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Introduction

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Anthropogenic resource subsidies and host–parasite dynamics in wildlife

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1. Introduction

For a wide range of wildlife, anthropogenic change and human activities modify the abundance, distribution and timing of food resources [1,2]. Although activities such as deforestation and overfishing deplete resources for many wildlife species, in other cases, urbanization, agriculture and supplemental feeding can provide wildlife with abundant and predictable food [3–8]. As a result, many wildlife have adapted their foraging behaviour to capitalize on these resources [9,10], leading to subsidized populations that are often larger, more aggregated and better fed than their naturally foraging counterparts [11–13]. Importantly, novel assemblages of species can form around anthropogenic resources [14,15], which could facilitate the cross-species transmission of pathogens among wildlife, humans and domestic animals [16]. For example, bird feeders have been implicated in the emergence of virulent pathogens such as *Mycoplasma gallisepticum* and *Trichomonas gallinae* in songbirds [17,18]. The 2014 Ebola outbreak in West Africa and 1998 emergence of Nipah virus in Malaysia also underscore the importance of understanding how anthropogenic resources can bring wildlife reservoirs of zoonotic pathogens into close proximity with humans and domesticated species [19–21].

Predicting how anthropogenic resources will impact host–parasite interactions is challenging owing to multiple underlying mechanisms with potentially opposing effects [22,23]. Although energy and nutrients from supplemental food can support robust immune function needed to resist and recover from infections [24], anthropogenic food containing toxins or lacking nutrients could reduce host immunity and increase susceptibility to infection and pathogen shedding [25–27]. Moreover, aggregation around food sources can increase contact rates and facilitate pathogen transmission [28–30]. These individual-scale effects and local interactions are embedded within landscapes characterized by patchily distributed resources; as such, the pattern of resource provisioning could influence host dispersal patterns and thus metapopulation dynamics of infectious disease [31–33]. Understanding how anthropogenic resources will alter wildlife infection and consequences for spillover risks thus requires integrating diverse expertise and approaches across multiple levels of biological organization.

This theme issue stemmed from a symposium on 'Resource provisioning and wildlife–pathogen interactions in human-altered landscapes' held at the 2016 Ecological Society of America Annual Meeting, where population ecologists, immunologists, epidemiologists and conservation biologists participated in six presentations and a panel discussion on supplemental feeding and wildlife disease. This theme issue breaks new ground by integrating field, experimental, socioeconomic and modelling studies from a diverse array of taxa and ecosystems to understand host–parasite responses to anthropogenic resource subsidies. Contributing papers synthesize emerging research and diverse perspectives on interactions between resource availability and infection processes across many scales of biology and highlight the applied importance of these findings for public health and wildlife conservation.

2. Topics addressed in this issue

Contributing papers of this theme issue examine questions that scale from individual-level processes (e.g. how anthropogenic resources affect within-host infection dynamics) up to regional- and community-level interactions (e.g. how the distribution of food resources influences parasite transmission across landscapes and host species barriers). The first series of papers asks how food availability affects host condition, immune defence and contact rates. The next set of papers examines the landscape determinants of supplemental feeding and its impacts on animal movement and parasite spread across large spatial scales. A final series of papers investigates the implications of food subsidies for the management of infectious diseases and cross-species transmission risks while also identifying future research priorities.

(a) Provisioning and individual-level processes

The theme issue's first section uses theoretical models, synthetic review, and observational and experimental studies to ask how resource availability affects individual-level infection processes such as host immune defence and contact rates. Hite & Cressler [34] use mathematical models to demonstrate that food resources affect parasite evolution via cross-scale effects on within-host and population-level dynamics. When food availability affects host density alone, parasite evolution favours a single high-virulence, high-transmissibility strategy that depresses host population size and its propensity to cycle at high resource availability. When resources also affect within-host parasite replication and host immune defence, a second, low-virulence, low-exploitation strategy can emerge in which host populations continue to cycle at high resource availability. Thus, abundant resources could alter the evolutionary trajectories of pathogens and their effects on host populations.

Strandin *et al*. [35] review empirical findings on how anthropogenic food provisioning influences wildlife immunity, using both field-based studies and captive studies with wildlife species. Although enhanced immune function results from supplemental feeding in wild and captive settings, toxic compounds associated with some anthropogenic resources can reduce host immunity in the wild, highlighting the complexity of this topic. The authors stress a need for further research, especially field studies, and highlight the potential for modern molecular techniques to enhance understanding of wildlife immunity.

Murray *et al*. [36] use an observational field study to examine the relationships between urban habituation and nutritional status, body condition and ectoparasite burdens of American white ibis (*Eudocimus albus*). Ibises in urban areas are often fed by people, and these anthropogenic resources likely result in a health trade-off: while provisioned birds had lower measures of body condition, they also showed lower ectoparasite burdens. The authors hypothesize that provisioned ibis spend less time foraging and more time preening to remove parasites. The net effect of provisioning on infection outcomes in urban ibis is still under study.

Becker *et al*. [37] examine how livestock abundance correlates with immunity and bacterial infection of vampire bats (*Desmodus rotundus*) in Peru and Belize. They find that bats with access to more livestock prey show greater investment in innate relative to adaptive immunity and that this pattern provides a mechanistic link to lower bacterial prevalence in provisioned bats. They conclude that predicting how provisioning influences infection requires considering how within-host processes and transmission modes respond to resource shifts.

Moyers *et al*. [38] use experiments with house finches (*Haemorhous mexicanus*) and bird feeders to ask how provisioning intensity affects host behaviour and transmission of a bacterial pathogen (*Mycoplasma gallisepticum*). They find that low feeder density frequently exposes birds to subclinical pathogen doses, whereas high feeder density results in higher pathogen transmission rates. Their results suggest that the intensity of supplemental feeding practices can influence infection outcomes.

Lawson *et al*. [39] present findings on the long-term surveillance of wild birds in Great Britain and infections by protozoan (finch trichomonosis), viral (Paridae pox) and bacterial (salmonellosis) pathogens. In each case, human activities influence transmission dynamics, but in different ways. The need to balance the risks and benefits of supplementary feeding for both birds and people is highlighted, as is the importance of engaging with the general public and relevant interest groups to promote and encourage compliance with best-practice guidelines.

(b) Landscape context and provisioning

The next section of this theme issue examines the landscape determinants of anthropogenic resources and how their distribution influences host movement and parasite spread across large spatial scales. Cox & Gaston [40] review the links between supplemental feeding in urban habitats and their impacts on wildlife and human–nature experiences. They suggest that wildlife attraction to provisioned food provides a positive feedback that encourages more interactions among humans and wildlife. While these interactions can benefit humans (e.g. mental health) and foster connections to nature, potential negative effects of provisioning (e.g. pathogen transmission) are unlikely to be apparent to the public. The authors suggest education campaigns that incorporate animal welfare concerns could help manage human feeding behaviour by increasing public awareness of harm caused by supplemental feeding in some contexts.

Human-provided resources can change animal movement behaviour, including long-distance migrations. Satterfield *et al*. [41] review how migratory species respond to anthropogenic food resources and present a conceptual framework for understanding how these changes can alter infection risk. They highlight the example of *Ophryocystis elektroscirrha* (a protozoan pathogen) in monarch butterflies (*Danaus plexippus*) and the importance of cross-disciplinary research to advance understanding of this topic. In particular, the authors encourage study on a wider range of migratory taxa and emphasize that new tracking technologies (e.g. geolocators, isotopes) can better examine mechanisms underlying interactions between food resources, animal migration and infectious disease.

Brown & Hall [42] ask how provisioning that promotes residency in partially migratory animals can influence pathogen dynamics and, in turn, the persistence of migration. Using mathematical models for a partially migratory bird species experiencing vector-borne pathogen transmission at its breeding grounds, they demonstrate how provisioning that increases resident nonbreeding survival extends the window of pathogen transmission. This can allow sustained transmission of pathogens that are highly virulent to hosts during migration, which in turn erodes the benefits of migratory escape from pathogens.

Their work highlights how local food subsidies can have range-wide consequences for pathogen impacts on highly mobile wildlife species.

Paez *et al*. [43] apply optimal foraging theory to understand drivers of patch residency in the context of recent urban habituation of flying foxes (*Pteropus* spp.) in Australia. They use theoretical models to show that expected patch residence time increases with the search time needed to find new food resources. These models reveal that small increases in searching times produce large increases in residence time, which may explain the recent surge of flying foxes in urban Australia which has been concomitant with the loss of critical winter nectar habitats [44].

(c) Implications for disease control and future research

The final section focuses on how anthropogenic resources affect disease risk from management perspectives and identifies future research priorities. Cotteril *et al*. [45] review a challenge that arises from intentional supplementation of wildlife for game and livestock management. The practice of feeding elk (*Cervus canadensis*) in the Greater Yellowstone Ecosystem has increased the prevalence of brucellosis but has also reduced opportunities for contact between elk and cattle. A major challenge in the Greater Yellowstone Ecosystem is how to reduce feeding elk without triggering an increase in elk-to-cattle contact that can cause the spillover of *Brucella abortis*. This review highlights how partnerships between research and management, guided by hypothesis testing, can provide adaptive management insights of wildlife disease.

Civitello *et al*. [46] expand the breadth of work included in this theme issue by reviewing the similarities and differences in the epidemiological impacts of widespread forms of nutrient input from human activities: agricultural fertilization and aquatic nutrient enrichment. They further develop mathematical models to assess whether including trophic complexity affects the relationship between resource enrichment and host–pathogen interactions. When trophic complexity is ignored, infection prevalence increases with resources; however, including competitors or predators of provisioned hosts can reverse this prediction, causing infection prevalence to stabilize or even decline at high degrees of resource enrichment.

In the closing paper, Altizer *et al*. [47] identify common threads from the contributions of this theme issue and highlight outstanding areas for future research. Research priorities include: developing mechanistic models that link the effects of resource provisioning across scales (within-host, population and landscape scales); manipulating food resources in field-based experiments and quantifying host and pathogen responses; quantifying feedback between wildlife disease and human behaviours that provision animals; and designing ecological interventions to limit opportunities for cross-species transmission by building upon a mechanistic understanding of host and pathogen biology.

3. Conclusion

Globally, wildlife are capitalizing on food provided by human activities, which has important implications for host–parasite interactions. This theme issue provides multi-displinary insights to help unravel the complex interactions among individual-, population- and landscape-level processes that determine infection outcomes in provisioned wildlife.

The included contributions highlight that novel immunological and ecological conditions associated with provisioning have profound impacts on the transmission of wildlife pathogens. Greater host aggregation, loss of migratory behaviour, improved demographic rates, immune impairment and increased overlap between wildlife and spillover hosts with provisioning can all increase infection risks. Yet contributions also highlight that such risks may not universally increase with provisioning. Parasite evolution, increased time and energy allocation to immune defence or anti-parasite behaviours, and trophic interactions can, under certain conditions, reduce parasite transmission and limit spillover. Importantly, this theme issue highlights that public education and adaptive management can contribute to 'win–win' scenarios for feeding wildlife that optimize benefits for conservation, disease management and human health.

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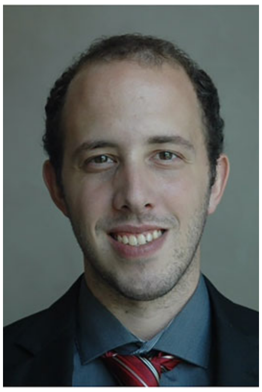

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