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How to study parasites and host migration: a roadmap for empiricists

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ABSTRACT

Animal migration (round-trip, predictable movements) takes individuals across space and time, bringing them into contact with new communities of organisms. In particular, migratory movements shape (and are shaped by) the costs and risk of parasite transmission. Unfortunately, our understanding of how migration and parasite infection interact has not proceeded evenly. Although numerous conceptual frameworks (e.g. mathematical models) have been developed, most empirical evidence of migration–parasite interactions are drawn from pre-existing empirical studies that were conducted using other conceptual frameworks, which limits our understanding. Here, we synthesise and analyse existing work, and then provide a roadmap for future (especially empirical) studies. First, we synthesise the conceptual frameworks that have been developed to understand interactions between migration and parasites (e.g. migratory exposure, escape, allopatry, recovery, culling, separation, stalling and relapse). Second, we highlight current challenges to studying migration and parasites empirically, and to integrating empirical and theoretical perspectives, particularly emphasizing the challenge of feedback loops. Finally, we provide a guide to overcoming these challenges in empirical studies, using comparative, observational and experimental approaches. Beyond guiding future empirical work, this review aims to inspire stronger collaboration between empiricists and theorists studying the intersection of migration and parasite infection. Such collaboration will help overcome current limits to our understanding of how migration and parasites interact, and allow us to predict how these critical ecological processes will change in the future.

Key words: disease ecology, evolutionary feedback, host–parasite interaction, life-history strategy, mathematical model, movement ecology, partial migration, pathogen infection

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I INTRODUCTION

Animal migration, the round-trip movement of individuals between distinct habitats, has fascinated ecologists for centuries. Although long-distance seasonal movements of large vertebrates such as blue wildebeest (*Connochaetes taurinus*), Canada geese (*Branta canadensis*) or humpback whales (*Megaptera novaeangliae*) often first come to mind, migratory behaviours are widespread in both vertebrates and invertebrates and can take many different forms. For instance, migration can occur over short distances (i.e. tens of meters), on a daily basis (e.g. diel migrations in some marine fish and water fleas) and/or involve only a fraction of the population [i.e. partial migration in fishes and ungulates (Alerstam, Hedenström & Åkesson, 2003; Hays, 2003; Chapman *et al*., 2011; Dingle, 2014)]. Scientists have a rich theoretical and empirical understanding of the ecological and evolutionary drivers of migratory behaviour across multiple systems and taxa (e.g. Olsson *et al*., 2006; Avgar, Street & Fryxell, 2013; Dingle, 2014; Gnanadesikan, Pearse & Shaw, 2017; Hegemann, Fudickar & Nilsson, 2019). Factors such as resource availability, predator avoidance, and tracking favourable climates are most commonly identified as important drivers of animal migration (Alerstam *et al*., 2003; Olsson *et al*., 2006; Avgar *et al*., 2013; Dingle, 2014; Gnanadesikan *et al*., 2017). Understanding the importance of these drivers in a given system allows researchers to predict better the responses of migrants to environmental change, and is crucial for informing management and conservation strategies for migratory species.

In the last decade, the field of animal migration/animal movement ecology began to integrate consideration of parasites and pathogens, hereafter parasites (Altizer, Bartel & Han, 2011; Bartel *et al*., 2011; Møller & Szep, 2011; Poulin & de Angeli Dutra, 2021). The transport of parasites on migrants has long been recognized as a by-product of host movement across landscapes. Parasite community composition can be used to elucidate migration routes, population origin and time since arrival in a new habitat (Criscione, Cooper & Blouin, 2006; Thieltges *et al*., 2010; Alarcos & Timi, 2013) even for use as a conservation tool (Gagne *et al*., 2021). Yet, parasites are now increasingly recognized as drivers of animal migration as opposed to passive passengers along for the ride (Altizer *et al*., 2011). Similarly, movement across different habitats represents increased disease risks to migrants, a cost to migration that has important implications for energy allocation, life-history trade-offs and parasite evolution (Poulin & de Angeli Dutra, 2021). Without explicitly considering the role of parasite infection and/or the risk of parasite infection on the behaviour of migratory hosts, researchers risk overlooking a key determinant in animal movement ecology. As anthropogenic changes increasingly threaten migratory behaviours and alter cycles of disease transmission globally (Wilcove & Wikelski, 2008; Altizer *et al*., 2013; Hall, Brown & Altizer, 2016), it is imperative to incorporate these often-overlooked variables into predictive animal migration frameworks.

Advances in the field of migration–parasite interactions have been asymmetrical. While multiple conceptual frameworks (many of which are mathematical models) exist to help predict patterns of migration and parasite infection (Table 1; see online Supporting Information, Table S1; Poulin & de Angeli Dutra, 2021; Peacock *et al*., 2020), empirical evidence of the effects of parasites on host migratory behaviour is mostly drawn from studies designed for other purposes. For instance, studies reporting differences in parasite fauna among migrants at a breeding site may be designed to test differences in host arrival time or migrant population origin rather than the influence of infection on host migratory decisions (Thieltges *et al*., 2010; Alarcos & Timi, 2013). The lack of empirical studies explicitly testing migration–parasite interactions may be due to the inherent difficulty in studying complicated ecological processes like migration and parasite infection. The tendency to work on questions of theory and empirical systems separately, without integration of these ways of understanding a phenomenon (but see Bradley & Altizer, 2005; Bartel *et al*., 2011; Hall *et al*., 2014) also means that our understanding of parasite–migration interactions is currently weak, hampering our ability to predict how these ecological processes will change. To understand the interactions between host migration and parasite infection, we need empirical studies explicitly designed to test the effects of parasites on host migration (and *vice versa*) as well as the parallel development of mathematical studies that explore these ideas from different perspectives (e.g. longer timescales). We also need iterative communication and collaboration between the two perspectives (Restif *et al*., 2012).

Table 1. Summary of known mathematical models that focus on each of the conceptual frameworks without a feedback loop between migration and infection, and with feedback loops. We did not include models that were parameterized to a particular study system

Conceptual framework	Models without feedbacks	Models with feedbacks
Migratory allopatry	none	none
Migratory culling	Hall, Altizer & Bartel (2014); Hall *et al.* (2016); Brown & Hall (2018); Johns & Shaw (2016)	Peacock *et al.* (2018, 2020)
Migratory escape (environmental)	Hall *et al.* (2016); Brown & Hall (2018)	Peacock *et al.* (2018, 2020); Balstad *et al.* (2021); Naven Narayanan, Binning & Shaw (2020); Shaw & Binning (2016); Shaw *et al.* (2019)
Migratory escape (social)	Hall *et al.* (2014); Johns & Shaw (2016); Hurtado (2008)	Shaw *et al.* (2019); Shaw & Binning (2020)
Migratory exposure	none	Shaw *et al.* (2018)
Migratory recovery	none	Naven Narayanan *et al.* (2020); Shaw & Binning (2016, 2020); Shaw *et al.* (2019); Peacock *et al.* (2020)
Migratory relapse	Becker, Ketterson & Hall (2020)	none
Migratory separation	none	Galsworthy *et al.* (2011)
Migratory stalling	none	Peacock *et al.* (2018, 2020)

Accomplishing this multidisciplinary goal requires that researchers tackle the problem using multiple different, yet complementary, approaches (i.e. comparative, observational, experimental and theoretical studies).

Here, we offer guidelines for how a range of scientists including behavioural ecologists, parasitologists, theoreticians, epidemiologists and eco-physiologists interested in animal movement can think about designing studies that test for interactions between migration and parasites. We first synthesise different conceptual frameworks developed to understand the interactions between parasites and host migration. Next, we point out some of the challenges inherent to study of animal migration and parasitism as well as the difficulties in linking theoretical and empirical research together in these fields. Finally, we generate a roadmap for overcoming the above challenges, to guide how future empirical research (including comparative, observational and experimental studies) can be structured within these frameworks to provide strong evidence for these ideas. Our goal is to encourage researchers to explore this challenging, yet fascinating, avenue of research, and to foster collaboration and communication between empirical and theoretical perspectives.

II CONCEPTUAL FRAMEWORKS

(1) What are conceptual frameworks and how are they used?

Conceptual frameworks are a common research tool in the fields of ecology and evolutionary biology, as they are in many areas of science (Zuk & Travisano, 2018). One tool for developing conceptual frameworks is mathematical models, which generally have the goal of understanding more clearly the link between assumptions and predictions. Such conceptual models can serve as 'proof of concept' tests of verbal models, paralleling the way that empirical data serve as tests of hypotheses of field or laboratory studies (Servedio *et al.*, 2014). These models are thus derived from general concepts that often span different biological systems, which has the double advantage of allowing one to draw parallels between disparate sets of species (which researchers focusing on particular species might not have compared), and to generate predictions that can be used to guide future studies in many species.

Conceptual models serve numerous roles, all of which can inform empirical work (Fig. 1). These roles include suggesting new ways of looking at empirical data, identifying the simplest model that generates an observed pattern, generating a novel conceptual framework, exploring the link between assumptions and outcomes, uncovering hidden assumptions in verbal explanations, and generating predictions that can be tested with data (Caswell, 1988; Servedio *et al.*, 2014). For example, models can generate predictions that can be tested with empirical studies. Hall *et al.* (2014) demonstrated that the further migrants travel and the longer they spend away from breeding grounds, the lower their infection prevalence. This model demonstrates that migratory escape and migratory culling (*M*; Fig. 1) can generate a pattern (*P*; Fig. 1) of lower infection in migrants. A comparative study on monarch (*Danaus plexippus*) butterflies, a system where both migratory escape and culling are present (Bradley & Altizer, 2005; Bartel *et al.*, 2011), documented an extreme version of this predicted pattern: parasite prevalence was higher for non-migratory butterfly populations than for migratory ones (Satterfield *et al.*, 2016).

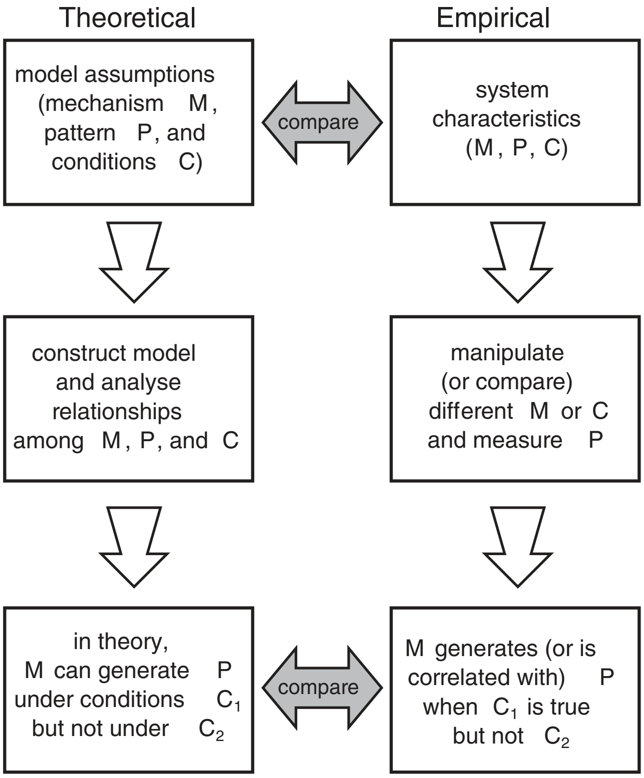

Fig. 1. Schematic demonstrating one set of relationships between theoretical models and empirical data. In the left panel, models are built on a set of assumptions, here relating to a potential mechanism (*M*, e.g. migratory escape) and/or a pattern (*P*, e.g. some individuals migrate and others do not) and/or a set of conditions (*C*, e.g., range of mortality costs of migration). Once model assumptions are set, the model is constructed and analysed, and the theoretical results are described, e.g. that mechanism *M* can lead to pattern *P* under some conditions *C*. In the right panel, empirical studies can build on existing theory in a number of steps. First, by comparing model assumptions to a particular empirical system (does mechanism *M* exist? Does it co-occur with *P* and/or *C*?). Next, an empirical study can manipulate *M* or *C* explicitly, or compare across systems that differ in *M* and *C*, to determine an empirical relationship between *M*, *P*, and *C*. Finally, the empirical result can be compared to the model results.

Models can also synthesise across systems, suggesting new ways of looking at empirical data. Empirical studies have documented two patterns: infection can increase (Koprivnikar & Leung, 2015) or decrease (Folstad *et al.*, 1991) with migration. Shaw *et al.* (2018) demonstrated that the observed pattern (*P*; Fig. 1) depends on the conditions (*C*; Fig. 1): in theory, migration both increases infection (in terms of diversity of parasite species) and decreases infection (in terms of prevalence of infection across hosts). To test this, empirical work could investigate a relationship between the conditions (*C*) and the patterns (*P*). Normandeau *et al.* (2020) measured infection intensity and prevalence simultaneously, finding that migrants had higher infection in terms of both metrics, which only partially matches theoretical predictions. This empirical finding of higher infection intensity in migrants could represent the rare theoretical case of the reverse pattern (which occurs when transmission of parasites in the migrant environment is high and their survival cost low, compared to parasites in the resident environment; Shaw *et al.*, 2018). Further empirical work estimating the transmission rates and survival costs of parasites could test this idea. Alternatively, this finding may represent a mechanism that is missing from the model (e.g. hosts being infected by more than two parasite species). Further theoretical work extending the model of Shaw *et al.* (2018) could test this idea.

As a final example, models can generate a novel conceptual framework. As described in more detail below, Shaw & Binning (2016) proposed that if individuals can migrate to a new environment that promotes recovery from infection, this could provide a selective pressure favouring migration, thus suggesting both a new mechanism (*M*; Fig. 1) as well as a resulting evolutionary pattern (*P*; Fig. 1). Daversa *et al.* (2018b) provided empirical support for this mechanism by demonstrating that individual spiny toads (*Bufo spinosus*) do indeed recover from infection as they migrate across an environmental gradient. Ideally a next empirical step would be testing for the pattern (*P*): whether recovery from infection itself is a selective pressure favouring toad migration. A number of different conceptual frameworks have been developed to study migration and parasites, which we describe below.

(2) Conceptual framework 1: migratory exposure

As animals migrate, they move across a range of habitats exposing them to new food sources and different environmental conditions as well as different predators and parasites. As increased encounters with different parasites can occur at any point on the host's breeding grounds, stopover sites, and wintering grounds, 'migratory exposure' predicts that migrants accumulate a greater diversity, intensity and/or prevalence of infection compared with non-migratory species or populations (Altizer *et al.*, 2011). This concept originally stems from ideas surrounding parasite infection risk and host geographic range size. Price, Westoby & Rice (1988) hypothesized that the number of parasite species per host should increase as the area occupied by that host population increases. Gregory (1990) provided correlational evidence for a positive relationship between the number of helminth species per host and the geographic range of the host species in waterfowl. Since harbouring more and different types of parasites is likely detrimental to hosts, migratory exposure is considered an additional cost of migration. Empirical support comes from studies on birds (Figuerola & Green, 2000; Waldenström *et al.*, 2002a; Jenkins *et al.*, 2012; Koprivnikar & Leung, 2015; Hannon *et al.*, 2016), ungulates (Teitelbaum *et al.*, 2018), and fish (Shaw *et al.*, 2018). For example, migratory species of anseriform birds harboured more hematozoa than did sedentary species, and infection prevalence was positively correlated with distance migrated (Figuerola & Green, 2000).

(3) Conceptual framework 2: migratory escape

Although exposure to and acquisition of more and new parasites as a result of travelling through different habitats is a potential negative consequence of migration (Koprivnikar & Leung, 2015; Teitelbaum *et al.*, 2018), researchers have been exploring infection-related benefits of host migratory movements since at least the early 1990s. Folstad *et al.* (1991) and Folstad & Nilssen (1990) were the first to suggest that post-calving migrations in reindeer (*Rangifer tarandus*) may be an important parasite-avoidance strategy in some populations. They documented decreased infection from warble-fly (*Hypoderma tarandi*) larvae as reindeer moved further away from calving grounds (Folstad *et al.*, 1991). Loehle (1995) suggested that migratory species may benefit from moving away from infected habitats for part of the year. This conceptual framework was built around the notion that continued habitat use by hosts allows parasites to accumulate in the environment over time. Thus, periodically moving away from these infested areas promotes the 'cleaning' of habitats as parasites die off without access to hosts (Loehle, 1995). Empirical evidence for this framework, eventually called 'migratory escape' (Bradley & Altizer, 2005), comes mostly from ungulates infected with endo- or ectoparasites (Folstad *et al.*, 1991; Qviller *et al.*, 2013; Mysterud *et al.*, 2016; Pruvot *et al.*, 2016), but also includes birds infected with haemosporidian parasites (Slowinski *et al.*, 2018). The benefits of migratory escape were originally framed in terms of avoiding infected habitats, and are thus most relevant for parasites transmitted from the environment (i.e. environmental migratory escape; Shaw & Binning, 2020). However, migration can also lead to the spatial separation of individuals within a population, and thus, may independently impart a benefit in terms of reducing direct transmission from infected conspecifics, or closely related heterospecifics. For example, house finches (*Carpodacus mexicanus*) are partially migratory in eastern North America. Resident populations tend to congregate around bird feeders in the winter, where they can directly transmit the bacterial infection, mycoplasmal conjunctivitis, suggesting that migrating may benefit finches by allowing them seasonal escape from infected individuals (Hurtado, 2008). The 'social migratory escape' framework has recently been formalized mathematically, but most empirical evidence supporting this phenomenon comes from studies that were not designed to test this idea (see Table 1 in Shaw & Binning, 2020).

(4) Conceptual framework 3: migratory allopatry

A framework similar to migratory escape, 'migratory allopatry', posits that uninfected juveniles benefit from spatial separation from infected adults through reduced parasite transmission among cohorts (Krkošek *et al.*, 2007). This idea was initially inspired by juvenile pink salmon (*Oncorhynchus gorbuscha*), who spend several months in their early lives occupying a different marine habitat from adults. During this time, juveniles experience low infection prevalence from harmful, directly transmitted salmon lice (*Lepeophtheirus salmonsis*). Such parasite-related benefits of this separation period are seen when adult salmon migrate back to coastal habitats from the open sea and are no longer allopatric with younger cohorts (Krkošek *et al.*, 2007). This mechanism is suggested as a potential evolutionary explanation for the bipartite life cycle of many coral reef fishes, whereby larvae migrate to the water column where they spend a period of days to weeks before settling on reefs. This pelagic larval period allows vulnerable larval stages to escape benthic-dwelling parasites and/or directly transmitted parasites through reduced population densities in the water column (Strathmann *et al.*, 2002).

(5) Conceptual framework 4: migratory recovery

Migration can also have benefits *via* host recovery from infection. As animals move between habitats along their migratory route, some ecto- or endoparasites die or fall off as external and/or internal environmental conditions become unfavourable for parasite survival (i.e. 'migratory recovery'; Shaw & Binning, 2016). In this scenario, migration benefits infected individuals, and evolutionary models suggest that this can lead to mixed strategies (partial migration) where each year some individuals migrate while others stay resident (Shaw & Binning, 2016). Migratory recovery and migratory escape are not mutually exclusive mechanisms: migration may allow individuals both to escape further infection and to recover from existing infection (Shaw & Binning, 2016). Indirect evidence of migratory recovery exists across a range of taxa (see Table 1 in Shaw & Binning, 2016). For example, the distance decay of parasite fauna as host fish migrate from fresh to salt water or *vice versa* is a well-documented phenomenon in many anadromous and catadromous species (Thieltges *et al.*, 2010). More recently, Daversa *et al.* (2018b) explicitly attribute migratory recovery to explain why spiny toads appear to recover from chytrid fungus (*Batrachochytrium dendrobatidis*) infections when they move from humid ponds to dry terrestrial burrows in the autumn and winter months. Migration across environments that differ in temperature, oxygen availability, or that lead to changes in host internal environments could also be investigated for evidence of migratory recovery.

(6) Conceptual framework 5: migratory culling

Migration and parasite infection are both energetically costly (Schmidt-Nielsen, 1972; McElroy & de Buron, 2014; Binning, Shaw & Roche, 2017). Individuals that are both infected and attempting to migrate may therefore have difficulty completing their journey and die *en route*. This idea was first described as 'migratory culling' by Bradley & Altizer (2005), citing evidence that fall armyworms (*Spodoptera frugiperda*) are less able to migrate long distances when infected with the nematode *Noctuidonema guyanense* (Simmons & Rogers, 1991). The culling of infected individuals from migratory populations can lead to reduced pathogen prevalence and rates of spread among migrants (Bradley & Altizer, 2005). Migratory culling of parasitized individuals has been extensively studied in monarch butterfly populations infected with the protozoan, *Ophryocystis elektroscirrha* (Bartel *et al.*, 2011). This model system illustrates how theoretical models, experimental tests and observational studies can be integrated to understand the role of parasites in migration (Bradley & Altizer, 2005; Bartel *et al.*, 2011; Hall *et al.*, 2014; Satterfield *et al.*, 2016). Other empirical systems for migratory culling include birds infected with haemosporidian parasites (Slowinski *et al.*, 2018), Bewick's swans (*Cygnus columbianus bewickii*) infected with avian influenza (van Gils *et al.*, 2007) and salmon infected with infectious haematopoietic necrosis virus (Furey *et al.*, 2021). Unlike the other conceptual frameworks above, which represent either a cost or benefit of migration (in terms of infection) to hosts, migratory culling represents a tension in selective pressures, being both a cost at the individual level (increased mortality for infected hosts) and a benefit at the population level (reduced prevalence and thus transmission within migratory populations).

(7) Emerging conceptual frameworks: migratory separation, stalling and relapse

New conceptual frameworks aimed at understanding interactions between migration and parasites are also being developed. In addition to affecting survival (see migratory culling), the energetic burden imposed by parasites can also affect host migration phenology such that infected individuals delay the start of their migration relative to uninfected conspecifics (coined 'migratory separation' by Risely, Klaassen & Hoye, 2018). Such migration delays have been observed in Bewick's swans infected with avian influenza (van Gils *et al.*, 2007). A model of mallard (*Anas platyrhynchos*) migration found that delayed migration of infected individuals results in a period of spatial separation between infected and uninfected hosts, thus reducing disease transmission (Galsworthy *et al.*, 2011). Alternatively, parasite-induced energetic costs can reduce an individual's mobility [as occurs in monarchs and salmon (Bradley & Altizer, 2005; Nendick *et al.*, 2011)], thus interrupting migration at stopover sites [i.e. 'migratory stalling' (Peacock *et al.*, 2018, 2020)]. For instance, stopover duration of juvenile mallards shedding more avian influenza virus is longer than those shedding less (Latorre-Margalef *et al.*, 2009). In their population model, Galsworthy *et al.* (2011) also show how stopover delays induced by infection alter disease transmission in concert with migratory separation. The intense energetic costs and/or physiological changes experienced by migrants while moving can also lead to flare-ups of latent infections, which can affect host migratory ability [i.e. 'migratory relapse' (Gylfe *et al.*, 2000; Becker *et al.*, 2020)]. As is true for migratory culling, all of these mechanisms can have important infection-related benefits at the population level, but may impose infection-related costs at the individual level.

III CHALLENGES

(1) Challenges to studying migration and parasites

Empirically studying the effects of parasites on animal migration is difficult for a number of reasons. Practical challenges in terms of data collection exist for both studies of host–parasite interactions and migratory behaviour independently due to their ecological complexities. Microparasites such as viruses, bacteria, protozoa or prions often require molecular tools to identify and quantify them accurately. Quantification of macroparasite (e.g. helminths and flukes) presence and burden can be time-consuming and often involves sacrificing hosts. Both microparasites and macroparasites can be transmitted by direct routes (close contact with an infectious individual) or indirect routes (transmitted *via* the environment). Some micro- and macroparasites (e.g. *Babesia* spp., *Francisella tularensis*, tapeworms) can be transmitted by ectoparasites (e.g. ticks, fleas), which may be relatively easy to see and count especially when externally visible on hosts. Furthermore, many parasites have low virulence at low intensities, and wild animals tend to conceal outward signs of sickness. All of these considerations make infected individuals difficult to detect and thus, observe and monitor. Conversely, very sick individuals often die before they are identified and studied. Co-infections by multiple parasite species or life stages can also make observed differences among individuals difficult to attribute conclusively to one parasite or another (Hafer & Milinski, 2016). Infection dynamics also operate across multiple spatial (i.e. within host, among hosts, across landscapes; Restif *et al.*, 2012), and temporal (i.e. seasonal, developmental) scales, both of which can vary simultaneously. This makes choosing the appropriate scale at which to target research effort an important consideration and constraint in disease and parasite ecology. Studying migration in the wild presents similar challenges in terms of sampling logistics: studying individuals across their entire migratory route is not yet tractable in many species, making it challenging to determine when and where parasites are picked up and lost across the migratory route. Indeed, for many species we lack a basic understanding of what routes migrants take (Bauer *et al.*, 2019; Kauffman *et al.*, 2021) and when and where mortality of migrants occurs (Bowlin *et al.*, 2010), and much less to what extent infection might contribute to migrant mortality. Sampling designs for studying migration and parasite infection may also be in conflict. For instance, repeated capture and sampling of the same individual may affect their movement behaviour, but may be necessary for tracking disease status, especially where assessing recovery from infection is a study goal. The combined challenges of studying disease dynamics across the often-large spatial and temporal scales required for migratory species present a huge barrier to developing model systems on these questions.

Evolutionary (in contrast to ecological) impacts of parasite infection, or the threat of parasite infection, can shape the evolution of host behaviour through feedback loops that may not be obvious when studying contemporary patterns (Poulin *et al.*, 2020). Whereas host–parasite systems that promote recovery from infection should evolve to exhibit dynamic infection cycles in a population (i.e. cycling between infected and uninfected states), hosts that become very effective at avoiding infections may evolve to never becoming infected at all. If avoidance behaviours are themselves not costly to maintain, or impart additional host benefits in terms of resource use etc., they may persist in a population even after the infection threat disappears. The "Ghost of parasitism past" hypothesis suggests that strong, sustained selection on parasite avoidance strategies in hosts should canalize certain host behavioural, morphological and/or physiological traits that persist in populations long after the threat of infection is gone (Poulin *et al.*, 2020). Empirically testing evolutionary models that suggest migration evolves as a mechanism to escape or recover from infection may face this difficulty: the observation of migratory behaviour in an empirical system may represent the endpoint of an evolutionary process involving parasites that no longer infect the host population.

Aligning selective pressures imposed by both infection risk and other environmental factors may drive reinforcement of migratory behaviours as well. For instance, an individual may start moving further and further away to exploit novel foraging opportunities while simultaneously experiencing reduced infection. Alternatively, infected individuals may display different microhabitat preferences to uninfected individuals, leading to their movement away from uninfected group members. This behaviour may be reinforced if individuals simultaneously experience infection recovery and benefit from increased access to resources through reduced competition. Because the evolutionary signatures left by past parasites on migratory hosts cannot be tested experimentally, there are limits to the types of causal inferences that can be made empirically. As a result, deconstructing the conceptual frameworks into explicit assumptions and predictions that could be expected if parasites are important drivers of animal migration may provide a more tractable avenue for empiricists to tackle large-scale ecological questions such as these. However, combining empirical and theoretical work presents its own sets of challenges.

(2) Challenges to linking theoretical and empirical research together

In some cases, theoretical work on infection-related consequences of migration has generated predictions that lend themselves to empirical tests and exploration of natural systems (see Bradley & Altizer, 2005; Bartel *et al.*, 2011; Hall *et al.*, 2014; Satterfield *et al.*, 2016). Yet, theoretical findings are not always easy to test empirically. A key complicating factor is the presence of feedback loops (e.g. infection alters migration, which in turn alters infection; Table 1, Fig. 2). Mathematical models that rely on a feedback loop will be much harder to test empirically (Fig. 2B, C). At best, this requires an experimental setup with a suitably long temporal scale to capture both sets of changes. At worst, these changes will happen so quickly (a tight feedback loop) that they will be hard to decouple. Within studies on migration and parasites, evolutionary models tend to incorporate feedback loops more frequently than ecological models, and thus may be more difficult to test empirically. However this association is not perfect – some ecological models include feedback loops and some evolutionary models lack them.

Another way of viewing the distinction between feedback presence and absence is whether an empirical comparative test is possible *versus* whether a manipulative test is required. For example, without a feedback loop, the idea that migration alters infection can be tested by comparing two existing populations: one migratory and one resident. We predict resident populations to have higher infection prevalence and/or intensity than migrants if migratory escape, recovery or culling are operating. Conversely, migrants should have higher parasite intensity and/or prevalence if migratory exposure is more likely (Table 2). By contrast, with a feedback loop, the comparison would need to be between the migratory population and the same population if it were not to migrate, a comparison only achievable through manipulation.

Mathematical models without a feedback loop, say one that predicts that migration should alter infection without any assumption that migratory behaviour will be affected (e.g. Johns & Shaw, 2016) should be relatively easy to test empirically (Fig. 2A). Empirical studies could include comparisons of infection prevalence, parasite richness or intensity between migratory and resident populations of the same species, or cross-species comparisons (Poulin *et al.*, 2012; Shaw *et al.*, 2018). For example, larvae from migratory *Galaxia brevipinnis* move to pelagic marine habitats post-hatching whereas larvae from non-migratory species (*G. depressiceps* and *G. gollumoides*) reside year-long in the same river habitats as adult conspecifics (Poulin *et al.*, 2012). Migratory *G. brevipinnis* experience lower infection prevalence and intensity by indirectly transmitted trematodes than non-migratory species (Poulin *et al.*, 2012).

IV OVERCOMING CHALLENGES TO GUIDE EMPIRICAL STUDIES

(1) Comparative studies

One way to test some of the above ideas empirically is to compare studies across previously published data sets. For example, Shaw *et al.* (2018) combined data sets on fish parasites and on fish life history to test whether migratory fish were more infected (e.g. migratory exposure) or less infected (e.g. migratory escape) than non-migratory fish (Table 2). A recent meta-analysis addressed a similar question across a wider range of taxa (Poulin & de Angeli Dutra, 2021). Correlational studies need to be done with care, by appropriately controlling for confounding factors. For example, many comparative studies on the relationship between migration and parasite diversity account for host phylogeny, sampling

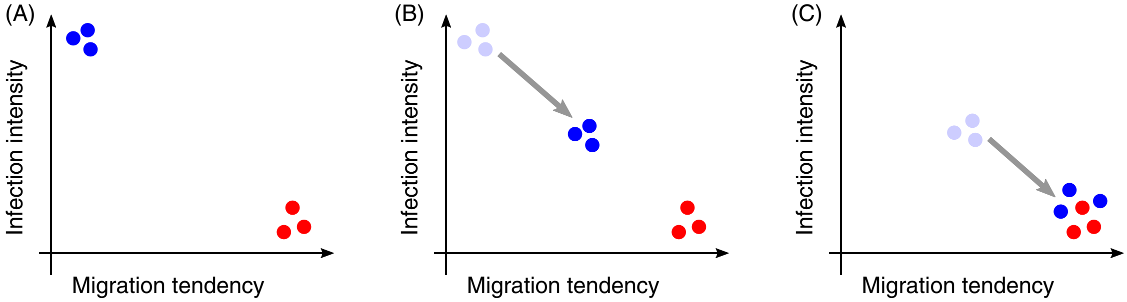

Fig. 2. The presence of feedback loops can make it challenging to understand the interactions between migration and infection. Each panel shows the relationship between infection intensity and migration tendency across several populations (each shown as a dot). (A) If migration and infection interact without a feedback loop, there may be a clear relationship between the two. Here, individuals in populations that migrate (solid red dots) have lower infection intensity than those in populations that do not migrate (solid blue dots). (B) If there is a feedback loop, the relationship between migration and infection may change over time (grey arrows, i.e. moving from light blue to dark blue dots). Here, if migration leads to lower infection intensity, this can favour an increased migration tendency in individuals that do not migrate, thus lowering their infection intensity. (C) The end result of a feedback loop may be no clear relationship between migration and infection.

effort, host body size and other traits (Poulin & de Angeli Dutra, 2021). However, to our knowledge, some factors specifically related to migration and infection are not typically controlled for. For example, transmission mode is key. Species that migrate along an environmental gradient may be able to escape (or recover) from environmentally transmitted parasites more easily than from directly transmitted parasites. Similarly, when testing migratory recovery, drawing on studies that sampled migrants at the start of their migration (i.e. before recovery) will give different results than drawing on studies that sampled migrants at the end of their migration (i.e. after recovery). It may also be important to consider the intensity of infection. Comparative analyses that bin all infected individuals together to contrast against healthy individuals may overlook patterns based on infection intensity. Finally, comparative studies are inherently correlative and thus are poor tools for understanding causality, especially for systems where there is a feedback loop between migration and infection. Possible ways to circumvent this include using closely related species to reconstruct past selective pressures on migration, or using dated phylogenies to reconstruct the evolution of migration (Poulin *et al.*, 2020). New studies that take these factors into account, by explicitly thinking about which mechanisms (migratory recovery, migratory escape, migratory exposure) are being studied may thus be able to uncover new or different patterns between migratory behaviour and infection that previously have not been reported in comparative studies.

(2) Observational studies

Observational studies aim to examine and understand ecological processes through the collection of data that has not been purposefully manipulated (Sagarin & Pauchard, 2010). For example, infection metrics can be sampled and compared between migrants and residents in partially migratory populations or species, or between closely related species where one species migrates and the other does not (Table 2). The advent of new technologies in pathogen detection, unmanned aerial vehicles (drones), animal tracking and biologging, as well as the continued emphasis on mark–recapture studies and natural experiments have enhanced the ability of observational studies to make meaningful inferences, especially in systems where manipulative experiments are not feasible, ethical or ecologically relevant. Choosing the infectious agent to be monitored is also a critical decision when choosing a study system. In observational studies, systems where parasite load or infection status can be assessed quickly and non-lethally are preferable when the same individual is to be sampled multiple times. Where an individual can be captured and handled, skin and genital swabs can be performed quickly to assess microparasite infections. Blood parasites can be screened through small samples of collected blood. Where capture and handling is not possible or where such procedures may influence movement behaviours, non-invasive techniques such as faecal or urine sampling may also allow researchers to screen individuals or stopover areas for parasites. Some infections may also be visible. Ectoparasites, such as ticks, lice, isopods and copepods, can often be seen and counted directly on infected hosts. Some encysted trematodes cause melanisation of host tissues that can be easily counted (e.g. black spot disease in many fishes). Other visible signs of disease including gland swelling, warts, rashes, skin lesions, altered colouration, as well as fur, scale or feather loss, can be noted during routine monitoring of migrating individuals. The passive nature of the data collection techniques involved in many observational studies makes them particularly amenable to research on animal movement patterns and disease status. Below, we highlight some common techniques used in observational studies, and how they may apply to questions related to migration and parasite infection.

(*a*) *Pathogen detection*

Continued advances in pathogen detection methods can help us not only to understand the disease status of individuals

Table 2. Summary of main predictions derived from conceptual frameworks and suggestions for how they can be tested empirically. Each row is a prediction that, if found, would provide support for the conceptual framework; not all predictions are required for a conceptual framework to be supported and conversely not all predictions are unique to a conceptual framework

Predictions	How can these be tested (comparative, observational, experimental)	Model system requirements
Migratory allopatry		
Species where juveniles migrate have lower infection prevalence in early life stages than those where juveniles reside with adults	Comparative: mine databases of parasite–host pairs with migratory behaviour, correct for phylogeny Observational: sample infection of closely related migratory and resident species	No or minimal parental care Good data on migratory behaviour and parasites (fish) No or minimal parental care (some fishes, insects, reptiles, amphibians)
Juvenile infection prevalence and intensity increases as more time is spent around adults	Experimental: manipulate time and proximity of juveniles and adults	No or minimal parental care (some fishes, insects, reptiles, amphibians) Ethical to restrict migration (in wild populations)
Migratory culling		
Infection reduces locomotor performance and/or has high energetic costs	Observational: fit individuals with accelerometers to record average movement speeds during migration Experimental: test for performance decreases following infection or increases following recovery (i.e. swim or wind tunnels, treadmills)	Feasible to exercise in the laboratory (i.e. some fishes, birds, bats, reptiles, small mammals, insects)
Prevalence of infection in population decreases the further and/or longer individuals migrate	Observational: capture sampling across migratory route to track changes in infection prevalence throughout migration	Known migratory route
Migratory escape (environmental)		
Environments that residents and migrants inhabit during their separate phase differ in parasite quantity	Observational: sample parasite quantity (i.e. eDNA) in both environments	Hosts with indirectly transmitted parasites, aquatic systems, air-borne pathogens
Migratory individuals within a species have lower abundance and/or prevalence of infection than resident individuals	Observational: sample migrant and resident individuals and compare parasite infection abundance and prevalence	Hosts with indirectly transmitted parasites
Hosts are more likely to migrate away from habitats with lots of parasites	Experimental: add or remove parasites from the environment and track movement behaviour	Indirectly transmitted parasites, which can be removed from the environment (i.e. using insecticides, fungicides)
Hosts avoid environments with parasites present	Experimental: measure parasite avoidance behaviour in hosts using cue choice arenas and/or habitat preference experiments	Hosts with indirectly transmitted parasites
Migratory escape (environmental and social)		
Migratory species have lower abundance, intensity and/or prevalence of infection than resident species	Comparative: mine databases of parasite–host pairs with migratory behaviour, correct for phylogeny	Good data on migratory behaviour and parasites (fish, mammals, birds)
Migratory individuals are less infected than resident individuals	Experimental: manipulate migration (e.g. provisioning food, altering release date), measure infection	Feeding site aggregations (social) Ethical to restrict migration (in wild populations)
Migratory escape (social)		
Hosts avoid infected conspecifics	Experimental: measure social avoidance behaviour in hosts using cue choice arenas and/or habitat preference experiments	Breeding aggregation Solitary migrations
Migratory exposure		
Prevalence of infection increases throughout migration	Observational: capture sampling across migratory route to track changes in infection prevalence throughout migration	Known and accessible migratory route
Migratory species have higher diversity, abundance, intensity and/or prevalence of infection than resident species	Comparative: mine databases of parasite–host pairs with migratory behaviour, correct for phylogeny	Good data on migratory behaviour and parasites (fish, mammals, birds)

Table 2. *(Cont.)*

Predictions	How can these be tested (comparative, observational, experimental)	Model system requirements
Parasite diversity increases with migration distance	Observational: use eDNA to create parasite species–area curves along migration route	Known migratory route
Migratory individuals within a species have higher diversity, abundance, intensity and/or prevalence of infection than resident individuals	Observational: capture sampling across migratory route to track changes in infection intensity, abundance, diversity and/or prevalence throughout migration	Known and accessible migratory route
Migratory individuals are more infected than resident individuals	Experimental: manipulate migration (e.g. provisioning food, altering release date), measure infection	Ethical to restrict migration (in wild populations)
Migratory recovery		
Infected individuals recover from infection when they migrate	Observational: sample individuals over the course of their migration	Migrations across distinct environments (i.e. across gradients of salinity, temperature, humidity, oxygen availability) such as anadromous/catadromous fishes, amphibians, birds
Reducing infection leads to less time spent in the recovery environment	Experimental: remove parasites from hosts and then track migratory behaviour	Feasible experimentally to remove infection through anti-parasite treatments (i.e. anti-helminths, delousing, tick treatments, etc.): fish, mammals, birds
Increasing infection leads to more time spent in the recovery environment	Experimental: infect individuals and then track migratory behaviour	Ethical to infect individuals experimentally (e.g. insects)
Microhabitat preference changes depending on infection status	Experimental: host habitat preference tests (i.e. biologgers, animal tracking)	Individual tracking is feasible (i.e. larger vertebrates)
Microhabitat preference changes depending on infection status	Experimental: host habitat preference tests (i.e. shuttleboxes, choice flumes)	Amenable to laboratory manipulation (i.e. smaller vertebrates, invertebrates)
Parasite survival is affected by environmental conditions and reduced when conditions change during migration	Experimental: test environmental tolerance of parasites to the environmental gradient experienced by hosts during migration	Feasible to assess changes in parasite infection through time (i.e. ectoparasites)
Migratory relapse		
Strenuous activity causes latent infections to flare up	Experimental: induce strenuous physical activity similar to migration and measure effect on infection intensity	Feasible to quantify infection intensity through non-lethal sampling Feasible to exercise in the laboratory (i.e. treadmills, swim tunnels, wind tunnels, etc.)
Prevalence of infection increases throughout migration	Observational: capture sampling across migratory route to track changes in infection prevalence throughout migration	Known and accessible migratory route
Migratory separation		
Individuals that migrate earlier are less infected than those that migrate later	Observational: track individual arrival times at a fixed location along the migratory route and record the infection status of hosts Track changes in parasite abundance through time at stopover sites (eDNA)	Known and accessible migratory stopover site Feasible to assess infection status
Infected individuals migrate later than uninfected ones	Observational: measure host infection status and then use animal tracking to record the timing of migration departure	Feasible to assess infection status and track individuals
Infected individual migrate later than uninfected ones	Experimental: manipulate infection of individuals and then record migratory behaviour (field) or correlates of migratory behaviour like restlessness (laboratory)	Ethical to manipulate parasites experimentally (e.g. insects)

(Continues)

Table 2. *(Cont.)*

Predictions	How can these be tested (comparative, observational, experimental)	Model system requirements
Migratory stalling		
Infected individuals take longer to complete migration than uninfected ones	Observational: record individual infection status and track migratory departure and arrival time (animal tracking)	Feasible to assess infection status and track individuals
Infected individuals spend more time at stopover sites than uninfected ones	Observational: measure infection of individuals and length of time spent at stopover sites (animal tracking)	Feasible to assess infection status and track individuals
	Experimental: manipulate infection of individuals and then record migratory behaviour	Ethical to manipulate parasites experimentally (e.g. insects)
Infected individuals travel shorter distances than uninfected ones	Observational: record individual infection status and track individuals during migration	Feasible to assess infection status and track individuals

better, but also pathogen loads deposited into various environments. New technologies can help with non-invasive pathogen sampling of wildlife *via* saliva, urine or faeces (Waldenström *et al*., 2002b; Smiley Evans *et al*., 2015). Additionally with environmental DNA (eDNA), environmental samples (including water, air, soil, snow) are collected and filtered for DNA remains from organisms; these are then amplified with polymerase chain reaction (PCR) to detect the presence and abundance of particular species, including parasites (Sengupta *et al*., 2019). For example, Fossøy *et al*. (2020) collected water samples upstream and downstream of an artificial migration barrier to assess the abundance of gyrodactylids, which are ectoparasites of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Such techniques could be used to test for patterns consistent with migratory recovery and migratory culling (i.e. lower parasite abundance and/or prevalence detected as hosts move further across the environmental gradient; Table 2).

(*b*) *Unmanned aerial vehicles (drones)*

High-tech solutions to studying wild animal behaviour are growing in popularity. Unmanned aerial vehicles, commonly referred to as drones, offer a safer, cheaper, less disruptive and often more precise alternative to identifying species or tracking animal migration than manned aircrafts like helicopters, which can lead to fatal crashes (Sasse, 2003; Christie *et al*., 2016). Drones carry cameras and/or sensors allowing animal tracking and sampling in hard-to-access places such as densely vegetated areas or in marine environments (Christie *et al*., 2016; Raoult *et al*., 2020). These devices can also be equipped to collect biological samples. For instance, drones equipped with petri dishes can collect blowhole discharge from whales to assess animal health non-invasively, culture respiratory microbes and look for patterns of disease emergence and spread (Pirotta *et al*., 2017; Geoghegan *et al*., 2018). While still in its infancy, the potential for drones to revolutionize the monitoring and sampling of migratory animals and of their health status is exciting and may help fill some of the gaps in our understanding that were identified above, including a better understanding of migratory routes as well as where and how mortality along migration routes occurs.

(*c*) *Animal tracking and biologging*

Tracking animals using superficial or implantable transmitting devices is a powerful way to explore the movement behaviour of sick and healthy individuals in the wild. These devices are attached to an animal and emit a unique signal and/or Global Positioning System (GPS) location that is detected by receivers (Crossin *et al*., 2017; Abecasis *et al*., 2018; Whitford & Klimley, 2019). New advances have shrunk transmitters, improved receivers and incorporated sensors allowing researchers to study animals across a range of body sizes and environments.

Biotelemetry can help explore mechanisms related to infection and host migration. Daversa *et al*. (2018b) used radiotelemetry on adult spiny toads to track the movement behaviour of individuals and monitor the status of infection with the fungus *Batrachochytrium dendrobatidis* (*Bd*). Post-breeding migrations of toads from pools to terrestrial burrows coincided with recovery from *Bd* infection, providing support for migratory recovery (Daversa *et al*., 2018b). Similarly, Halttunen *et al*. (2018) used acoustic telemetry to study the migratory behaviour of sea trout (*Salmo trutta*). Sea trout migrate to freshwater areas earlier in the season when sea lice (*Lepeophtheirus salmonis*) infestation levels are high. As lice die off once trout reach fresh water, this pattern is consistent with migratory recovery. Telemetry techniques could be expanded to test for patterns consistent with migratory exposure, culling, stalling and separation (Table 2).

In addition to tracking individual location, equipping animals with biologgers such as heart-rate monitors and accelerometers is increasing in popularity as technologies improve (Wilmers *et al*., 2015; Sherub *et al*., 2017; Whitford &

Klimley, 2019). The aim of these devices is to record various aspects of an individual's physiology (i.e. heart rate, body temperature), behaviour (i.e. movement speed, acceleration) and/or movement (i.e. tail beats, footsteps) while in the wild (Abecasis *et al.*, 2018). Sometimes abiotic parameters (i.e. temperature, depth, altitude, etc.) are logged simultaneously. This technology has become popular for use in animals which are difficult to study in captivity, including in the marine environment and in long-distance migratory species such as birds (Sherub *et al.*, 2017). However, devices must be recovered or released from the tagged individuals and/or transmitted *via* satellite technology in order for the information to be retrieved, limiting the number and types of animals that can be tagged. Battery shelf life may also make biologgers more practical in studies where data can be collected within a relatively short time frame.

Interest in using biologgers to monitor wild animal stress and health is growing (Wilmers *et al.*, 2015; Lennox *et al.*, 2019). Symptoms of disease can be monitored, such as detecting fevers (Kamerman *et al.*, 2001) or failed reproductive events (e.g. abortions in elk, *Cervus elaphus canadensis*, correlated with *Brucella abortus*; Cross *et al.*, 2015). Recently, Jax *et al.* (2021) used biologgers measuring 3D acceleration, heart rate and body temperature to detect the magnitude and timing of changes in these parameters in mallard ducks while mounting an acute-phase immune response. These tools could be used to explore migratory relapse (Table 2). Using multisensor loggers, Emmenegger *et al.* (2021) found that infected great reed warblers (*Acrocephalus arundinaceus*) had later onset of migration, longer migratory bouts, shorter resting times, and overall shorter migratory distances that uninfected birds (i.e. migratory separation, stalling). Aside from these and a few other examples (see Jourdain *et al.*, 2010; Bengtsson *et al.*, 2016), biologgers have not been used to study infection and animal movement despite ways in which this technology could be employed in research. For instance, slower movement speeds, longer periods of time resting, and/or altered patterns of acceleration/deceleration in infected relative to healthy individuals can be assessed using accelerometers, and may provide evidence of migratory culling, stalling and/or relapse (Table 2). Similarly, physiological metrics like heart rate may also give an indication of the energetic costs of movement depending on health status, providing additional evidence for migratory stalling. Loggers that record external environmental parameters can be used to examine habitat preference (e.g. migratory recovery) depending on infection status (Table 2). A preference for environments of higher or lower temperature or salinity when infected or when infections in a population are high may be evidence of migratory recovery and/or migratory escape. Indeed, the timing of sea trout migration to rivers and estuaries is related to infection with sea lice, suggesting that changing microhabitat preferences when infection levels are high influence migratory behaviour (Birkeland & Jakobsen, 1997; Halttunen *et al.*, 2018); studies using biologgers could provide more detailed insight into these findings.

(*d*) *Mark–recapture or transect studies*

Even without the use of electronic technology, mark–recapture studies, where an animal is given a unique identifying tag and then released into nature with the goal of recapturing or resighting them at a later time, can be set up to address questions of migration and infection (Table 2). These low-cost techniques are useful for long-lived individuals that can be tracked over long distances and timeframes. Structured parasite sampling of populations along a known migratory route can be used to determine whether and how migration and infection might interact. For example, transect studies can be set up to encompass a network of capture sites at known stopover sites (i.e. watering hole, forest patch) or bottlenecks (i.e. river mouth, waterfall) along a migratory route. Random sampling of individuals across various sections of their route could help answer whether individuals are losing key parasites (e.g. migratory recovery) or acquiring new infections (e.g. migratory exposure) as they move further away from their origin. Recording the timing of arrival at key sites could also provide evidence for or against migratory stalling and/or migratory separation.

(*e*) *Natural experiments*

Natural experiments are empirical studies where the experimental conditions are imposed by external factors outside of the researcher's control. Researchers can take advantage of natural experiments that affect the ability of populations to migrate to explore changes in infection dynamics. For example, new barriers either natural (landslides, fires, floods) or manufactured (dams, roads, fences, urban areas) could hinder passage across traditional migration routes (Bolger *et al.*, 2008). If these barriers lead to migration failure, researchers could monitor whether infections increase (consistent with migratory escape, allopatry, recovery, and/or culling) or decrease (consistent with migratory exposure) in now-resident populations. Comparisons can also be made locally with still-migratory populations if infection cycles prior to the barrier presence are unknown.

Changing environmental conditions altering migration routes may also provide interesting natural experiments. For example, warming winter temperatures are altering the migratory behaviour of blackcaps (*Sylvia atricapilla*), whereby some birds now overwinter closer to their breeding grounds (Pulido & Berthold, 2010). Similarly, changing ocean circulation patterns have led to changes in the migratory routes and spawning location of Atlantic herring (*Clupea harengus*) (Corten, 1999). The effect of migration shifts on infection can be explored by observing whether migration distance or route travelled is related to parasite prevalence in historic (if available) and contemporary individuals. Shorter migration distances associated with increased parasite prevalence or intensity would be evidence of migratory escape, whereas decreases in these parameters would suggest migratory exposure. If altered migration routes take migrants across new environments or to new stopover or breeding sites, migratory recovery may also occur if these new habitats lead to parasite mortality and host recovery from infection.

The availability of anthropogenic food can also alter the migratory behaviour of animals (Satterfield *et al.*, 2018). For instance, elk on supplemental feeding grounds during winter months migrate shorter distances, spend longer at stopover sites and arrive at summer ranges later than unfed elk (Jones *et al.*, 2014). This altered movement behaviour and congregation around feeders may affect disease transmission (Cross *et al.*, 2007). Bird feeders can also be a source of disease transmission, especially in the winter when birds tend to congregate around them (Altizer, Hochachka & Dhondt, 2004; Becker, Streicker & Altizer, 2015; Becker *et al.*, 2018; Moyers *et al.*, 2018). Reduced migratory behaviours have also been reported in many species of birds, butterflies, bats and sharks as a result of recreational feeding (reviewed in Satterfield *et al.*, 2018). Examining whether supplemental feeding and loss of migratory behaviour is related to increased disease transmission could provide indirect evidence of social and/or environmental migratory escape (Table 2).

Outbreaks of novel diseases in natural populations can also provide an opportunity to study how infection influences migration. For instance, amphibians infected with the emerging fungal disease caused by *Batrachochytrium dendrobatidis* have been studied in the context of migration and infection recovery. Through a series of radio-tracking and mark–recapture experiments, Daversa *et al.* (2018b) showed that spiny toads recover from *Bd* infections during post-breeding migrations, providing support for both migratory recovery and escape in response to this novel pathogen. As another example, the invasive nematode *Anguillicoloides crassus* infects the swimbladders of European eels (*Anguilla anguilla*), which may affect swim performance. Laboratory-based tests have confirmed that severe nematode infections can interfere with swim bladder functionality (Currie *et al.*, 2020), but field-based studies are needed to determine the extent to which this interferes with the ability of eels to migrate successfully, and thus provide evidence of migratory culling or stalling. Finally, the current epidemic of the fungal disease caused by *Pseudogymnoascus destructans* (i.e. white nose syndrome) in North American bat populations may be interesting to monitor in terms of changes to bat movement, roosting and migratory behaviours and infection transmission (Langwig *et al.*, 2021).

(3) Experimental studies

Although most empirical studies of migration and infection are correlational or observational, manipulative studies (particularly randomized experiments) remain the gold standard for causal inference in ecology (Larsen, Meng & Kendall, 2019). Experimental studies can help untangle the causes of migratory behaviour (Birnie-Gauvin *et al.*, 2020). Empirical studies can take two directions: (*i*) manipulating infection (adding or removing infection) to measure the effect on migration, or (*ii*) manipulating migration (affecting migration timing or incentivizing residency) to measure the effects on infection. Both approaches require serious consideration of the potential ethical and ecological consequences on the individuals and populations affected. Some of these challenges can be potentially overcome by using invertebrates as model systems, which have historically been underrepresented in studies of animal migration (Satterfield *et al.*, 2020). When manipulating infection, care must be taken to choose parasites with low potential to lead to outbreaks or spillover to unintended wild populations. For instance, parasites with complex life cycles are unlikely to lead to serious outbreaks since transmission is indirect and dependent on the presence of intermediate hosts. Alternatively, simulating infection, for example, through administering immune-stimulating agents such as heat-killed microbes, endotoxins such as lipopolysaccharide, or attenuated viruses, could also be used to induce sickness-like behaviours in vertebrates (Lopes *et al.*, 2021). This technique could be used to see whether migrants respond by delaying migration start date (i.e. migratory separation), increasing stopover duration (migratory stalling) or seeking out warmer or cooler microhabitats (i.e. behavioural fever/chilling; consistent with migratory recovery). In some cases, administering these agents as a vaccine to protect against future infections may be an ethical way of exploring the role of sickness behaviours in the movement decisions of migratory hosts. While theoretically possible, experimental manipulation of many migratory species also poses a logistic challenge, given the large temporal and spatial scales often involved. Here again, invertebrate models may provide an interesting avenue for future research (Satterfield *et al.*, 2020).

(*a*) *Manipulate infection*

Field manipulations could increase infection and measure how migratory behaviour changes. Manipulated individuals would be expected to decrease their migratory behaviour if movement is very costly for infected individuals. For example, birds that were given a simulated infection prolonged their migratory stopovers compared to healthy individuals as predicted by migratory stalling (Hegemann *et al.*, 2018). Alternatively, if movement facilitates recovery from infection, manipulated individuals would be expected to increase the time spent in whichever environment enables recovery (migratory recovery; Table 2). For example, sea trout experimentally infected with sea lice spent less time migrating out at sea than control fish (18 *versus* 100 days); instead they returned prematurely to fresh water, where they can recover from lice infection (Serra-Llinares *et al.*, 2020). For systems where migration is thought to be driven by migratory recovery, one could infect non-migratory individuals to see whether increased migration is favoured in newly infected hosts (Table 2); we do not know of any studies to date that have attempted this. Finally, expected results are more complex in the case of social and environmental migratory escape. If infections are equivalent (infection intensity does not matter), newly infected individuals or individuals in newly infected environments would be expected to decrease time spent in the escape environment (Table 2). If infection intensity is critical, newly manipulated individuals may spend increased time in the escape environment to escape further infection. Uninfected individuals may also increase time in the escape environment if infection is transmitted socially and infection prevalence is high (social migratory escape).

Experimentally reducing parasite infection in wild populations may present ethical challenges with unintended consequences (see Ezenwa & Jolles, 2015). However, this practice has nonetheless been used in experiments in a wide range of wild animal populations (e.g. Reed *et al.*, 2008; Ballesteros *et al.*, 2012; Provencher *et al.*, 2017; Roznik *et al.*, 2020), including to study movement behaviours in treated *versus* untreated individuals (Butler & Roper, 1996). For instance, European badgers (*Meles meles*) were treated with antiparasite spray removing lice, fleas and mites to examine whether nest site switching frequency is used as a defence against infection in burrowing species (Butler & Roper, 1996). Surprisingly, this type of manipulation seems to be less common when studying migration. Treating sea trout with a prophylaxis against sea lice had no significant effect on migration route, although hosts may be compensating for infection in other ways (Halttunen *et al.*, 2018). If migratory stalling and/or separation shape migration, newly uninfected individuals should migrate earlier and/or faster than infected ones (Table 2). If migratory recovery is important, newly uninfected individuals should decrease the time spent in the recovery environment (Table 2). Finally, if environmental or social migratory escape drives migration, individuals living in newly uninfected environments or with newly uninfected conspecifics should spend less time in the escape environment or forego migration altogether (Table 2).

(*b*) *Manipulate migratory behaviour*

Perhaps less intuitively, but nevertheless tractable in some systems, migratory behaviour itself could be manipulated and the subsequent effects on infection dynamics observed (Birnie-Gauvin *et al.*, 2020). This could include manipulating the release date of some migratory animals, or even preventing migration altogether by keeping individuals in pens during the migration season (Calabrese *et al.*, 2018). For example, the management system of red deer (*Cervus elaphus*) in Germany allowed researchers to manipulate the release date of deer from winter enclosures in the spring experimentally to test the forage maturation hypothesis for ungulate migratory movements (Rivrud *et al.*, 2016). A similar approach could be used to test whether parasite loads in migrants released early or late in a season differ: migratory escape would predict that early-released migrants should accumulate fewer infections than late-released migrants (Table 2). Varying the release date or densities of stocked fish may also provide an interesting test of parasite accumulation and the importance of migration phenology in terms of parasite exposure and/or social escape from infection. In some systems, manipulating the time that juveniles and adults are in proximity to each other by preventing or delaying migration may provide evidence for migratory allopatry (Table 2). Experimental introduction of feeding stations in target locations to incentivize residency may also be ethical in some species and/or areas. As described above (see Section IV.2e on natural experiments), food supplementation can be used to explore questions related to migratory escape and migratory exposure (Table 2).

(*c*) *Laboratory experiments*

Whether field manipulations are feasible to carry out or not, some systems may be amenable to laboratory manipulation, which can be used in parallel with field experiments to understand infection–movement dynamics better in migratory populations. Laboratory experiments can function as proofs of concept and allow researchers to test whether specific predictions derived from conceptual frameworks hold in isolation from other confounding factors. For example, environmental tolerances of ectoparasites to the environmental gradient experienced along the migration route can help determine the potential for migratory recovery in a system. Host-level performance metrics can similarly be tested in the laboratory. Bradley & Altizer (2005) measured monarch butterfly flight performance in the laboratory to infer that infection likely hampers migration success as predicted by migratory culling. Similarly, strenuous physical activity can be induced in hosts to see whether latent infections flare up (migratory relapse). Small-scale (e.g. diel) movements or microhabitat preferences of infected and uninfected individuals can be measured and compared as a way of assessing whether certain environments favour infection recovery, a precursor for migratory recovery (Table 2). Daversa *et al.* (2018a) showed experimentally that habitat switching between aquatic and terrestrial habitats generated *Bd* infection patterns in alpine newts (*Icthyosaura alpestris*) akin to that observed in nature, suggesting that mechanisms similar to migratory recovery operate in this system. Parasite avoidance behaviour, which may be an important precursor for migratory escape, can also be tested in a laboratory setting using cue choice arenas or habitat preference experiments (Table 2). For example, rainbow trout (*Oncorhynchus mykiss*) will avoid areas with high densities of *Diplostomum spathaceum* trematode cercaria in laboratory experiments (Karvonen, Seppälä & Valtonen, 2004). Motivation to migrate can be tested simultaneously by quantifying individual activity patterns. For example, captive birds show increased activity in the lead-up to their normal migration time (i.e. 'migratory restlessness'; Mewaldt & Rose, 1960). These changes in activity patterns can be used as a proxy for departure time in the wild (Eikenaar *et al.*, 2014). This technique could be used to test whether the timing of migratory restlessness differs between infected and uninfected hosts (migratory separation). Proof of concept studies can help reveal the cellular, physiological and/or behavioural mechanisms underlying infection–migration dynamics that can be expanded and tested explicitly in field-based studies.

V FINAL THOUGHTS

We hope the guidelines provided herein help stimulate future empirical work to be framed within existing conceptual frameworks. Despite the abundance of conceptual frameworks developed to study different mechanisms linking migration and parasites (Table 1), there appears to be only substantial empirical work on three: migratory culling, exposure and escape, while the other mechanisms (migratory allopatry, recovery, relapse, separation, stalling) have each only been considered by, at most, one empirical study (Table S1). Note that although the concept of migratory exposure is widespread (Figuerola & Green, 2000; Teitelbaum *et al*., 2018), few studies use this term explicitly, thus the key word search terms used for Table S1 captured few papers. Publication bias, whereby researchers may be more likely to publish results supporting a conceptual framework than those finding no effect, may also be limiting our ability to discern patterns in natural systems. Future empirical work on each of these under-studied mechanisms will advance both empirical work and theory by informing to what extent these mechanisms act in natural systems and, in turn, to what extent they merit future theoretical exploration.

Progress in science relies on advances in both empirical and theoretical work, ideally with regular feedback among different approaches and with the emphasis that no one approach is better than others (Plowright *et al*., 2008). Despite this ideal, it can be challenging to communicate ideas across theoretical and empirical perspectives (Haller, 2014; Servedio *et al*., 2014). We hope that the roadmap presented here will both guide future empirical work and foster stronger collaboration and communication between empirical and theoretical researchers.

VI CONCLUSIONS

(1) A recent exciting development in the field of animal migration is understanding its interaction with parasites. Many conceptual frameworks have been developed to understand how host migratory behaviour and parasites might interact (e.g. migratory exposure, escape, allopatry, recovery, culling, relapse, stalling and separation).

(2) Theoretical work explicitly designed to investigate the links between migration and infection is currently outpacing empirical work, which has led to two problems. First, we do not have a good sense of how valid these conceptual frameworks are in empirical systems, since empirical studies of migration and parasites are rarely conducted using existing conceptual frameworks that link migration and parasites. Second, without regular validation from empirical systems to ensure that assumptions and parameters built into theoretical models are ecologically relevant and plausible based on data, there is a risk that the theory on these subjects will become an exercise in navel gazing.

(3) There are numerous logistical challenges to studying migration and parasites empirically, and to integrating empirical and theoretical perspectives. In particular, feedback loops between migration and infection (e.g. migration shapes infection, which in turn shapes the selective pressures on migration) make it challenging empirically to test theoretical findings that rely on these feedbacks.

(4) Despite these challenges, there are a number of ways comparative (using existing data), observational (pathogen detection, animal tracking and biologging, mark–recapture, natural experiments), and experimental (generating data through manipulations) approaches can be leveraged to test many of the conceptual ideas empirically. We have described many of these both in the text and in Table 2, which is effectively our 'roadmap' for future empirical studies.

(5) We hope the guidelines provided here both inspire stronger collaboration between empiricists and theorists studying the intersection of migration and parasite infection, and stimulate future empirical work to be framed within existing conceptual frameworks.

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IX. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Summary of literature search for migration–parasite conceptual frameworks.

Table S2. References for studies counted in the 'model' and 'empirical' columns of Table S1.

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