Biological Conservation 248 (2020) 108702

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Parasites are endangered by the conservation of their hosts: Meta-analyses of the effect of host captivity on the odds of parasite infection

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ARTICLE INFO

Keywords:
Parasite extinction
Parasite decline
Captive management
Parasitism
Conservation-driven extinction
Conservation

ABSTRACT

Parasites are important drivers of ecosystem functions and play a key role in the maintenance of ecosystem health. However, parasites may be threatened by host conservation, as well as by host extinction. Captive management is of increasing importance for conserving threatened host species, but captivity represents a drastic environmental change that may in turn threaten parasites. To address this concern, we examined how host captivity affects the odds of parasite infection and identified which parasite life-history traits (particularly modes of transmission) are the strongest predictors of parasite decline. Data were collated from 45 studies examining parasite prevalence in both captive and free-range host populations across a total of 55 host and 158 parasite species. We performed meta-analyses of these studies and found that overall, the odds of infection by parasites were not different between host populations in captive and free-range environments. However, the odds of infection by helminths were lower in captivity. Parasites with indirect life cycles, especially helminths with complex life cycles and vector-borne protozoa, also had lower odds of infecting hosts in captivity. Finally, parasites transmitted through the environment with direct life cycles, particularly environmentally-transmitted helminths, had lower odds of infecting hosts in captivity. Parasite losses in captivity are likely caused by the use of antiparasitic drugs, and the biotic and abiotic differences between captive and free-range environments. If the goals of activities such as captive breeding are to re-establish self-sustaining ecosystems, then conservation efforts need to include both hosts and their parasites in captive management programs.

1. Introduction

The world is currently experiencing its sixth mass extinction event (Regnier et al., 2015; Ceballos et al., 2015; Ceballos et al., 2017). With hundreds of species becoming extinct each year through anthropogenic causes (Ceballos et al., 2017), conservation efforts to save the most threatened species are of increasing importance. To date, such efforts have mainly focused on large, charismatic megafauna (Albert et al., 2018), some of which depend on captivity for persistence (Mysterud et al., 2007). However, these species comprise only a small percentage of overall biodiversity, with the majority of biodiversity contained in groups that are less charismatic, more obscure and more neglected by conservation efforts, including symbiotic organisms such as parasites (Windsor, 1997; Gompper and Williams, 1998; Marcogliese, 2005; Dunn et al., 2009).

Parasites are integral parts of every ecosystem; they regulate host populations, they contribute to energy flow through the many links in food webs, and they are a major component of biodiversity (Lafferty et al., 2006; Dobson et al., 2008; Sato et al., 2011; Hatcher et al., 2012). Despite their importance, parasite extinction risks and their potential impacts on ecosystem health have rarely been studied and are poorly described. Since they co-evolve with their hosts, parasites are especially vulnerable to co-extinction. Co-extinction occurs when a parasite, dependent on its host, becomes extinct as a result of the host's extinction, and this is thought to be one of the most common ways in which biodiversity is lost (Koh et al., 2004). Unfortunately, as well as being threatened by co-extinction events per se, parasites can even become extinct before their hosts, as a direct consequence of host decline (de Castro and Bolker, 2005). In addition, conservation efforts to restore declining host populations can actually endanger parasite fauna (Windsor, 1997; Gompper and Williams, 1998; Gomez and Nichols, 2013; Rozsa and Vas, 2015). Here, we refer to this phenomenon as

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https://doi.org/10.1016/j.biocon.2020.108702
Received 26 December 2019; Received in revised form 30 June 2020; Accepted 4 July 2020

"conservation-driven extinction". Although conservation-driven extinction has been poorly studied, there are a number of examples of parasite extinctions due to host conservation efforts. For example, the lice *Neotrichodectes* sp. and *Colpocephalum californici* from the black-footed ferret (*Mustela nigripes*) and the Californian condor (*Gymnogyps californianus*), respectively, went extinct when host captive breeding programs included de-lousing protocols (Gompper and Williams, 1998; Koh et al., 2004). Most estimates of parasite extinctions focus only on co-extinction risks in the wild, without considering the possibility that parasites may go extinct before their hosts due to natural or human-driven causes (Koh et al., 2004; Dunn et al., 2009; Cizauskas et al., 2017). Understanding how methods used in host conservation impact parasite fauna and determining which factors contribute to parasite survival or demise are important next steps in conserving parasites and thus, maintaining wider ecosystem function (Gompper and Williams, 1998; Viney and Graham, 2013).

Captive animal management (e.g. zoos, captive breeding facilities, rehabilitation centres, and enclosures) is an important strategy for ensuring the survival of some endangered animals through raising public awareness (Balmford et al., 1995), providing opportunities for captive breeding programs, and supplementing natural populations (Kleiman, 1989). There are currently 38 animal species listed as extinct in the wild on the IUCN Red List of Threatened Species (IUCN, 2020), which survive only because of human intervention through captivity and captive breeding. Examples include the scimitar-horned oryx (*Oryx dammah*), the Hawaiian crow (*Corvus hawaiiensis*), the black softshell turtle (*Nilssonia nigricans*), the Polynesian tree snail (*Partula nodosa*), and the Socorro isopod (*Thermosphaeroma thermophilum*) (IUCN, 2020). Despite the growing number of animals destined for captivity, our understanding of how captivity affects associated fauna such as parasites is largely unexplored.

When a subset of hosts is transferred from a free-range/wild environment to captivity, some parasite species may be lost simply by chance because only uninfected hosts are taken (MacLeod et al., 2010), resulting in a new host population devoid of those parasites. This potential loss can be exacerbated by the already diminished parasite diversity associated with small populations of endangered hosts (Altizer et al., 2007). Even when parasites are successfully transferred to a captive environment, they may not survive in the new, unfamiliar conditions. In many ways, this is akin to the reduced diversity and abundance of parasites recorded for invasive species after they are introduced into a new environment (i.e. the enemy release hypothesis) (Keane and Crawley, 2002; Torchin and Mitchell, 2004; MacLeod et al., 2010). In captivity, the most obvious way in which parasites are lost is through direct parasite control, such as the use of antiparasitic drugs (Stringer and Linklater, 2014). Parasites can also be lost from captive populations indirectly, because of environmental differences experienced between captive and wild populations. For example, parasite survival may be affected through changes in host density, home range, the absence/change of intermediate hosts or vectors, or a change in the biotic or abiotic environment (Nunn et al., 2005; Krasnov et al., 2004; Lindenfors et al., 2007; Kutz et al., 2009; Wood et al., 2011). The magnitude of the effect that these variables will have on parasite survival is thought to be largely determined by the parasites' life-history traits (Thompson et al., 2018).

Most parasite extinction models examine the role that host-specificity could play in parasite co-extinctions, with disagreement on whether it is generalist or specialist parasites that suffer the most with host declines (Koh et al., 2004; Dunn et al., 2009; Strona, 2015; Strona and Fattorini, 2016; Cizauskas et al., 2017). However, the effect of other life-history traits, such as mode of transmission, on parasite loss has been poorly studied (Thompson et al., 2018), especially in the context of captive management. The only other large-scale study comparing parasites of captive and free-range animals focuses on parasite richness in captive and wild primates, where it was found that total parasite species richness in captive primates was similar to the wild. However, the species compositions were almost entirely different, suggesting both loss of endemic parasites and a gain of foreign parasites in captivity (Herrera et al., 2019). In our current study, we ask whether there is a general tendency for hosts in captive environments to have lower odds of being infected by any parasite species compared to hosts in a free-range environment, and whether this tendency depends on parasite life-history traits. The magnitude of the decline of specific parasites may be determined by the combination of biotic and abiotic factors they are faced with in captivity that affect their transmission from host to host. We predicted that the odds of infection by parasites with indirect modes of transmission will be lower for hosts in a captive environment than in a free-range environment, because of the potential for these transmission pathways to be disrupted in captivity. Conversely, we predicted that the odds of infection by parasites which are transmitted by direct host to host contact will be higher for hosts in captivity because increased host density in captive facilities may facilitate transmission.

2. Methods

2.1. Data selection and inclusion criteria

Data for meta-analyses were compiled from studies of parasites in any terrestrial host animal species that were examined in both a captive (fenced enclosures including zoos, reserves, research colonies, captive-breeding facilities, or rehabilitation/rescue centres) and free-range (living in a wild free-range environment) environment. Both microparasites and macroparasites were selected for this study. Microparasites included viruses, bacteria, and protozoa, whereas macroparasites included helminths (nematodes, cestodes, trematodes, and acanthocephalans) as well as arthropods (ectoparasites such as fleas and ticks). We searched Web of Science, selecting 'all databases' using the terms "captiv* AND (wild OR "free-range" OR "free range" OR "free-living" OR "free living") AND (parasit*) AND compar* NOT parasitoid NOT freshwater NOT aquatic". Only terrestrial hosts were selected to remove the possible confounding factor that an aquatic environment might introduce when examining different modes of transmission. We expect parasite transmission to differ between the two environments, especially vector-borne and environmentally transmitted parasites. Within 2064 articles spanning through the years 1980 to 2019 inclusively, only 303 papers were selected for detailed inspection because they examined parasite infections for host populations in both captive and free-range environments. From these, 45 articles provided suitable data on parasite prevalence (used to calculate odds ratios, see below) from the same host species in both a captive and free-range environment, where sample collection was comparable for both population types. Unfortunately, most of the studies do not describe where the captive populations originated from, so we were unable to confirm that captive populations originated from the free-range populations with which they were compared.

Parasite prevalence was often based on molecular work, morphology, and/or serology, depending on the parasite species in question. We included data from studies based on serology because previous

Table 1
Definitions for each parasite mode of transmission. Note that our definition of "complex life cycle" excludes vector-borne transmission.

Direct (one host in life cycle) Parasites with direct life cycles require only one type of host to reproduce and complete their life cycle.	
Host contact	Close transmission between hosts via biting, scratching, aerosols, exchange of bodily fluids. This often includes bacteria and viruses.
Environmental contact	Ingestion of faecal matter or urine via contaminated environment, food or water. This includes many gastrointestinal nematodes and protozoa spread through a contaminated environment.
Indirect (two or more hosts in life cycle) Parasites with indirect life cycles require two or more types of hosts to reproduce and complete their life cycle.	
Vector-borne	Transmission by a biting arthropod that carries the parasite. This often involves parasites found in the blood, e.g. protozoa such as trypanosomes and *Plasmodium* spp., and even some nematodes.
Complex life cycle	Transmission through ingestion (trophic transmission) of an infected intermediate host (host infected with a larval, non-reproductive parasite form) or via free-living infectious stages. Examples include many helminths (trematodes, cestodes, acanthocephalans, and even some nematodes) and protozoa.

large-scale analyses found that discarding this type of data did not affect the results (Olival et al., 2017; Pandit et al., 2018) and is acceptable even when examining parasite richness (Herrera et al., 2019). We excluded studies if parasite prevalence was estimated based on the number of samples and not individual animals, or if multiple host species were pooled together. Data consisted of parasite taxonomy (based on contemporary literature), and host taxonomy, based on contemporary literature and corrected with TimeTree (Hedges et al., 2006). TimeTree is an up-to-date tool for building phylogenetic trees, consisting of thousands of published studies with up-to-date phylogenetic data (Hedges et al., 2006). Data also consisted of sample type (blood, faeces, etc.), captivity type (fenced enclosures including zoos, reserves, research colonies, captive-breeding facilities, or rehabilitation/rescue centres), total number of hosts examined in the captive and free-range environments, and number of infected hosts found in each environment. Mode of transmission (Table 1) for each parasite species was determined separately by comparison with a previously compiled database, the Global Mammal Parasite Database (GMPD) (Nunn and Altizer, 2005; Stephens et al., 2017). When the parasite was not listed in the GMPD, we searched the literature for a description of its life cycle and mode of transmission (in some cases, parasites utilized more than one transmission mode). Otherwise, for all other modes of transmission, when data were unavailable for a specific parasite species, we used the mode of transmission that is typical for that taxonomic group (at the genus or family level). When a study examined the same parasite species across multiple host species, or when multiple parasite species were examined in a single host species, each host-parasite association was considered as a unique case in our analysis. Finally, while we acknowledge that host-specificity is an important parasite life-history trait when studying parasite extinction, we have not included this trait in our study because determining host-specificity is not straightforward (Poulin et al., 2011).

2.2. Determining phylogenetic signal

A phylogenetic signal measures whether there is a tendency for closely related species to show a more similar response due to their evolutionary relatedness (Muenkemueller et al., 2012). To determine whether the relationship between the odds of parasite infection and environment was influenced by host phylogeny, we calculated Pagel's lambda (Pagel, 1999), which ranges from 0 to 1. Values closer to 1 indicate that closely related taxa show a more similar response, and values close to 0 mean that closely related taxa do not show a more similar response. A phylogenetic tree was constructed for host species using TimeTree (Kumar et al., 2017). In R version 3.5.2 (R Core Team, 2018), we used the match.phylo.data() function from package *picante* v 1.8 (Kembel et al., 2010) to match our odds ratios to the species on the phylogenetic tree and calculate Pagel's lambda using the phylosig() function from the *phytools* v 0.6-99 package (Revell, 2012). Since we had multiple odds ratios for the same parasite species, we bootstrapped our Pagel's lambda so that each host was represented only once in the dataset; for each bootstrap, the parasite selected was randomly resampled with replacement. This was done 1000 times to account for any possible combinations of hosts and parasites. Since the phylogenetic signal was high (mean Pagel's $\lambda = 0.362$, 95% CI: 0.333–0.390), we can assume that host phylogeny had an effect on the relationship between odds of infection and environment and we therefore performed phylogenetic meta-analyses (Lajeunesse, 2009; Chamberlain et al., 2012) to account for host phylogeny. Although we did not make phylogenetically independent contrasts for parasites because robust phylogenies were not available for all parasite taxa, we undertook separate analyses for the major taxonomic groups.

2.3. Meta-analysis procedures

All meta-analyses were performed with the OpenMEE software (Wallace et al., 2017). We used a random effects model, which allows for different true effect sizes in different studies, because of the differences across studies (sampling method, geographic location, and host and parasite species). Since our data were binary for the predictor variable (captive and free-range) and consisted of number of infected hosts versus the number of uninfected hosts, we calculated odds ratios for each parasite (in each host species, if there were multiple host species examined) in each study as a measure of effect size. An odds ratio greater than 1 means that the odds of infection in captive host populations are higher, and less than 1 means that they are lower than in free-range host populations. Because of multiple comparisons (see below), and because corrections for multiple testing in meta-analyses are not universally agreed upon (Borenstein et al., 2009; Schmidt and Hunter, 2015), we opted for a more conservative approach by setting $\alpha = 0.01$ to reduce the chances of committing a Type I error (i.e. confidence intervals were set to 99%), which is recommended for analyses that may contribute to future policy decisions (Borenstein et al., 2009).

Table 2
The total number of parasite species (n = 158), counting unknown parasite species as unique, organized by taxonomic group and mode of transmission. Direct life cycles include parasites that utilize exclusively host-contact, exclusively environmental contact and parasites utilizing both modes of transmission, so the total number of species is greater than the two sub-categories combined. The same applies to indirect transmission methods.

Taxonomic group	Number of species (% of total)	Mode of transmission					
		Direct	Exclusively host-contact	Exclusively environmental contact	Indirect	Exclusively vector-borne	Exclusively complex life cycle
Helminth	65 (41.1%)	47	0	46	18	0	18
Protozoa	43 (27.2%)	24	0	5	19	9	7
Bacteria	41 (26.0%)	38	10	7	3	3	0
Virus	4 (2.5%)	4	2	0	0	0	0
Arthropod	5 (3.2%)	4	0	3	1	0	1
Total	158	117	12	61	41	12	26

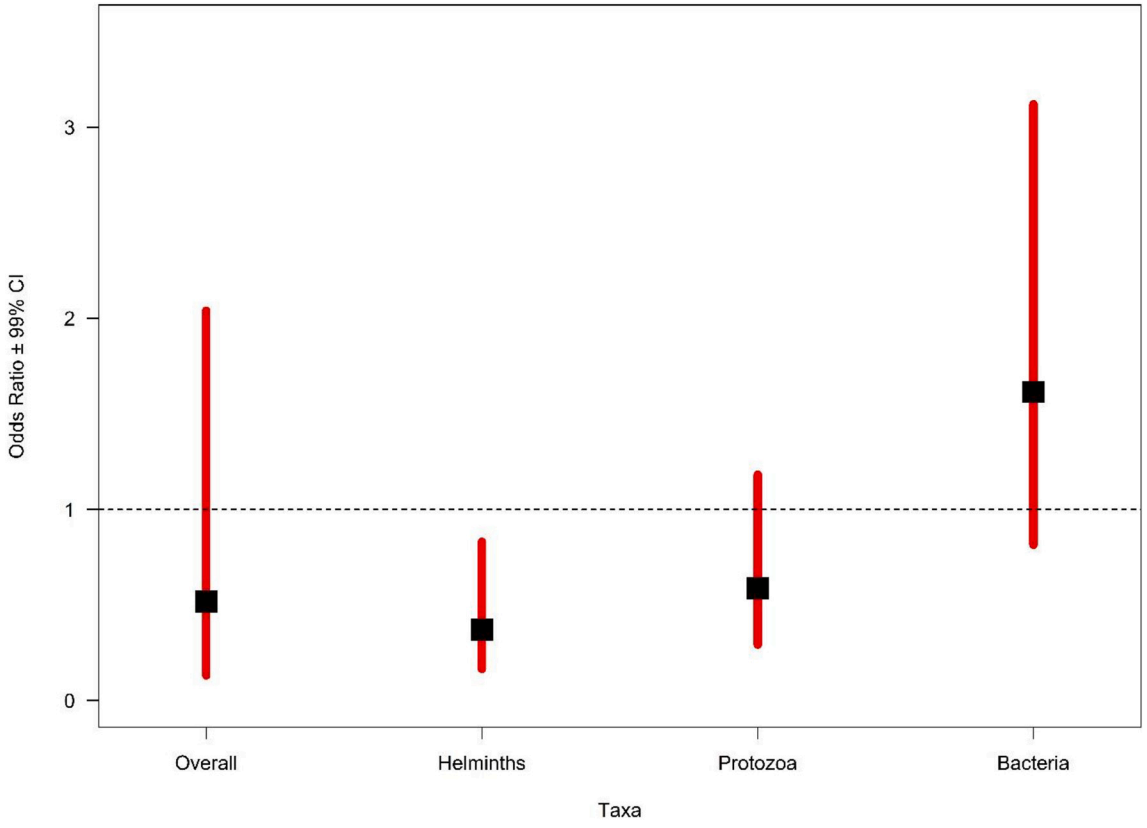

Fig. 1. Odds ratios (with confidence intervals) from meta-analyses examining the odds of infection by parasites in captive vs. free-range hosts, both over all examined studies, and for different taxa. Values below 1 mean lower odds of infection for hosts in captivity and values above 1 mean higher odds of infection for hosts in captivity. Odds are different if the confidence interval does not overlap with 1.

We initially examined the odds of infection in captive and free-range host populations over all parasites, then separately for helminths, protozoa, and bacteria. The effect of captivity on viruses and arthropods were not analyzed separately due to a small study sample size for each, but these groups were included in other analyses. Separate analyses were then performed for parasites with different modes of transmission (direct life cycle, host contact, environmental contact, indirect life cycle, vector-borne, and complex life cycle). Analyses for direct life cycles included parasites with both host contact and environmental contact and similarly, indirect life cycle analyses included both vector-borne parasites and those with complex life cycles. If a parasite utilized more than one mode of transmission (e.g. host contact and environmental contact), then it was included for analysis at the level of the highest category (i.e. direct life cycles in this case), but not for analysis at the level of the lowest category (e.g. not included in either host-contact or environmental contact analyses). Where sample sizes permitted (5 or more host-parasite associations, to reduce the chances of a false positive result), we undertook separate analyses for helminths and

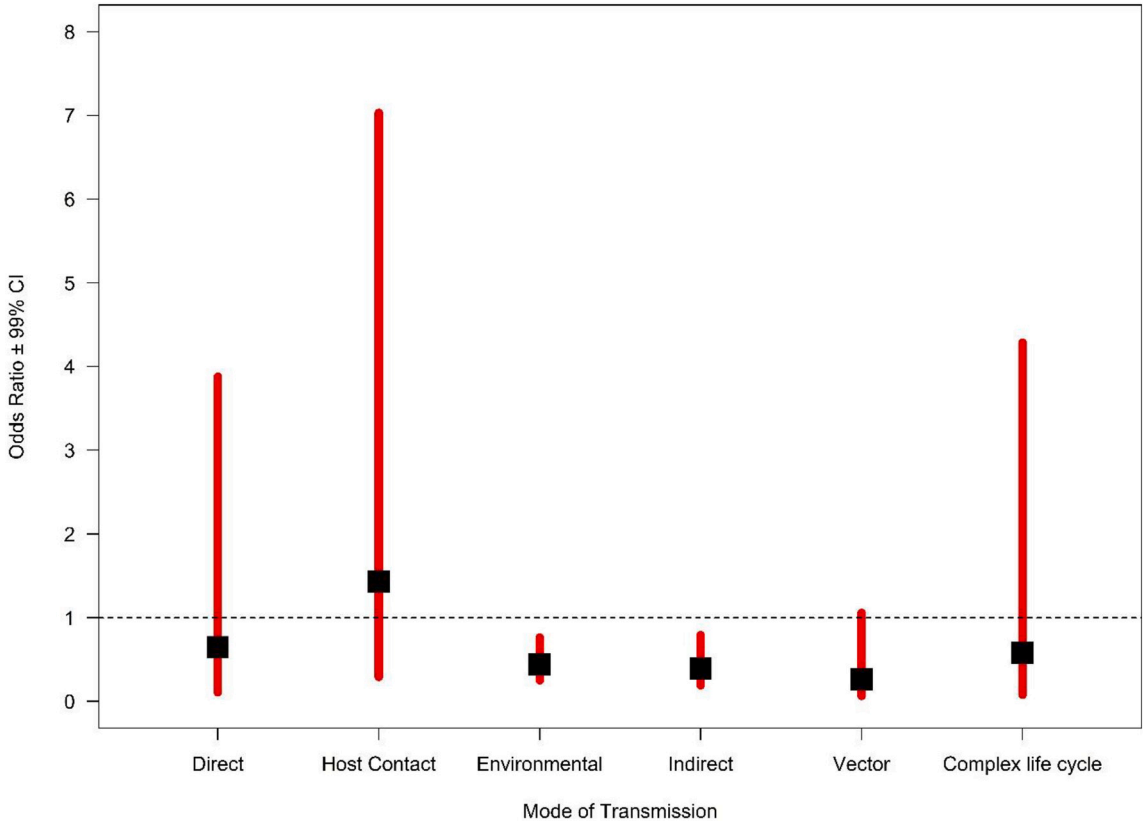

Fig. 2. Odds ratios (with confidence intervals) from meta-analyses examining the odds of infection by parasites in captive vs. free-range hosts for parasites with different modes of transmission. Direct transmission is composed of host-contact and environmental, and indirect transmission is composed of vector and complex life cycle. Values below 1 mean lower odds of infection for hosts in captivity and values above 1 mean higher odds of infection for hosts in captivity. Odds are different if the confidence interval does not overlap with 1.

protozoa with different modes of transmission.

3. Results

From the 45 selected studies investigating parasitism in both captive and free-range host populations, there were 86 parasite species identified. However, an additional 72 parasite taxa that were not identified to species level were also included; we have treated these as 72 separate species, but it is possible that some of them could have been repeats of the 86 identified species (Table 2). In total, there were 222 host-parasite associations (Appendix Table 1). Parasite taxa spanned 17 phyla, 26 classes, 41 orders, 71 families, and 84 genera. The most common parasite order in host-parasite associations was Rhabditida (n = 41), followed by Eucoccidiorida (n = 23), Enterobacterales (n = 17), Strongylida (n = 15), Amoebida (n = 13), and Trypanosomatida (n = 11). The most common genera were *Entamoeba* (n = 13), *Tachygonetria* (n = 10), *Cryptosporidium* (n = 5), and *Balantidium* (n = 7). The genus could not be determined for 21 parasites, so they were classified to the lowest possible taxonomic level. The most common modes of transmission were environmental contact (n = 73) and complex life cycles (n = 39) (Table 2).

Across the 45 studies, there were 55 host species spanning 4 classes, 15 orders, 30 families, and 49 genera. The most common host orders in host-parasite associations were Primates (n = 102), Testudines (n = 28), Squamata (n = 16), Carnivora (n = 13), Accipitriformes (n = 12), and Artiodactyla (n = 11). The most common families were Hominidae (n = 36), Testudinidae (n = 28), Lemuridae (n = 26), and Cercopithecidae (n = 20).

Henceforth, all differences in odds of infection are significant unless stated otherwise. Over all taxonomic groups and across all modes of transmission, there was no difference in the odds of hosts being infected in captivity compared to hosts being infected in a free-range environment (Fig. 1, Appendix Table 1). However, by separating parasite groups, we found that captive hosts had 2.71 times lower odds of being infected by helminths (Appendix Fig. 1), but there was no difference in the odds of infection by protozoa (Appendix Fig. 2) and bacteria in captive and free-range environments (Fig. 1, Appendix Table 1).

Stratifying by modes of transmission, the odds of infection by parasites with indirect life cycles were 2.57 times lower in captivity, whereas there was no difference in the odds of infection by parasites with direct life cycles in the captive and free-range environments (Fig. 2, Appendix Table 1). Comparing the different modes of transmission in more detail, captivity had the largest effect on environmentally transmitted parasites with direct life cycles, with hosts in captivity having 2.30 times lower odds of infection (Appendix Fig. 3). There was also a non-significant trend for lower odds of infection by vector-borne parasites with indirect life cycles in captivity (3.80 times lower odds) (Fig. 2, Appendix Table 1, Appendix Fig. 4). Further, there

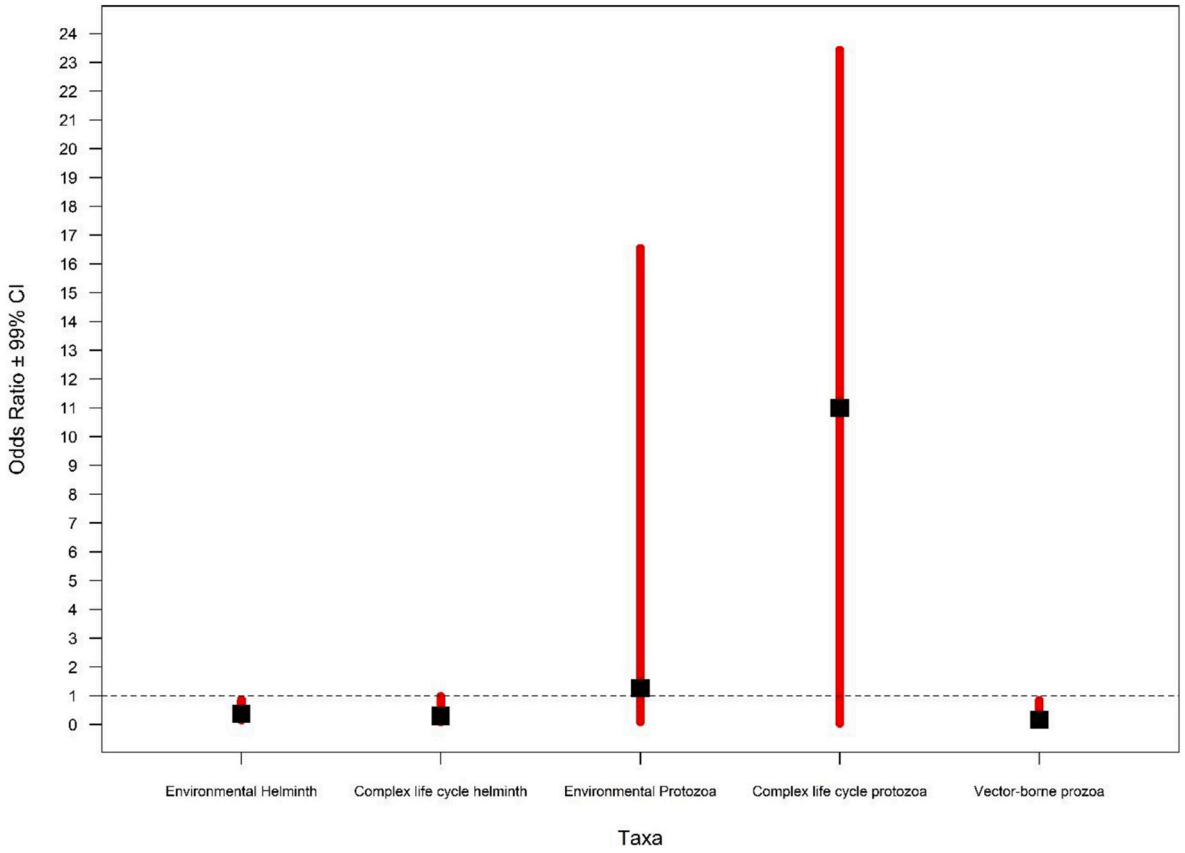

Fig. 3. Odds ratios (with confidence intervals) from meta-analyses examining the odds of infection by parasites in captive vs. free-range hosts for helminth and protozoan parasites with different modes of transmission. Values below 1 mean lower odds of infection for hosts in captivity and values above 1 mean higher odds of infection for hosts in captivity. Odds are different if the confidence interval does not overlap with 1.

was no difference in the odds of infection by parasites transmitted by direct host-host contact, or with indirect, complex life cycles (Appendix Fig. 5) in the two environments (Fig. 2, Appendix Table 1).

When different modes of transmission were examined separately for helminths and protozoa, the odds of infection by helminths with direct life cycles and environmental transmission were 2.70 times lower in captivity (Fig. 3, Appendix Table 1). Similarly, the odds of infection by helminths with indirect, complex life cycles were 3.40 times lower in captivity (Fig. 3, Appendix Table 1). Among protozoa, vector transmission was the only important mode of transmission, with hosts in captivity having 5.74 times lower odds of infection by vector-borne protozoa (Fig. 3, Appendix Table 1) while there was no difference in the odds of infection by protozoa with indirect, complex life cycles in captive and free-range environments.

4. Discussion

Overall, there was no difference in the odds of infection by parasites for hosts in a captive or free-range environment. However, the environment type may have affected some parasite taxa and not others. For example, while there was no difference in the odds of infection by bacteria or protozoa, helminths had lower odds of infecting hosts in captivity. The odds of infection were not just influenced by parasite taxa, but by the mode of transmission as well. As predicted, hosts in captivity had lower odds of being infected by parasites with indirect life cycles, and this was especially true for helminths with complex life cycles and vector-borne protozoa. We also predicted that hosts in captivity would have higher odds of infection by parasites with direct life cycles but instead, we found that the odds of infection by parasites with direct life cycles did not differ between the two environments. This was largely due to parasites with transmission depending on host-contact because the odds of infection by these parasites were not different in the two environments and there was a lot of variation associated with this sub-group. However, the odds of infection by parasites with direct life cycles and environmental transmission were lower in captivity, especially for environmentally transmitted helminths. Overall, our results show that the mode of transmission does indeed play a role in how parasites respond to captivity, but there may also be other, taxon-specific factors that influence the odds of parasite infection in a captive environment.

4.1. Climate and geography

Animals in captivity often undergo significant changes in their environment, which may have implications for host-parasite associations, particularly for vector-borne parasites and parasites with complex life cycles, where free-living stages require a period of development in the environment. A change in abiotic factors such as geography or climate

can also change the biotic factors of an area, such as the composition of definitive or intermediate hosts, vectors, as well as parasites (Nunn et al., 2005; Krasnov et al., 2004; Lindenfors et al., 2007; Kutz et al., 2009; Wood et al., 2011; Eriksson et al., 2020). Indeed, hosts in foreign, non-native ranges sometimes lose nearly half of their usual parasite species in the new environment (MacLeod et al., 2010). Our results for helminths and vector-borne protozoa are consistent with the hypothesis that parasites with more complex modes of transmission may be more prone to extinction because of a change in environment (Koh et al., 2004; Dobson et al., 2008; Rohr et al., 2011; Poulin and Morand, 2014). This could occur because of the direct effects of climatic variables, such as changes in temperature, light, UV radiation and moisture, on the survival of infective, free-living parasite stages (Pietrock and Marcogliese, 2003; Lafferty, 2009; O'Connor et al., 2006; Okulewicz, 2017), or because of the disruption of normal transmission pathways through the loss of vectors and intermediate hosts (Krasnov et al., 2004; Lindenfors et al., 2007; Kutz et al., 2009; Wood et al., 2011). In addition, since most captive animals in our study were held in close proximity to urban areas, urbanization itself may have had negative impacts on parasite transmission (Hess, 1994; Werner and Nunn, 2020). Urbanization brings with it pollution in the form of agricultural and industrial effluents, acidification, sewage, pesticides, and thermal pollution, which may all harm free-living stages of parasites (Pietrock et al., 2002; Marcogliese, 2005; Koprivnikar et al., 2006; Koprivnikar et al., 2007) and even intermediate hosts (Poulin, 1992; Lafferty, 1997; Milotic et al., 2018), potentially affecting parasites with complex life cycles (Werner and Nunn, 2020), particularly helminths.

The impact of captivity on vectors is still poorly understood and seems to be context-dependent. In some cases, there may be greater potential for the introduction of novel diseases when in captivity (Pung et al., 1998, Ratterree et al., 2003), as vectors may have a wider range of host species on which to feed (Tuten et al., 2012). In addition, the density of flying vectors can be higher in captivity than in the wild (Derraik et al., 2003; Bradley and Altizer, 2007). Despite some factors that seem to suggest a higher possibility of vector-borne pathogen transmission in captivity, there are four possible reasons as to why we found a non-significant trend for lower odds of infection by vector-borne parasites overall, but lower odds of infection by vector-borne protozoa. First, vector-borne parasites may experience a dilution effect in the presence of a high diversity of host species serving as decoys, and this can be especially important for zoos (Schmidt and Ostfeld, 2001; Ezenwa et al., 2006). Biting arthropod vectors are often generalists (Kettle, 1995), so the chances of a successful blood meal with the correct host become slimmer as the diversity of host species increases in captivity. Secondly, even when captive facilities are in a similar geographical area, the composition of flying vector species can differ (LaDeau et al., 2013; Heym et al., 2018) and different vectors may not always be capable of transmitting the same parasites (Kampen and Werner, 2015). Thirdly, a highly species-diverse vector population can lower the transmission of vector-born parasites (Chaves et al., 2011). Lastly, targeted or non-targeted parasite control may be causing the loss of non-flying ectoparasites serving as vectors, indirectly leading to a lower odds of infection by vector-borne parasites (Panayotova-Pencheva, 2016). The interplay between all these factors may be why we only saw a non-significant trend for lower odds of infection by vector-borne parasites, but did see lower odds of infection by vector-born protozoa in captivity.

4.2. Parasite control

Other factors may also explain why we saw lower odds of infection by parasites, particularly with helminths, with both direct and indirect life cycles that were observed in our study. Parasite control, such as the administration of antiparasitic drugs, is likely the most direct cause of parasite loss. Drugs are routinely administered to captive animals to clear parasite infections and improve host health (Stringer and Linklater, 2014). This is particularly the case for endangered host species and those which are to be used in a captive breeding program, although there is not always a demonstrated improvement of host health from parasite control, in either captive or free-range populations (Pedersen and Fenton, 2015; Panayotova-Pencheva, 2016). Moreover, drugs are often non-specific and may affect more than one type of parasite. Ivermectin, a drug that targets both nematodes and some ectoparasites, has been used since 1981 as a cheap, effective anthelmintic and is commonly used to eradicate nematodes in captive animals (Campbell et al., 1984; Panayotova-Pencheva, 2016). Some ectoparasites are capable of transmitting vector-borne parasites, and their reduction through the use of non-specific drugs may be another reason why we may see a loss of vector-borne parasites, although we cannot draw this direct conclusion from our study. For captive ruminants, it is common for ivermectin treatment to be administered as frequently as every 2–3 months (Isaza et al., 1990) because of the perception that environmentally transmitted helminths (often nematodes) pose a major threat for captive animals (Kahn et al., 2005). Quarantine procedures may exacerbate parasite loss from captive animals because quarantine often involves vaccinations, antiparasitic drug treatments and even barriers against vectors, in addition to animal isolation (Kahn et al., 2005; Backues et al., 2011). Vector control is also recommended outside of quarantine as an additional way of controlling vector-borne parasite transmission (Derrickson and Snyder, 1992; Tuten, 2011). Lastly, dung removal is common for the prevention of environmentally transmitted parasites (Fagiolini et al., 2010). Thus, direct parasite control may be a major driving factor behind our observed lower odds of infection in captivity for certain parasite types, especially helminths that may be targeted due to their high prevalence in captivity (Panayotova-Pencheva, 2013; Jorgensen, 2015) and not other parasites such as protozoa or bacteria.

4.3. Implications and future directions

In our study, we observed lower odds of infection by parasites with indirect life cycles and parasites transmitted via direct, environmental contact in captive hosts. This means that in captivity, hosts are less likely to be infected by parasites with these modes of transmission. As a group, helminths and vector-borne protozoa were most vulnerable in captivity. While we cannot draw direct conclusions about conservation-driven parasite extinction from these results, this pattern does suggest that bringing animals into captivity may result in reduced odds of infection by certain types of parasites, leading to potential losses of parasite diversity down the line. This may have implications for parasite extinction if captive animals are threatened and have low numbers left in the wild, or no wild populations at all, because any parasites lost due to captivity may not be replaceable. With the progression of the sixth mass extinction, captivity may be an increasingly common way to save host species while dooming parasites to extinction, if captive management practices stay the same. In addition, if captive animals and/or their progeny are released back into the wild to establish new

populations, the resulting 'restored' ecosystem will forever be devoid of the parasites that once existed and will thus never truly be restored. It is unclear how losing parasites may affect ecosystems on a larger scale (Wood and Johnson, 2015), but drawing from what is known on the effect of losing top predators, losing parasites could have similar cascading effects on the whole ecosystem (Polis et al., 2000; Ripple et al., 2016). However, unlike top predators, parasites are both consumers and prey items, and they regulate organisms in all trophic levels, including top predators themselves (Anaya-Rojas et al., 2019), so the effects of losing parasites could have even greater repercussions. Invasive animals may serve as an example of how losing some natural enemies could potentially have both ecological and economic consequences.

Although host conservation is evidently a contributing factor in parasite extinctions, it also presents a unique avenue for control and intervention. By incorporating parasites into conservation programs along with their hosts, there is an opportunity to control how parasites are treated as well. However, conserving parasites is risky, particularly in a captive environment where there is potential for harming captive animals. Firstly, stress associated with captivity can make animals more susceptible to infection, and under the wrong circumstances, parasites that are normally benign can become pathogenic (Mason, 2010). Secondly, confined areas may promote transmission of density-dependent parasites (Lyles and Dobson, 1993), and finally, there is also potential for infection by novel parasites to which hosts are naïve (Lyles and Dobson, 1993). It has been suggested that if the risk of host morbidity is low, and host health or fitness is unaffected by the presence of the parasite, and/or if keeping the parasite is beneficial in the long-term, then parasites should be conserved with the host (Stringer and Linklater, 2014). However, finding this balance is not an easy task, especially with the difficulty of trying to conserve parasites with indirect life cycles, as well as the difficulty of controlling instead of eradicating parasites. Our lack of understanding of these processes highlights the importance of further research needed to better understand how parasite conservation might work in captivity.

We are not alone in suggesting that parasites should be targets for conservation (Windsor, 1997; Koh et al., 2004; Gomez and Nichols, 2013; Dougherty et al., 2016) and there are several examples of host conservation programs that do take parasites into account. For example, a host-specific louse, *Felicola isidoroi*, from wild Iberian lynx (*Lynx pardinus*), has been transferred to lynx in a captive-breeding program to ensure the persistence of the louse (Perez et al., 2013). Tasmanian devil (*Sarcophilus harrisii*) management also includes provisions for conserving parasites in captivity (Wait et al., 2017), because the retention of parasites is thought to confer long-term benefits. These programs have recognized that, counterintuitively, parasite-free hosts can become highly susceptible to infection upon re-introduction into the wild, whereas hosts that retain their parasites may actually be more successful in the long term (van Oosterhout et al., 2007; Almberg et al., 2012) not just through strengthening the immune system, but also because elimination of some parasites (e.g. nematodes) could lead to an increased prevalence of other, more harmful parasites (e.g. coccidians) (Pedersen and Antonovics, 2013; Knowles et al., 2013; Northover et al., 2018). Retaining parasites in captivity may thus be not only beneficial for the host, but would also allow for later re-establishment of evolutionary and ecological processes, and ecosystem services in the wild (Marcogliese, 2004; Almberg et al., 2012), providing a more complete restoration of a given ecosystem.

CRediT author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Jaye Moors, Alan Eriksson, Antoine Filion and Dino Milotic for their valuable assistance with various methods, data compilation or analysis, programming, graphing or grunt work. MM was supported by a University of Otago Doctoral Scholarship.

Appendix A

Table 1
Odds ratios (OR) with confidence intervals (CI) from meta-analyses examining the odds of infection by parasites in captive vs. free-range hosts for different parasites grouped by taxa and modes of transmission. Each host-parasite interaction counts as one 'study' and thus, some parasite species are repeated and the sample size is higher than shown in Table 1 in the main body of the manuscript. Values below 1 including the CI mean lower odds of infection for hosts in captivity and values above 1 including the CI mean higher odds of infection for hosts in captivity. Significant results are bolded.

	Sample size	OR	99% CI	Magnitude of effect	P
Overall	222	0.5177	0.1313–2.0401	1.93 times lower odds in captivity	0.216
Helminth	85	0.3694	0.1643–0.8305	2.71 times lower odds in captivity	**0.002**
Protozoa	72	0.5880	0.2925–1.1822	1.70 times lower odds in captivity	0.050
Bacteria	56	1.6143	0.8147–3.1200	1.61 times higher odds in captivity	0.071
Direct	159	0.6449	0.1073–3.8772	1.55 times lower odds in captivity	0.529
Host contact	15	1.4331	0.2922–7.0287	1.43 times higher odds in captivity	0.560
Environmental	73	0.4380	0.2519–0.7616	2.30 times lower odds in captivity	**0.001**
Indirect	63	0.3891	0.1912–0.7919	2.57 times lower odds in captivity	< **0.001**
Vector	20	0.2632	0.0656–1.0556	3.80 times lower odds in captivity	0.013
Complex life cycle	39	0.5804	0.0786–4.2855	1.72 times lower odds in captivity	0.483
Helminth - direct (same as environmental)	57	0.3720	0.1593–0.8688	2.70 times lower odds in captivity	**0.003**
Helminth - indirect (same as complex life cycle)	24	0.2954	0.0891–0.9795	3.40 times lower odds in captivity	**0.009**
Protozoa – direct	37	1.5067	0.0331–68.6414	1.50 times higher odds in captivity	0.782
Protozoa –environmental	5	1.2613	0.0962–16.5403	1.26 times higher odds in captivity	0.816
Protozoa –indirect	35	0.3705	0.0582–2.3588	2.70 times lower odds in captivity	0.167
Protozoa – complex life cycle	14	10.9928	0.0421–23.4267	11 times higher odds in captivity	0.995
Protozoa - vector	17	0.1741	0.0360–0.8418	5.74 times lower odds of infection in captivity	**0.004**

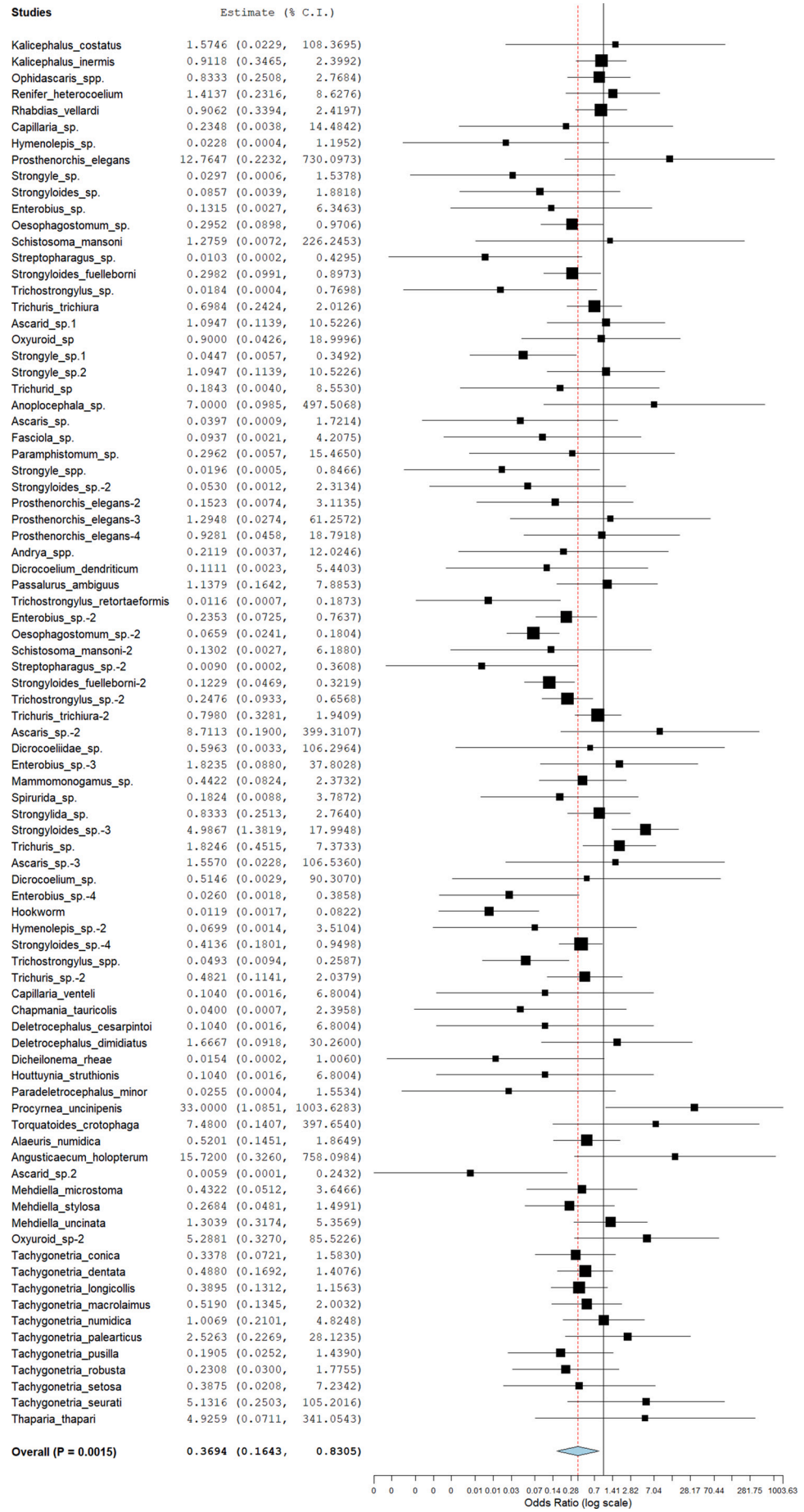

Fig. 1. Forest plot of odds ratios (rectangles) and confidence intervals (bars) for helminth species. Dashed line and diamond show the odds ratio and confidence intervals for all helminth species. Size of the points corresponds to the weight placed on individual 'studies'.

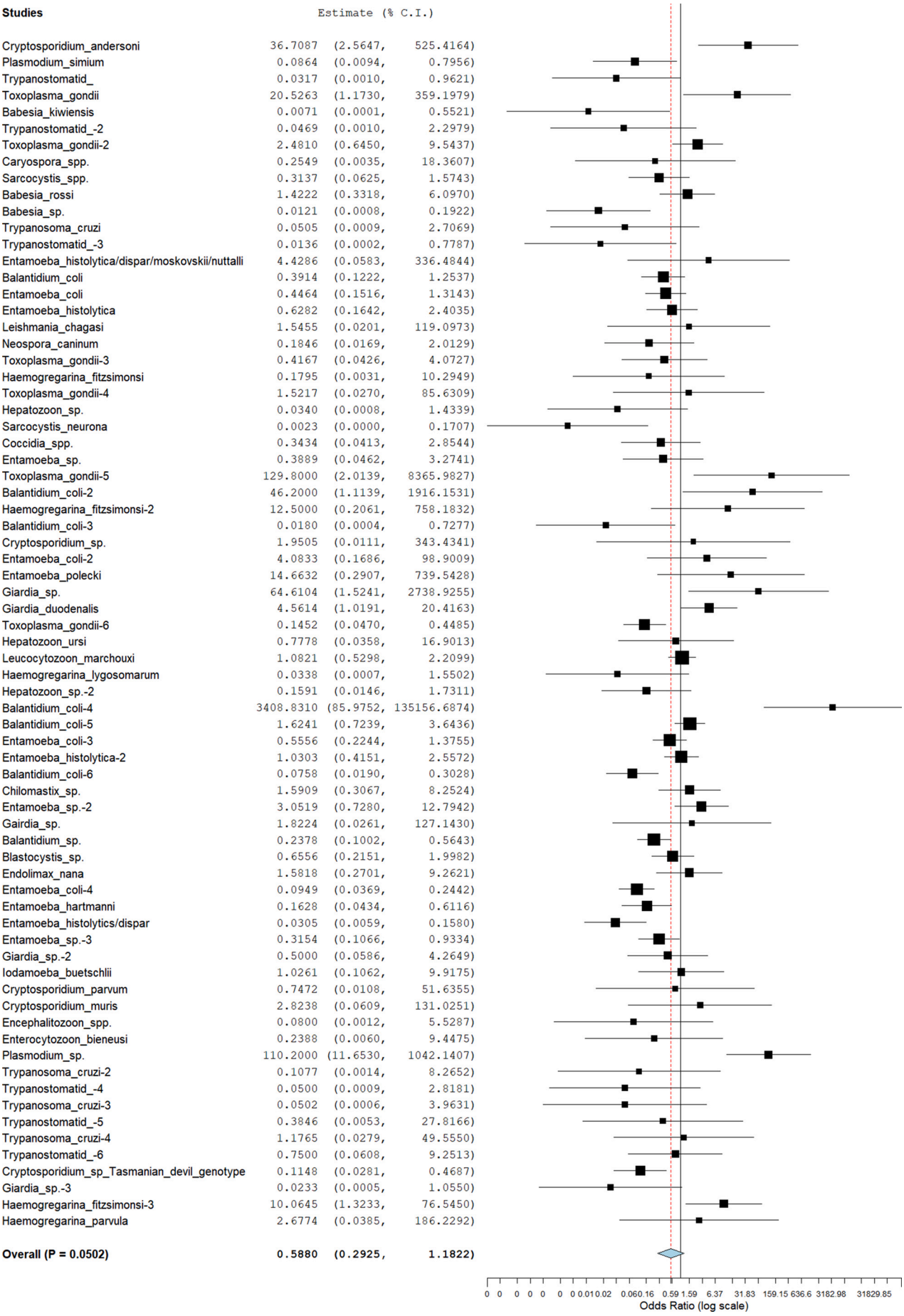

Fig. 2. Forest plot of odds ratios (rectangles) and confidence intervals (bars) for protozoan species. Dashed line and diamond show the odds ratio and confidence intervals for all protozoan species. Size of the points corresponds to the weight placed on individual 'studies'.

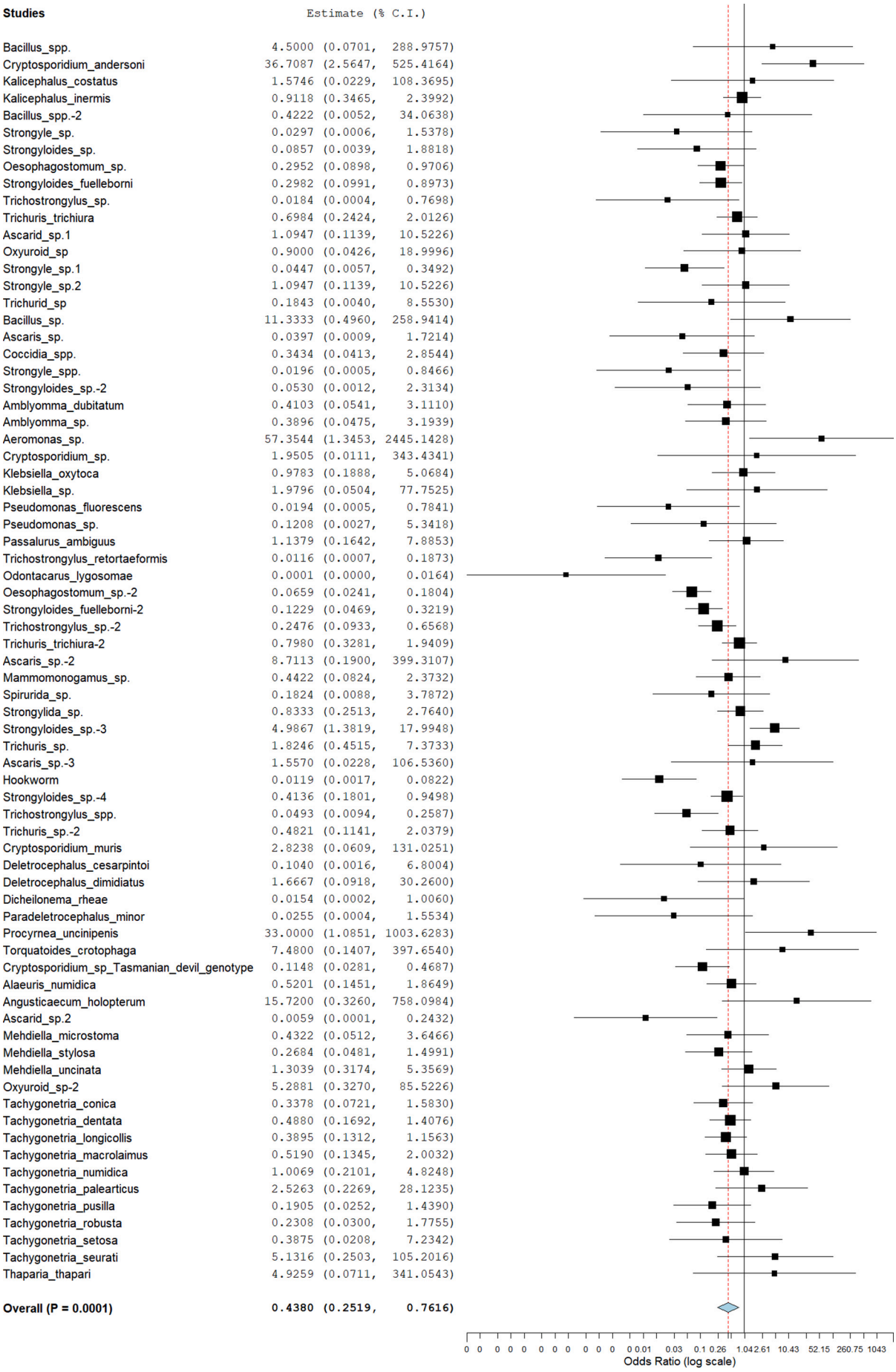

Fig. 3. Forest plot of odds ratios (rectangles) and confidence intervals (bars) for environmentally transmitted species. Dashed line and diamond show the odds ratio and confidence intervals for all environmentally transmitted species. Size of the points corresponds to the weight placed on individual 'studies'.

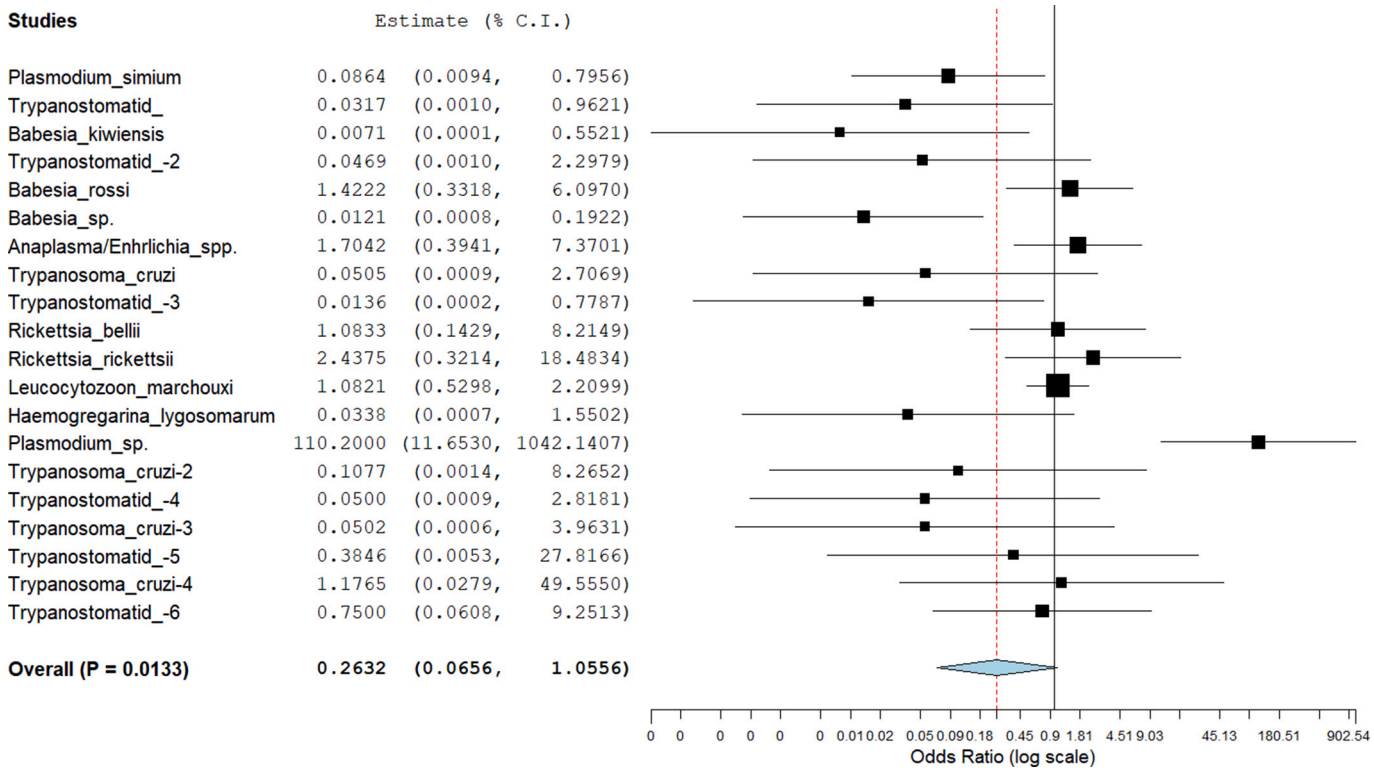

Fig. 4. Forest plot of odds ratios (rectangles) and confidence intervals (bars) for vector-borne species. Dashed line and diamond show the odds ratio and confidence intervals for all vector-borne species. Size of the points corresponds to the weight placed on individual 'studies'.

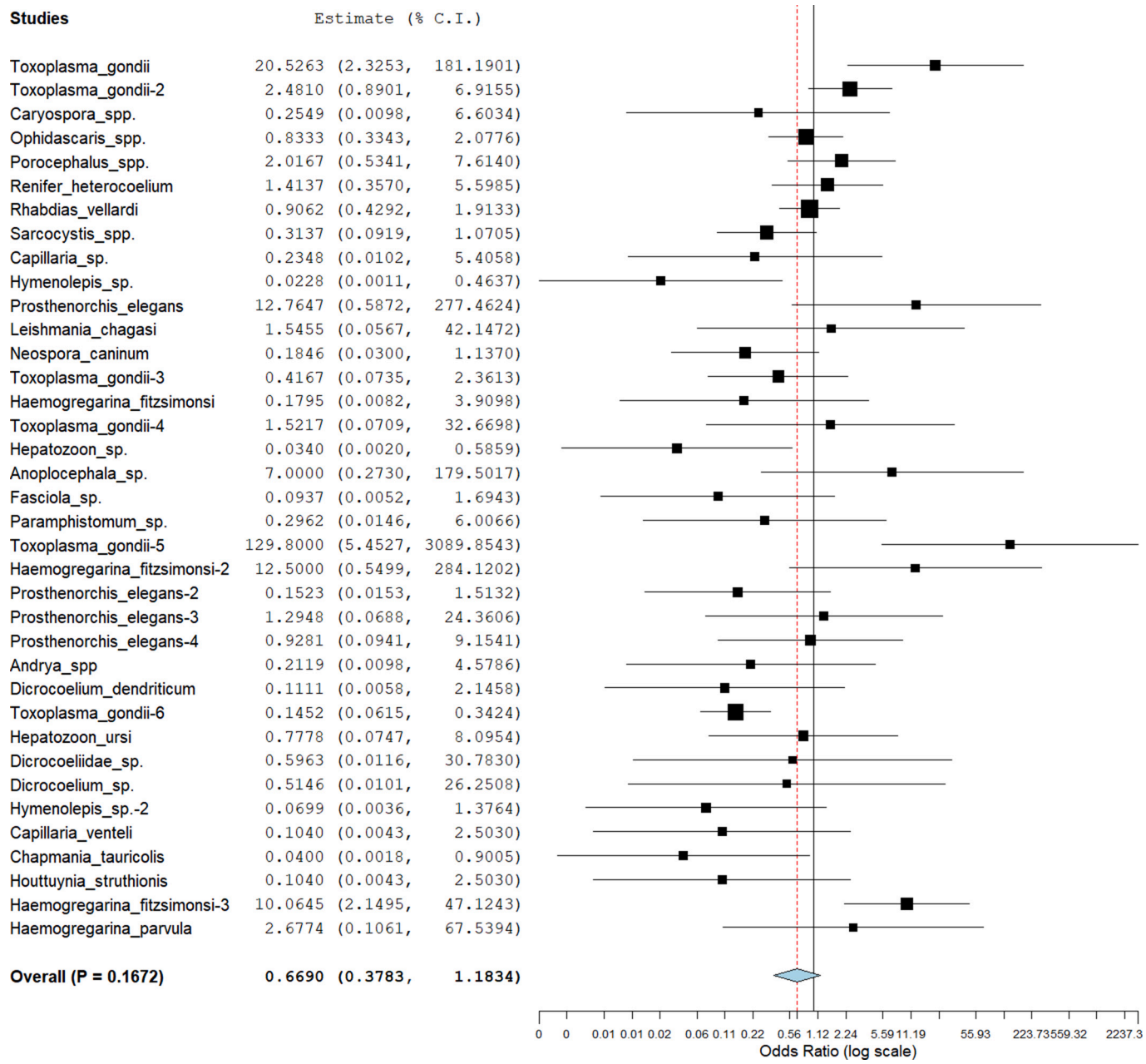

Fig. 5. Forest plot of odds ratios (rectangles) and confidence intervals (bars) for parasites with complex life cycles. Dashed line and diamond show the odds ratio and confidence intervals for all parasites with complex life cycles. Size of the points corresponds to the weight placed on individual 'studies'.

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108702.

References

Albert, C., Luque, G.M., Courchamp, F., 2018. The twenty most charismatic species. PLoS One 13, 12. https://doi.org/10.1371/journal.pone.0199149.

Almberg, E.S., Cross, P.C., Dobson, A.P., Smith, D.W., Hudson, P.J., 2012. Parasite invasion following host reintroduction: a case study of Yellowstone's wolves. Philosophical Transactions of the Royal Society B-Biological Sciences 367, 2840–2851. https://doi.org/10.1098/rstb.2011.0369.

Altizer, S., Nunn, C.L., Lindenfors, P., 2007. Do threatened hosts have fewer parasites? A comparative study in primates. J. Anim. Ecol. 76, 304–314. https://doi.org/10.1111/j.1365-2656.2007.01214.x.

Anaya-Rojas, J.M., Best, R.J., Brunner, F.S., Eizaguirre, C., Leal, M.C., Melian, C.J., Seehausen, O., Matthews, B., 2019. An experimental test of how parasites of predators can influence trophic cascades and ecosystem functioning. Ecology 100, 12. https://doi.org/10.1002/ecy.2744.

Backues, K., Clyde, V., Denver, M., Fiorello, C., Hilsenroth, R., Lamberski, N., Larson, S., Meehan, T., Murray, M., Ramer, J., Ramsay, E., Suedmeyer, K., Whiteside, D., 2011. Guidelines for zoo and aquarium veterinary medical programs and veterinary hospitals. Journal of Zoo and Wildlife Medicine 42, 176–192.

Balmford, A., Leaderwilliams, N., Green, M.J.B., 1995. Parks or arks - where to conserve threatened mammals. Biodivers. Conserv. 4, 595–607. https://doi.org/10.1007/bf00222516.

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H., 2009. Introduction to Meta-analysis. John Wiley & Sons, Chichester, U.K.

Bradley, C.A., Altizer, S., 2007. Urbanization and the ecology of wildlife diseases. Trends Ecol. Evol. 22, 95–102. https://doi.org/10.1016/j.tree.2006.11.001.

Campbell, W.C., Burg, R.W., Fisher, M.H., Dybas, R.A., 1984. The discovery of ivermectin

and other avermectins. ACS Symp. Ser. 255, 5–20.
Ceballos, G., Ehrlich, P.R., Barnosky, A.D., Garcia, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci. Adv. 1 (5), 5. https://doi.org/10.1126/sciadv.1400253.
Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences of the United States of America 114, E6089–E6096. https://doi.org/10.1073/pnas.1704949114.
Chamberlain, S.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S., Ahern, J.R., Bell-Dereske, L.P., Roy, C.L., Meza-Lopez, M., Carrillo, J., Siemann, E., Lajeunesse, M.J., Whitney, K.D., 2012. Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. Ecol. Lett. 15, 627–636. https://doi.org/10.1111/j.1461-0248.2012.01776.x.
Chaves, L.F., Hamer, G.L., Walker, E.D., Brown, W.M., Ruiz, M.O., Kitron, U.D., 2011. Climatic variability and landscape heterogeneity impact urban mosquito diversity and vector abundance and infection. Ecosphere 2, 1–21.
Cizauskas, C.A., Carlson, C.J., Burgio, K.R., Clements, C.F., Dougherty, E.R., Harris, N.C., Phillips, A.J., 2017. Parasite vulnerability to climate change: an evidence-based functional trait approach. Royal Society Open Science 4. https://doi.org/10.1098/rsos.160535.
de Castro, F., Bolker, B., 2005. Mechanisms of disease-induced extinction. Ecol. Lett. 8, 117–126. https://doi.org/10.1111/j.1461-0248.2004.00693.x.
Derraik, J.G.B., Slaney, D., Weinstein, P., Lester, P., Purdie, G., 2003. Presence of adult *Ochlerotatus* (*Finlaya*) notoscriptus (Skuse) and *Culex* (*Culex*) *pervigilans* Bergroth (Diptera: Culicidae) in tree canopy in Wellington, New Zealand. New Zealand Entomologist 26, 105–107.
Derrickson, S.R., Snyder, N.F., 1992. Potentials and Limits of Captive Breeding in Parrot Conservation. New world parrots in crisis. Smithsonian Institution Press, Washington, DC, pp. 133–163.
Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F., Jetz, W., 2008. Homage to Linnaeus: how many parasites? How many hosts? Proceedings of the National Academy of Sciences of the United States of America, 105, 11482–11489. https://doi.org/10.1073/pnas.0803232105.
Dougherty, E.R., Carlson, C.J., Bueno, V.M., Burgio, K.R., Cizauskas, C.A., Clements, C.F., Seidel, D.P., Harris, N.C., 2016. Paradigms for parasite conservation. Conserv. Biol. 30, 724–733. https://doi.org/10.1111/cobi.12634.
Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P., Sodhi, N.S., 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? Proceedings of the Royal Society B-Biological Sciences, 276, 3037–3045. https://doi.org/10.1098/rspb.2009.0413.
Eriksson, A., Doherty, J.-F., Fischer, E., Graciolli, G., Poulin, R., 2020. Hosts and environment overshadow spatial distance as drivers of bat fly species composition in the Neotropics. J. Biogeogr. 47, 736–747.
Ezenwa, V.O., Godsey, M.S., King, R.J., Guptill, S.C., 2006. Avian diversity and West Nile virus: testing associations between biodiversity and infectious disease risk. Proceedings of the Royal Society B-Biological Sciences 273, 109–117. https://doi.org/10.1098/rspb.2005.3284.
Fagiolini, M., Lia, R.P., Laricchiuta, P., Cavicchio, P., Mannella, R., Cafarchia, C., Otranto, D., Finotello, R., Perrucci, S., 2010. Gastrointestinal parasites in mammals of two Italian zoological gardens. Journal of Zoo and Wildlife Medicine 41, 662–670. https://doi.org/10.1638/2010-0049.1.
Gomez, A., Nichols, E., 2013. Neglected wild life: parasitic biodiversity as a conservation target. International Journal for Parasitology Parasites and Wildlife 2, 222–227. https://doi.org/10.1016/j.ijppaw.2013.07.002.
Gompper, M.E., Williams, E.S., 1998. Parasite conservation and the black-footed ferret recovery program. Conserv. Biol. 12, 730–732. https://doi.org/10.1046/j.1523-1739.1998.97196.x.
Hatcher, M.J., Dick, J.T.A., Dunn, A.M., 2012. Diverse effects of parasites in ecosystems: linking interdependent processes. Front. Ecol. Environ. 10, 186–194. https://doi.org/10.1890/110016.
Hedges, S.B., Dudley, J., Kumar, S., 2006. TimeTree: a public knowledge-base of divergence times among organisms. Bioinformatics 22, 2971–2972. https://doi.org/10.1093/bioinformatics/btl505.
Herrera, J.P., Chakraborty, D., Rushmore, J., Altizer, S., Nunn, C., 2019. The changing ecology of primate parasites: insights from wild-captive comparisons. Am. J. Primatol. 81. https://doi.org/10.1002/ajp.22991.
Hess, G.R., 1994. Conservation corridors and contagious-disease - a cautionary note. Conserv. Biol. 8, 256–262. https://doi.org/10.1046/j.1523-1739.1994.08010256.x.
Heym, E.C., Kampen, H., Walther, D., 2018. Mosquito species composition and phenology (Diptera, Culicidae) in two German zoological gardens imply different risks of mosquito-borne pathogen transmission. Journal of Vector Ecology 43, 80–88.
Isaza, R., Courtney, C.H., Kollias, G.V., 1990. Survey of parasite control programs used in captive ruminants. Zoo Biology 9, 385–392. https://doi.org/10.1002/zoo.1430090506.
IUCN, 2020. The IUCN red list of threatened species. Version 2020-1. https://www.iucnredlist.org.
Jorgensen, D., 2015. Conservation implications of parasite co-reintroduction. Conserv. Biol. 29, 602–604. https://doi.org/10.1111/cobi.12421.
Kahn, C.M., Line, S., Aiello, S.E., 2005. The Merck Veterinary Manual. Merck & Co. Inc., Whitehouse Station, NJ.
Kampen, H., Werner, D., 2015. The recurring necessity of mosquito surveillance and research. Bundesgesundheitsblatt-Gesundheitsforschung-Gesundheitsschutz 58, 1101–1109. https://doi.org/10.1007/s00103-015-2218-2.
Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17, 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0.
Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166.
Kettle, D.S., 1995. Medical and Veterinary Entomology. CAB International, Wallingford, UK.
Kleiman, D.G., 1989. Reintroduction of captive mammals for conservation. Bioscience 39, 152–161. https://doi.org/10.2307/1311025.
Knowles, S.C.L., Fenton, A., Petchey, O.L., Jones, T.R., Barber, R., Pedersen, A.B., 2013. Stability of within-host-parasite communities in a wild mammal system. Biological Sciences, Proceedings of the Royal Society B, pp. 280. https://doi.org/10.1098/rspb.2013.0598.
Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S., 2004. Species coextinctions and the biodiversity crisis. Science 305, 1632–1634. https://doi.org/10.1126/science.1101101.
Koprivnikar, J., Forbes, M.R., Baker, R.L., 2006. Effects of atrazine on cercarial longevity, activity, and infectivity. J. Parasitol. 92, 306–311. https://doi.org/10.1645/ge-624r.1.
Koprivnikar, J., Forbes, M.R., Baker, R.L., 2007. Contaminant effects on host-parasite interactions: atrazine, frogs, and trematodes. Environ. Toxicol. Chem. 26, 2166–2170. https://doi.org/10.1897/07-220.1.
Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Degen, A.A., 2004. Flea species richness and parameters of host body, host geography and host 'milieu'. J. Anim. Ecol. 73, 1121–1128. https://doi.org/10.1111/j.0021-8790.2004.00883.x.
Kumar, S., Stecher, G., Suleski, M., Hedges, S.B., 2017. TimeTree: a resource for timelines, timetrees, and divergence times. Mol. Biol. Evol. 34, 1812–1819. https://doi.org/10.1093/molbev/msx116.
Kutz, S.J., Jenkins, E.J., Veitch, A.M., Ducrocq, J., Polley, L., Elkin, B., Lair, S., 2009. The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host-parasite interactions. Vet. Parasitol. 163, 217–228. https://doi.org/10.1016/j.vetpar.2009.06.008.
LaDeau, S.L., Leisnham, P.T., Biehler, D., Bodner, D., 2013. Higher mosquito production in low-income neighborhoods of Baltimore and Washington, DC: understanding ecological drivers and mosquito-borne disease risk in temperate cities. Int. J. Environ. Res. Public Health 10, 1505–1526. https://doi.org/10.3390/ijerph10041505.
Lafferty, K.D., 1997. Environmental parasitology: what can parasites tell us about human impacts on the environment? Parasitol. Today 13, 251–255. https://doi.org/10.1016/s0169-4758(97)01072-7.
Lafferty, K.D., 2009. The ecology of climate change and infectious diseases. Ecology 90, 888–900. https://doi.org/10.1890/08-0079.1.
Lafferty, K.D., Dobson, A.P., Kuris, A.M., 2006. Parasites dominate food web links. Proceedings of the National Academy of Sciences of the United States of America 103, 11211–11216. https://doi.org/10.1073/pnas.0604755103.
Lajeunesse, M.J., 2009. Meta-analysis and the comparative phylogenetic method. Am. Nat. 174, 369–381. https://doi.org/10.1086/603628.
Lindenfors, P., Nunn, C.L., Jones, K.E., Cunningham, A.A., Sechrest, W., Gittleman, J.L., 2007. Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. Glob. Ecol. Biogeogr. 16, 496–509. https://doi.org/10.1111/j.1466-8238.2006.00301.x.
Lyles, A.M., Dobson, A.P., 1993. Infectious-disease and intensive management - population-dynamics, threatened hosts, and their parasites. Journal of Zoo and Wildlife Medicine 24, 315–326.
MacLeod, C.J., Paterson, A.M., Tompkins, D.M., Duncan, R.P., 2010. Parasites lost - do invaders miss the boat or drown on arrival? Ecol. Lett. 13, 516–527. https://doi.org/10.1111/j.1461-0248.2010.01446.x.
Marcogliese, D.J., 2004. Parasites: small players with crucial roles in the ecological theater. Ecohealth 1, 151–164. https://doi.org/10.1007/s10393-004-0028-3.
Marcogliese, D.J., 2005. Parasites of the superorganism: are they indicators of ecosystem health? Int. J. Parasitol. 35, 705–716. https://doi.org/10.1016/j.ijpara.2005.01.015.
Mason, G.J., 2010. Species differences in responses to captivity: stress, welfare and the comparative method. Trends Ecol. Evol. 25, 713–721. https://doi.org/10.1016/j.tree.2010.08.011.
Milotic, M., Milotic, D., Koprivnikar, J., 2018. Exposure to a cyanobacterial toxin increases larval amphibian susceptibility to parasitism. Parasitol. Res. 117, 513–520. https://doi.org/10.1007/s00436-017-5727-0.
Muenkemueller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., Thuiller, W., 2012. How to measure and test phylogenetic signal. Methods Ecol. Evol. 3, 743–756. https://doi.org/10.1111/j.2041-210X.2012.00196.x.
Mysterud, A., Barton, K.A., Jedrzejewska, B., Krasinski, Z.A., Niedzialkowska, M., Kamler, J.F., Yoccoz, N.G., Stenseth, N.C., 2007. Population ecology and conservation of endangered megafauna: the case of European bison in Bialowieza Primeval Forest, Poland. Anim. Conserv. 10, 77–87. https://doi.org/10.1111/j.1469-1795.2006.00075.x.
Northover, A.S., Lymbery, A.J., Wayne, A.F., Godfrey, S.S., Thompson, R.C.A., 2018. The hidden consequences of altering host-parasite relationships during fauna translocations. Biol. Conserv. 220, 140–148. https://doi.org/10.1016/j.biocon.2017.12.037.
Nunn, C.L., Altizer, S.M., 2005. The global mammal parasite database: an online resource for infectious disease records in wild primates. Evol. Anthropol. 14, 1–2. https://doi.org/10.1002/evan.20041.
Nunn, C.L., Altizer, S.M., Sechrest, W., Cunningham, A.A., 2005. Latitudinal gradients of parasite species richness in primates. Divers. Distrib. 11, 249–256. https://doi.org/10.1111/j.1366-9516.2005.00160.x.
O'Connor, L.J., Walkden-Brown, S.W., Kahn, L.P., 2006. Ecology of the free-living stages of major trichostrongylid parasites of sheep. Vet. Parasitol. 142, 1–15. https://doi.org/10.1016/j.vetpar.2006.08.035.
Okulewicz, A., 2017. The impact of global climate change on the spread of parasitic

nematodes. Annals of Parasitiology 63, 15–20. https://doi.org/10.17420/ap6301.79.
Olival, K.J., Hosseini, P.R., Zambrana-Torrelio, C., Ross, N., Bogich, T.L., Daszak, P., 2017. Host and viral traits predict zoonotic spillover from mammals. Nature 546, 646–650. https://doi.org/10.1038/nature22975.
Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877–884. https://doi.org/10.1038/44766.
Panayotova-Pencheva, M.S., 2013. Parasites in captive animals: a review of studies in some European zoos. Zoologische Garten 82, 60–71.
Panayotova-Pencheva, M.S., 2016. Experience in the Ivermectin treatment of internal parasites in zoo and captive wild animals: a review. Zoologische Garten 85, 280–308.
Pandit, P.S., Doyle, M.M., Smart, K.M., Young, C.C.W., Drape, G.W., Johnson, C.K., 2018. Predicting wildlife reservoirs and global vulnerability to zoonotic Flaviviruses. Nat. Commun. 9, 5425. https://doi.org/10.1038/s41467-018-07896-2.
Pedersen, A.B., Antonovics, J., 2013. Anthelmintic treatment alters the parasite community in a wild mouse host. Biol. Lett. 9. https://doi.org/10.1098/rsbl.2013.0205.
Pedersen, A.B., Fenton, A., 2015. The role of antiparasite treatment experiments in assessing the impact of parasites on wildlife. Trends Parasitol. 31, 200–211. https://doi.org/10.1016/j.pt.2015.02.004.
Perez, J.M., Sanchez, I., Palma, R.L., 2013. The dilemma of conserving parasites: the case of *Felicola* (*Lorisicola*) *isidoroi* (Phthiraptera: Trichodectidae) and its host, the endangered Iberian lynx (*Lynx pardinus*). Insect Conservation and Diversity 6, 680–686. https://doi.org/10.1111/icad.12021.
Pietrock, M., Marcogliese, D.J., 2003. Free-living endohelminth stages: at the mercy of environmental conditions. Trends Parasitol. 19, 293–299. https://doi.org/10.1016/s1471-4922(03)00117-x.
Pietrock, M., Marcogliese, D.J., McLaughlin, J.D., 2002. Effects of cadmium upon longevity of *Diplostomum* sp. (Trematoda: Diplostomidae) cercariae. Chemosphere 47, 29–33. https://doi.org/10.1016/s0045-6535(01)00283-1.
Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., Maron, J., 2000. When is a trophic cascade a trophic cascade? Trends in Ecology and Evolution 15, 473–475. https://doi.org/10.1016/S0169-5347(00)01971-6.
Poulin, R., 1992. Toxic pollution and parasitism in fresh-water fish. Parasitol. Today 8, 58–61. https://doi.org/10.1016/0169-4758(92)90090-o.
Poulin, R., Morand, S., 2014. Parasite Biodiversity. (Smithsonian Institution).
Poulin, R., Krasnov, B.R., Mouillot, D., 2011. Host specificity in phylogenetic and geographic space. Trends Parasitol. 27, 355–361.
Pung, O.J., Spratt, J., Clark, C.G., Norton, T.M., Carter, J., 1998. Trypanosoma cruzi infection of free-ranging lion-tailed macaques (*Macaca silenus*) and ring-tailed lemurs (Lemur catta) on St. Catherine's Island, Georgia, USA. Journal of Zoo and Wildlife Medicine 29, 25–30.
R Core Team, 2018. R: a language and environment for statistical computing. In: R Foundation for Statistical Computing. Austria. URL, Vienna. https://www.R-project.org/.
Ratterree, M.S., da Rosa, A.P.T., Bohm Jr., R.P., Cogswell, F.B., Phillippi, K.M., Caillouet, K., Schwanberger, S., Shope, R.E., Tesh, R.B., 2003. West Nile virus infection in nonhuman primate breeding colony, concurrent with human epidemic, southern Louisiana. Emerg. Infect. Dis. 9, 1388–1394. https://doi.org/10.3201/eid0911.030226.
Regnier, C., Achaz, G., Lambert, A., Cowie, R.H., Bouchet, P., Fontaine, B., 2015. Mass extinction in poorly known taxa. Proceedings of the National Academy of Sciences of the United States of America 112, 7761–7766. https://doi.org/10.1073/pnas.1502350112.
Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x.
Ripple, W.J., Estes, J.A., Schmitz, O.J., Constant, V., Kaylor, M.J., Lenz, A., Motley, J.L., Self, K.E., Taylor, D.S., Wolf, C., 2016. What is a trophic cascade? Trends in Ecology and Evolution 31, 842–849. https://doi.org/10.1016/j.tree.2016.08.010.
Rohr, J.R., Dobson, A.P., Johnson, P.T.J., Kilpatrick, A.M., Paull, S.H., Raffel, T.R., Ruiz-Moreno, D, Thomas, M.B., 2011. Frontiers in climate change-disease research. Trends in Ecology and Evolution 26 (6), 270–277. https://doi.org/10.1016/j.tree.2011.03.002.
Rozsa, L., Vas, Z., 2015. Co-extinct and critically co-endangered species of parasitic lice, and conservation-induced extinction: should lice be reintroduced to their hosts? Oryx 49, 107–110. https://doi.org/10.1017/s0030605313000628.
Sato, T., Watanabe, K., Kanaiwa, M., Niizuma, Y., Harada, Y., Lafferty, K.D., 2011. Nematomorph parasites drive energy flow through a riparian ecosystem. Ecology 92, 201–207. https://doi.org/10.1890/09-1565.1.
Schmidt, F.L., Hunter, J.E., 2015. Methods of Meta-analysis, Correction Error and Bias in Research Findings, 3rd edition. Sage, Washington, DC.
Schmidt, K.A., Ostfeld, R.S., 2001. Biodiversity and the dilution effect in disease ecology. Ecology 82, 609–619. https://doi.org/10.2307/2680183.
Stephens, P.R., Pappalardo, P., Huang, S., Byers, J.E., Farrell, M.J., Gehman, A., Ghai, R.R., Haas, S.E., Han, B., Park, A.W., Schmidt, J.P., Altizer, S., Ezenwa, V.O., Nunn, C.L., 2017. Global mammal parasite database version 2.0. Ecology 98, 1476. https://doi.org/10.1002/ecy.1799.
Stringer, A.P., Linklater, W., 2014. Everything in moderation: principles of parasite control for wildlife conservation. Bioscience 64, 932–937. https://doi.org/10.1093/biosci/biu135.
Strona, G, 2015. Past, present and future of host-parasite co-extinctions. International Journal for Parasitology: Parasites and Wildlife 4 (3), 431–441. https://doi.org/10.1016/j.ijppaw.2015.08.007.
Strona, G, Fattorini, S, 2016. Are generalist parasites being lost from their hosts? Journal of Animal Ecology 85 (3), 621–623. https://doi.org/10.1111/1365-2656.12443.
Thompson, R.C.A., Lymbery, A.J., Godfrey, S.S., 2018. Parasites at risk - insights from an endangered marsupial. Trends Parasitol. 34 (1), 12–22. https://doi.org/10.1016/j.pt.2017.09.001.
Torchin, M.E., Mitchell, C.E., 2004. Parasites, pathogens, and invasions by plants and animals. Front. Ecol. Environ. 2, 183–190.
Tuten, H.C., 2011. Habitat characteristics of larval mosquitoes in zoos of South Carolina, USA. J. Am. Mosq. Control Assoc. 27, 111–119. https://doi.org/10.2987/10-6061.1.
Tuten, H.C., Bridges, W.C., Paul, K.S., Adler, P.H., 2012. Blood-feeding ecology of mosquitoes in zoos. Med. Vet. Entomol. 26, 407–416. https://doi.org/10.1111/j.1365-2915.2012.01012.x.
Van Oosterhout, C., Smith, A.M., Haenfling, B., Ramnarine, I.W., Mohammed, R.S., Cable, J., 2007. The guppy as a conservation model: implications of parasitism and inbreeding for reintroduction success. Conserv. Biol. 21, 1573–1583. https://doi.org/10.1111/j.1523-1739.2007.00809.x.
Viney, M.E., Graham, A.L., 2013. Patterns and processes in parasite co-infection. Adv. Parasitol. 82, 321–369. https://doi.org/10.1016/b978-0-12-407706-5.00005-8.
Wait, L.F., Peck, S., Fox, S., Power, M.L., 2017. A review of parasites in the Tasmanian devil (*Sarcophilus harrisii*). Biodivers. Conserv. 26, 509–526. https://doi.org/10.1007/s10531-016-1256-x.
Wallace, B.C., Lajeunesse, M.J., Dietz, G., Dahabreh, I.J., Trikalinos, T.A., Schmid, C.H., Gurevitch, J., 2017. OpenMEE: intuitive, open-source software for meta-analysis in ecology and evolutionary biology. Methods Ecol. Evol. 8, 941–947. https://doi.org/10.1111/2041-210x.12708.
Werner, C.S., Nunn, C.L., 2020. Effect of urban habitat use on parasitism in mammals: a meta-analysis. Proceedings.Biological Sciences 287, 20200397. https://doi.org/10.1098/rspb.2020.0397.
Windsor, D.A., 1997. Stand up for parasites. Trends Ecol. Evol. 12, 32. https://doi.org/10.1016/s0169-5347(97)88390-5.
Wood, C.L., Johnson, P.T., 2015. A world without parasites: exploring the hidden ecology of infection. Front. Ecol. Environ. 13, 425–434. https://doi.org/10.1890/140368.
Wood, A.M., Haro, C.R., Haro, R.J., Sandland, G.J., 2011. Effects of desiccation on two life stages of an invasive snail and its native cohabitant. Hydrobiologia 675, 167–174. https://doi.org/10.1007/s10750-011-0814-1.