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Behavioural ecology and infectious disease: implications for conservation of biodiversity

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Main Text

Summary

Behaviour underpins interactions among conspecifics and between species, with consequences for the transmission of disease-causing parasites. Because many parasites lead to declines in population size and increased risk of extinction for threatened species, understanding the link between host behaviour and disease transmission is particularly important for conservation management. Here, we consider the intersection of behaviour, ecology, and parasite transmission, broadly encompassing micro- and macroparasites. We focus on behaviours that have direct impacts on transmission, as well as the behaviours that result from infection. Given the important role of parasites in host survival and reproduction, the effects of behaviour on parasitism can scale up to population level processes, thus affecting species conservation. Understanding how conservation and infectious disease control strategies actually affect transmission potential can therefore often only be understood through a behavioural lens. We highlight how behavioural perspectives of disease ecology apply to conservation by reviewing the different ways that behavioural ecology influences parasite transmission and conservation goals.

1. Introduction:

Parasites and their hosts co-evolve, often in an arms race in which hosts exhibit behavioural strategies for clearing or avoiding parasites, and parasite traits facilitate transmission and evade host immunity [1, 2]. Host behaviours include strategies to mitigate parasite exposure, such as foraging to avoid contaminated areas [3], and reduced contact with sick conspecifics [4, 5].

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Other behaviours, however, facilitate the transmission of parasites, including promiscuous mating [6], and feeding on infected prey [7]. The interplay of behaviour and parasite transmission has consequences that scale up to populations [8], as well as communities and ecosystems [9] (Fig. 1). It is therefore necessary to understand the many connections between host behaviour and parasitism to effectively model population and community dynamics.

In the modern age of anthropogenic impacts on biodiversity, multiple compounding factors are putting species at risk of extinction. Infectious diseases are among the top five causes of species extinctions and have been implicated in the extirpation or extinction of 4% of species [10, 11]. Many more species are currently threatened by the combined effects of disease and anthropogenic factors such as habitat loss, fragmentation, and harvesting [12, 13]. Parasitism can negatively impact host population density [14, 15], and behaviours related to parasite avoidance, such as monogamy, can reduce effective population size [16, 17]. When parasites cause declines in host population sizes, the host becomes more vulnerable to extinction due to other behavioural phenomena, such as Allee effects and demographic stochasticity [Sæther and Engen, this issue, 18]. Thus, the interactions between behaviour and disease are essential for understanding population viability.

Several definitions are important for the review that follows. Throughout, we use an ecological definition of a parasite as any organism that lives in or on a host at some cost to that host, including micro-parasites such as bacteria, protozoa and viruses, and macroparasites, such as helminths and arthropods [11]. Parasites are transmitted via direct contact among individuals – e.g., grooming, mating, fighting – and indirectly via shared space and exposure to infectious stages of parasites in the environment. Vector-borne parasites are transmitted when infected vectors, such as mosquitoes and arthropod ectoparasites, feed on hosts. Parasites can also have

49 multiple hosts throughout their life cycles, and can be transmitted through intermediate hosts to
50 definitive hosts, including trophic transmission when a predator eats infected prey [11, 19, 20].
51 We generally consider three measures of parasitism. Prevalence refers to the proportion of
52 individuals that are infected. Intensity or parasite "load" is a measure of how many parasites
53 infect a host individual. Richness is the number of parasite species found in an individual host, a
54 group, or a species.

55 Here, we review how behaviour influences parasite transmission, with impacts on
56 individuals, populations, communities, and ecosystems (Fig. 1). We especially focus on the
57 nexus of disease, behaviour, and ecological principles that can be leveraged for management and
58 conservation (Table 1). First, we examine the effects of behaviours on parasite transmission
59 because behaviour affects how hosts interaction with the environment and other individuals,
60 influencing parasite exposure and infection risk. Second, we investigate the effects of parasite
61 infection on behaviour because infection then influences the acquisition of resources, fecundity,
62 and predation risk, including through sickness behaviours, mating patterns, and manipulation of
63 host behaviour by parasites. Recognizing that these concepts are not mutually exclusive, we
64 illustrate how they are often involved in feedbacks of transmission.

65 **1. Behaviours that influence parasite transmission**

66 The behavioural interactions among individuals, with the environment, and vectors affect the
67 transmission of parasites (Fig. 1). While some behaviours increase the risk of parasite
68 transmission, others are counterstrategies to avoid parasites. The interactions among individuals,
69 driven by their social organization, network dynamics, and patterns of range use, influence the
70 probability of contacts that can facilitate transmission. When parasites infect multiple hosts, the
71 patterns of interactions among species in communities creates a complex system of transmission

potential. In this section, we discuss each of these phenomena in turn, illustrating how behaviour affects transmission with consequences for species viability and conservation.

a. Social organization

Ecological and social factors lead many species to be solitary throughout most of the year, while others have a tendency to form aggregations of social groups. Parasitism is hypothesized to be a significant cost of group living [21-23]. Species that live in larger groups are predicted to have higher rates of parasitism than those that are solitary or form smaller groups due to the higher local density of hosts [14], accumulation of infectious material in the environment [24], and migrants that carry new parasites into groups [25]. Indeed, larger flocks of birds had higher parasite prevalence than solitary birds [26, 27], and group-living gorillas had higher mortality rates from Ebola (97%) than solitary males [77%, 28]. It would therefore appear that living in groups can have significant costs due to parasitism.

Despite the theory outlined above that predicts a positive relationship between group size and parasitism, empirical results have often found no relationship, or even a negative association, between group size and parasitism. In African bovids, for example, group size was not correlated with parasitism in eleven sympatric species, and only buffalo and hartebeest had higher prevalence of helminth infection in larger groups than smaller ones [29]. In comparative studies of primates and rodents, as well as meta-analyses across multiple taxa, there were weak or nonsignificant relationships between group size and parasite species richness [30-33]. These results suggest that other mechanisms are buffering individuals in larger groups from the higher risk of parasitism.

The benefits of group living, such as herd immunity, may offset the costs of parasitism in larger groups [34-37]. Other mechanisms by which the benefits of group living outweigh the costs of parasitism include increased vigilance for predators and access to resources. For example, although parasite infection risk was higher in larger groups of Grant's gazelles (*Nanger granti*) than in smaller groups, the cumulative benefit of vigilance allowed individuals to spend more time feeding in larger groups [38]. Solitary wolves (*Canis lupus*) were more likely to die from mange infection than those that lived in packs, most likely due to the increased probability of prey capture in groups [39]. Thus, sociality can increase the probability that individuals gain access to resources, and decrease the threat of predation and competition. Increased nutrient intake and decreased stress could offset deleterious impacts of parasites, such as decreased foraging due to lethargy or nutrients lost to helminths. As habitats are lost and degraded, however, the availability of resources often declines, making it more difficult to sustain large social groups and therefore there may be consequences for the health of populations beyond that expected based on nutrients or parasites alone [40].

b. Social networks and transmission

The patterns of behavioural interactions among individuals also affect the probability of parasite transmission over and above what would be expected based on random interactions among individuals (i.e., a mass action model). Heterogeneity in contact rates leads some individuals to be more connected in social networks than others. The highly connected, or more central, individuals likely play key roles in parasite transmission, potentially serving as super-spreaders [41]. Heterogeneities in contacts led to the "20 / 80 rule," in which a small proportion of the population (20%) is predicted to account for a large majority of the contacts and transmission potential (80%)[42]. Variation in contact rates among individuals and through time is especially important for predicting characteristics of networks with impacts for disease outbreaks [Silk et al, this issue, 43, 44-47], and to clarify why the relationship between group size and parasitism is inconsistent and weak across studies [48, 49].

In addition to properties of individuals, variation in pair-wise interactions can produce structure in the overall network. In primate social groups, for example, subgroups often emerge, within which interactions are more frequent relative to interactions between subgroups [50, 51]. In social network theory, subgrouping is measured using metrics such as community modularity [52]. High modularity can decrease transmission because fragmentation of the network and cohesion within subgroups tend to 'trap' parasites within a subgroup, leading to lower outbreak size and delayed transmission dynamics [43, 48, 49, 51, 53]. These features of network structure and individual centrality can therefore have important applications to conservation management strategies.

Social network theory can be applied in designing intervention strategies such as vaccination or culling (Table 1). Because only a subset of individuals accounts for the majority of disease transmission, targeting those individuals for treatment or removal would be more effective than random treatment [42]. In an epidemiological simulation on observed networks of chimpanzees (*Pan troglodytes*), vaccinating the most central individuals in social networks would reduce the proportion of the population that would have to be treated by 10%, compared to random treatment [44]. When parasites are highly contagious, however, all individuals become infected quickly and connectivity in the network does not affect outbreak dynamics.

Though centrality-based approaches have potential applications to disease interventions and population management, the effectiveness is dependent on properties of the whole network. One such case is the Tasmanian devil facial tumour disease, in which Tasmanian devils (*Sarcophilus harrisii*) transmit cancerous cells among individuals through biting [54] (Table 1). The disease

140 reduces fecundity and increases mortality, leading to a 60% decline in population size [55].
141 Although contact networks of Tasmanian devils exhibit heterogeneities in potential disease
142 transmission, their networks show low modularity [56]. Targeted vaccination programs focused
143 on central individuals would therefore have little effect on slowing the transmission of facial-
144 tumour disease [57]. Instead, isolating uninfected populations is an important priority. For
145 conservation, it is important to understand how the pattern of interactions among hosts as well as
146 overall network structure affect the process of parasite transmission, but also how parasite
147 infections affect the dynamics of the network. In future research, dynamic network models
148 should be investigated to better incorporate the spatiotemporal variation in contacts that are
149 important for parasite transmission [45, 46].

150 Due to the difficulty of studying the social relationships of a whole population, social
151 networks of subgroups can be used to identify individual traits linked to parasite transmission,
152 such as sex, body size, and relative location in foraging parties, which can be used in lieu of
153 quantitative data on individual network centrality. For example, larger-bodied and more
154 aggressive deer mice (*Peromyscus maniculatus*) have higher contact rates and probability of
155 hantavirus infection than smaller individuals [58], and large male mice had higher prevalence of
156 *Leptospira* infection than small males and females [59]. Chimpanzee individuals that foraged
157 with the rest of the group had higher centrality than those that foraged alone, and this salient
158 behaviour could be used to target individuals for vaccination [44]. Targeted intervention
159 programs that account for these transmission-related behavioural traits could improve the
160 efficacy of management, and also allow managers to forecast the spread of diseases by predicting
161 contact rates based on the frequency of individuals with specific behavioural traits in the
162 population, thus improving recommendations for interventions.

c. Range use, intergroup encounters, and dispersal

Living in distinct, stable home ranges creates structure in population networks, and can lead to barriers that act to quarantine infectious diseases, thus potentially reducing disease risk at the population level [60, 61]. In this context, it is important to consider the influence of territoriality, intergroup encounters, and dispersal on parasite transmission. Territorial behaviour can act as a parasite-avoidance strategy to reduce contacts with neighbouring individuals or groups, but it may also promote environmental transmission through increased intensity of the home range [19]. Territorial species must patrol and defend their range boundaries, and this tends to increase the intensity of range use compared to non-territorial species [62, 63]. In a spatially-explicit individual-based model of faecal-oral parasite transmission in a socially-structured population, range-use intensity was a strong predictor of parasite prevalence [24]. Further, greater use of core areas was positively related to parasite prevalence, while home-range overlap among groups was not [24]. Across primate species, range-use intensity and territoriality were positively associated with parasite species richness, including parasites with direct and indirect transmission modes [64]. The association between range-use intensity and the probability of exposure to infectious agents in the environment leads to increased threat of parasitism for species forced into small patches due to habitat loss and fragmentation [e.g., 65]. Thus, parasitism can compound other effects of anthropogenic habitat loss, such as limited resources.

As discussed above, group size alone did not explain variation in helminth infection in most African bovids. Instead, nuances of sociality and territoriality explain variation in parasitism. Among Grant's gazelles, territorial males have higher infection intensity with directly-transmitted strongyle worms than non-territorial males and nursery herds which float among territorial males [29]. Further, gregarious and territorial ungulate species had higher parasite

186 richness than solitary and non-territorial species [29]. These effects may be partially explained
187 by higher exposure to more highly contaminated soils in territorial than non-territorial species [3,
188 66]. Variation in physiology also plays a proximate role, with aggression linked to higher
189 testosterone and therefore potentially compromising the immune system compared to less
190 aggressive males [67]. The intrinsic and extrinsic traits that affect heterogeneity in exposure and
191 susceptibility are important for future research to understand variation in parasitism.

192 Dispersal, including leaving the natal territory, can facilitate disease transmission, especially
193 in group-living species. The effects of sex-biased dispersal may lead to different outcomes for
194 parasite transmission. For example, theoretical models showed that dispersal of low-ranking
195 males in a socially-structured population had little effect on intergroup STD transmission, given
196 that these males were less likely to have access to mates and therefore had lower STD prevalence
197 [68]. In contrast, an individual-based model revealed that parasite transmission was driven by
198 the dispersal of infected females from groups when males died due to the disease, which the
199 authors termed "parasite-mediated dispersal" [25]. Consistent with this theoretical model,
200 empirical data on primate species show that prevalence and richness of STDs are higher when
201 females disperse [68].

202 To apply these behavioural perspectives in a conservation context, managers will need to
203 account for the combined effects of intergroup encounters and dispersal patterns. For example,
204 dispersing individuals may not always be the disease super-spreaders. In lions, dispersing
205 bachelor males were not the most important individuals in the spread of canine distemper virus
206 as they rarely come into contact with resident individuals; instead, intergroup encounters among
207 female prides with resident males were more likely to transmit the virus [69]. Modelling
208 approaches that can integrate data on behavioural ecology, including social networks, range-use

209 intensity, intergroup encounters, and dispersal patterns, allow for more realistic predictions of parasite transmission. Further, these models can produce nuanced understanding of the most important factors driving transmission.

212 Similarly, the combined effects of territoriality and dispersal behaviours have important applications to strategies for mitigating the impacts of disease spread in wildlife management. Culling or harvesting involves removing a subset of the population to manage disease and overpopulation (Table 1). Culling can be effective because host population density is a limiting factor for parasite transmission [13, 70, 71], and can alleviate both the threat of disease and the negative impacts of overpopulation [e.g., white-tailed deer, 72, 73]. Such strategies may require extremely large proportions of the population be removed, which is problematic for endangered wildlife [71]However, when individuals are removed, territories may open, with individuals dispersing into those vacant areas and increasing parasite transmission [74, 75]. Predicting the efficacy of culling for disease management must therefore incorporate aspects of behavioural ecology.

223 European badgers (*Meles meles*) in the UK, for example, are implicated in the spread of bovine tuberculosis to cattle, posing problems for livestock [76]. Culling was used to control badger populations but also destabilized their territories, which led to immigration into the culled area, greater overlap in ranges, and less stable range boundaries [76]. This destabilizing effect can increase disease prevalence if the rate, duration, and spatial extent of culling are inadequate to properly control the population [76, 77]. An area for future research is to model the effects of culling and vaccination regimes that apply knowledge of territorial behaviour to dynamic social networks. For example, male badgers are responsible for most between-group contacts that could facilitate parasite transmission among groups [78]. Using simulations, one approach

would be to test the prediction that maintaining populations of territory-holding males via vaccination will decrease dispersal by stabilizing territories. Though badgers are not an endangered species, the system is important for understanding how behaviour affects disease transmission, and how strategies to mitigate spill-over to livestock can implement behavioural ecology theory. The findings from the badger system can then be used to inform disease management of endangered species.

d. Shared use of limited resources

The spatial distribution and abundance of resources influence the probability of contacts and thus parasite transmission. Illustrating the feedbacks among behaviours, intergroup encounters often occur at shared resources, which can lead to the transmission of parasites, both within and between species (Fig. 1). In gorillas, for example, different groups overlapped in the fruit trees they visited and were exposed to potentially infectious agents that could lead to parasite transmission [79]. These observations are especially worrisome because Ebola is an important parasite that could be transmitted among groups, with devastating impacts on ape populations [28, 79-81]. The patterns of shared space and resource use among groups of gorillas is mirrored in many species, and can be modelled to understand the general effects of space use and intergroup encounters for the transmission of parasites.

Behavioural choices associated with drinking water can also influence parasitism. For example, when water is limited, sharing waterholes can generate intense exposure to parasites. Empirical results illustrate how sharing limited water sources was related to bovine tuberculosis (*Mycobacterium tuberculosis*) prevalence in wild boars and red deer [82, 83] and mass outbreaks of anthrax (*Baccillus anthracus*) in hippos (*Hippopotamus amphibius*) [84]. In theoretical models, seasonal waterhole sharing markedly increased disease prevalence, and seasonal migration increased disease risk at shared resources, but also enabled hosts to escape parasites that built up in their "normal" home ranges [85]. Understanding the impacts of the distribution and use of limited resources on the probability of disease transmission can be important for managing diseases in wildlife and livestock, especially as anthropogenic pressures cause declines in the abundance of resources and as a result changes in ranging patterns.

The union of movement and landscape ecology with disease epidemiology has important applications to conservation given anthropogenic habitat degradation [86]. In simulations of intergroup encounters based on data from long-term studies of endangered primates, direct transmission of a parasite was related to the abundance of resources in the landscape [87]. The highest probability of intergroup encounters and thus parasite transmission occurred at intermediate levels of resource density. In contrast, the probability of parasite transmission was low when resources were highly abundant or scarce. As natural habitats shrink and animals are forced into smaller, lower quality ranges, the effects of ranging behaviour on parasite transmission potential will be important for predicting future population dynamics.

e. Cross-species transmission

Many behaviours affect parasite transmission among multiple hosts (Fig. 1). Cross-species transmission involves a source or reservoir host that transmits a parasite to a target species, with deleterious effects for the target species [41, 88]. Reservoir species are susceptible to the parasite but live long enough to support transmission, use spaces that expose them to parasites and vectors, and are physiologically similar to other hosts such that the parasite can establish in multiple hosts [89]. The probability of transmission among species is predicted to be higher for species that have similar behavioural and ecological niches. Examples of cross-species transmission illustrate the negative impacts of reservoirs on the management and conservation of target species [88, 90]. Reservoirs allow the parasite to persist, even if the population size of the target is small. Developing management plans to mitigate a disease outbreak in an endangered species must therefore also consider if it a disease caused by a multispecies parasite and how to manage the potential reservoirs as well as the target threatened species.

Overlap in space and shared resources among species creates opportunities for transmission [79, 83, 91]. Canine distemper virus in lions most likely had multiple spill-over events from sympatric hyenas and jackals, which could transmit the virus at shared resources such as carcasses [92]. Therefore, in most complex communities with multiple, closely-related species, the opportunities for parasite transmission are greater than would be predicted from a single-species model. Management strategies should incorporate these multi-host dynamics to accurately represent transmission risks to threatened species [e.g., 92].

2. Effects of infection on behaviour and transmission

The review above illustrates how host behaviour affects parasite transmission patterns. While many of these behaviours are likely independent of parasite infection, infection itself can change the behaviour of hosts in many ways. Some behaviours, including sickness behaviours, are outcomes of infection that help to clear the parasite. Parasitic infection has long been hypothesized to drive mate choice decisions, with concomitant effects on fitness and the evolution of phenotypes. In other cases, the parasites themselves have evolved mechanisms to manipulate host behaviour to promote their own transmission. This section describes the feedback between parasitic infection and host behaviour that affects transmission dynamics. The effects of infection on behaviour can be especially important for the management of wildlife because infection often increases the chances of onward transmission and the risk of predation.

a. Sickness behaviour

The most direct way that parasitic infection can affect the behaviour of an individual is through sickness behaviour. Sickness behaviours include a suite of behavioural changes related to infection, such as general inactivity or lethargy, increased sleep, reduced social interactions and feeding, and postures that help to reduce heat loss and mount a fever response [93]. Although these behaviours have benefits for conserving energy and mounting an immune response to clear the parasite, they also probably entail significant fitness costs, such as susceptibility to predation [94] or losing competitive interactions.

Changes to interactions among individuals in relation to infection status affects the probability of parasite transmission. Infected mice used fewer nest sites than uninfected mice, leading to reduced interactions with other individuals [95]. This change in behaviour would likely decrease the probability of transmission due to the decreased interactions between infected and susceptible individuals. Sickness behaviour is generally expected to reduce contact rates and social transmission of parasites; however, in captive house finches (*Carpodacus mexicanus*), healthy males increased their time spent feeding in proximity to males experimentally infected with *Mycoplasma gallisepticum,* and won aggressive interactions more often than with uninfected males [4]. This change in behavioural interactions due to parasitic infection likely increases the probability of transmission. Individual-based models revealed that the decreased activity of infected individuals can result in increased contact rates and transmission when resources are limited and individuals are crowded in space [96]. Therefore, sickness behaviours can have opposing outcomes for the probability of onward transmission. This highlights that quantitative assessments of sickness behaviours in wildlife are important for understanding how the recovery of infected animals affects population dynamics via effects on disease transmission and the potential for increased predation risk. Conservation strategies may aim at using sickness behaviour to reduce transmission rates by isolating infected individuals.

b. Mate Choice

For many sexually-reproducing animals, direct physical contact is needed for fertilization. As we discussed previously, contacts among individuals are fundamental to the social network, and provide opportunities for the exchange of infectious agents. Mate choice behaviour, therefore, has important impacts on individuals' reproductive success and the probability of infection with a parasite, effects which may scale up to population-level phenomena such as host population growth rates and parasite prevalence. Understanding the causes and consequences of mate choice behaviour can clarify the roles of co-evolved parasites in driving host phenotypes.

Parasitism is hypothesized to affect mate choice, with the exaggeration of male advertisement characteristics commonly posited to be driven by female choice, including in relation to parasitism. Females may choose males with exaggerated sexual traits because males have heritable genetic resistance to infectious disease [97]. In meta-analyses of inter- and intraspecific studies with ecto- and endoparasites, half of the studies found positive associations between exaggerated male sexual traits and parasite intensity, but the overall relationship was not significant [98]. Rather than choosing males based on indirect signals of genetic resistance to parasites, females seem to use direct signals of infection to avoid sick males [6, 99]. Experimental evidence across studies of more than 15 host species has shown that females chose healthy males over infected males in the absence of exaggerated sexual traits [99-101]. Therefore, the cues of infection status may directly influence female mating preferences, affecting male reproductive success as well as the possibility of parasite transmission.

A counter-example is found in Tasmanian devil facial tumour disease described above. Animals with the highest reproductive success are the most socially dominant and most frequent biters – behaviours that result in a high probability of infecting others with facial tumour disease [102]. Thus, Tasmanian devils that have the highest fitness are also most exposed to the parasite. Management options available to conserve the population include large-scale removal of all potentially infected individuals (those greater than 2 years of age) and isolation of uninfected populations [57].

Regardless of the proximate and ultimate mechanisms of sexual selection, the subsequent influence of infection on mating behaviours and reproductive success has important implications for population growth. The links between individual behaviours, especially mate selection, and parasite transmission are important to consider in assessing population viability and wildlife management [16]. Selective mating affects an individual's probability of finding a mate and thereby influences effective population size, variance in fecundity, and the probability of extinction [18, 103]. Thus, information on mate choice and reproductive success increases the accuracy of population viability models. Further, high reproductive skew may increase the frequency of beneficial genes, but may also eliminate genetic variation that is important for adapting to future change and coevolving parasites [104]. Awareness of these consequences is important for population management and breeding programs. These behaviours scale up to population-level phenomena, with impacts on social organization, networks, territoriality, and range use and thus, again the transmission of parasites

c. Mating system

The mating system of organisms may be a selective response to infected individuals and the risk of parasite transmission. While mate choice refers to which individuals choose to mate with one another, mating systems refer to the ways in which individuals associate for reproduction, including short- and long-term associations. Lifetime monogamy is a potential behavioural counter-strategy to STDs because mating with only a single partner would reduce exposure to STDs [61]. In support of this hypothesis, promiscuity was positively related to the number of basal white blood cells, a measure of investment in immune defence, in a comparative study across species of primates and carnivores [105, 106]. While monogamy may reduce parasite transmission, it is also a mating strategy that reduces the effective population size by decreasing the proportion of mated females because of the difficulty of finding bachelor males, and thus increases demographic stochasticity and extinction probability [16]. Therefore, different optimal strategies exist between avoiding infectious disease and maximizing reproductive success.

Monogamy can be a safe strategy in the context of STDs, but variation in other factors, especially STD prevalence, is correlated with changes in the probability of infection that can outweigh the protective effects of monogamy [107]. Based on simulations of a single host species with multiple mating strategies and a theoretical STD that was sterilizing but not deadly, when STD transmissibility and prevalence were low, monogamy reduced the probability of individual infection. When transmissibility and prevalence were high, however, the chances of mating with an infected male were high whether females were monogamous or promiscuous, and females maximized their chances of conception by having multiple mates [107, 108]. These results highlight that while monogamy should generally reduce STD transmission, variation in STD prevalence and other factors also affect the optimal mating strategy.

d. Parasite manipulation of host behaviour

Selection can act on parasite traits to manipulate host behaviour when the traits benefit transmission. Parasites often exhibit exquisite adaptations to manipulate host behaviours in ways that increase the probability of onward transmission, often at substantial costs to the host [109]. These "parasite manipulation" behaviours are distinct from sickness behaviours because they increase parasite transmission, while sickness behaviours are aimed at clearing infection and thus reducing transmission. Parasites manipulate the behaviour of hosts in a variety of ways, including within- and among-species transmission. Many parasites have complex life cycles including multiple hosts, such as those nematodes and trematodes that encyst in the flesh of intermediate hosts that will be preyed upon by the definitive host. These parasites benefit from increased predation on the intermediate host, as increasing predation rates increase transmission.

Several parasites exploit their hosts' central nervous systems to promote their own transmission [110]. Rabies, a lyssavirus that is transmitted through saliva, causes behavioural changes in the host that increase aggression and decrease fearful responses, both of which promote transmission by increasing biting [110, 111]. Rabies has important impacts on wildlife management, such as when it was introduced to threatened Ethiopian wolves by a feral dog, causing increased aggression and salivation, and killed 10% of the known population [Table 1, 112]. Effective rabies management will necessarily include multiple perspectives that combine population ecology, epidemiology, behavioural modelling [113], as well as treatment and population control of feral dogs [111].

STDs generally benefit from increased sexual behaviour of infected hosts [114]. One way to achieve this, at least in female mammals, is through sterility: by eliminating gestation and lactational amenorrhea, a sterilizing STD would increase the frequency of mating and thus transmission. STDs can have major impacts on individual host fitness, causing severe damage to reproductive organs [115] and infertility [116] that have negative consequences for population growth and are important for wildlife management and captive breeding [116, 117].

Parasites with complex life cycles can manipulate host behaviour to promote trophic transmission by affecting the likelihood of predation (Table 1). *Toxoplasma*, for example, is a protozoan parasite with a complex life cycle. Infectious stages reside in multiple hosts, especially rodents and carnivores, such as cats [118]. Rodents, the intermediate hosts, become infected by exposure to oocytes in the faeces of cats or in the environment, and the parasite transmits back to the cat, the definitive host, through predation. Consistent with the manipulation hypothesis, infected rodents exhibited increased exploratory behaviour and became less fearful when confronted with cat odour's [119]. Similarly, killifish infected with trematodes which encyst their brains were preyed on significantly more frequently by herons, the definitive host, than were uninfected fish [7]. By affecting host population growth and the behaviour of hosts that make them more vulnerable to predation, parasites have important impacts on food webs [15, 119-123], with potentially destabilizing effects for ecosystems. Addressing how behavioural changes due to parasitic infections at lower trophic levels may affect higher levels of the food chain is therefore important to assess the resilience of an ecosystem to environmental change.

3. Conclusions

We reviewed the connections between parasitism and the behaviour of animals, and how those behaviours affect ecology and conservation. Our review reveals how feedbacks between parasitism and behaviour affect population dynamics via survival and fecundity are linked across scales, from individuals to ecosystems. Transmission begins with individual-level behavioural interactions with conspecifics, with the environment, and with other species. These processes affect population-level phenomena, and ultimately they can impact ecosystem dynamics. This review illustrates the ways in which host behaviour affects the dynamics of parasite transmission, via ecological and social mechanisms, and how those dynamics affect host population viability. The interconnections among mechanisms lead to a complex system in which many factors may simultaneously facilitate and impede parasite transmission (Fig. 2). To understand the outcome of behavioural effects on parasite transmission, research needs to account for the trade-offs of ecological and social processes for parasite transmission.

Basic epidemiological models can be made significantly more realistic when incorporating information on behaviour. Disease-driven population declines or extinctions have led to wildlife management approaches that apply principles of population ecology, epidemiology, and network theory (Table 1). In the future, with habitat loss, degradation, and climate change, the important interplay between parasitism, behaviour, and population dynamics will be perturbed, with consequences for the conservation of wildlife. Incorporating information on behavioural ecology can improve the efficacy of wildlife management decisions in light of future threats to biodiversity.

Areas of future research in this realm include modelling approaches that incorporate heterogeneities in contacts among individuals, social groups, and species through time [46, 69, 92]. Further, combined intervention strategies including culling, vaccination, and contraception may elicit the desired effects of decreased transmission without adversely perturbing the social organization of populations. Realistic models that incorporate these nuances can give finer insights into the utility of different intervention strategies [e.g., 72], such as in African carnivores suffering from canine distemper virus [69, 92]. Another area requiring further research includes comparing multiple measures of infection together. In fish, for example, parasite species richness was higher in migratory species than non-migratory, but prevalence and intensity did not differ [124]. Therefore, it is important to make clear predictions and interpretations in light of the variables measured to understand how behavioural mechanisms might affect richness, prevalence, and intensity. A significant gap remains to understand how natural host-parasite interactions should be integrated into conservation and management practices [122, 125]. In closing, the links between parasites and host behaviour is important for theories of population, community, and ecosystem ecology. An integrated theory of disease ecology and behaviour will ultimately help us forecast and manage the consequences of anthropogenic effects on ecosystem health.

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Authors' Contributions

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Competing Interests

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References

Tables

Behaviour	Effect of parasites on populations	Conservation & management	Example host-parasite system
Behaviours that affect parasite transmission			
Group size	Group-living can increase parasitism with negative consequences for mortality Benefits of group-living can offset costs of parasites	Group-living species monitored for parasite, and larger colonies targeted for interventions	Mange in wolves [39] Helminths in ungulates [29] Ebola in gorillas [28]
Social network properties	Variation among individuals in contact rates predict outbreak patterns Individuals highly connected in networks can be super-spreaders Overall network subdivision impacts outbreak dynamics	Individuals with high centrality targeted for intervention (e.g., vaccination/removal) Understanding how network subdivision affects parasite transmission	Hantavirus in rodents [58] Facial tumour disease in Tasmanian devils [56, 57] Viruses in chimpanzees [44]
Parasite infection affects behaviour			
Sickness behaviour	Sick individuals reduce activity and social interactions, decreasing potential for transmission Healthy individuals may preferentially interact with sick individuals because they are poor competitors, increasing transmission potential	Recognizing sickness behaviour important for culling / treating target individuals	Finches and *Mycoplasma* [4]
Mate choice	Females choose healthy males as mates, decreasing	Monitoring transmission of STDs important for management	Meta-analyses of birds, fish, amphibians, lizards

	transmission from infected males	Mate choice affects breeding population size and variation in population size due to demographic stochasticity	and endo- and ecto-parasites [98, 99]
Parasite manipulation of hosts	Parasites affect host behaviour to promote transmission	Recognizing how trophic transmission affects predator-prey dynamics Monitoring rabies, feral dogs, & endangered carnivores	*Toxoplasma* transmission, especially from small prey to carnivores [126] Ethiopian wolves and rabies lyssavirus [112]

Figure and table captions

Table 1. Links between empirical examples of animal behaviour and parasite transmission with consequences and applications to conservation and management.

Figure 1. Schematic illustrating the links between behaviour and infectious disease transmission across levels of biological organization. From individual behaviours, such as avoiding sick conspecifics, to group- and population-levels, parasites can affect parasite dynamics within species. Parasitism affects communities and ecosystems via cross-species spillover and food webs dynamics.

Figure 2. Venn diagram illustrating the overlap in processes of behavioural ecology that affect parasite transmission dynamics. Plus and minus signs indicate whether the behavioural mechanism facilitates or impedes parasite transmission. For example, social behaviours can have both positive (increased transmission within social units) and negative effects on parasite transmission (heterogeneous contact rates among individuals, modularity in social units / populations). The relationships between behavioural concepts demonstrate how variation in social and mating behaviour (e.g., monogamy), can decrease parasite transmission, while mate-seeking behaviours can increase transmission (e.g., via parasite-mediated dispersal).

Figures

Fig. 1

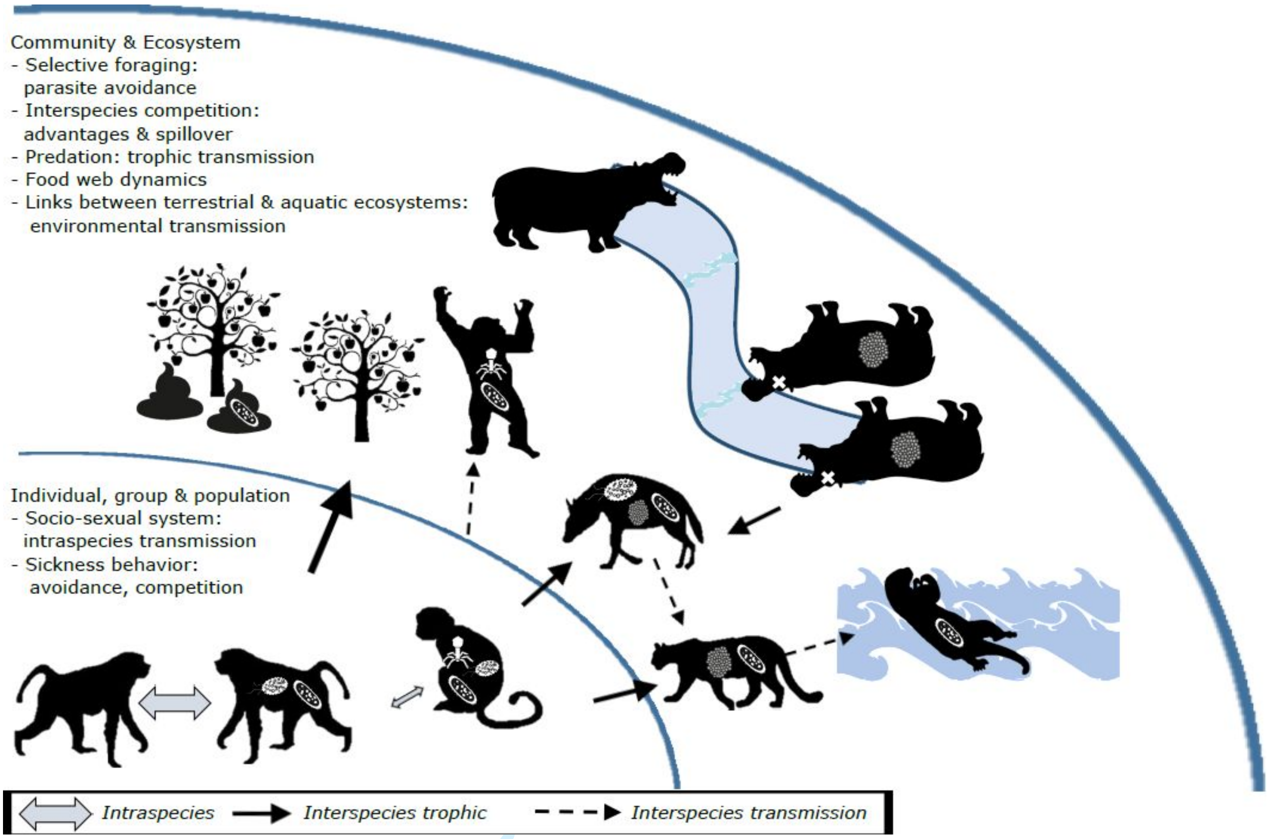
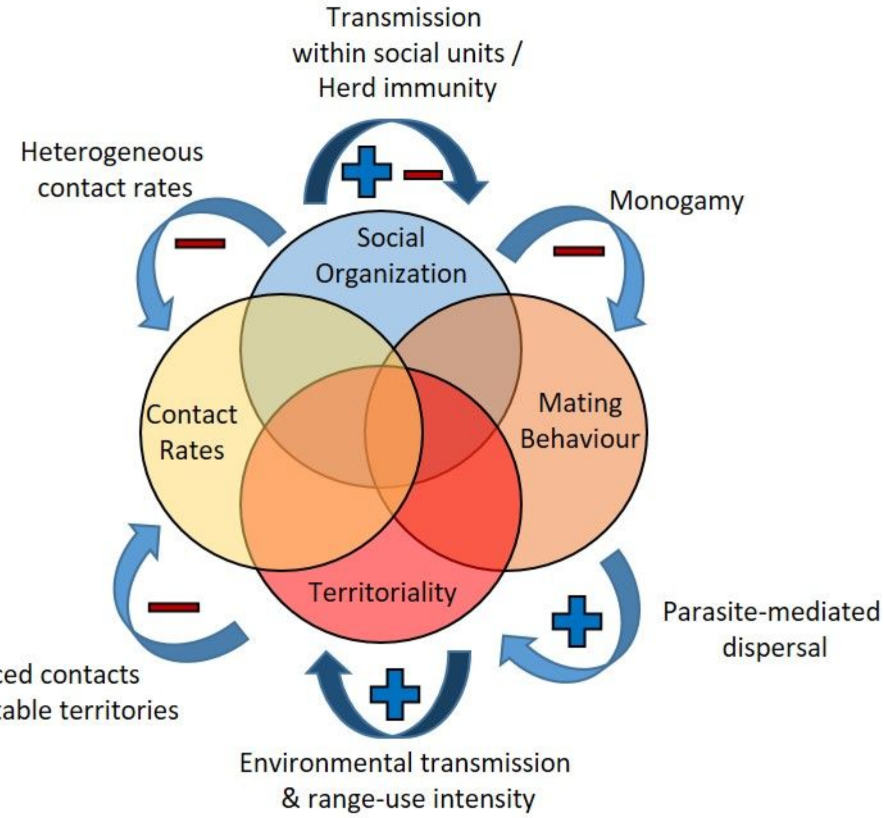


Fig. 2



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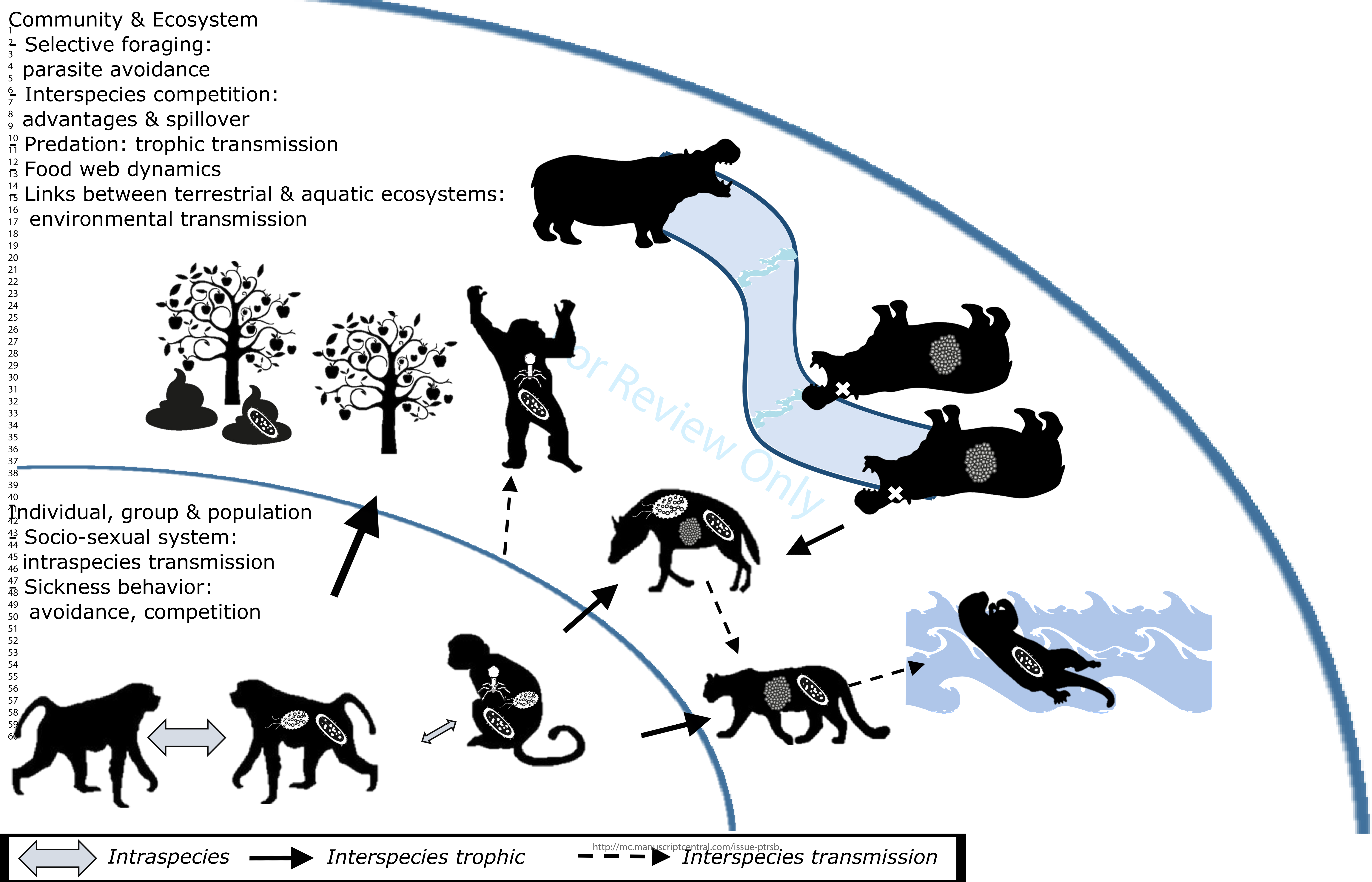
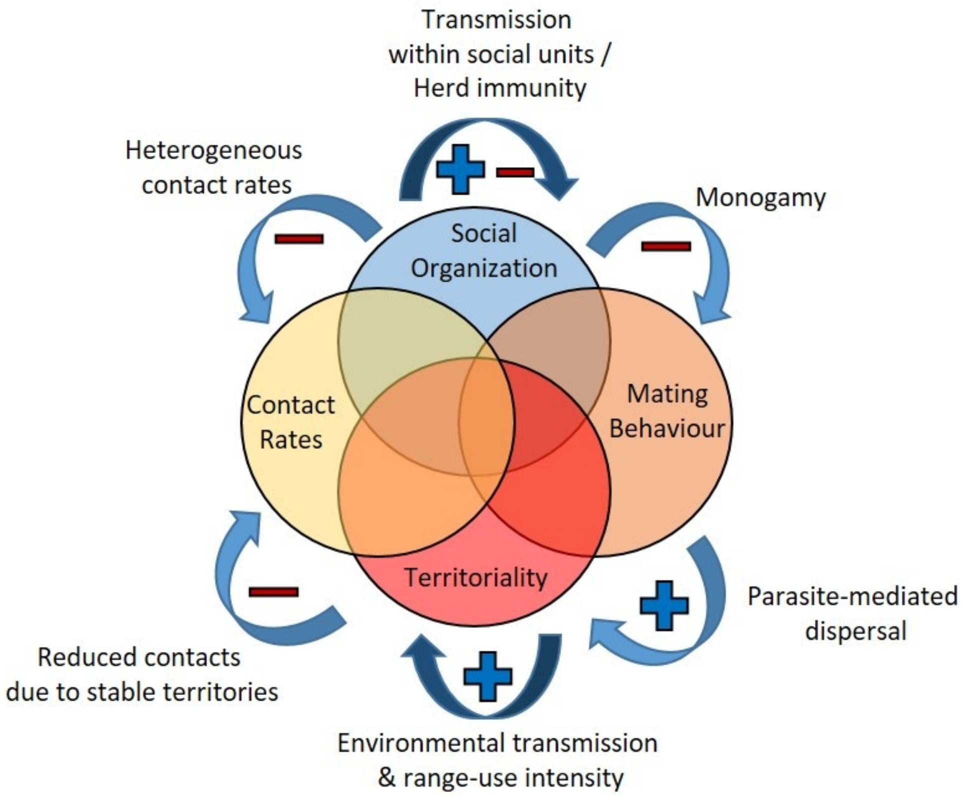

Community & Ecosystem
Selective foraging:
parasite avoidance
Interspecies competition:
advantages & spillover
Predation: trophic transmission
Food web dynamics
Links between terrestrial & aquatic ecosystems:
environmental transmission
Individual, group & population
Socio-sexual system:
intraspecies transmission
Sickness behavior:
avoidance, competition
Intraspecies
Interspecies trophic
Interspecies transmission



Venn diagram illustrating the overlap in processes of behavioural ecology that affect parasite transmission dynamics. Plus and minus signs indicate whether the behavioural mechanism facilitates or impedes parasite transmission. For example, social behaviours can have both positive (increased transmission within social units) and negative effects on parasite transmission (heterogeneous contact rates among individuals, modularity in social units / populations). The relationships between behavioural concepts demonstrate how variation in social and mating behaviour (e.g., monogamy), can decrease parasite transmission, while mate-seeking behaviours can increase transmission (e.g., via parasite-mediated dispersal).

136x111mm (150 x 150 DPI)