Biological Conservation 220 (2018) 140–148

Contents lists available at ScienceDirect

Biological Conservation

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

Perspective

The hidden consequences of altering host-parasite relationships during fauna translocations

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ARTICLE INFO

Keywords:
Polyparasitism
Wildlife
Anti-parasitic drug treatment
Parasite conservation

ABSTRACT

Host-parasite relationships are complex, and in wild animal populations individuals are commonly co-infected with various parasite species or intraspecific strains. While it is widely recognised that polyparasitism has the potential to reduce host fitness and increase susceptibility to predation or disease, the role of polyparasitism in influencing translocation success has never been investigated. Here we review the consequences of translocation for the host-parasite infracommunity and demonstrate how translocation-induced perturbations to within-host-parasite relationships may exacerbate the negative impacts of polyparasitism to the detriment of host health and translocation success. We also consider the ecological and immunological effects of altering host-parasite assemblages during translocation, and illustrate how the use of anti-parasitic drugs can further modify parasite infracommunity dynamics, with unintended impacts on target and non-target parasites. Importantly, as the evolutionary and ecological significance of the host-parasite relationship is increasingly recognised, we discuss the benefits of conserving parasites during fauna translocations.

1. Introduction

Fauna translocations have become a widely employed conservation tool for the management of threatened species worldwide (IUCN, 2013). Translocations for conservation are occurring at an ever-increasing frequency (Seddon et al., 2007) with their value extending beyond conservation management, by also benefiting conservation and biological research, ecosystem restoration and the wider human community (Parker, 2008). Despite their pertinent role, the success rate of fauna translocations remains poor (Fischer and Lindenmayer, 2000). In a recent assessment of species relocations within Australia (Sheean et al., 2012), only 46% were successful. While there are a range of factors influencing translocation success, it is increasingly (albeit inconsistently) recognised that parasites (using the term broadly to include viruses, bacteria, fungi, protozoa, helminths and arthropods; Viney and Graham, 2013) impose a risk to host fitness and translocation success (Griffith et al., 1993; Viggers et al., 1993; Cunningham, 1996; Sainsbury and Vaughan-Higgins, 2012).

Hosts are usually infected by multiple parasite species (polyparasitism). In essence, therefore, fauna translocations involve the movement of complete "biological packages" from one ecosystem to another, during which the disruption of normal host-parasite relationships can have various outcomes for both the host and the parasites it carries (Corn and Nettles, 2001; Telfer et al., 2010; Moir et al., 2012). In contrast to the widely recognised disease risks associated with translocating wildlife (see Table 1 for examples), the way in which fauna translocations disrupt the dynamics of within-host parasite communities (infracommunities) is far less well understood, as is the impact of such perturbations on host fitness and translocation success.

We know for example, that a translocated host can acquire novel parasites (using the term "novel" to refer to any parasite that an individual has not previously encountered) within the destination site with devastating consequences for host health and survival. What we don't know is the mechanism behind this outcome. The presence of both canine distemper virus (CDV) and *Sarcoptes scabiei* (mange) reduced pack growth rates of Yellowstone's reintroduced grey wolves (*Canis lupus*), and in severe cases mange was associated with pack extinctions (Almberg et al., 2012). While host density and connectivity appeared to influence the spatio-temporal spread of sarcoptic mange, there were some packs that remained mange-free despite close proximity or territorial overlap with other infected packs. Likewise the spread and severity of mange varied among individuals within the same pack.

Inconsistencies such as these raise a number of important questions with regard to host-parasite dynamics and resistance to infection within

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https://doi.org/10.1016/j.biocon.2017.12.037
Received 28 July 2017; Received in revised form 22 December 2017; Accepted 24 December 2017
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Table 1
Examples of disease transmission risks during fauna translocations.

Risk	Example	Effect/outcome	References
Translocated host introduces novel parasite into naïve wild population	Parapoxvirus introduced into the United Kingdom by grey squirrels (*Sciurus carolinensis*)	Debilitating skin disease, catastrophic mortality and local extinction of native red squirrels (*Sciurus vulgaris*)	Tompkins et al. (2002) Sainsbury et al. (2008)
	Crayfish plague (*Aphanomyces astaci*) introduced into Europe by infected North American crayfish.	Local extinction of native European crayfish (*Austropotamobius pallipes*).	Holdich and Reeve (1991) Prenter et al. (2004)
Translocated host exposed to local endemic parasite	Caribou (*Rangifer tarandus*) and moose (*Alces americana*) translocated into areas inhabited by white-tailed deer (*Odocoileus virginianus*) exposed to the meningeal worm *Parelaphostrongylus tenuis*.	Major morbidity and mortality among translocated hosts due to the development of cerebrospinal nematodiasis (the meningeal worm does not affect local white-tailed deer, which have coevolved with this parasite).	Anderson (1972) Viggers et al. (1993)
	North American elk (*Cervus canadensis*) translocated into the Gila Forest, New Mexico, exposed to the arterial worm (*Elaeophora schneideri*), which is endemic in local mule deer (*Odocoileus hemionus*)	Morbidity (blindness, neurological symptoms, facial gangrene and abnormal antler growth) and mortality of elk calves (15–20% survival rate). Arterial worm infection is asymptomatic in mule deer.	Hibler et al. (1969) Viggers et al. (1993)
Parasite spillover from translocated wild host to domestic/human host and vice versa	Translocated bighorn sheep (*Ovis canadensis*) contracted pasteurellosis from direct contact with healthy domestic sheep.	Bighorn sheep developed fatal *Mannheimia haemolytica* pneumonia.	Foreyt (1989) Kock et al. (2010)
	Brush-tailed possums (*Trichosurus vulpecula*) translocated from Australia to New Zealand acquired bovine tuberculosis (*Mycobacterium bovis*) from infected dairy cattle.	Possums became a new reservoir host for the disease (i.e. amplified parasite transmission) with significant economic consequences for the New Zealand dairy industry.	Coleman (1988) Daszak et al. (2001) Kock et al. (2010)

an individual. For example, does the presence of *S. scabiei* directly influence host health? What role does stress and immune function play in enabling *S. scabiei* acquisition and persistence, particularly in the presence of CDV? Does exposure to *S. scabiei* (or any other novel parasite) affect the abundance or pathogenicity of other pre-existing parasites within a host? One can see how this aspect of host-parasite ecology is of great importance, yet there is a lack of research evaluating how fauna translocations influence host-parasite assemblages at the individual level; and the serious, often permanent consequences of using anti-parasitic drugs to remove parasites during translocation.

Our aim in this paper is to illustrate how fauna translocations have the potential to alter within host-parasite relationships and how translocation-induced perturbations to parasite infracommunities may affect host health and translocation success. We also highlight the potential positive and negative consequences of anti-parasitic drug treatment and investigate the possible benefits of conserving parasites during translocation.

2. Polyparasitism and infracommunity interactions

In the past, studies have focused on the effects of single parasite species within a host (Bordes and Morand, 2011; Holmstad et al., 2005) despite polyparasitism (co-infection, multiparasitism or concomitant infection) being the norm in wild animal populations (Keusch and Migasena, 1982; Graham, 2008). Theoretical studies have suggested that polyparasitism will reduce host fitness more than single infections (Bordes and Morand, 2011). This may occur because polyparasitism can lead to competitive interactions between parasite species or strains, resulting in increased virulence, which we define as the degree of parasite-induced reduction in host fitness (Lymbrey and Thompson, 2012). For example, experimental coinfection of laboratory rats (*Rattus norvegicus*) with *Trypanosoma lewisi* and *Toxoplasma gondii* resulted in higher numbers of *T. gondii* tachyzoites compared to rats infected with *T. gondii* alone (Guerrero et al., 1997; Catarinella et al., 1998), suggesting that in co-infected hosts *T. gondii* had increased virulence.

In addition, polyparasitism has the potential to reduce host fitness and increase susceptibility to predation or disease through synergistic effects on the course and severity of infection (Irvine, 2006). Observational studies in wildlife have detected a negative correlation between polyparasitism and host body condition (Holmstad et al., 2005; Lello et al., 2005; Jolles et al., 2008); although a causal connection has rarely been demonstrated experimentally. Gibson et al. (2011) found that California sea lions (*Zalophus californianus*) parasitised with *Sarcocystis neurona* and *T. gondii* succumbed to severe protozoal encephalitis and death, while sea lions with single *S. neurona* infections showed no disease symptoms. Likewise, domestic piglets (*Sus scrofa domesticus*) experimentally infected with *Ascaris suum* and *Escherichia coli* displayed severe signs of respiratory disease and weight loss, due to migrating *A. suum* larvae transporting *E. coli* to the lungs (Adedeji et al., 1989).

On the other hand, interactions between parasites may suppress pathogenicity within a host, reducing the impact of disease. In a murine coinfection model, prior infection with the filarial nematode *Litomosoides sigmodontis* protected the host against malarial (*Plasmodium berghei*) pathology via immunomodulation (Ruiz-Fernández, 2008). Mixed trypanosome infections in woylies (*Bettongia penicillata*) also suggest that interspecific competition may sometimes be important in reducing pathogenic effects on the host (Thompson et al., 2014). Woylies initially infected with *Trypanosoma vegrandis* never developed subsequent *Trypanosoma copemani* infections, while several woylies that initially tested positive to *T. copemani*, later also tested positive to *T. vegrandis*. This is of significance because *T. copemani* appears to be more pathogenic than other trypanosome species found in woylies, because of its propensity for intracellular invasion (Botero et al., 2013).

3. Fauna translocations and within-host-parasite dynamics

Because wildlife are host to a variety of parasites, there is inherent difficulty in not only determining what parasite species and/or strains are present, but also predicting how these parasites interact with each other and their host during translocation (Sainsbury and Vaughan-Higgins, 2012; Aiello et al., 2014). Translocating fauna can alter existing cycles of parasite transmission among translocated hosts, and establish new transmission cycles between translocated hosts and the recipient host community, thereby altering parasite infracommunity structure and establishing new parasite interactions within hosts. To demonstrate the basic processes by which translocation may influence within-host parasite interactions, parasite persistence and host health, we provide a conceptual framework (Fig. 1), which we refer to in the

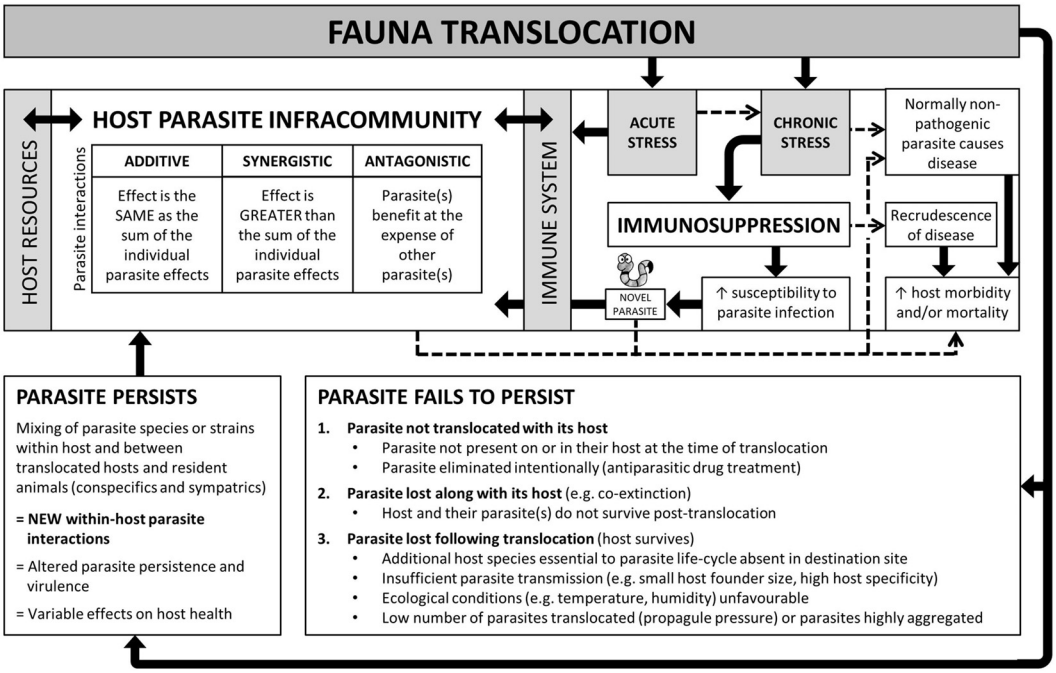

Fig. 1. Conceptual flowchart depicting how fauna translocations may influence within-host parasite interactions, parasite persistence and host health. Solid arrows represent known, predictable outcomes (e.g. translocation almost always causes acute stress), whereas dashed arrows indicate potential, less predictable outcomes (e.g. acute stress may lead to chronic stress, but, this is not always the case).

sections below.

To better understand how fauna translocations may influence polyparasitism within a host, a basic understanding of within-host competitive interactions is required. Romansic et al. (2011) highlight that the presence of multiple parasites within a single host can have additive, synergistic, or antagonistic effects; and competition between parasites may be direct (e.g. competition for physical space), or indirect via "bottom-up" (e.g. antagonism for mutual host resources) or "top-down" processes (e.g. immune-mediated competition or collaboration) (Pedersen and Fenton, 2006; Knowles et al., 2013) (Fig. 1). Interactions between parasites, particularly helminth-microparasite coinfection, have been described using a "hypothetical within-host-parasite community interaction network" (Pedersen and Fenton, 2006) comprising three levels of trophic structure; host resources, parasite community and host immune system (Pedersen and Fenton, 2006; Graham, 2008). This network can be used to predict the outcome of polyparasitism using ecological first principles. In helminth-microparasite coinfected mice for example, Graham (2008) demonstrates how "bottom-up" resource-based (Fig. 2a) and "top-down" immunological control (Fig. 2b) can regulate microparasite population size.

While ecological first principles provide a theoretical framework that enables us to comprehend how "bottom-up" and "top-down" processes may influence parasite interactions within a host, the immunological response to different parasites varies considerably both between and within-hosts depending on the parasite(s) in question [see Cox (2001) and Supali et al. (2010) for examples]; thus the outcome of infection is not easily predictable. For translocated hosts with known parasites, knowledge of how each parasite may influence immune function could theoretically be used to inform parasite management protocols using ecological first principles. While this is by no means straight-forward, it provides a starting point for decision making, particularly with regard to the use of anti-parasitic drugs (see Section 6).

4. Stress and immunocompetence of the host

As the epidemiology of individual parasite species within a host is governed by interactions between co-infecting parasites, we must also consider how resistance to infection may be influenced by immunocompetence of the host; an important concept for translocated hosts. During translocation, prolonged or recurrent exposure to multiple acute stressors (e.g. capture, clinical examination, transportation, captivity and release into a novel environment) can cause chronic stress, which may depress immunity and reduce the ability of a host to resist infection (Dickens et al., 2009; Poulin et al., 2011; Aiello et al., 2014) (Fig. 1). Captivity in particular has been identified as a "critical step" in inducing chronic stress in birds (Dickens et al., 2009), which may compromise post-translocation survival by enhancing vulnerability to disease (Dickens et al., 2010). Stress associated with handling, captivity and release into a new environment has been linked to high mortality rates in translocated beavers (*Castor fiber*), which succumbed to leptospirosis and yersiniosis infection post-translocation (Nolet et al., 1997). Stress-mediated immunosuppression has also been associated with recrudescence of latent disease in zoo translocations (e.g. toxoplasmosis in macropods; Adkesson et al., 2007; Bermudez et al., 2009). While there is a link between chronic stress and disease during translocation, the precise mechanisms by which stress influences within-host-parasite relationships is yet to be determined.

Translocations involving captive-bred animals also suggest that immunological naivety is linked with decreased survival post-translocation (Jule et al., 2008; Faria et al., 2010; Boyce et al., 2011; Ewen et al., 2012a). During captivity, regular contact with parasites is lost, which enhances vulnerability to infection due to loss of acquired immunogenic variation (Viggers et al., 1993; Mathews et al., 2006; Faria et al., 2010). Parasites may also be removed intentionally, which may have adverse consequences for the host when they are released into the wild. In captive-bred guppies (*Poecilia reticulata*) that underwent experimental reintroduction, those that were pre-exposed to native parasites had significantly lower parasite loads at the end of the experiment and their ability to eliminate parasite infection was higher, compared to naïve guppies (Faria et al., 2010). These effects may be exacerbated in endangered species that often have reduced immunocompetence associated with inbreeding and low genetic diversity (e.g. Cassinello et al., 2001).

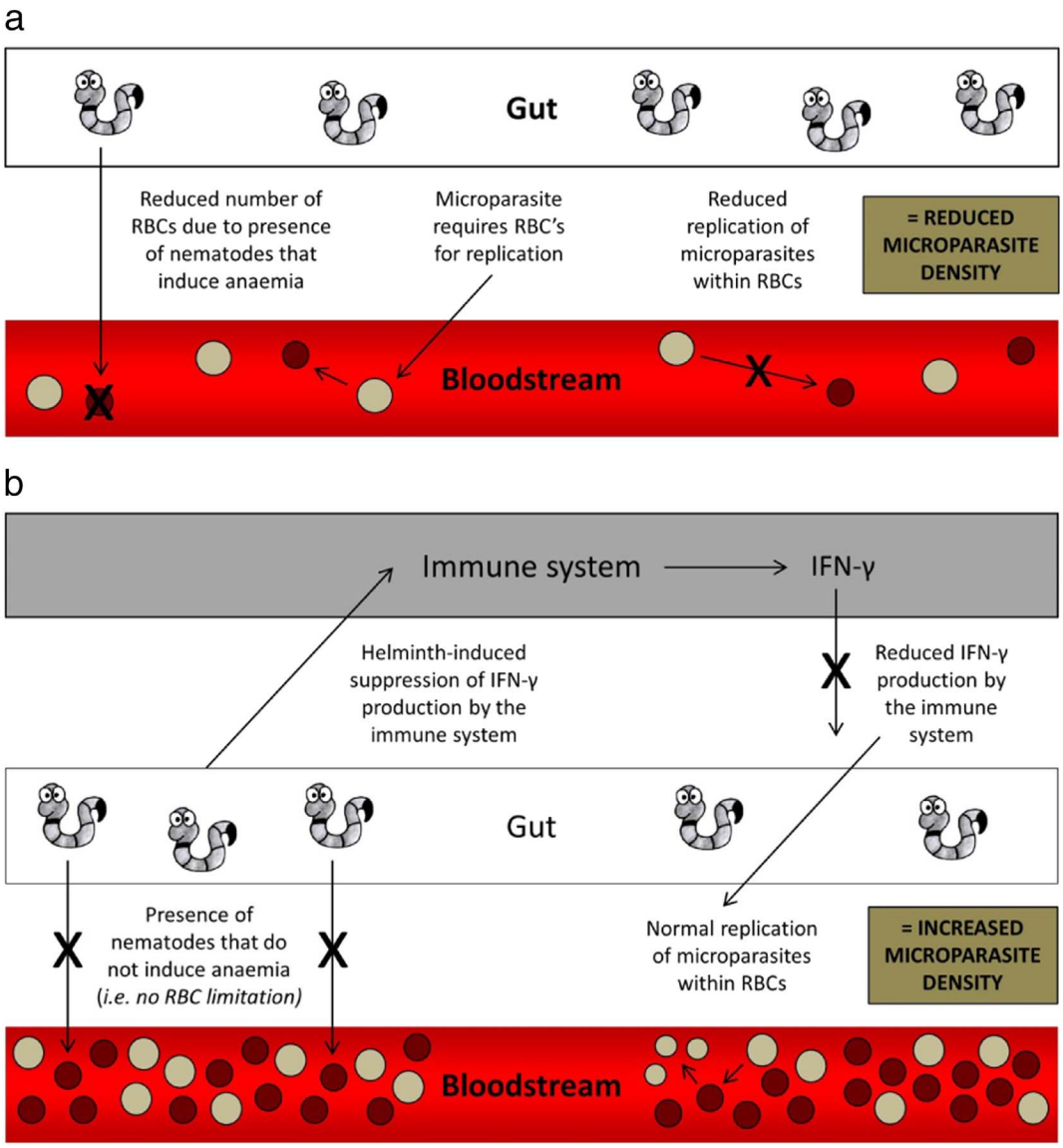

Fig. 2. a: A schematic representation of "bottom-up" resource-based control.
In this scenario, helminth-induced changes in RBC availability impose "bottom-up" control of microparasites that require RBCs for replication (i.e. resource limitation), decreasing microparasite population size.
b: A schematic representation of "top-down" immunological control.
In this coinfection model, helminth-induced suppression of IFN-γ predictably increases microparasite population size. Importantly, this picture also illustrates how microparasites may be positively influenced by helminth co-infection in the absence of resource limitation.

5. Factors influencing parasite persistence

Selection pressures imposed on parasites during and post-translocation may lead to parasite extinction, and parasite loss, whether incidental or intentional, is commonplace (Torchin et al., 2003; MacLeod et al., 2010). In reintroduced Eastern bettongs (*Bettongia gaimardi*), five ectoparasite species recorded at the point of translocation failed to persist following translocation (Portas et al., 2016). Parasites may fail to persist because they are either not translocated with their host in the first place, or they do not survive following translocation (Fig. 1; Torchin et al., 2003; MacLeod et al., 2010). For chewing lice on New Zealand's introduced bird species, 40% of native parasite genera were absent post-introduction and parasites were more likely to be lost following translocation than not translocated with their host (MacLeod et al., 2010).

Parasite loss during and post-translocation may have important consequences for coinfecting parasites and host health, where the presence of one parasite may indirectly regulate another (Fig. 3). For example, if parasite A (nematode) were lost during translocation, parasite B (microparasite) may thrive and negatively influence host health. This has been demonstrated experimentally, with elimination of *H. polygyrus* in wild wood mice (*Apodemus sylvaticus*) resulting in a 15-fold increase in *Eimeria* spp. intensity, suggesting dynamic localised competition between *H. polygyrus* and *Eimeria* spp. (Knowles et al., 2013). As *Eimeria* spp. are classified as "high risk" parasites during the stress of translocation for some species (e.g. *E. reichenowi* in cranes, Ellis et al., 1996), the loss of a coinfecting regulatory parasite may intensify the negative effects of infection with *Eimeria* spp. Equally, resistance to one parasite may confer resistance against other parasites that the host may encounter following translocation (Spencer and Zuk, 2016). In flies (*Drosophila melanogaster*), the experimental removal of the bacterium *Wolbachia pipientis* reduced the survival of its virus-challenged hosts, suggesting protection against virus-induced mortality (Hedges et al., 2008). In mice, bacteria (e.g. *Corynebacterium parvum*) and bacterial products likewise protect their host from intraerythrocytic protozoal infections (e.g. *Plasmodium falciparum*) via immunomodulatory

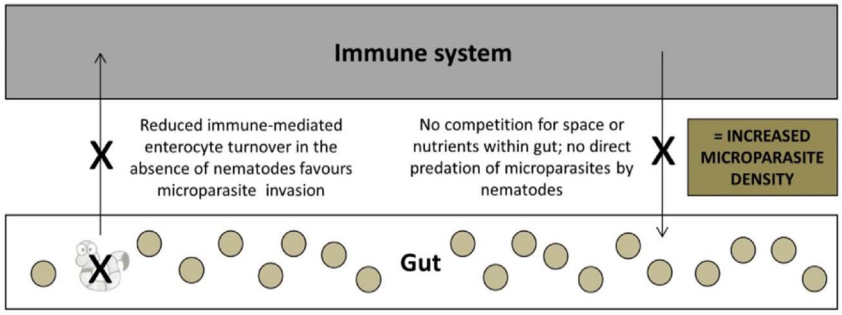

Fig. 3. Mechanisms by which anti-parasitic drug treatment can indirectly affect non-target microparasites within a host.
In this scenario, the elimination of nematodes alters the within-host-parasite network to benefit microparasites within the gastrointestinal tract.

mediators (Cox, 1975).

6. Anti-parasitic drug treatment

In an effort to enhance host health and translocation outcomes, wildlife are often treated with anti-parasitic drugs prior to translocation. For critically endangered species with parasites that impose a risk to host survival, or when every individual is imperative for species survival (e.g. small population size), parasite treatment may be warranted (Stringer and Linklater, 2014). The decision regarding whether or not to implement parasite control during fauna translocations however, is constrained by our lack of knowledge about most parasite infracommunities of wildlife. One of the main limitations in using anti-parasitic drugs in wildlife is that few clinical trials have been carried out to evaluate the safety or efficacy of these drugs. Dose rates, routes of administration, and dosage regimes are often extrapolated from closely related species, and may not be feasible in the context of translocating fauna (e.g. administering repeat doses). Thus we cannot be certain whether (a) anti-parasitic drug treatment will actually work, and (b) what parasite species will be affected (directly or indirectly) by treatment.

Regrettably, anti-parasitic drugs are also often administered in an inconsistent manner without any attempt to assess the effectiveness of treatment following translocation (Pedersen and Fenton, 2015). Routine translocation protocols often use parasite control in an analogous manner to the enemy release hypothesis, by inferring that treated individuals may benefit from reduced parasite burden post-release (Almberg et al., 2012). Studies in invasive animal species show that invaders have fewer parasites (Torchin et al., 2003), and the absence of such parasites may explain their success. Introduced populations of the European green crab (*Carcinus maenas*) for instance, have fewer parasites than native European populations, and are larger and heavier than native crabs (Torchin et al., 2002). However, while there is evidence to support the fact that translocated hosts have fewer parasites, there are no equivalent studies in translocated hosts that empirically demonstrate that parasite loss offers any competitive advantage post-translocation, thus this outdated practice can no longer be justified.

In studies that do evaluate the efficacy of anti-parasitic drug treatment in wildlife, there isn't always a benefit of treatment to host health. Experimental anthelmintic treatment in juvenile eastern grey kangaroos (*Macropus giganteus*) did not significantly improve body condition, weight or growth rates (leg or pes length), despite oral albendazole significantly reducing strongylid egg counts in treated individuals (Cripps et al., 2014). Equally, ivermectin administered to woylies prior to translocation did not improve body condition post-translocation (Northover et al., 2015), nor did it alleviate physiological stress (measured using faecal cortisol metabolites) associated with parasite infection (Hing et al., 2017). Thomas and Morgan (2013) reported reduced host health (i.e. poorer live weight gain) in anthelmintic treated alpacas compared to control animals.

Despite efforts to 'control' parasites during translocation, the effect of anti-parasitic drug treatment is unpredictable and only transitory, and translocated hosts will in due course be exposed to an array of parasites with variable outcomes. Almberg et al. (2012) found that vaccination and anti-parasitic drug treatment only conferred short-term benefits to reintroduced grey wolves (*Canis lupus*), which eventually succumbed to infection with endemic parasites, thus highlighting that this strategy does not eliminate the risk of translocated hosts acquiring parasites from the resident host community (Larkin et al., 2003). While the effects of anti-parasitic treatment are infrequently examined during and/or post-translocation, field studies in non-translocated populations also highlight the transient nature of these drugs. Ivermectin treated free-ranging Australian sea lions (*Neophoca cinerea*) for example, were re-infected with lice (*Antarctophthirus microchir*) at the same prevalence and intensity as control animals two months post-treatment (Marcus et al., 2015). Cripps et al. (2014) also found a transient reduction in strongyle egg counts in juvenile eastern grey kangaroos following albendazole treatment, however mean faecal egg counts were significantly greater in the treated group compared to the control group at some points post-treatment.

6.1. Anti-parasitic drug treatment and within-host-parasite dynamics

The administration of any anti-parasitic drug prior to translocation will to some degree disrupt parasite infracommunity structure. Even in the case of 'targeted' anti-parasitic drug treatment, the drugs selected often target more than one parasite group (e.g. ivermectin; nematodes and arthropods) and treatment is in fact not targeted at all. This raises a number of important questions. Does targeting one part of the parasite community create more 'space' for coinfecting parasites to thrive or facilitate parasite invasion? What are the effects of treatment in non-target parasites? Notably, there will also be instances where we have identified parasites of concern (e.g. *Trypanosoma copemani* in woylies; Thompson et al., 2014), however drugs are not available to treat these parasites in wildlife. Targeting other parasite genera and disrupting host-parasite relationships may inadvertently potentiate the adverse effects of such parasites.

Experimental studies in mice demonstrate how anti-parasitic drug treatment can indirectly influence the abundance of coinfecting parasites. In white-footed mice (*Peromyscus leucopus*), anthelmintic treatment resulted in a reciprocal increase in coccidia prevalence (Pedersen and Antonovics, 2013). As the presence of gastrointestinal nematodes may elicit some form of protective immunity for the host against co-infecting microparasites, or down-regulate their negative impact on host health, anthelmintic treatment has the potential to negatively influence host health (Fenton, 2013). In free-living yellow-necked mice (*Apodemus flavicollis*), anthelmintic treatment unexpectedly increased non-target tick (*Ixodes ricinus*) numbers, an effect that may negatively influence host health (*I. ricinus* is the vector for tick-borne encephalitis virus; Labuda et al., 1997) and potentially impact tick-borne disease dynamics within the population (Ferrari et al., 2009).

Parasite treatment may even enhance host susceptibility to disease

upon re-exposure (Viggers et al., 1993). Hosts reintroduced to supplement wild populations that are likely to encounter parasites that have evolved to exploit them, may be particularly vulnerable to parasite invasion (Almberg et al., 2012). Thus in circumstances where the host is likely to encounter a host-specific parasite with a prolonged period of coevolution, eradication of the parasite prior to translocation is not recommended (De Leo and Dobson, 2002; McGill et al., 2010).

6.2. Justification for anti-parasitic drug use

As "treating for good health" and eliminating parasites can disrupt parasite community composition (Pedersen and Antonovics, 2013), enhance susceptibility to disease (Viggers et al., 1993; Hedges et al., 2008), and increase morbidity and mortality post-translocation (Almberg et al., 2012), there needs to be strong justification for the use of anti-parasitic drugs, such as targeting a parasite with demonstrated negative effects on host health. Host monitoring should also be carried out to determine whether parasite treatment has (a) controlled the parasite of concern, and (b) whether treatment has benefited host health. Monitoring non-target parasite genera is also important for identifying any indirect effects of parasite treatment. While adopting an appropriate experimental framework (e.g. having treatment and control cohorts, replicates and repeated trials over space and time) would be ideal for reliably improving our knowledge in this area and informing parasite management protocols in future translocations, this expectation is likely to be unrealistic when dealing with small numbers of threatened species. Undertaking studies such as these in closely related or more common species however, may help fill the knowledge gap in this area. In cases where the effects of anti-parasitic drug treatment are poorly understood, or there is no clear justification for their use, a precautionary approach is advised and parasite conservation, rather than parasite elimination, should be considered.

Ideally parasite control must offer benefits to host health that outweigh the cost of disrupting host-parasite relationships (Stringer and Linklater, 2014) and should aim to minimise disease rather than eliminate parasites in their entirety. For parasites that are capable of inducing epidemic disease in their host during the stress of translocation (e.g. coccidia), translocation outcomes have improved following the implementation of such protocols. Immature Eurasian Cranes (*Grus grus*) receive prophylactic treatment to reduce but not eliminate coccidian parasites during captive-rearing, as exposure to this parasite during development stimulates immunity and reduces the likelihood of disease outbreaks during translocation (Sainsbury and Vaughan-Higgins, 2012). Strict hygiene and prophylactic treatment to control disease but not eradicate the coccidian parasite *Isospora normanlevinei* has similarly contributed to the success of cirl bunting (*Emberiza cirlus*) translocations, even though this parasite has been associated with mortality of translocated hosts in the past (McGill et al., 2010). In captive black-footed ferrets (*Mustela nigripes*), two species of *Eimeria* were likewise conserved rather than eradicated from the population (Williams et al., 1992; Gompper and Williams, 1998). Exposure to low levels of *Eimeria* spp. during captivity is believed to stimulate immunity, which serves to protect the host during re-exposure in the wild.

7. Parasite conservation

More recently, studies have started to acknowledge the benefit of conserving parasites (Hudson et al., 2006; Gomez et al., 2012; Hatcher et al., 2012; Spencer and Zuk, 2016). Given the innate ability of parasites to influence host health and population dynamics, parasite conservation may be crucial for preserving overall ecosystem integrity (Thompson et al., 2010; Gomez et al., 2012). In addition, the loss of parasites is likely to affect the evolutionary trajectory of a host population. Parasites and their host are classically described as being in an 'arms race' in which selective pressures placed on one species by another drive the process of evolution. Continual adaptation between a parasite and its host or between parasites within a host, elicit selection for adaptations that enhance competitive fitness and therefore survival (Strickberger, 2000). Translocation and anti-parasitic drug treatment can interfere with this host-parasite arms race, which ultimately disrupts host adaptation and evolution (Nunn et al., 2004), and may have unintended impacts on non-target parasite species (Spratt, 1997).

Of particular concern for threatened species, is that translocation may induce parasite extinction cascades for host-specific parasites that are likely to be endangered themselves (Colwell et al., 2012) and anti-parasitic drug treatment may further compound this effect. For example, the host-specific louse *Rallicola* (*Aptericola*) *pilgrimi* did not survive translocation to predator-free islands along with its host the spotted kiwi (*Apteryx owenii*) and is now extinct (Buckley et al., 2012). Targeted ectoparasite removal in black-footed ferrets (*Mustela nigripes*) is suspected of causing the extinction of the host-specific louse (*Neotrichodectes* sp.) and this species is now host to a low diversity of generalist ectoparasites (Harris et al., 2014). Delousing treatment is also believed to be responsible for the extinction of the host-specific louse *Colpocephalum californici* in the California condor (*Gymnogyps californianus*) (Rozsa and Vas, 2015). A recently discovered species of tick (*Ixodes woyliei*) found almost exclusively on critically endangered woylies is considered to be at risk of coextinction due to its apparent host specificity and the extensive use of fauna translocations in the management of its host; a risk that is heightened by the use of anti-parasitic drugs (Ash et al., 2017). Thus, parasites may be particularly vulnerable to extinction through processes designed to conserve the host.

7.1. Embracing the concept of parasite co-introduction

With our increasing awareness of the ecological and evolutionary importance of parasites (Almberg et al., 2012), the concept of parasite co-introduction has recently come into focus. Essentially we cannot translocate a species in order to "save" it without considering what else needs to be translocated with it, thus we can no longer view a translocated host as an entity on its own. We must consider the entire "biological package." Parasites are now considered meaningful conservation targets (Gomez and Nichols, 2013) and the IUCN Species Survival Commission appeals for deliberation of parasite co-introduction during fauna translocations (IUCN/SSC, 2013). Rebuilding ecosystems is one of the aims of translocating fauna, and parasite co-introduction should be encouraged for native parasites that have coevolved with their host (Jørgensen, 2014; Rideout et al., 2016). For endangered species with host-specific parasites, in which the likelihood of parasite extinction outweighs that of the host, co-introduction offers a means of conserving biological diversity (Moir et al., 2012) and preserving the host-parasite arms race, which promotes the maintenance of genetic diversity (Stringer and Linklater, 2014).

The host-specific louse, *Felicola* (*Lorisicola*) *isidoroi*, found on the endangered Iberian lynx (*Lynx pardinus*) is now considered a conservation target, and any live lice that are found on lynx during translocation are manually removed and transferred to captive lynx for preservation (Perez et al., 2013). In the case of translocating fauna, maintaining host-parasite relationships can enhance host immunity (Pizzi, 2009; McGill et al., 2010; Boyce et al., 2011), which ultimately reduces disease susceptibility and thus morbidity and mortality, thereby improving translocation outcomes (Rideout et al., 2016). During captive breeding and translocation of the brush-tailed rock wallaby (*Petrogale penicillata*), *Eimeria* spp. community structure within wild, captive bred and supplemented populations has been maintained by not administering anti-coccidial drugs to hosts before release or during translocation between sites (Vermeulen et al., 2016). Similarly, the Save the Tasmanian Devil Program aims to conserve parasites and symbionts during captive management and translocations to enhance immunity, a practice that is particularly important for a species with low genetic diversity, which may be more susceptible to disease (Wait

Box 1

Parasite management during fauna translocations - Key questions:

1. How is post-release survival affected by parasite management?
2. How do parasites within the release site affect suitability for translocation?
3. Are parasites native to the ecosystem?
4. How will the ecosystem be affected by the parasites?

et al., 2017). Tasmanian devil insurance populations were routinely treated with prophylactic anti-parasitic drugs in the past (Jones et al., 2007); this is no longer the case (Wait et al., 2017).

While the concept of parasite conservation has been given significant attention, the practicalities of implementing parasite conservation are largely neglected, with consideration needed for how dependent parasite species will survive on their host within a new environment (summarised by MacLeod et al., 2010). In many cases, the number of translocated hosts may be too small to support sustainable populations of dependent parasite species (Moir et al., 2012), or ecological conditions (e.g. temperature, humidity) may be unfavourable. Parasites with high host specificity such as *Eimeria* spp. (Duszynski and Wilber, 1997) are strongly influenced by host density and are more likely to undergo declines with their host. This is also true for parasites with complex life-cycles (e.g. helminths). If a host population is too small for adequate transmission, parasites may fail to persist following translocation (Fig. 1). The absence of coccidia in Gunner's Quoin night geckos (*Nactus coindemirensis*) has been attributed to a population bottleneck, where the host population size fell below the threshold density required to sustain infection (Leinwand et al., 2005). Likewise, when parasite control programs aim to reduce but not eliminate certain parasites, they may in fact cause the extinction of species due to sub-optimal numbers being translocated. As the very act of translocating fauna decreases the diversity of dependent parasite species (Moir et al., 2012), parasite control may exacerbate this process.

In an effort to conserve host-parasite assemblages and thus ecological function post-translocation, the IUCN Guidelines for Reintroductions and Other Conservation Translocations (IUCN/SSC, 2013) provide a framework for maintaining and/or restoring host-parasite relationships, while minimising disease risk. The ten key questions proposed by Armstrong and Seddon (2007) likewise provide an integrated approach to fauna reintroduction biology, with four of these questions being applicable to parasite management (Ewen et al., 2012b; see Box 1). It is important to note there are cases where (a) parasites have been identified as a threat, (b) parasites are verified not to be a threat (e.g. non-pathogenic commensal parasites), or (c) the potential pathogenicity of a parasite is uncertain. The decision regarding whether or not to implement anti-parasitic drug treatment will vary in each case. To gain a greater understanding of host-parasite assemblages and their impact on host health post-translocation, the value of parasite monitoring cannot be over-emphasised. Evaluating the efficacy of anti-parasitic drugs in wildlife is also of paramount importance. Once we have a better understanding of the parasite infra-communities we are dealing with, guidelines such as those proposed above can be used as an evolving tool (i.e. an adaptive management approach) and form the basis for decision making with the overall aim of improving the outcome of wildlife translocations.

8. Concluding remarks

Determining the best way to manage parasites during fauna translocations requires a multifaceted approach. On the one hand, parasites provide vital ecosystem services, drive host adaptation and evolution, and constitute an important component of biodiversity; on the other hand parasites are capable of compromising host health and population survival post-translocation. We highlight the importance of the fundamental host-parasite relationship and demonstrate how translocation- and treatment-induced perturbations to host-parasite assemblages can negatively influence host health and translocation outcomes. We also stress the need for parasite conservation and preservation of host-parasite relationships during fauna translocations, where it is deemed safe to do so. While we do not discredit the value of anti-parasitic drug treatment, we do question the ad-hoc use of anti-parasitic drugs without clear purpose or adequate monitoring to validate treatment efficacy. Given the potential ramifications of anti-parasitic drugs in both target and non-target species, parasite control must be justified and preservation of the host-parasite relationship should be a key consideration in the design and implementation of fauna translocation programs. We identify the need for ongoing surveillance and screening of native wildlife in conjunction with field-based studies to further elucidate the impacts of translocation and anti-parasitic drug treatment on parasite assemblages in translocated hosts and co-habiting species.

Role of the funding source

This review paper forms part of a PhD project that is predominantly funded by the Australian Research Council and the Department of Biodiversity, Conservation and Attractions (Western Australia). We have also been supported by grants from the Holsworth Wildlife Research Endowment (ANZ Trustees Foundation) and the Ecological Society of Australia, the Royal Zoological Society of New South Wales (Paddy Pallin Grant), and the Australian Wildlife Society.

Competing interests statement

The authors have no competing interests to declare.

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Glossary

Translocation: "Deliberate and mediated movement of wild individuals or populations from one part of their range to another" (IUCN, 1998). Frequently used as an overarching term to describe species relocations and introductions, and typically undertaken for the purposes of species conservation and recovery.

Reintroduction: "An attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct" (IUCN, 1998).

Reinforcement/supplementation: "The addition of individuals to an existing population of conspecifics" (IUCN, 1998).

Conservation/benign introduction: "An attempt to establish a species, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat and ecogeographical area" (IUCN, 1998).

Species relocation: Collective term used to describe reintroductions, supplementations and conservation introductions (Sheean et al., 2012).

Parasite infracommunities: Parasite assemblages found in individuals hosts (Holmes and Price, 1986).

Polyparasitism: Simultaneous infection with various parasite species or intraspecific strains (Keusch and Migasena, 1982; Graham, 2008).