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Opinion

Effects of migratory animals on resident parasite dynamics

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Migratory animals can bring parasites into resident animal (i.e., non-migratory) home ranges (transport effects) and exert trophic effects that either promote or reduce parasite exposure to resident hosts. Here, we examine the importance of these transport and trophic effects and their interactions for resident parasite dynamics. We propose that migrant transport and trophic effects are impacted by the number of migratory animals entering a resident's home range (migration intensity), the amount of time that migrants spend within a resident's home range (migration duration), and the timing of migrant–resident interactions. We then incorporate migration intensity, duration, and timing into a framework for exploring the net impact of migrant trophic and transport effects on resident animal parasite prevalence.

Highlights

Migratory movement shapes infectious disease dynamics within migratory populations, but also impacts the disease dynamics of resident (non-migratory) species by transporting pathogens along migratory routes.

Migratory animals often dominate local animal biomass and exert strong trophic effects on the resident species that they encounter. Many of these trophic effects could impact infectious disease transmission, yet very little is known about the role of migrant trophic effects in shaping resident disease dynamics.

We propose mechanisms via which migrant trophic effects change the local infection risk for resident animals. We then describe a framework that captures the role of migration intensity and duration in modifying migrant transport and trophic effects that can be used to investigate the complex ecological interactions that determine resident parasite dynamics in nature.

Effects of animal migration on resident parasite dynamics

Migratory animals can move parasites that infect resident (i.e., non-migratory) animals into resident home ranges and also modify resource availability, thereby imposing both transport and trophic effects on resident parasite dynamics [1,2]. To date, studies of infectious disease in migrant–resident interactions have focused almost exclusively on transport effects (e.g., the spread of the haemosporidian parasites by migrating birds to resident birds in South America [3]). By contrast, intra- and inter-specific trophic interactions are a largely unrecognized component of migrant–resident parasite dynamics, despite being a common feature of migratory systems with the potential to change resident parasite transmission [2]. For example, seasonal diet-switching by Alaskan brown bears (*Ursus arctos*) from moose (*Alces alces*) to Pacific salmon (*Oncorhynchus* spp.) during the salmon migration could reduce exposure of resident bears to tapeworms (*Taenia arctos*) ingested in infected moose prey [4]. The impact of migration on resident parasite dynamics should depend on a combination of migrant transport effects, direct and indirect trophic effects, and their interactions. In this opinion article, we propose that the impact of migrant transport and trophic effects on resident parasite transmission should be determined by: (i) the number of migrants entering resident home ranges (migration intensity); (ii) the length of time that migrants spend in resident home ranges (migration duration); (iii) the infection status of the migrants, and (iv) the seasonality of migrant–resident interactions. We then generate a set of hypotheses for exploring the consequences of migrant–resident interactions on resident parasite transmission.

A non-binary view of migratory movement: migration intensity and duration

From the perspective of resident animals, migrants entering and subsequently departing resident home ranges represent discrete events. The intensity and duration of these events can vary substantially among, and within, study systems [5,6]. Importantly, migration intensity and duration are inter-related because resource requirements for migrating animals should scale with intensity (Box 1). For example, among migrating passerine birds using island stopover sites in the North Sea, birds that arrive in larger groups consume the dominant resource, black elder (*Sambucus nigra*) fruit, faster and therefore leave earlier than birds arriving in smaller groups [7]. Thus, for

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Box 1. The migration intensity and duration trade-off: migrating wildebeest as a case study

The number of animals involved in individual migration events (intensity) can range from hundreds of thousands of animals to long-distance individual movements [57]. The period of time that these animals spend in any single location (migration duration) also varies widely, with migrating animals moving for a wide range of reasons, including breeding opportunities, predator avoidance, or resource access [58]. However, the upper boundary of migration duration will be determined by resource limitation and this limitation should scale with intensity as more animals deplete resources faster. Thus, an intensity-duration trade-off should exist within migratory systems, with large groups of animals (high intensity) remaining for shorter durations than small groups of animals (low intensity). The seasonal migration of Serengeti blue wildebeest (*Connochaetes taurinus*) provides an illustrative example of this phenomenon

Approximately 1.3 million wildebeest follow a seasonal migration pattern in the Serengeti-Mara ecosystem in East Africa that is driven by availability of fresh grass growth [59,60]. The absolute limit for herds of migrating wildebeest to remain in any given location is set by local resource availability and should scale with resource demand (i.e., herd size) [60]. This relationship should result in a herd size (intensity) versus duration trade-off, such that large herds (high intensity) are unable to spend long periods (long duration) in a single location.

The snapshot Serengeti camera grid is an array of 150+ camera traps that cover the south-eastern section of the annual wildebeest migratory route (Figure IA [61]). Observations from 7 years of images in the grid identify an intensity/duration trade-off in the wildebeest migration (Figure IB). The number of wildebeest involved (intensity = number of wildebeest images captured per day) in discrete migration events (contiguous days of wildebeest presence) sets an upper threshold for the number of days (duration) that herds remain at any given camera trap location. This is clear from the complete absence of high-intensity/long-duration migration events recorded in over 3000 documented events. At the extreme end of the intensity gradient, wildebeest become limited by resource availability and move on quickly, resulting in high-intensity/short-duration events. Conversely, long-duration events only involve a few animals. Below this resource-associated threshold, individual groups of wildebeest make movement decisions due to myriad other local drivers that are unrelated to resource limitation [60] and there are numerous events involving herds of animals leaving prior to resource depletion (i.e., low-intensity/short duration).

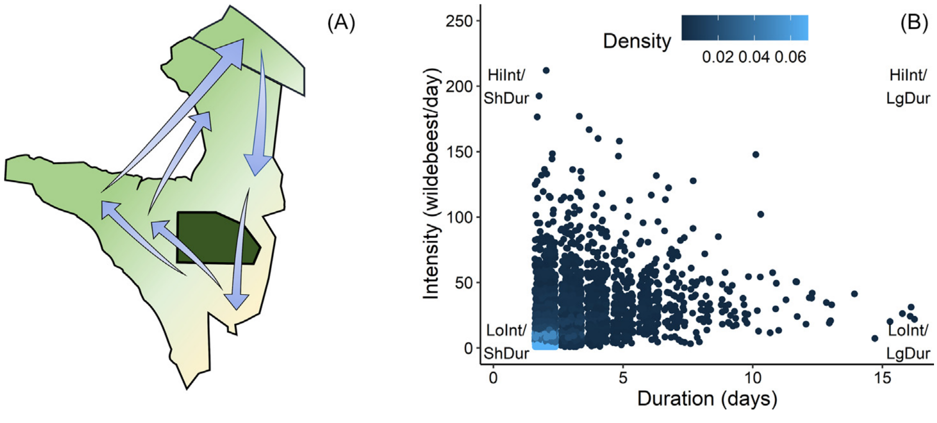

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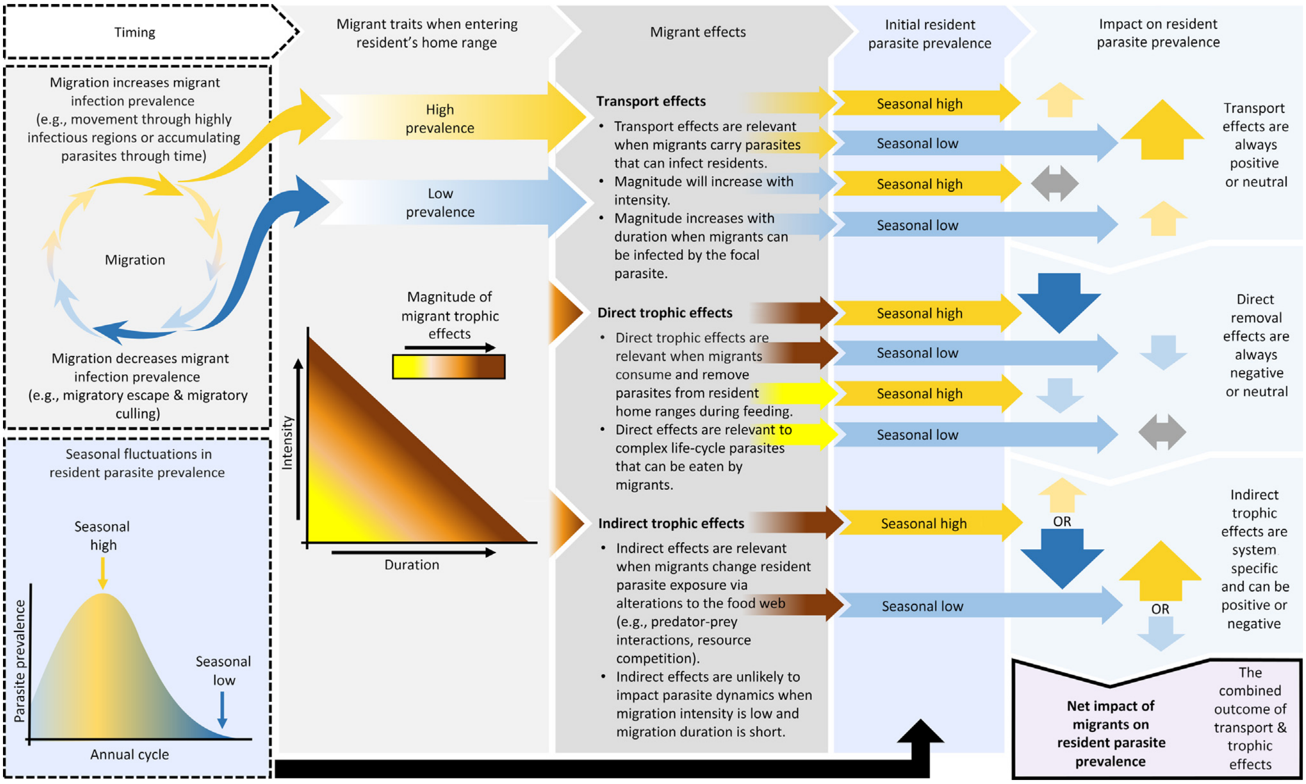
Figure I. Intensity (number of daily captures of wildebeest) as a function of duration (number of contiguous days with wildebeest captures) for individual migration events captured by 150 cameras within the Snapshot Serengeti camera trap grid from 2012 to 2018. Note the presence of high-intensity/short-duration (HiInt/ShDur), low-intensity/long-duration (LoInt/LgDur), and low-intensity/short-duration (LoInt/ShDur) events and the absence of high-intensity/long-duration events (HiInt/LgDur).

any migratory system, the intensity of the migration event should dictate the upper boundary of the duration of that event, resulting in an intensity–duration trade-off, with high intensity events having short durations and vice versa (see Figure I in Box 1). Given this trade-off, high intensity/long duration migration events should be rare and largely restricted to non-forage driven migrations, for example, high numbers of European roach (*Rutilus rutilus*) avoid predation by restricting their feeding to spend winter in low-resource refuge streams [8]. The vast majority of migrant–resident interactions should exhibit a range of intensities and durations below some resource-imposed threshold, with migrants leaving an area for myriad reasons beyond local resource depletion (e.g., predation risk [9], or mating opportunities [10]).

Transport and trophic effects are generally considered separately within the contexts of animal migration and parasite transmission. While it has been established that both transport and trophic effects independently influence parasite dynamics by modifying host exposure risk [11,12], these two processes may act simultaneously. For example, the trematode *Telogaster opisthorchis* can be transported by migratory inanga (*Galaxias maculatus*) upstream, where they infect longfin eels (*Anguilla dieffenbachii*), when the latter consume infected inanga [13,14]. Crucially, both the magnitude of transport and trophic effects and their interactions should depend on migration intensity and duration. For example, during periods of overlap between migrants and residents, migration events temporarily increase the combined (migrant + resident) local animal population density. Increasing host densities raises the risk of parasite transmission [15,16] and, therefore, greater migration intensity can drive higher infection rates in migrants [17], which should impact the transmission risk for susceptible resident hosts. This effect is exacerbated by the fact that larger groups of migrants are more likely to include highly infected individuals in systems where parasite infection is aggregated [18]. Thus, the intensity of transport effects should scale, possibly nonlinearly, with migration intensity. Likewise, extending the duration of a migration event also increases the period of time during which contacts between migratory and resident hosts can occur [19]. Finally, because migration can influence migrant population parasite prevalence through the processes of migratory culling and migratory escape [17], and because seasonality can impact resident host–pathogen dynamics [20], the timing of migrant–resident spatial overlap may be a key factor modulating the strength of transport effects (Figure 1).

Transport effects are only relevant when migrants carry parasites that infect resident animals. Conversely, trophic effects can manifest whenever migrants share resources with, or alter the habitat of, resident animals. Trophic interactions can be direct or indirect and consumer-resource ecology suggests that both processes should increase in strength with migration intensity and duration. A direct trophic effect can occur when migrants feed in resident home ranges and ingest (and therefore remove, if migrants either leave before becoming infectious or act as dead-end hosts) parasites that infect residents. This trophic effect has been demonstrated with invasive dace (*Leuciscus leuciscus*), which ingest the helminth *Pomphorhynchus tereticollis* during feeding. Since dace are incompetent hosts for *P. tereticollis*, their presence reduces infection risk for native brown trout (*Salmo trutta*) [21]. Migrants could exert similar trophic effects if they act as parasite sinks in systems with trophically transmitted parasites or parasites that have free-living life stages that can be eaten by migrants (e.g., ticks, helminths). In these situations, greater migration intensity or duration should lead to increased consumption and stronger direct effects (Figure 1).

Indirect trophic effects occur when migrants impact resource availability, modifying resident exposure to parasites. For example, many apex predators are infected by trophically transmitted parasites (e.g., cestodes), and during migration events resident predators regularly switch from feeding on resident prey to predominantly consuming more abundant migratory prey [22,23]. If parasites are more abundant in resident than migratory prey, migration events could reduce predator exposure to trophically transmitted parasites (and vice versa if parasites are more abundant in migratory prey). Greater migration intensity and duration both increase migrant–resident trophic interactions [24,25], and migrant indirect trophic effects should scale with migration intensity and duration. Unlike direct trophic effects, indirect effects could alter resident infection risk from directly transmitted parasites if they change resident host behavior. For example, in Tanzania, the presence of migrating ungulate prey in the home ranges of resident spotted hyenas (*Crocuta crocuta*) results in increased adult hyena presence at den sites [26], and higher adult



Migration increases migrant infection prevalence (e.g., movement through highly infectious regions or accumulating parasites through time)

Migration decreases migrant infection prevalence (e.g., migratory escape & migratory culling)

Seasonal fluctuations in resident parasite prevalence

Transport effects

- Transport effects are relevant when migrants carry parasites that can infect residents.
- Magnitude will increase with intensity.
- Magnitude increases with duration when migrants can be infected by the focal parasite.

Direct trophic effects

- Direct trophic effects are relevant when migrants consume and remove parasites from resident home ranges during feeding.
- Direct effects are relevant to complex life-cycle parasites that can be eaten by migrants.

Indirect trophic effects

- Indirect effects are relevant when migrants change resident parasite exposure via alterations to the food web (e.g., predator-prey interactions, resource competition).
- Indirect effects are unlikely to impact parasite dynamics when migration intensity is low and migration duration is short.

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Figure 1. A framework for understanding migration effects on resident parasite burdens. The net response of resident parasite infection risk to migration events will be dictated by the relative strength of migrant transport effects and the trophic effects they exert on resident parasite transmission. The timing of migrant–resident overlap will impact the initial parasite prevalence of migrant and resident hosts because migrant parasite prevalence changes over the course of their migratory movement and resident infection prevalence fluctuates seasonally. The initial parasite prevalence of both migrants and residents will set the baseline for resident host responses to parasites transported by migrants. The intensity and duration of migration will impact the transport and direct trophic effects by increasing the magnitude of the response. However, if migration intensity is high enough or duration long enough to exert indirect trophic effects on resident parasite transmission, then indirect effects have the capacity to dominate the net response of resident parasite prevalence, particularly when migrations remain until their resource-imposed threshold.

presence at den sites in turn changes the transmission rates of directly transmitted hookworms (*Ancylostoma*) in juvenile hyenas [27].

A framework for integrating migration intensity and duration with transport and trophic effects

Transport effects are determined by initial conditions

Transport effects bring new parasites into areas occupied by residents and the effect on resident parasite burdens should always be positive or neutral. For example, studies of interactions between migratory saiga antelope (*Saiga tatarica*) and domestic sheep (*Ovis aries*) suggest that the transport of feces by saiga into pasture used by domestic sheep consistently elevates gastrointestinal helminth burdens in sheep [28]. In ecosystems where migrants do not exert trophic effects, the infection status of both the migratory and resident animals at the start of their spatial overlap should determine the strength of the transport effect (Figure 1). This happens because when residents are uninfected by focal parasites, any transport effect from migrants (even those with low parasite prevalence) increases resident exposure risk. This phenomenon may account for documented cases of migration resulting in the introduction and dissemination of parasites into new areas/hosts (e.g., the protozoan parasite *Toxoplasma gondii* transported by migratory geese [29]). Conversely, resident populations with already high parasite prevalence will be less likely to experience further increases in prevalence as a result of migrant inputs. Because seasonality has strong impacts on parasite prevalence [30], the seasonal timing of migrant–resident overlap may determine the strength of transport effects (Figure 1). For example, in China, migrating waterbirds that transport haemosporidian parasites may have a lower impact on avian malaria infections in resident birds if they arrive in summer, when prevalence in resident birds is already high, than if they arrive in spring when prevalence is low [31].

The timing of migrant–resident encounters along the migratory trajectory should also affect outcomes for residents (Figure 1). Migration can either decrease migrant parasite prevalence (via the mechanisms of migratory culling and migratory escape [32–34]), or increase it if migrants move through regions with high infection risk [35]. Residents that encounter migrants during the early stages of migration, when migrant parasite loads are often high, for example, monarch butterflies (*Danaus plexippus*) in North America at the beginning of their fall migration southward [36], may experience a net increase in parasite burdens. Conversely, residents encountering the same migrants at the end of the migration cycle may not experience an increased risk of infection, if highly infected migrants have been culled from the population (e.g., monarch butterflies toward the end of their southward migration [36]). Alternatively, some migrants may accumulate parasites over the course of migration with parasite loads higher during later stages of migration. For example, sea lice (*Lepeophtheirus salmonis*) infections on migrating juvenile pink salmon (*Oncorhynchus gorbuscha*) increase with greater exposure of salmon to sea lice during seaward migration [37]. In this case, exposure risk to residents would increase toward the end of the migratory period.

Transport effects interact with direct trophic effects

The capacity for migrants to transport parasites of public health or economic concern has driven research on animal migrations as superspreader events [38]. However, consumptive effects by migrants may simultaneously remove parasites and this can reduce exposure in residents [2]. This interpretation is supported by observations from mixed livestock grazing systems, where gastrointestinal helminth burdens in horses are lower on farms with mixed horse–cattle grazing compared with specialized horse farms, likely because cattle (which are incompetent hosts for horse helminths) inadvertently consume horse-specific helminth larvae on pasture during grazing, thereby reducing horse exposure to these parasites [39]. Similar effects could be driven by migrants that do not transport the focal parasite.

When migratory hosts transport parasites while simultaneously removing them through feeding, the overall effect on resident parasite prevalence should be determined by the combined transport inputs and direct trophic removal effects (Figure 1). There is growing evidence that migration can reduce parasite prevalence in migrant hosts [18,34,40] and migrants with low infection rates entering resident home ranges could act to reduce resident exposure if they remove more parasites than they transport in. An applied implication of this phenomenon relates to the management of free-ranging livestock, which overlap spatially with migratory herbivores in many systems globally [41]. If migratory species remove more parasites than they bring into livestock ranges, they may reduce overall infection risk for livestock.

Variation in migration duration is also important for resident parasite dynamics. If migrants have low parasite prevalence when entering a resident home range, they may initially impose direct consumptive effects that remove more parasites than are added. However, if migrants remain in a resident home range until they become infected and are capable of infecting others, the high host population density (migrants + residents) may introduce higher parasite numbers than are removed. A mechanism for this process has recently been demonstrated in the water flea *Daphnia dentifera*; a change from low to high host density initially diluted host encounters with the fungal parasite *Metschnikowia bicuspidate*, reducing inadvertent ingestion of infective spores [42]. However, over time, higher host densities supported greater spore production and resulted in increased infection risk [42]. Under these scenarios, the intensity–duration trade-off suggests that high-intensity/short-duration events are most likely to result in decreases in infection risk, while low-intensity/long-duration events could increase it.

Indirect trophic effects are strongly linked to intensity and duration

Migrants can profoundly affect available resources and alter habitat utilization and/or foraging rates of resident species [1], possibly increasing (if the effect is facilitative) or decreasing (if the effect is competitive) resident exposure to parasites in the environment. For example, when resident animals compete with migratory animals for food (e.g., migrating insectivorous birds compete with, and slow down feeding rates of, resident insectivorous rufous-capped warblers (*Basileuterus rufifrons*) in Mexico [43]), then the presence of migrants should slow down resource and parasite intake by residents. A similar mechanism has been observed in *D. dentifera*, which consume infective fungal spores during grazing: infection prevalence declines when *Daphnia* densities become high enough that interference competition suppresses feeding rates and individual fungal spore intake declines [44]. Crucially, indirect trophic effects are driven by migrant resource utilization and will require a threshold intensity or duration to impact resident parasite transmission (Figure 1). For example, migratory snow geese (*Anser caerulescens*) facilitate grazing by resident species through the formation of grazing lawns [45] and may indirectly stimulate parasite intake. This same trophic effect will not occur if geese numbers are too low to drive grazing lawn formation and low-intensity/short-duration events are unlikely to have strong indirect trophic effects on residents. Conversely, high-intensity or long-duration events that remain until a resource-imposed threshold is reached (e.g., migratory snow geese flocks can reach extremely high abundances and completely remove local vegetation, resulting in long-term trophic effects on resident herbivores [46]) could exert extreme indirect trophic effects on resident parasite transmission risk and need to be considered in any system where indirect trophic interactions occur.

Seasonal environmental conditions that change resource availability will impact the time it takes for a migration to begin displaying indirect trophic effects. If migrants overlap with residents during a period of limitation (e.g., insectivorous songbirds migrate to the neotropics and overlap with resident insectivorous birds during the dry season when insect abundance is relatively low [47]), then indirect trophic effects would require fewer migrants to manifest, or occur faster, than would be the case when resources are plentiful (e.g., in North America, migrating sandhill cranes (*Antigone canadensis*) have winter ranges that overlap with multiple bird species on supplemental corn crops that provide an essentially unlimited food resource [48]). Extreme trophic scenarios may also occur when unusually long periods of migrant–resident overlap are enforced by perturbations that restrict migrant dispersal (e.g., dams restricting migrating fish, or severe weather grounding avian migrants for long periods), or during rare high-intensity/long-duration events when migrants remain at limited resource sites in the absence of viable alternative locations (e.g., the persistent use of stopover sites in the Yellow Sea by migrating shorebirds despite declining resource availability [49]). The timing of migration events in relation to seasonal resource availability will therefore impact the migration intensity and duration required to initiate indirect trophic effects.

Concluding remarks

The potential impact of animal migrations on parasite transmission in resident species is of global relevance to both animal and human health. Our conceptual framework (Figure 1), which captures the role of migration intensity and duration in modifying transport and trophic effects of migration on parasite transmission, uncovers a set of novel hypotheses (Figure 2) that can help move research on migrant–resident parasite transmission away from a binary (presence/

Outstanding questions

How is the effect of interactions between transport and trophic effects and migration intensity and duration on transmission influenced by parasite life history strategy (e.g., transmission mode, host specificity, host exploitation strategy, virulence).

How do parasite-induced changes in the behavior of migrants affect the magnitude of transport and trophic effects?

Can migrant–resident interactions and the intensity and duration of migratory events affect immune responses of resident species? How do these effects translate to variation in the quality and quantity of parasite defenses in residents?

How do abiotic factors (e.g., temperature, rainfall, fire, etc.) modify the transport and trophic effects that migrants exert on residents?

Migrant effects & hypothesis	Migrant-resident-parasite system	Possible case studies
Transport only **H1)** Encounters occurring when migrant parasite prevalence is high and resident prevalence is low will result in explosive increases in resident parasite prevalence.		Song thrushes (*Turdus philomelos*) and other migratory passerine birds import hundreds of thousands of ixodid ticks (e.g., *Ixodes ricinus*) to northern latitudes annually. In areas where local tick populations are established, these imported ticks should not have seasonal impacts on resident tick dynamics. On the other hand, in areas without established tick populations, resident mammals like sheep (*Ovis aries*) may consistently experience seasonal increases in tick parasitism linked to bird migrations.
Direct trophic only **H2)** Resident parasite prevalence will decrease in response to migrations when migrants have no transport effects, because they do not carry the focal parasite, but can remove parasites occurring at high prevalence in resident hosts.		Migrating brent geese (*Branta bernicla*) that feed in the same pasture as resident brown hares (*Lepus europaeus*) should not transport mammal specific gastrointestinal nematodes (e.g., *Trichostrongylus retortaeformis*). However, geese feeding in the same pasture as brown hares may consume and remove infective life-stages from the shared pasture and reduce the risk of infection for hares.
Indirect trophic only **H3)** Indirect effects of migrations on resident parasite dynamics are most likely to manifest when migrations are either intense, have extended durations or remain until resources become limiting.		Migrating sockeye salmon (*Oncorhynchus nerka*) change local stream resources by disturbing sediment during nest digging and laying high numbers of eggs. When salmon reach threshold densities, nest digging can drive declines in benthic invertebrate communities. Resident Artic grayling (*Thymallus arcticus*) respond by feeding on salmon eggs and reduce feeding on less abundant invertebrates. When salmon migrations are intense, then strong dietary changes could reduce Artic graylings exposure to the parasites ingested in invertebrate prey (e.g., cestodes).
Indirect trophic only **H4)** High-intensity migration events that persist until resource depletion will drive the strongest indirect trophic effects on residents.		American redstarts (*Motacilla ruticilla*) and other songbirds migrate to the neo-tropics each dry-season. The feeding rates of resident rufous-capped warblers (*Basileuterus rufifrons*) decline during overlap with migrants due to resource competition. These competitive effects should be greatest in areas with the highest densities of migrants or in years when insect densities are lower than normal. Declines in intake rates should drive declines in the burdens of gastrointestinal parasites ingested during feeding (e.g., trematodes).
Transport + trophic **H5)** If trophic effects on parasite transmission outweigh transport effects, animal migrations should reduce parasite prevalence		Migrating blue wildebeest (*Connochaetes taurinus*) that can host gastrointestinal nematode (GIN) parasites that infect resident ruminant herbivores may transport GIN parasites into resident home ranges, but also consume infective GIN larvae within shared pasture and may reduce the exposure of resident ruminant grazers such as buffalo (*Syncerus caffer*) to GIN infection.

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Figure 2. Hypotheses for resident parasite responses to different migrant–resident interactions and potential migrant–resident–parasite systems that allow for these hypotheses to be tested. Supporting references [47,53–56]. Photograph credits from top to bottom: Anna Karp (Unsplash), Jason Donaldson, Erik Karitz (Unsplash), Bob Brewer (Unsplash), Steffi Wacker (Pexels), Basil Senso, OVasik (iStock), Mirecca (iStock), Sinhyu (iStock), Patrice Bouchard (Unsplash), Edwin Pérez (Pexels), Josef Reischig, Jason Donaldson, Jason Donaldson, Basil Senso.

absence) perspective of migration and towards a more nuanced view of the complex ecological interactions that determine the outcomes of host–parasite interactions in nature. It also raises a number of novel questions about other aspects of the migrant–host interaction that may affect parasite dynamics in migratory systems (see Outstanding questions). More generally, it provides useful insight into how human-driven changes that are increasingly altering or stopping animal migrations [50–52] could have cascading consequences for parasite dynamics in resident species.

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Declaration of interests

No interests are declared.

References

1. Holdo, R.M. *et al.* (2013) Migration impacts on communities and ecosystems: empirical evidence and theoretical insights. In *Animal Migration - A Synthesis* (Milner-Gulland, E.J. *et al.*, eds), pp. 130–143, Oxford University Press
2. Bauer, S. and Hoye, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* 344, 1242552
3. de Angeli Dutra, D. *et al.* (2021) Migrant birds disperse haemosporidian parasites and affect their transmission in avian communities. *Oikos* 130, 979–988
4. Walsh, J.C. *et al.* (2020) Relationships between Pacific salmon and aquatic and terrestrial ecosystems: implications for ecosystem-based management. *Ecology* 101, e03060
5. Mueller, T. and Fagan, W.F. (2008) Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos* 117, 654–664
6. Benhamou, S. and Riotte-Lambert, L. (2012) Beyond the utilization distribution: identifying home range areas that are intensively exploited or repeatedly visited. *Ecol. Model.* 227, 112–116
7. Ottich, I. and Dierschke, V. (2003) Exploitation of resources modulates stopover behaviour of passerine migrants. *J. Ornithol.* 144, 307–316
8. Brönmark, C. *et al.* (2008) Seasonal migration determined by a trade-off between predator avoidance and growth. *PLoS One* 3, e1957
9. Berg, J.E. *et al.* (2023) Summer elk calf survival in a partially migratory population. *J. Wildl. Manag.* 87, e22330
10. Lassis, R. *et al.* (2022) Breeding migrations by bighorn sheep males are driven by mating opportunities. *Ecol. Evol.* 12, e8692
11. Richards, R.L. *et al.* (2023) Unhealthy herds and the predator–spreader: understanding when predation increases disease incidence and prevalence. *Ecol. Evol.* 13, e9918
12. Hoffman, T. *et al.* (2023) The biological and ecological features of northbound migratory birds, ticks, and tick-borne microorganisms in the African–Western palearctic. *Microorganisms* 11, 158
13. Stewart, S.D. *et al.* (2022) Sea to the mountains: quantifying freshwater eel and trout diet reliance on marine subsidies from upstream migrating fish. *N. Z. J. Mar. Freshw. Res.* 56, 466–490
14. Cirtwill, A.R. *et al.* (2015) Are parasite richness and abundance linked to prey species richness and individual feeding preferences in fish hosts? *Parasitology* 143, 75–86
15. Arneberg, P. *et al.* (1998) Host densities as determinants of abundance in parasite communities. *Proc. R. Soc. B* 265, 1283–1289
16. Morand, S. and Poulin, R. (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evol. Ecol.* 12, 717–727
17. Majewska, A.A. *et al.* (2022) Parasite dynamics in North American monarchs predicted by host density and seasonal migratory culling. *J. Anim. Ecol.* 91, 780–793
18. Poulin, R. and de Angeli Dutra, D. (2021) Animal migrations and parasitism: reciprocal effects within a unified framework. *Biol. Rev.* 96, 1331–1348
19. Krkošek, M. *et al.* (2009) Sea lice and salmon population dynamics: effects of exposure time for migratory fish. *Proc. R. Soc. B* 276, 2819–2828
20. Altizer, S. *et al.* (2006) Seasonality and the dynamics of infectious diseases. *Ecol. Lett.* 9, 467–484
21. Tierney, P.A. *et al.* (2020) Invasive freshwater fish (*Leuciscus leuciscus*) acts as a sink for a parasite of native brown trout *Salmo trutta*. *Biol. Invasions* 22, 2235–2250
22. Vettorazzi, M. *et al.* (2022) Understanding the effects of seasonal variation in prey availability on prey switching by large carnivores. *J. Zool.* 318, 218–227
23. Hansen, J.H. *et al.* (2020) Ecological consequences of animal migration: prey partial migration affects predator ecology and prey communities. *Ecosystems* 23, 292–306
24. Coblentz, K.E. (2020) Relative prey abundance and predator preference predict individual diet variation in prey-switching experiments. *Ecology* 101, e02911
25. McDonald, R.S. *et al.* (2017) Goose persistence in fall strongly influences Arctic fox diet, but not reproductive success, in the southern Arctic. *Polar Res.* 36, 5
26. Gicquel, M. *et al.* (2022) Climate change does not decouple interactions between a central-place-foraging predator and its migratory prey. *Ecosphere* 13, e4012
27. Ferreira, S.C.M. *et al.* (2019) Parasite infections in a social carnivore: evidence of their fitness consequences and factors modulating infection load. *Ecol. Evol.* 9, 8783–8799
28. Morgan, E.R. *et al.* (2004) Ruminating on complexity: macroparasites of wildlife and livestock. *Trends Ecol. Evol.* 19, 181–188
29. Elmore, S.A. *et al.* (2015) Evidence for *Toxoplasma gondii* in migratory vs. nonmigratory herbivores in a terrestrial arctic ecosystem. *Can. J. Zool.* 93, 671–675
30. Poulin, R. (2020) Meta-analysis of seasonal dynamics of parasite infections in aquatic ecosystems. *Int. J. Parasitol.* 50, 501–510
31. Han, Y. *et al.* (2023) Seasonal variations of intensity of avian malaria infection in the Thousand Island Lake System, China. *Parasit. Vectors* 16, 218
32. Daversa, D.R. *et al.* (2017) Infections on the move: how transient phases of host movement influence disease spread. *Proc. R. Soc. B* 284, 20171807
33. Hall, R.J. *et al.* (2022) Animal migration and infection dynamics: recent advances and future frontiers. In *Animal Behavior and Parasitism* (Ezenwa, V.O. *et al.*, eds), pp. 111–127, Oxford University Press

34. Kendzel, M.J. *et al.* (2023) Interactions between parasitism and migration in monarch butterflies. *Curr. Opin. Insect Sci.* 59, 101089
35. Von Rönn, J.A.C. *et al.* (2015) Transcontinental migratory connectivity predicts parasite prevalence in breeding populations of the European barn swallow. *J. Evol. Biol.* 28, 535–546
36. Bartel, R.A. *et al.* (2011) Monarch butterfly migration and parasite transmission in eastern North America. *Ecology* 92, 342–351
37. Krkošek, M. *et al.* (2007) Effects of host migration, diversity and aquaculture on sea lice threats to Pacific salmon populations. *Proc. R. Soc. B* 274, 3141–3149
38. Mckay, A.F. and Hoye, B.J. (2016) Are migratory animals superspreaders of infection? *Integr. Comp. Biol.* 56, 260–267
39. Forteau, L. *et al.* (2020) Horses grazing with cattle have reduced strongyle egg count due to the dilution effect and increased reliance on macrocyclic lactones in mixed farms. *Animal* 14, 1076–1082
40. Peacock, S.J. *et al.* (2020) A unifying framework for the transient parasite dynamics of migratory hosts. *Proc. Natl. Acad. Sci. U. S. A.* 117, 10897–10903
41. Behnke, R.H. *et al.* (2011) Pastoral migration: mobile systems of livestock husbandry. In *Animal Migration: A Synthesis* (Milner-Gulland, E.J. *et al.*, eds), pp. 145–171, Oxford University Press
42. Stewart Merrill, T.E. *et al.* (2022) Timescale reverses the relationship between host density and infection risk. *Proc. R. Soc. B* 289, 20221106
43. Jedlicka, J.A. *et al.* (2006) Seasonal shift in the foraging niche of a tropical avian resident: resource competition at work? *J. Trop. Ecol.* 22, 385–395
44. Civitello, D.J. *et al.* (2013) Parasite consumption and host interference can inhibit disease spread in dense populations. *Ecol. Lett.* 16, 626–634
45. Cargill, S.M. and Jefferies, R.L. (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-Arctic salt marsh. *J. Appl. Ecol.* 21, 669–686
46. Peterson, S.L. *et al.* (2013) The legacy of destructive snow goose foraging on supratidal marsh habitat in the Hudson Bay lowlands. *Arct. Antarct. Alp. Res.* 45, 575–583
47. Powell, L.L. *et al.* (2021) Interspecific competition between resident and wintering birds: experimental evidence and consequences of coexistence. *Ecology* 102, e03208
48. Boggie, M.A. *et al.* (2023) Availability of supplemental corn for sandhill cranes, light geese, and dabbling ducks wintering in New Mexico. *J. Fish Wildl. Manag.* 14, 51–61
49. Wang, X. *et al.* (2022) Impacts of habitat loss on migratory shorebird populations and communities at stopover sites in the Yellow Sea. *Biol. Conserv*. 269, 109547
50. Kauffman, M.J. *et al.* (2021) Mapping out a future for ungulate migrations. *Science* 372, 566–569
51. Satterfield, D.A. *et al.* (2020) Seasonal insect migrations: massive, influential, and overlooked. *Front. Ecol. Environ.* 18, 335–344
52. Kubelka, V. *et al.* (2022) Animal migration to northern latitudes: environmental changes and increasing threats. *Trends Ecol. Evol.* 37, 30–41
53. van der Wal, R. *et al.* (1998) Interactions between hare and brent goose in a salt marsh system: evidence for food competition? *Oecologia* 117, 227–234
54. Mijele, D. *et al.* (2016) Influence of massive and long distance migration on parasite epidemiology: lessons from the great wildebeest migration. *Ecohealth* 13, 708–719
55. Hasle, G. *et al.* (2009) Transport of ticks by migratory passerine birds to Norway. *J. Parasitol.* 95, 1342–1351
56. Scheuerell, M.D. *et al.* (2007) Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. *Freshw. Biol.* 52, 1944–1956
57. Dingle, H. and Drake, V.A. (2007) What is migration? *Bioscience* 57, 113–121
58. Alerstam, T. *et al.* (2003) Long-distance migration: evolution and determinants. *Oikos* 103, 247–260
59. Holdo, R.M. *et al.* (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *Am. Nat.* 173, 431–445
60. Hopcraft, J.G.C. *et al.* (2014) Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecol. Monogr.* 84, 355–372
61. Anderson, T.M. *et al.* (2016) The spatial distribution of African savannah herbivores: species associations and habitat occupancy in a landscape context. *Philos. Trans. R. Soc. B* 371, 20150314