REVIEW ARTICLE

Dung beetles and fecal helminth transmission: patterns, mechanisms and questions

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SUMMARY

Dung beetles are detrivorous insects that feed on and reproduce in the fecal material of vertebrates. This dependency on vertebrate feces implies frequent contact between dung beetles and parasitic helminths with a fecal component to their life-cycle. Interactions between dung beetles and helminths carry both positive and negative consequences for successful parasite transmission, however to date there has been no systematic review of dung beetle-helminth interactions, their epidemiological importance, or their underlying mechanisms. Here we review the observational evidence of beetle biodiversity–helminth transmission relationships, propose five mechanisms by which dung beetles influence helminth survival and transmission, and highlight areas for future research. Efforts to understand how anthropogenic impacts on biodiversity may influence parasite transmission must include the development of detailed, mechanistic understanding of the multiple interactions between free-living and parasitic species within ecological communities. The dung beetle–helminth system may be a promising future model system with which to understand these complex relationships.

Key words: Scarabaeinae, disease ecology, environmental change, parasite ecology, macroparasite, microparasite.

INTRODUCTION

Changes in the community composition of free-living biodiversity can greatly influence parasite transmission intensity in positive and negative ways (Randolph and Dobson, 2012; Johnson *et al.* 2013). A mechanistic understanding of the observed patterns between free-living and parasitic diversity is a prerequisite to explorations of the consistency of diversity-transmission relationships across parasites with diverse ecologies.

Macroparasite-based model systems with which to explore these relationships remain relatively scarce (Thieltges *et al.* 2008; Johnson and Thieltges, 2010). From a basic ecology perspective, this paucity of macroparasite systems precludes a wider view of the complex ecological networks that link parasitic life stages and free-living biodiversity. From an applied perspective, macroparasitic diseases (e.g. helminthiases) present a tremendous global disease burden to both domestic (Over *et al.* 1992) and wild animals (Albon *et al.* 2002), and represent the most common infectious agents of humans in developing countries (Lustigman *et al.* 2012). The expansion of

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drug resistance across several helminth families (Prichard *et al.* 2012) has further led to recent calls to consider complementary preventative approaches, turning research on the biological regulation of macroparasites into a frontier applied concern (Lustigman *et al.* 2012). In addition, as free-living infectious stages (e.g. eggs, larvae or oncospheres) and complex life-cycles that involve multiple hosts are both common features of helminth natural histories (Johnson and Thieltges, 2010; Johnson *et al.* 2012*a*), macroparasite transmission success is strongly influenced by interactions with free-living biodiversity and by external environmental conditions. Understanding how these interactions suppress, maintain or amplify transmission requires a mechanistic understanding of the ecological context of parasite transmission.

Here we review the current knowledge of the mechanisms underlying interactions between the fecal helminths of vertebrates and coprophagous dung beetles. Dung beetles are a diverse and cosmopolitan group of detrivorous insects that use vertebrate feces for both adult feeding and reproduction, an association dating back to the Cenozoic (Davis, 2009). As a consequence of this resource use, many coprophagous species in families Scarabaeidae (subfamilies Scarabaeinae and Aphodiinae) and Geotrupidae (subfamily Geotrupinae) play roles in the transmission of vertebrate parasites. Previous

Table 1. Common fecal parasitic helminths of vertebrates expected to interact with coprophagous beetle fauna during their life-cycle. Asterisks denote helminth genera known to use dung beetles as obligate intermediate hosts. Compiled from Bowman (2008) and Schmidt *et al*. (2000)

	Phyla	Order	Family	Example genera
Direct transmission	Nematoda	Ascaridida	Toxocaridae	*Toxocara*
	Nematoda	Oxyurida	Oxyuridae	*Enterobius*
	Nematoda	Rhabditida	Strongyloididae	*Strongyloides*
	Nematoda	Rhabditida	Ancylostomatidae	*Ancylostoma*
	Nematoda	Rhabditida	Filaroididae	*Filaroides*
	Nematoda	Rhabditida	Strongylidae	*Strongylus*
	Nematoda	Rhabditida	Trichostrongylidae	*Ostertagia*
	Nematoda	Trichocephalida	Trichuridae	*Trichuris*
Indirect transmission	Platyhelminthes	Cyclophyllidea	Anoplocephalidae	*Moniezia*
	Platyhelminthes	Cyclophyllidea	Taeniidae	*Taenia**
	Platyhelminthes	Cyclophyllidea	Davaineidae	*Raillietina**
	Nematoda	Rhabditida	Stephanuridae	*Stephanurus*
	Nematoda	Rhabditida	Syngamidae	*Mammomonogamus* (*Syngamus*)
	Nematoda	Rhabditida	Crenosomatidae	*Crenosoma*
	Nematoda	Rhabditida	Angiostrongylidae	*Aelurostrongylus*
	Nematoda	Rhabditida	Metastrongylidae	*Metastrongylus*
	Nematoda	Spirurida	Gongylonematidae	*Gongylonema**
	Nematoda	Spirurida	Thelaziidae	*Spirocerca**

studies have shown that some species of dung beetles reduce the number of emergent nematode larvae in livestock pastures (Mfitilodze and Hutchinson, 1988; Hutchinson *et al*. 1989) and contribute to lower parasite loads in vertebrate hosts (Fincher, 1973), while others are also involved in the maintenance of helminth transmission cycles, through their roles as intermediate hosts (Gottlieb *et al*. 2011). As these interactions with helminths consequently result in both positive and negative parasite transmission outcomes, the net epidemiological effect of these interactions may ultimately be context-dependent. Understanding whether dung beetle communities buffer, maintain, or amplify parasite transmission, and how these outcomes depend on local environmental conditions is a key basic and applied ecology question.

Here we synthesize over five decades of study on dung beetle-helminth relationships. We propose a series of five underlying mechanisms by which dung beetles may influence helminth survival and transmission, review the observational evidence that links dung beetles to parasite survival and transmission outcomes, and highlight areas for future research. While we focus on interactions between dung beetles and mammal macroparasites, other coprophagous invertebrate species also influence parasite transmission cycles, and dung beetles also interact with other parasites of vertebrates.

IMPLICATIONS OF DUNG BEETLE-HELMINTH INTERACTIONS FOR HELMINTH SURVIVAL AND TRANSMISSION

The frequent interaction with fecal material puts dung beetles in contact with at least 19 families of parasitic helminths with a fecal component in their life-cycle, predominantly within the phyla Platyhelminthes (flatworms) and Nematoda (roundworms) (Table 1; Fig. 1). Dung beetles may influence helminth survival and transmission success through both direct and indirect effects on the viability, survivorship or transport of parasite eggs or larvae, and/or by directly participating in transmission cycles (Table S1).

Direct mechanical interference

Adult dung beetles feed on the microorganism-rich liquid in feces by first collecting fecal particles using their maxillary galeae and then removing larger particles before ingestion by passing fecal material through a set of filtering setae (Madle, 1934; Holter, 2000). The remaining small particles are then further squeezed between the beetle's molar ridges, removing excess liquid and concentrating the ingestible microorganisms and dead vertebrate epithelial cell components that together represent the adult beetle's primary diet. Together, these feeding activities can restrict food ingestion to particles with diameters in the range of 2–150 μm (Holter *et al*. 2002; Holter, 2004; Holter and Scholtz, 2005, 2007), and significantly reduce the likelihood of successful passage of helminth eggs (Miller, 1954; Bílý and Prokopic, 1977; Bílý *et al*. 1978; Holter, 2000). The strength of this reduction varies depending on the identity of both the helminth and beetle species. For example, Miller *et al*. (1961) observed that the feeding actions of four species in the genera *Canthon* and *Phanaeus* reduced the passage of hook and roundworm eggs by nearly 100%, while *Dichotomius carolinus* had little effect. Similarly, although *Ascaris* sp., *Trichuris* sp.,

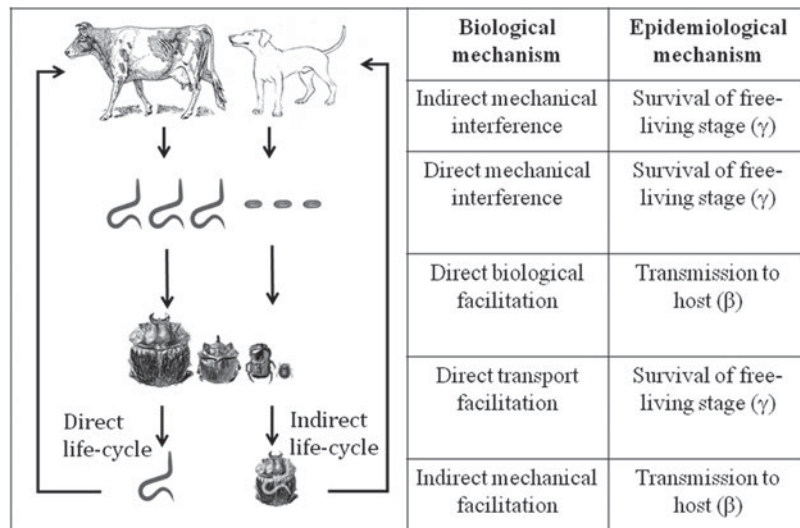| Biological mechanism	Epidemiological mechanism
Indirect mechanical interference	Survival of free-living stage (γ)
Direct mechanical interference	Survival of free-living stage (γ)
Direct biological facilitation	Transmission to host (β)
Direct transport facilitation	Survival of free-living stage (γ)
Indirect mechanical facilitation	Transmission to host (β)

Fig. 1. Biological and epidemiological mechanisms by which dung beetles influence the transmission outcomes of direct and indirect life-cycle helminths.

and *Taenia* sp. eggs ingested by *Canthon* species showed varying degrees of external and internal damage, a significant fraction of those ingested by beetles in the genus *Phanaeus* were still recognizable after passage (Miller *et al*. 1961). A recent experiment in Australia found beetle feces burial significantly reduced the number of emergent helminth larvae compared with human hand-burial of infected sheep feces – a difference the authors attributed to the mechanical impacts of beetles on larval survival (Coldham, 2011). While such direct mechanical interference may result both from the feeding actions of beetle adults and larvae as well as subsequent digestive processes within the beetles' gastrointestinal tract, we are not aware of published reports that separate out these effects, nor explicitly examine the viability of helminth eggs after passage.

Indirect mechanical interference

Most adult dung beetles craft brood balls from the fibrous components of feces, oviposit directly within these balls, and store brood balls in excavated chambers under the soil surface to provision developing larvae (Halffter and Edmonds, 1982; Edwards and Aschenborn, 1987). Such extensive manipulation of fecal material during these activities may interfere with helminth survival, through inducing microclimate changes to the fecal deposit itself (Bryan, 1973), and through underground burial of feces containing helminth free-living infectious stages (Bornemissza, 1960).

As adult beetles tunnel through vertebrate fecal deposits during feeding and nesting activities, they contribute to pat-fracturing and eventual breakdown (Bryan, 1973). The subsequent increase in pat desiccation rates can have strong effects on parasite development and survival (Durie, 1961; Williams

and Bilkovich, 1971; Mfitilodze and Hutchinson, 1988). These impacts may be particularly important for direct life-cycle parasites, where definitive hosts are (re)infected by free-living infectious larvae released during or immediately following defecation (Fig. 1). For example, Bryan (1973) found that under relatively dry seasonal conditions, fecal pat aeration by small dung beetles led to the complete desiccation of the fecal pat and the rapid death of parasitic nematode larvae. The burial of parasitic larvae or eggs as a consequence of beetle brood ball relocation may also reduce the number of emerging larvae (Bryan, 1976; Bryan and Kerr, 1989), and therefore overall contact rates with the final host. This negative influence of dung beetle feces burial should be most pronounced when brood balls are buried at depths that exceed each helminth species' maximum vertical migration distance within a given soil type (Lucker, 1936, 1938).

Finally, beetle burial activities also reduce the likelihood of splash dispersal – a passive parasite dispersal mechanism that occurs with contact between rain droplets and infective stage larvae (Grønvold *et al*. 1992, 1996). For example, Grønvold *et al*. (1992) reported a 70–90% reduction in splash dispersal of infective (L3) *Cooperia* spp. from cattle feces experimentally exposed to a single dung beetle species (*Diastellopalpus quinquedens*), compared with beetle-free controls.

Indirect mechanical facilitation

Beetle-mediated changes in the abiotic conditions of feces may alternatively enhance parasite survival by fostering a temperature-buffered and oxygenated environment, although empirical evidence for this role is lacking (Bryan, 1976; Houston *et al*. 1984; Chirico *et al*. 2003; Coldham, 2011). Waghorn *et al*.
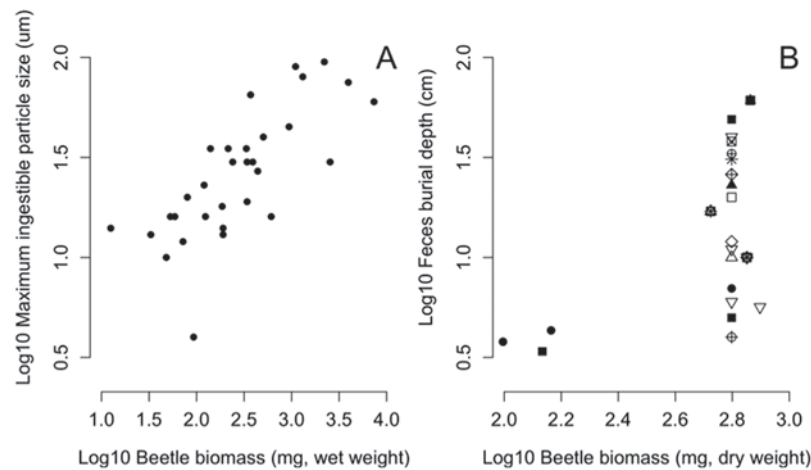
Fig. 2. Relationship between dung beetle body mass and two mechanisms of beetle-macroparasite interactions. (A) Intermediate host competence for a given parasite with an indirect life-cycle is likely to be in part a function of the maximum ingestible food particles (MDIP), and therefore related to beetle body size. Parasite eggs that exceed a given dung beetle's maximum MDIP value are less likely to be ingested by that beetle, potentially reducing potential host competency. Data from Holter (2000, 2004), Holter *et al.* (2002), Holter and Scholtz (2005) and du Toit *et al.* (2012). (B) Indirect mechanical interference as a function of dung burial depth is positively related to beetle body mass. For macroparasites with direct life-cycles, beetle feces burial depth is likely negatively related to helminth survival. Different symbols represent different dung beetle species: *Canthon aequinoctialis, C. triangularis, Dichotomius batesi, D. lucasi, Eurysternus caribaeus, Oxysternon conspicillatum, Phanaeus cambeforti, P. chalcomelas, Scybalocanthon pygidialis*, burial depth (Vulinec, 2002), body mass (Vulinec, 2000); *D. carolinus*, burial depth (Lindquist, 1933), body mass (Estrada and Coates-Estrada, 2002); *Onitis alexis, O. fulgidus, O. unicatus, O. viridulus*, burial depth (Edwards and Aschenborn, 1987), body mass (Davis *et al.* 2012).

(2002) reported an increase in parasite abundance in experimental soil columns in treatments where dung was experimentally hand-buried at a distance of 5 cm, relative to an unburied control. The same shallow experimental burial had no clear influence on final parasite emergence above ground (i.e. where contact with definitive hosts occurs). Shallow hand-burial trials may be an ecologically unrealistic proxy for beetle-mediated facilitation of parasite survival, as the maximum feces burial depth for many dung beetle species can much deeper: e.g. 8 cm Vulinec (2002), 12 m (Estrada and Coates-Estrada, 1991), 27 cm (Shepherd and Chapman, 1998), 102 cm (Lindquist, 1933), and 130 cm (Edwards and Aschenborn, 1987). However, as burial depth is positively associated with beetle body size (Fig. 2b), dung beetle communities dominated by small-bodied beetle species may have a neutral or positive community-level influence on helminth transmission. While these ideas require further exploration, if dung beetles indeed demonstrate size-ordered sensitivity to environmental change as has been suggested (Larsen *et al.* 2005; Gardner *et al.* 2008), this inverse relationship between body size and fecal helminth survival may contribute to enhanced transmission risk in degraded landscapes.

Direct biological facilitation

Beetles are obligate intermediate hosts for a diverse group of helminths with indirect life-cycles (i.e. those involving a definitive and one or more intermediate hosts) (Table 1; Fig. 1). Here, beetles ingest eggs from infected feces, parasites develop into an infective larval stage within the dung beetle's body, and successful transmission occurs upon beetle consumption by a definitive host. Species from least 18 dung beetle genera (*Anomiopsoides, Ateuchus, Canthon, Copris Catharsius, Dichotomius, Epirinus, Eucranium, Euonthophagus, Geotrupes, Gymnopleurus Megathopa, Onthophagus, Onitis, Phanaeus, Sarophorus, Scarabaeus* and *Sisyphus*) have been reported as likely or confirmed intermediate hosts of parasites of omnivores and carnivores, including *Ascarops strongylina, Physocephalus sexalatus, Macracanthorhynchus hirudinaceus, Gongylonema verrucosum* and *Spirocerca lupi* (Alicata, 1935; Martínez, 1959; Bailey *et al.* 1963; Stewart and Kent, 1963; Bailey, 1972; Fincher and Marti, 1982; Stumpf, 1986; Mukaratirwa *et al.* 2010; Gottlieb *et al.* 2011; du Toit *et al.* 2012). For a given helminth species, prevalence can range widely across dung beetle hosts. For example, Bílý and Prokopic (1977) reported post experimental infection prevalence of *Ascaris suum* in dung beetles to range from 90% (*Geotrupes stercorosus*), 66·7% (*Aphodius fimetarius*), 27% (*Onthophagus fracticornis*) to 5% (*Onthophagus verticornis*). To our knowledge, the mechanisms of this variability in prevalence such as dung beetle exposure to infection, and infection susceptibility remain uncharacterized for even a single parasite species to date.

Direct transport facilitation

Dung beetles can play a role in helminth transmission and dispersal when a fraction of ingested eggs survive passage through the beetles' masticatory and gastro-intestinal systems. For example, *Trichuris trichuria* eggs have been found in the excrement of *Phanaeus vindex* and *D. carolinus* (Miller *et al.* 1961). *Taenia saginata* ova have been reported as viable in *Onitis* sp. and *Heliocopris* sp. feces for at least 4 days, with some unfragmented ova recovered up to 10 days after ingestion (Mutinga and Madel, 1981). In contrast, Bergstrom *et al.* (1976) found no trichostrongylid eggs (*Trichostrongylus colubriformis*, *Nematodirus* sp., *Ostertagia* sp., or *Marshallagia marshalli*) in the intestinal tract of four different species of *Aphodius* and *Canthon* beetles following parasite egg consumption.

Finally, dung beetles may theoretically act as transport hosts for parasite eggs or larvae that adhere to beetle exoskeletons, although empirical evidence for this role is lacking. For example, Bergstrom *et al.* (1976) found no trichostrongylid eggs (*T. colubriformis*, *Nematodirus* sp., *Ostertagia* sp. or *M. marshalli*) either within the intestinal tract or on the exoskeleton of four different species of *Aphodius* and *Canthon*. Other coprophagous invertebrates (e.g. earthworms) have been investigated for their role as transport or paratenic hosts (i.e. intermediate hosts that contribute to parasite life-cycles, but are not required for development), also with generally inconclusive results (Roepstorff *et al.* 2002).

LINKING BIOLOGICAL AND EPIDEMIOLOGICAL MECHANISMS

Predicting the overall impact of dung beetles on parasitic helminth transmission risk will ultimately require information on the per-capita impact of each dung beetle species in a given community on parasite transmission success. A simplified view of helminth transmission can be given as:

$$\frac{dW}{dt} = \lambda P - \gamma W - \beta W H \tag{1}$$

(modified from Dobson and Hudson, 1992), where the impact on transmission of free-living helminths (W) by a dung beetle community (H) depends upon the production of infectious parasitic stages (λ) by infected definitive hosts (P), subsequent survival of infectious stages in the environment (γ), the probability of an infectious stage encountering the beetle community (WH), and the proportion of helminths that successfully produce an infective unit following an interaction with the beetle community (β) – a parameter directly linked to the likelihood of transmission to the definitive host, following a parasite encounter with the dung beetle community. For direct life-cycle helminths, infective units are free-living infective larvae that directly infect final hosts (Fig. 1). Dung beetles interact with direct life-cycle

helminths during nesting, where the burial of brood balls containing feces and helminths can interfere with helminth vertical migration to the soil surface. An estimate of the proportion of free-living infectious units (helminths) that survive an encounter with the entire beetle community could be given as:

$$\beta = \sum_i^j B_i \times S_i \times E_i \tag{2}$$

where helminth survival depends on the per-capita proportion of a fecal mass buried by beetle species i (B_i), the proportion of helminths that survive direct mechanical interference during the feeding activities of beetle species i (S_i), and the proportion of helminths able to successfully emerge from the average burial depth of beetle species i (E_i). The proportion of beetle diet represented by definitive host feces (P_i) will also be an important parameter, as beetle-helminth interactions cannot occur if a given beetle is not attracted to infected feces of the appropriate mammal host. For those indirect life-cycle helminths for which dung beetles act as intermediate hosts (Fig. 1), the infective unit of interest is the proportion of infected beetles within the community:

$$\beta = \sum_i^j C_i \times S_i \times P_i \tag{3}$$

which depends upon the capacity of a given beetle species i to become successfully infected and transmit that infection (i.e. competence, C_i), and the same S_i and P_i terms as above.

FUTURE RESEARCH PRIORITIES

Community-level influences on parasite transmission

Understanding the influence of biological communities on parasitic disease transmission requires an integrative view of the ecological mechanisms by which overall community structure influences variation in transmission success (Johnson *et al.* 2012*a*; Randolph and Dobson, 2012; Wood and Lafferty, 2012). For example, host species diversity may inversely correlate with transmission success, either when additional host species have low or zero competence and therefore act as epidemiological dead ends, or when increased host diversity is associated with a decrease in the density of competent hosts (Keesing *et al.* 2006; Suzán *et al.* 2009). We found no published work that quantified the relevance of different dung beetle community compositions on the survival or transmission of parasitic helminths. Future studies that link such observational data with experimental manipulation will be critical to investigations of the influence of beetle community structure on parasite transmission.

Species traits

Species' traits are hereditary morphological, physiological or phenological characteristics that influence

individual fitness through impacts on organism growth, reproduction or survival, which can be measured without reference to the external environment (Arnold, 1983; Violle *et al.* 2007). Traits interact with contemporary environmental conditions and historical biogeographic conditions to influence species' patterns of abundance and distribution (Nichols *et al.* 2013), including those of hosts and parasites. The application of trait-based models in disease ecology is remarkably recent (Johnson *et al.* 2012*b*) and have been used to predict intermediate host competency (du Toit *et al.* 2012) as well as which hosts may function as pathogen reservoirs (Cronin *et al.* 2010; Hawley and Altizer, 2010). Given the diversity of mechanisms that link free-living biodiversity to infection outcomes in macroparasite systems (Orlofske *et al.* 2012) and the strong influence of individual variation in host susceptibility on host-parasite interactions, trait-based disease ecology models are likely to be extremely useful in efforts to understand the role of complex community structure on infection risk.

Beetle body mass may be a useful predictor of the impacts of dung beetles on indirect life-cycle helminths (via interspecific variation in host competence; Fig. 2a), as well as on direct life-cycle helminths (via per-capita influences on burial depth; Fig 2b). Given the positive relationship between beetle body mass and burial depth (e.g. Vulinec, 2002), indirect mechanical interference between larger-bodied beetles and direct life-cycle helminths may reduce overall helminth survivorship and transmission risk. However, the relationship between beetle body size and other mechanisms anticipated to influence the survivorship of direct life-cycle helminths (e.g. direct mechanical interference) remains unexplored to date.

Dung beetle influence on indirect life-cycle helminths is also likely to be related to beetle body mass, as well as other physiological traits. For example, beetle body mass and the intensity of *Spirocerca lupi* infections of beetles appear to be positively related (Mukaratirwa *et al.* 2010). This may be driven by the positive correlation between beetle body size and the maximum diameter of ingestible particles (Fig. 2a) (du Toit *et al.* 2012). Large beetles also appear less choosy about particle size than smaller beetles, potentially due to evolutionary trade-offs between high food quality (ingestion of very small particles only) and quantity (ingestion of larger particles too) that contributes to reduced 'pickiness' about particle size by large beetles (Holter *et al.* 2002; Holter and Scholtz, 2005). These mechanisms are likely to interact, and suggest that beetle body size may be a key morphological trait determining beetle exposure to infection, an important component of competence.

Beetle nesting strategy may also play a role in determining maximum ingestible particle size (Holter and Scholtz, 2005). Roller species tend to accept larger particles than tunnellers of similar body mass, potentially as a consequence of reduced feces selectivity by tunnellers due to reduced exploitative competition pressures at the feces deposition site (Holter and Scholtz, 2005). Finally, while host immunology clearly plays a key role in the probability of infection and survivorship (and therefore competence), these parameters remain unexplored for dung beetles.

Diet breadth

A key attribute that shapes dung beetle–vertebrate–parasite ecological networks is beetle diet breadth. For this diverse group as a whole, we lack basic data about feeding ecology, including diet breadth, plasticity and their ecological correlates (Nichols *et al.* 2009). As attraction to infected feces is a prerequisite of beetle interaction with fecal helminths, there is a dire need for basic investigation into these aspects of dung beetle natural history. The few existing published cafeteria studies demonstrate that dung beetle species range from extreme dietary specialism (e.g. obligate on single species) to extreme generalists (e.g. capable of feeding across multiple vertebrate guilds) (Whipple and Hoback, 2012). Given the ephemeral nature of dung beetle-vertebrate interactions, both traditional field observations and cafeteria experiments are limited in their ability to cost-effectively evaluate dietary preferences in the wild (Nichols *et al.* 2009; García-Robledo *et al.* 2013). Recently, the use of molecular methods has helped expand our knowledge about animal diets in the wild (Pompanon *et al.* 2012) and may prove to be particularly useful in studying dung beetle feeding patterns.

Influence of seasonality and climate events

Environmental conditions (i.e. moisture and temperature) have a major impact on the development, survival and migratory behaviour of parasitic nematode larvae with direct life-cycles (Durie, 1961; Stromberg, 1997). Particularly in their ensheathed infective stage, the free-living larvae of many nematode species may survive for months after deposition, depending on environmental conditions, raising concern that the beetle-mediated burial of infected feces in arid regions or dry seasons may result in an infection 'time bomb', although no empirical evidence currently supports this concern (Coldham, 2011). For indirect life-cycle parasites, seasonal changes in the abundance of competent intermediate hosts will influence seasonal transmission dynamics. For example, the seasonal variation in *S. lupi* prevalence in Israel is correlated with the seasonal abundance variation of its principal intermediate host *Onthophagus sellatus* (Mazaki-Tovi *et al.* 2002).

Interactions with other pathogens: microparasites and fungi

The mechanisms that interfere with or facilitate macroparasite transmission by dung beetles may also modulate the transmission of fecal microparasites. Saitoh and Itagaki ([1990](#)) concluded that two species of *Onthophagus* beetles that emerged from cat feces infected with *Toxoplasma gondii* carried infective oocysts, both in their feces and on their bodies. These individuals subsequently transmitted toxoplasmosis to mice, and onwards to kittens that consumed them (1990). The same authors additionally detected two additional strains of feline coccidian (*Isopora felis* and *Isopora rivolta*) on dung beetles collected from urban dog feces. These dung beetles were also able to successfully transmit feline coccidia to kittens via dung beetle–mouse consumption, suggesting a paratenic or intermediate host role for some beetle species in feline coccidia (Saitoh and Itagaki, [1990](#)).

In contrast, in an investigation of the fate of *Cryptosporidium parvum* oocysts ingested by three beetle species (*Anoplotrupes stercorosus*, *Aphodius rufus* and *O. fracticornis*), Mathison and Ditrich ([1999](#)) reported that the majority of oocysts were destroyed following passage through dung beetle mouthparts and gastrointestinal tract, suggesting a potentially negative influence of beetles on *C. parvum* transmission. A similarly negative impact of beetle activity on *Cryptosporidium* oocysts' viability was reported by Ryan *et al*. ([2011](#)), who found that oocysts' viability in feces burial by seven pairs of *Bubas bison* declined from 58% (control) to 10% (burial treatment). In a study of the ability of the dung beetle species *Catharsius molossus* to act as transport host for the pathogenic *Escherichia coli* strain O157: H7, only 5% of dung beetles tested positive for its presence in their gut contents, leading the authors to conclude that dung beetles appeared to play no epidemiological role in its transmission (Xu *et al*. 2003). Dung beetles have also been implicated in the reduction in abundance of the exploding fungus *Pilobolus sporangia*, which forcefully disperses nematodes in pasture systems along with its own spores (Gormally, [1993](#); Biggane and Gormally, [1994](#)).

A background regulatory role for dung beetles in public health?

Given that open defecation is practiced by nearly 1 in 5 people in developing countries (*c*. 1·1 billion people worldwide (WHO and UNICEF, [2012](#)) and that dung beetles readily bury human feces (Miller, [1954](#); Nichols and Gardner, [2011](#)), it should be expected that dung beetles interact with the transmission of helminths of public health concern. Human helminth infections (also known as soil-transmitted helminths, or STHs) are associated with approximately 10 000–135 000 deaths annually, severe annual morbidity for an estimated 300 million people and the extensive impairment of physical and mental development in children (Lustigman *et al*. [2012](#)). The principal STH agents (i.e. *Ascaris lumbricoides*, *Trichuris trichiura*, *Necator americanus* and *Ancylostoma duodenale*) that disproportionately represent the morbidity burdens of the neglected tropical diseases recognized by the World Health Organization (WHO, [2004](#); Lopez and Mathers, [2006](#)) are all direct life-cycle helminths for which dung beetles are expected to play a strong regulatory role. Although chemotherapeutic intervention is clearly effective in reducing the prevalence, intensity and morbidity of STH infection (Hotez, [2009](#)), mass chemotherapy has its own challenges, including drug resistance risk (Vercruysse *et al*. [2011](#)) and barriers to the optimal treatment coverage required for acceptable reductions in the probability of reinfection (Prichard *et al*. [2012](#)). Given these constraints, it is generally accepted that anthelmintic treatment must be complemented by improvements in environmental sanitation, housing, health education and access, and vector control where relevant (Gazzinelli *et al*. [2012](#)). Dung beetle-mediated transmission suppression may be especially important in reducing environmental reservoirs of viable STH eggs or larvae (i.e. infected feces or soil), and therefore likely plays a positive role in the reduction of re-infection risk.

CONCLUSIONS

Two important factors emerge from consideration of the mechanisms that link dung beetle community composition to fecal helminth survival and transmission. First, beetle-parasite interactions may have divergent effects on transmission intensity within a given transmission cycle. For example, beetles above a body mass threshold may have a neutral or positive influence on transmission of indirect life-cycle parasites, while smaller species are likely to suppress the quantity of available infecting stages, by being fully incompetent hosts ([Fig 2](#)a). For direct life-cycle helminths, small beetles may exert relatively weak indirect mechanical interference as a consequence of their shallow feces burial, yet continue to reduce helminth viability through direct mechanical interference effects on parasite larvae and eggs.

Second, beetle-parasite interactions may have divergent effects on transmission intensity across transmission cycle types, given the divergent relationships between beetle body mass and parasite transmission and survival for direct and indirect-life-cycle parasites. Ultimately, the net epidemiological consequences of dung beetles on the parasitic helminths of vertebrates will be a function of the community-wide distribution and redundancy of beetle traits such as body size, diet breadth and feeding strategy. The dung beetle-fecal helminth

system is a potentially ideal model system to understand the epidemiological consequences of community disassembly under environmental change, given the cosmopolitan distribution of both beetles and helminths, as well as their amenability to experimental manipulation in both laboratory and field settings. Here we have sought to draw attention to the diverse ways in which coprophagous beetles may contribute towards the maintenance, amplification or dilution of parasitic helminth transmission. Enhanced understanding of such mechanistic links will be an important step in future efforts to understand how environmental change may influence the interactions between free-living and parasitic species that ultimately alter infection risk (Randolph and Dobson, 2012; Johnson *et al.* 2013).

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit http://dx.doi.org/S0031182013002011.

REFERENCES

Albon, S. D., Stien, A., Irvine, R. J., Langvatn, R., Ropstad, E. and Halvorsen, O. (2002). The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society B – Biological Sciences* **269**, 1625–1632. doi: 10.1098/rspb.2002.2064.

Alicata, J. E. (1935). *Early Development Stages of Nematodes Occurring in Swine*. U.S. Department of Agriculture Technical Bulletin No. 489. Washington, DC, USA.

Arnold, S. J. (1983). Morphology, performance and fitness. *American Zoologist* **23**, 347–361.

Bailey, W. S. (1972). *Spirocera lupi*: a continuing inquiry. *Journal of Parasitology* **58**, 3–22.

Bailey, W. S., Cabrera, D. J. and Diamond, D. L. (1963). Beetles of the family Scarabaeidae as intermediate hosts for *Spirocera lupi*. *Journal of Parasitology* **49**, 485–488.

Bergstrom, R. C., Maki, L. R. and Werner, B. A. (1976). Small dung beetles as biological control agents: laboratory studies of beetle action on trichostrongylid eggs in sheep and cattle feces. *Proceedings of the Helminthological Society of Washington* **43**, 171–174.

Biggane, R. P. J. and Gormally, M. J. (1994). The effect of dung beetle activity on the discharge of *Pilobolus* (Fungi, Mucorales) sporangia in cattle, sheep and horse faeces. *Entomophaga* **39**, 95–98.

Bílý, S. and Prokopic, J. (1977). Destruction of *Ascaris suum* eggs during their feeding to various species of beetles. *Folia Parasitologica* **24**, 343–345.

Bílý, S., Stěrba, J. and Dyková, I. (1978). Results of an artificial feeding of eggs of *Taenia saginata* Goeze, 1782 to various beetle species. *Folia Parasitologica* **25**, 257–260.

Bornemissza, G. F. (1960). Could dung eating insects improve our pastures? *Journal of the Australian Institute of Agricultural Science* **26**, 54–56.

Bowman, D. D. (2008). *Georgis' Parasitology for Veterinarians*, 9 Edn. Saunders, Amsterdam, the Netherlands.

Bryan, R. P. (1973). The effects of dung beetle activity on the numbers of parasitic gastrointestinal helmintic larvae recovered from pasture samples. *Australian Journal of Agricultural Research* **24**, 161–168.

Bryan, R. P. (1976). The effects of the dung beetle, *Onthophagus gazella*, on the ecology of the infective larvae of gastrointestinal nematodes of cattle. *Australian Journal of Agricultural Research* **27**, 567–574.

Bryan, R. P. and Kerr, J. D. (1989). Factors affecting the survival and migration of the free living stages of gastrointestinal nematode parasites of cattle in central Queensland. *Veterinary Parasitology* **30**, 315–326.

Chirico, J., Wiktelius, S. and Waller, P. J. (2003). Dung beetle activity and the development of trichostrongylid eggs into infective larvae in cattle faeces. *Veterinary Parasitology* **118**, 157–163.

Coldham, J. (2011). *Dung Beetles and Internal Parasites of Sheep*. Meat & Livestock Australia Limited, North Sydney, Australia.

Cronin, J. P., Welsh, M. E., Dekkers, M. G., Abercrombie, S. T. and Mitchell, C. E. (2010). Host physiological phenotype explains pathogen reservoir potential. *Ecology Letters* **13**, 1221–1232.

Davis, A. (2009). Outlines of composition, spatial pattern and hypothetical origins of regional dung beetle faunas. In *Evolutionary Biology and Conservation of Dung Beetles* (ed. Scholtz, C., Davis, A. L. V. and Kryger, U.), pp. 365–383. Pensoft, Sofia, Bulgaria.

Davis, A. L. V., Scholtz, C. H. and Swemmer, A. M. (2012). Effects of land usage on dung beetle assemblage structure: Kruger National Park versus adjacent farmland in South Africa. *Journal of Insect Conservation* **16**, 399–411.

Dobson, A. P. and Hudson, P. J. (1992). Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *Journal of Animal Ecology* **61**, 487–498.

Durie, P. H. (1961). Parasitic gastroenteritis of cattle: the distribution and survival of infective strongyle larvae on pasture. *Australian Journal of Agricultural Research* **12**, 1200–1211.

du Toit, C. A., Holter, P., Lutermann, H. and Scholtz, C. H. (2012). Role of dung beetle feeding mechanisms in limiting the suitability of species as hosts for the nematode *Spirocera lupi*. *Medical and Veterinary Entomology* **26**, 455–457.

Edwards, P. B. and Aschenborn, H. H. (1987). Patterns of nesting and dung burial in *Onitis* dung beetles: implications for pasture productivity and fly control. *Journal of Applied Ecology* **24**, 837–851.

Estrada, A. and Coates-Estrada, R. (1991). Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* **7**, 459–474.

Estrada, A. and Coates-Estrada, R. (2002). Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation* **11**, 1903–1918.

Fincher, G. T. (1973). Nidification and reproduction of *Phanaeus spp*. in three textural classes of soil (Coleoptera: Scarabaeidae). *Coleopterists Bulletin* **27**, 33–37.

Fincher, G. T. and Marti, O. G. (1982). *Onthophagus gazella* as an intermediate host for spiruroids in Georgia and Texas. *Southwestern Entomologist* **7**, 125–129.

García-Robledo, C., Erickson, D. L., Staines, C. L., Erwin, T. L. and Kress, W. J. (2013). Tropical plant-herbivore networks: reconstructing species interactions using DNA barcodes. *PLoS ONE* **8**, e52967.

Gardner, T. A., Hernandez, M. I. M., Barlow, J. and Peres, C. A. (2008). Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology* **45**, 883–893.

Gazzinelli, A., Correa-Oliveira, R., Yang, G. J., Boatin, B. A. and Kloos, H. (2012). A research agenda for helminth diseases of humans: social ecology, environmental determinants, and health systems. *PLoS Neglected Tropical Diseases* **6**, e1603.

Gormally, M. J. (1993). The effect of dung beetle activity on the discharge of *Pilobus* sporangia in cattle faeces. *Medical and Veterinary Entomology* **7**, 197–198.

Gottlieb, Y., Markovics, A., lKlementa, E., Naora, S., Samish, M., Arocha, I. and Lavya, E. (2011). Characterization of *Onthophagus sellatus* as the major intermediate host of the dog esophageal worm *Spirocera lupi* in Israel. *Veterinary Parasitology* **180**, 378–382.

Grønvold, J., Sommer, C., Holter, P. and Nansen, P. (1992). Reduced splash dispersal of bovine parasitic nematodes from cow pats by the dung beetle *Diastellopalpus quinquedens*. *Journal of Parasitology* **78**, 845–848.

Grønvold, J., Henriksen, S. A., Larsen, M., Nansen, P. and Wolstrup, J. (1996). Biological control. Aspects of biological control – with special reference to arthropods, protozoans and helminths of domesticated animals. *Veterinary Parasitology* **64**, 47–64.

Halffter, G. and Edmonds, W. D. (1982). *The Nesting Behavior of Dung Beetles (Scarabaeinae)*. An Ecological and Evolutive Approach. Instituto de Ecología, México, DF.

Hawley, D. M. and Altizer, S. M. (2010). Disease ecology meets ecological immunology: understanding the links between organismal immunity and infection dynamics in natural populations. *Functional Ecology* **25**, 48–60.

Holter, P. (2000). Particle feeding in *Aphodius* dung beetles (Scarabaeidae): old hypotheses and new experimental evidence. *Functional Ecology* **14**, 631–637.

Holter, P. (2004). Dung feeding in hydrophilid, geotrupid and scarabaeid beetles: examples of parallel evolution. *European Journal of Entomology* **101**, 365–372.

Holter, P. and Scholtz, C. H. (2005). Are ball-rolling (Scarabaeini, Gymnopleurini, Sisyphini) and tunnelling scarabaeine dung beetles equally choosy about the size of ingested dung particles? *Ecological Entomology* **30**, 700–705.

Holter, P. and Scholtz, C. H. (2007). What do dung beetles eat? *Ecological Entomology* **32**, 690–697.

Holter, P., Scholtz, C. H. and Wardhaugh, K. W. (2002). Dung feeding in adult scarabaeines (tunnellers and endocoprids): even large dung beetles eat small particles. *Ecological Entmology* **27**, 169–176.

Hotez, P. J. (2009). Mass drug administration and integrated control for the world's high-prevalence neglected tropical diseases. *Clinical Pharmacology and Therapeutics* **85**, 659–664.

Houston, R. S., Craig, T. M. and Fincher, G. T. (1984). Effects of *Onthophagus gazella* F (Coleoptera: Scarabaeidae) on free-living strongyloids of equids. *American Journal of Veterinary Research* **45**, 572–574.

Hutchinson, G. W., Abba, S. A. and Mfitilodze, M. W. (1989). Seasonal translation of equine strongyle infective larvae to herbage in tropical Australia. *Veterinary Parasitology* **33**, 251–263.

Johnson, P. T. J. and Thieltges, D. W. (2010). Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *Journal of Experimental Biology* **213**, 961–970.

Johnson, P. T. J., Preston, D. L., Hoverman, J. T., Henderson, J. S., Paull, S. H., Richgels, K. L. D. and Redmond, M. D. (2012*a*). Species diversity reduces parasite infection through cross-generational effects on host abundance. *Ecology* **93**, 56–64.

Johnson, P. T. J., Rohr, J. R., Hoverman, J. T., Kellermanns, E., Bowerman, J. and Lunde, K. B. (2012*b*). Living fast and dying of infection: host life history drives interspecific variation in infection and disease risk. *Ecology Letters* **15**, 235–242.

Johnson, P. T. J., Preston, D. L., Hoverman, J. T. and Richgels, K. L. D. (2013). Biodiversity decreases disease through predictable changes in host community competence. *Nature* **494**, 230–233.

Keesing, F., Holt, R. D. and Ostfeld, R. S. (2006). Effects of species diversity on disease risk. *Ecology Letters* **9**, 485–498.

Larsen, T., Williams, N. and Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* **8**, 538–547.

Lindquist, A. W. (1933). Amounts of dung buried and soil excavated by certain Coprini (Scarabaeideae). *Kansas Entomological Society* **6**, 109–125.

Lopez, A. D. and Mathers, C. D. (2006). Measuring the global burden of disease and epidemiological transitions: 2002–2030. *Annals of Tropical Medicine and Parasitology* **100**, 481–499.

Lucker, J. T. (1936). Extent of vertical migration of horse strongyle larvae in soils of different types. *Journal of Agricultural Research* **52**, 353–361.

Lucker, J. T. (1938). Vertical migration, distribution, and survival of infective horse strongyle larvae developing in feces buried in different soils. *Journal of Agricultural Research* **57**, 335–348.

Lustigman, S., Prichard, R. K., Gazzinelli, A., Grant, W. N., Boatin, B. A., McCarthy, J. S. and Basáñez, M.-G. (2012). A research agenda for helminth diseases of humans: the problem of helminthiases. *PLoS Neglected Tropical Diseases* **6**, e1582.

Madle, H. (1934). Zur Kenntnis der Morphologie, Ökologie und Physiologie von *Aphodius rufipes* Lin. und einigen verwandten Arten. *Zoologische Jahrbücher (Anatomie und Ontogenie der Tiere)* **58**, 303–396.

Martínez, A. (1959). Catálogo de los Scarabaeidae Argentinos (Coleoptera). *Revista del Museo de Ciencias Naturales Bernadino Rivadavia* **5**, 1–126.

Mathison, B. and Ditrich, O. (1999). The fate of *Cryptosporidium parvum* oocysts ingested by dung beetles and their possible role in the dissemination of cryptosporidiosis. *Journal of Parasitology* **85**, 678–681.

Mazaki-Tovi, M., Baneth, G., Aroch, I., Harrus, S., Kass, P.H., Ben-Ari, T., Zur, G., Aizenberg, I., Bark, H. and Lavy, E. (2002). Canine spirocercosis: clinical, diagnostic, pathologic, and epidemiologic characteristics. *Veterinary Parasitology* **107**, 235–250.

Mfitilodze, M. W. and Hutchinson, G. W. (1988). Development of free-living stages of equine strongyles in faeces on pasture in a tropical environment. *Veterinary Parasitology* **26**, 285–296.

Miller, A. (1954). Dung beetles (Coleoptera, Scarabaeidae) and other insects in relation to human feces in a hookworm area of southern Georgia. *American Journal of Tropical Medicine and Hygiene* **3**, 372–389.

Miller, A., Chi-Rodriquez, E. and Nichols, R. L. (1961). The fate of helminth eggs and protozoan cysts in human feces ingested by dung beetles (Coleoptera: Scarabeidae). *American Journal of Tropical Medicine and Hygiene* **10**, 748–754.

Mukaratirwa, S., Pillay, E. and Munsammy, K. (2010). Experimental infection of selected arthropods with spirurid nematodes *Spirocerca lupi* Railliet & Henry, 1911 and *Gongylonema ingluvicola* Molin, 1857. *Journal of Helminthology* **84**, 369–374. doi: 10.1017/s0022149x10000039.

Mutinga, M. J. and Madel, G. (1981). The role of coprophagous beetles in the dissemination of taeniasis in Kenya. *Insect Science and its Application* **1**, 379–382.

Nichols, E. and Gardner, T. A. (2011). Dung beetles as a candidate study taxon in applied biodiversity conservation research. In *Dung Beetle Ecology and Evolution* (ed. Simmons, L. W. and Ridsdill-Smith, J.), pp. 267–291. Wiley-Blackwell, Chichester, UK.

Nichols, E., Gardner, T. A., Peres, C. A., Spector, S. and the Scarabaeinae Research Network (2009). Co-declining mammals and dung beetles: an impending ecological cascade. *Oikos* **118**, 481–487.

Nichols, E., Uriarte, M., Bunker, D. E., Favila, M., Slade, E. M., Vulinec, K., Larsen, T., Mello, F. V. d., Louzada, J. N. C., Naeem, S. and Spector, S. H. (2013). Trait-dependent response of dung beetle populations to tropical forest conversion at local to global scales. *Ecology* **94**, 180–189.

Orlofske, S. A., Jadin, R. C., Preston, D. L. and Johnson, P. T. J. (2012). Parasite transmission in complex communities: predators and alternative hosts alter pathogenic infections in amphibians. *Ecology* **93**, 1247–1253.

Over, H. J., Jansen, J. and van Olm, P. W. (1992). *Distribution and Impact of Helminth Diseases of Livestock in Developing Countries*. Food and Agriculture Organization, Rome, Italy.

Pompanon, F., Deagle, B. E., Symondson, W. O. C., Brown, D. S., Jarman, S. N. and Taberlet, P. (2012). Who is eating what: diet assessment using next generation sequencing. *Molecular Ecology* **21**, 1931–1950.

Prichard, R. K., Basáñez, M.-G., Boatin, B. A., McCarthy, J. S., García, H. H., Yang, G.-J., Sripa, B. and Lustigman, S. (2012). A research agenda for helminth diseases of humans: intervention for control and elimination. *PLoS Neglected Tropical Diseases* **6**, e1549.

Randolph, S. E. and Dobson, A. D. M. (2012). Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology* **139**, 847–863.

Roepstorff, A., Grønvold, J., Larsen, M. N., Kraglund, H. O. and Fagerholm, H. P. (2002). The earthworm *Lumbricus terrestris* as a possible paratenic or intermediate host of the pig parasite *Ascaris suum*. *Comparative Parasitology* **69**, 206–210.

Ryan, U., Yang, R., Gordon, C. and Doube, B. (2011). Effect of dung burial by the dung beetle *Bubas bison* on numbers and viability of *Cryptosporidium oocysts* in cattle dung. *Experimental Parasitology* **129**, 1–4.

Saitoh, Y. and Itagaki, H. (1990). Dung beetles, *Onthophagus* spp., as potential transport hosts of feline coccidia. *Japanese Journal of Veterinary Science* **52**, 293–297.

Schmidt, G. D., Roberts, L. S. and Janovy, J. J. (2000). *Foundations of Parasitology*, 6th Edn. McGraw-Hill Education, New York, NY, USA.

Shepherd, V. E. and Chapman, C. A. (1998). Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal Of Tropical Ecology* **14**, 199–215.

Stewart, T. B. and Kent, K. M. (1963). Beetles serving as intermediate hosts of swine nematodes in southern Georgia. *Journal of Parasitology* **49**, 158–159.

Stromberg, B. (1997). Environmental factors influencing transmission. *Veterinary Parasitology* **72**, 247–264.

Stumpf, I. V. K. (1986). Hospedeiros intermediários de *Macracanthorynchus hirudinaceus* (Pallas, 1781) (Acanthocephala) em Mandirituba, Paraná, Brasil. *Acta Biologica Paranaense* **15**, 87–124.

Suzán, G., Marcé, E., Giermakowski, J. T., Mills, J. N., Ceballos, G., Ostfeld, R. S., Armién, B., Pascale, J. M. and Yates, T. L. (2009). Experimental evidence for reduced rodent diversity causing increased hantavirus prevalence. *PLoS ONE* **4**, e5461.

Thieltges, D. W., Jensen, K. T. and Poulin, R. (2008). The role of biotic factors in the transmission of free-living endohelminth stages. *Parasitology* **135**, 407–426.

Vercruysse, J., Albonico, M., Behnke, J. M., Kotze, A. C., Prichard, R. K., McCarthy, J. S., Montresor, A. and Levecke, B.

(2011). Is anthelmintic resistance a concern for the control of human soil-transmitted helminths? *International Journal for Parasitology: Drugs and Drug Resistance* **1**, 14–27.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. (2007). Let the concept of trait be functional! *Oikos* **116**, 882–892.

Vulinec, K. (2000). Dung beetles (Coleoptera: Scarabaeidae), monkeys, and conservation in Amazonia. *Florida Entomologist* **83**, 229–241.

Vulinec, K. (2002). Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. *Biotropica* **34**, 297–309.

Waghorn, T. S., Leathwick, D. M., Chen, L. Y., Gray, R. A. and Skipp, R. A. (2002). Influence of nematophagous fungi, earthworms and dung burial on development of the free-living stages of *Ostertagia* (*Teladorsagia*) *circumcincta* in New Zealand. *Veterinary Parasitology* **104**, 119–129.

Whipple, S. D. and Hoback, W. W. (2012). A comparison of dung beetle (Coleoptera: Scarabaeidae) attraction to native and exotic mammal dung. *Environmental Entomology* **41**, 238–244.

WHO (2004). *The World Health Report 2004: Changing History*. World Health Organization, Geneva, Switzerland.

WHO/UNICEF (2012). *Progress on Drinking Water and Sanitation: 2012 Update*. WHO/UNICEF, New York, NY, USA.

Williams, J. C. and Bilkovich, F. R. (1971). Development and survival of infective larvae of the cattle nematode, *Ostertagia ostertagi*. *Journal of Parasitology* **57**, 327–338.

Wood, C. L. and Lafferty, K. D. (2012). Biodiversity and disease: a synthesis of ecological perspectives on Lyme disease transmission. *Trends in Ecology and Evolution* **28**, 239–247.

Xu, J., Liu, Q., Jing, H., Pang, B., Yang, J., Zhao, G. and Li, H. (2003). Isolation of *Escherichia coli* O157:H7 from dung beetles *Catharsius molossus*. *Microbiology and Immunology* **47**, 45–49.