 2010). The level of population synchrony in timing of migration then results from the variability between individuals in the use of and response to these cues and the conditions experienced (Harrison et al. 2011). Additionally, migration synchrony might be influenced by a variety of processes: variation in fuelling rates (Seewagen et al. 2013), sex-specific constraints and selection pressures (Saino et al. 2010), or delayed departure of infected individuals (Hoye et al. 2012), and it may vary for different migratory steps or between breeding and non-breeding migration. Furthermore, the level of migration synchrony will be generally higher in migrants travelling in groups, e.g. fish shoals, herds, swarms, as migration routes and timing result from group decisions (Conradt and List 2009) and with a cultural transmission of migration behaviour (Harrison et al. 2010).

One might argue that the original definition of migratory connectivity implicitly contains a time-dimension as migrants visit the various places at different times of the year. However, we think that time needs to be made explicit, often at a higher resolution than implicitly contained in the original definition, as we would otherwise neglect consequences that are directly shaped by phenology and synchrony of migration. [An analogy of the implicit-versus-explicit consideration of time could be drawn from network analyses: In most ecological applications to date, networks are considered as time-aggregated networks; however, the dynamics, resilience and stability of time-ordered networks can be fundamentally different from time-aggregated networks (Blonder et al. 2012).]

As we have exemplarily shown, the disease dynamics in a migratory population can substantially differ if the timing of migration is considered explicitly – changes in synchrony and phenology led to very different prevalence over long periods although the underlying infection dynamics remained unchanged. Aggregating over time - as in the original definition of migratory connectivity - implicitly assumes that migrations are completely synchronous and disregards the relevance of other processes, which, however, are crucial for understanding its consequences.

Obviously, the relevance of timing may vary, e.g. between periods and places, but whether timing can be neglected or not depends on the consequences of migratory connectivity under consideration and their hypothesized mechanisms. Both consequences and mechanisms determine which spatial and temporal scales are required for their detection. In turn, the spatial and temporal scales required have implications for the choice of empirical methods: Various tracking methods exists to date, all of which set very different yet strict limits to the spatial and temporal resolutions that can be achieved (Boulet and Norris 2006), and therefore, the choice of methodology determines, and possibly restricts, the consequences and mechanisms that can be identified.

This sets the basis for several exciting challenges for future research. A prime need is a sound theoretical basis for the consequences of migratory connectivity. In particular, we need theoretical studies that develop predictions for specific consequences of migratory connectivity and explore their mechanisms (Taylor and Norris 2010).

Network approaches might be particularly useful when consequences are modified by the heterogeneity of contact structures and their changes over time. For instance, several community and ecosystem consequences of migratory connectivity result from direct interactions ('contacts') between migrants and residents but the intensity and nature of these interactions critically depend on the numbers of migrants and their timing – phenology and synchrony (Fig. 2): Whether parasites will be successfully introduced into a resident community, which pathways imported nutrients and energy take, or whether dispersed seeds establish in a resident community – depends on phenology and synchrony of migration and can be explored with dynamic network models.

Another promising approach might be behaviour-based migration models, which can explicitly take into account behavioural flexibility and constraints in responding to climatic and habitat changes (Fagan et al. 2012), the variable number of sites that constitute migration routes and the potential existence of key-sites (Iwamura et al. 2013) but also fundamental differences in migration strategies, such as different modes of locomotion (Hein et al. 2012).

Although for many species and populations we are still at the stage of identifying the places to which individuals migrate, we urge for an extension of the original, exclusively spatial definition of migratory connectivity into a spatio-temporal framework. Going beyond the descriptive stage of migratory connectivity requires us to be explicit about its consequences, their mechanisms and the spatial and temporal scales alike.

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454

Legends to figures

Fig. 1. The timing of migration – here exemplarily from a non-breeding site via an intermittent staging to a breeding site – can be characterised by synchrony (left panel) and phenology (right panel).

Migration synchrony describes in how far individual migrants travel at the same time, i.e. synchronously, or at different times, i.e. asynchronously. Migration phenology relates the timing of migration to the phenology of resources or to that of other populations and species, with which migrants interact, e.g. via competition, predation, etc. The degree of coincidence between migrant visitation and resource availability (upper-right panel) determines the migrants' fitness consequences, which under complete overlap can range from positive when resources are concerned to negative when it characterises the presence of predators.

Fig. 2. The consequences of migratory connectivity can be modified and shaped by migration phenology and synchrony, via a suite of different factors and mechanisms.

Fig. 3. Disease dynamics differed considerably in a dynamic network. Prevalence varied between the two locations (a-c starting location, b-d destination) and in dependence of migration synchrony (a-b) and phenology (c-d). Increasing variation around the mean migration date makes migration more asynchronous, which is exemplarily illustrated by underlying histograms: completely synchronous (dark grey bars), slightly (grey bars) and highly (light grey bars) asynchronous. While in the highly synchronized migration (dark blue and dark orange line) prevalence was similar at the two locations, asynchronous migration led to slowly decreasing prevalence in the starting location (a) and a slowly increasing prevalence at the destination (b).

Prevalence was also affected by the onset of a period of increased parasite pressure, which was varied relative to migration date (c-d). The highest prevalence resulted when migration coincided with the period of increased parasite pressure, while it was considerably lower for an onset before and unchanged for an onset after migration.

Timing of Migration

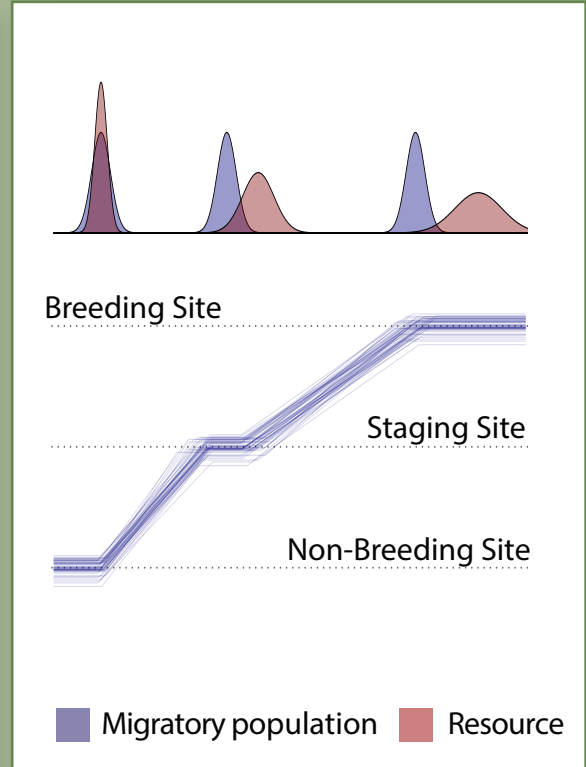
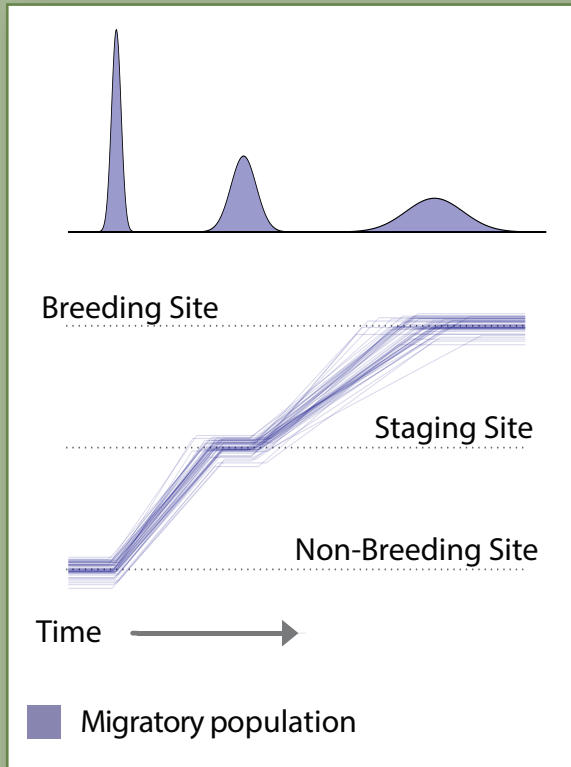
synchronous

asynchronous

matched

mismatched

Synchrony



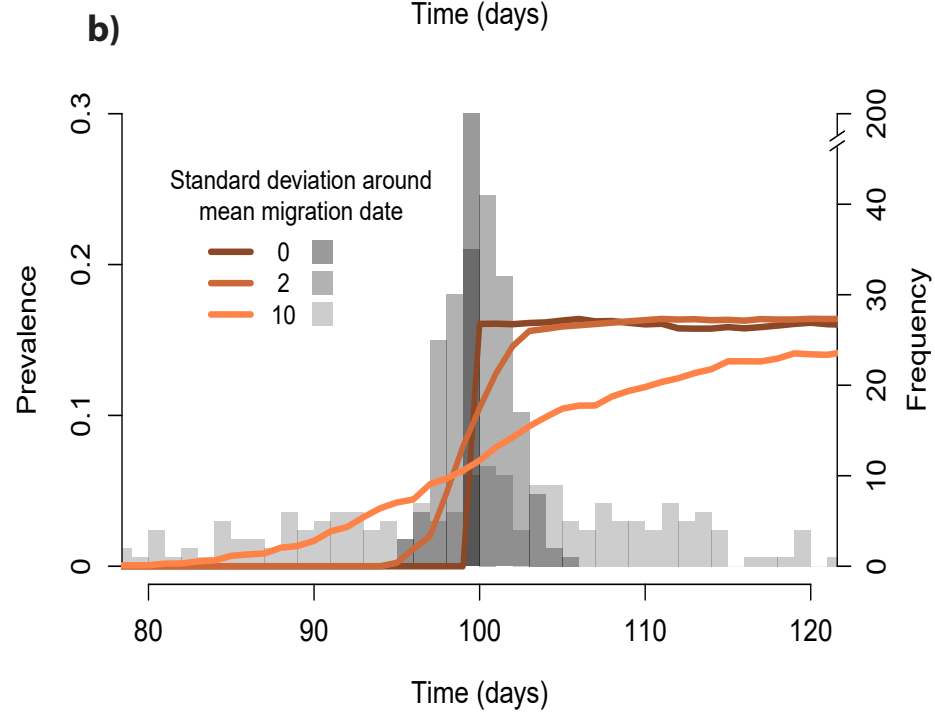
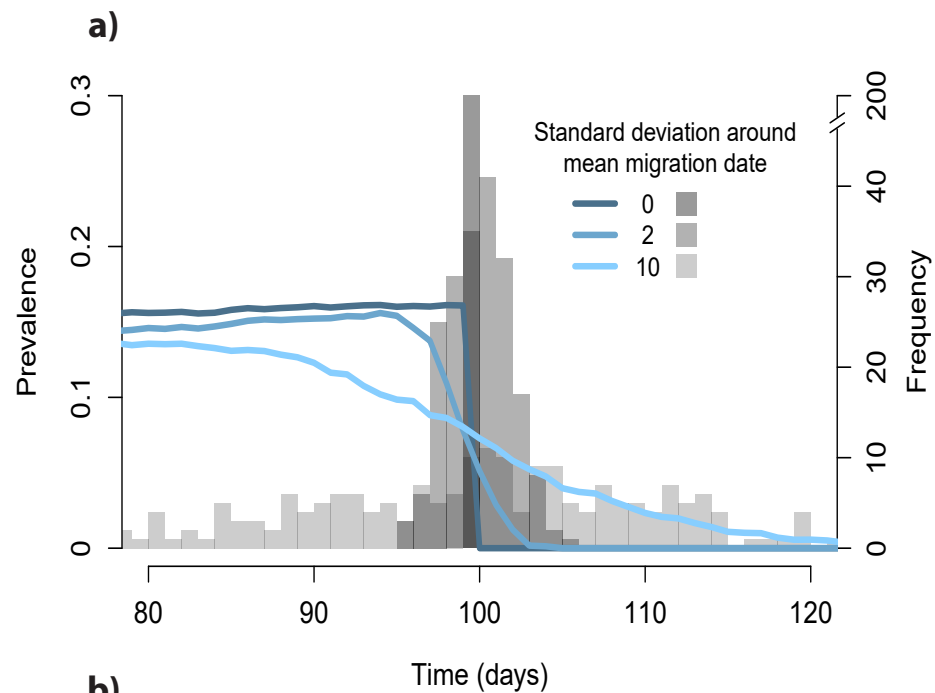
Phenology

Migration Synchrony		Migration Phenology	
modifies consequences if ...		relevant in relation to ...	
Resource availability	Climate & weather	... resource availability changes over visitation period	... phenology of resources (match/mismatch hypothesis)
	Density dependence	... weather conditions change over visitation period	... seasonality of places & variability of weather
	Predation, disturbance, hunting	... degree of synchrony determines magnitude of density-dependent interactions	... phenology of other species, resulting in specific levels of competition, facilitation or other interactions
	Gene flow & genetic mixing	... predation risk, hunting pressure or disturbance levels vary over visitation period	... predator phenology, schedules of hunting and disturbance
Parasite transmission	Transport of nutrients & energy	... synchrony affects pair formation and mating	... variation in reproductive success of early and late breeders
	Transport of propagules	... asynchronous migration separates infected & uninfected individuals	... variation in susceptibility or prevalence over time
Trophic effects	Transport of propagules	... simultaneous input of nutrients or energy results in resource pulses	... phenology of community as timing of input determines pathways of nutrients & energy into community
	Trophic effects	... simultaneous input of propagules enhances probability of establishment, e.g. via mass effect or numerical domination	... phenology of community as timing of input influences fate & effect of propagules, e.g. probability of establishment, pollination, etc.
Community & ecosystem		... it determines interaction strength	... trophic processes in community

Migrant individuals and their populations

Community & ecosystem

Changes in migration synchrony



Changes in migration phenology

