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Anthropogenic resource subsidies and host–parasite dynamics in wildlife

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Introduction

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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

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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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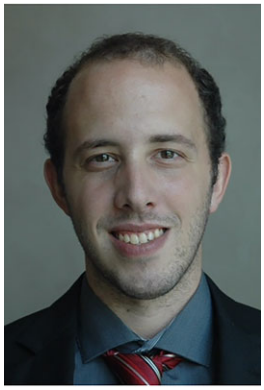

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References

1. Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013 Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* **16**, 1501–1514. (doi:10.1111/ele.12187)
2. Robb GN, McDonald RA, Chamberlain DE, Bearhop S. 2008 Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* **6**, 476–484. (doi:10.1890/060152)
3. Reynolds SJ, Galbraith JA, Smith JA, Jones DN. 2017 Garden bird feeding: insights and prospects from a north-south comparison of this global urban phenomenon. *Front. Ecol. Evol.* **5**, 24. (doi:10.3389/fevo.2017.00024)
4. Newsome D, Rodger K. 2008 To feed or not to feed: a contentious issue in wildlife tourism. *Aust. Zool.* **34**, 255–270. (doi:10.7882/FS.2008.029)

5. Ewen JG, Walker L, Canessa S, Groombridge JJ. 2014 Improving supplementary feeding in species conservation. *Conserv. Biol.* **29**, 341–349. (doi:10.1111/cobi.12410)
6. Jefferies RL, Rockwell RF, Abraham KF. 2004 Agricultural food subsidies, migratory connectivity and large-scale disturbance in Arctic coastal systems: a case study. *Integr. Comp. Biol.* **44**, 130–139. (doi:10.1093/icb/44.2.130)
7. Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR. 2014 The ecological effects of providing resource subsidies to predators. *Glob. Ecol. Biogeogr.* **24**, 1–11. (doi:10.1111/geb.12236)
8. McKinney ML. 2006 Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260. (doi:10.1016/j.biocon.2005.09.005)
9. Galbraith JA, Jones DN, Beggs JR, Parry K, Stanley MC. 2017 Urban bird feeders dominated by a few species and individuals. *Front. Ecol. Evol.* **5**, 81. (doi:10.3389/fevo.2017.00081)
10. Sih A, Ferrari MCO, Harris DJ. 2011 Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* **4**, 367–387. (doi:10.1111/j.1752-4571.2010.00166.x)
11. Fedriani JM, Fuller TK, Sauvajot RM. 2001 Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* **24**, 325–331. (doi:10.1034/j.1600-0587.2001.240310.x)
12. Corcoran MJ, Wetherbee BM, Shivji MS, Potenski MD, Chapman DD, Harvey GM. 2013 Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the southern stingray, *Dasyatis americana*. *PLoS ONE* **8**, e59235. (doi:10.1371/journal.pone.0059235)
13. Wilcoxen TE *et al.* 2015 Effects of bird-feeding activities on the health of wild birds. *Conserv. Physiol.* **3**, cov058. (doi:10.1093/conphys/cov058)
14. Ellis J, Shriner S, McLean H, Petersen L, Root J. 2017 Inventory of wildlife use of mortality pits as feeding sites: implications of pathogen exposure. *Hum. Wildl. Interact.* **11**, 8–18.
15. Galbraith JA, Beggs JR, Jones DN, Stanley MC. 2015 Supplementary feeding restructures urban bird communities. *Proc. Natl Acad. Sci. USA* **112**, E2648–E2657. (doi:10.1073/pnas.1501489112)
16. Becker DJ, Streicker DG, Altizer S. 2015 Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. *Ecol. Lett.* **18**, 483–495. (doi:10.1111/ele.12428)
17. Lawson B, Robinson RA, Colvile KM, Peck KM, Chantrey J, Pennycott TW, Simpson VR, Toms MP, Cunningham AA. 2012 The emergence and spread of finch trichomonosis in the British Isles. *Phil. Trans. R. Soc. B* **367**, 2852–2863. (doi:10.1098/rstb.2012.0130)
18. Fischer JR, Stallknecht DE, Luttrell P, Dhondt AA, Converse KA. 1997 Mycoplasmal conjunctivitis in wild songbirds: the spread of a new contagious disease in a mobile host population. *Emerg. Infect. Dis.* **3**, 69–72. (doi:10.3201/eid0301.970110)
19. Alexander KA *et al.* 2015 What factors might have led to the emergence of Ebola in West Africa? *PLoS Negl. Trop. Dis.* **9**, e0003652. (doi:10.1371/journal.pntd.0003652)
20. Pulliam JRC *et al.* 2012 Agricultural intensification, priming for persistence and the emergence of Nipah virus: a lethal bat-borne zoonosis. *J. R. Soc. Interface* **9**, 89–101. (doi:10.1098/rsif.2011.0223)
21. Epstein JH *et al.* 2008 The emergence of Nipah virus in Malaysia: the role of pteropus bats as hosts and agricultural expansion as a key factor for zoonotic spillover. *Int. J. Infect. Dis.* **12**, E46. (doi:10.1016/j.ijid.2008.05.007)
22. Becker DJ, Hall RJ. 2014 Too much of a good thing: resource provisioning alters infectious disease dynamics in wildlife. *Biol. Lett.* **10**, 20140309. (doi:10.1098/rsbl.2014.0309)
23. Hall SR, Knight CJ, Becker CR, Duffy MA, Tessier AJ, Caceres CE. 2009 Quality matters: resource quality for hosts and the timing of epidemics. *Ecol. Lett.* **12**, 118–128. (doi:10.1111/j.1461-0248.2008.01264.x)
24. Forbes KM, Mappes T, Sironen T, Strandin T, Stuart P, Meri S, Vapalahti O, Henttonen H, Huitu O. 2016 Food limitation constrains host immune responses to nematode infections. *Biol. Lett.* **12**, 20160471. (doi:10.1098/rsbl.2016.0471)
25. Blanco G, Lemus JA, García-Montijano M. 2011 When conservation management becomes contraindicated: impact of food supplementation on health of endangered wildlife. *Ecol. Appl.* **21**, 2469–2477. (doi:10.1890/11-0038.1)
26. Plowright RK, Peel AJ, Streicker DG, Gilbert AT, McCallum H, Wood J, Baker ML, Restif O. 2016 Transmission or within-host dynamics driving pulses of zoonotic viruses in reservoir–host populations. *PLoS Negl. Trop. Dis.* **10**, e0004796. (doi:10.1371/journal.pntd.0004796)
27. Becker DJ, Chumchal MM, Bentz AB, Platt SG, Czirják GÁ, Rainwater TR, Altizer S, Streicker DG. 2017 Predictors and immunological correlates of sublethal mercury exposure in vampire bats. *R. Soc. Open Sci.* **4**, 170073. (doi:10.1098/rsos.170073)
28. Cross PC, Edwards WH, Scurlock BM, Maichak EJ, Rogerson JD. 2007 Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. *Ecol. Appl.* **17**, 957–964. (doi:10.1890/06-1603)
29. Gompper ME, Wright AN. 2005 Altered prevalence of raccoon roundworm (*Baylisascaris procyonis*) owing to manipulated contact rates of hosts. *J. Zool.* **266**, 215–219. (doi:10.1017/S0952836905006813)
30. Becker DJ, Streicker DG, Altizer S. In press. Using host species traits to understand the consequences of resource provisioning for host–parasite interactions. *J. Anim. Ecol.* (doi:10.1111/1365-2656.12765)
31. Becker DJ, Hall RJ. 2016 Heterogeneity in patch quality buffers metapopulations from pathogen impacts. *Theor. Ecol.* **9**, 197–205. (doi:10.1007/s12080-015-0284-6)
32. Plowright RK, Foley P, Field HE, Dobson AP, Foley JE, Eby P, Daszak P. 2011 Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus* spp.). *Proc. R. Soc. B* **278**, 3703–3712. (doi:10.1098/rspb.2011.0522)
33. Leach CB, Webb CT, Cross PC. 2016 When environmentally persistent pathogens transform good habitat into ecological traps. *R. Soc. Open Sci.* **3**, 160051. (doi:10.1098/rsos.160051)
34. Hite JL, Cressler CE. 2018 Resource-driven changes to host population stability alter the evolution of virulence and transmission. *Phil. Trans. R. Soc. B* **373**, 20170087. (doi:10.1098/rstb.2017.0087)
35. Strandin T, Babayan SA, Forbes KM. 2018 Reviewing the effects of food provisioning on wildlife immunity. *Phil. Trans. R. Soc. B* **373**, 20170088. (doi:10.1098/rstb.2017.0088)
36. Murray MH, Kidd AD, Curry SE, Hepinstall-Cymerman J, Yabsley MJ, Adams HC, Ellison T, Welch CN, Hernandez SM. 2018 From wetland specialist to hand-fed generalist: shifts in diet and condition with provisioning for a recently urbanized wading bird. *Phil. Trans. R. Soc. B* **373**, 20170100. (doi:10.1098/rstb.2017.0100)
37. Becker DJ *et al.* 2018 Livestock abundance predicts vampire bat demography, immune profiles and bacterial infection risk. *Phil. Trans. R. Soc. B* **373**, 20170089. (doi:10.1098/rstb.2017.0089)
38. Moyers SC, Adelman JS, Farine DR, Thomason CA, Hawley DM. 2018 Feeder density enhances house finch disease transmission in experimental epidemics. *Phil. Trans. R. Soc. B* **373**, 20170090. (doi:10.1098/rstb.2017.0090)
39. Lawson B, Robinson RA, Toms MP, Risely K, MacDonald S, Cunningham AA. 2018 Health hazards to wild birds and risk factors associated with anthropogenic food provisioning. *Phil. Trans. R. Soc. B* **373**, 20170091. (doi:10.1098/rstb.2017.0091)
40. Cox DTC, Gaston KJ. 2018 Human–nature interactions and the consequences and drivers of provisioning wildlife. *Phil. Trans. R. Soc. B* **373**, 20170092. (doi:10.1098/rstb.2017.0092)
41. Satterfield DA, Marra PP, Sillett TS, Altizer S. 2018 Responses of migratory species and their pathogens to supplemental feeding. *Phil. Trans. R. Soc. B* **373**, 20170094. (doi:10.1098/rstb.2017.0094)
42. Brown LM, Hall RJ. 2018 Consequences of resource supplementation for disease risk in a partially migratory population. *Phil. Trans. R. Soc. B* **373**, 20170095. (doi:10.1098/rstb.2017.0095)
43. Páez DJ, Restif O, Eby P, Plowright RK. 2018 Optimal foraging in seasonal environments: implications for residency of Australian flying foxes in food-subsidized urban landscapes. *Phil. Trans. R. Soc. B* **373**, 20170097. (doi:10.1098/rstb.2017.0097)
44. Plowright RK *et al.* 2015 Ecological dynamics of emerging bat virus spillover. *Proc. R. Soc. B* **282**, 20142124. (doi:10.1098/rspb.2014.2124)

45. Cotterill GG, Cross PC, Cole EK, Fuda RK, Rogerson JD, Scurlock BM, du Toit JT. 2018 Winter feeding of elk in the Greater Yellowstone Ecosystem and its effects on disease dynamics. *Phil. Trans. R. Soc. B* **373**, 20170093. (doi:10.1098/rstb.2017.0093)

46. Civitello DJ, Allman BE, Morozumi C, Rohr JR. 2018 Assessing the direct and indirect effects of food provisioning and nutrient enrichment on wildlife infectious disease dynamics. *Phil. Trans. R. Soc. B* **373**, 20170101. (doi:10.1098/rstb.2017.0101)

47. Altizer S *et al.* 2018 Food for contagion: synthesis and future directions for studying host–parasite responses to resource shifts in anthropogenic environments. *Phil. Trans. R. Soc. B* **373**, 20170102. (doi:10.1098/rstb.2017.0102)