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Succinctus

## Big dung beetles dig deeper: trait-based consequences for faecal parasite transmission

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## ABSTRACT

Observational evidence suggests that burial of faeces by dung beetles negatively influences the transmission of directly transmitted gastrointestinal helminths. However, the mechanistic basis for these interactions is poorly characterised, limiting our ability to understand relationships between beetle community composition and helminth transmission. We demonstrate that beetle body size and sex significantly impact tunnel depth, a key variable affecting parasite survival. Additionally, high parasite loads reduce the depth of beetle faeces burial, suggesting that the local prevalence of parasites infecting beetles may impact beetle ecosystem function. Our study represents a first step towards a mechanistic understanding of a potentially epidemiologically relevant ecosystem function.

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An improved understanding of the ecology of parasitic biodiversity is critical to efforts aimed at the reduction of the disease burden associated with parasite transmission. Infections of humans and their domestic animals by parasitic helminths cause enormous health and economic costs across the global tropics (Perry and Randolph, 1999; Hotez et al., 2008; Lustigman et al., 2012). Despite major contributions of chemotherapy towards the reduction of helminth infection prevalence and intensity, it is increasingly accepted that an understanding of the ecological context of helminth transmission is a required complement to existing control efforts (Boatin et al., 2012).

Interactions between parasitic and free-living species are often a fundamental determinant of parasite transmission success. For example, interspecific variation in host competence can strongly influence microparasite prevalence (Johnson et al., 2013). The community structure of free-living biodiversity is therefore expected to influence the transmission dynamics of the parasites with which they interact.

Less understood is how interactions between parasitic and free-living species may influence macroparasite transmission (Johnson and Thieltges, 2010). As many important parasitic helminths have direct transmission and free-living infective stages, interactions between helminths and ambient free-living species (i.e. species external to the parasite life-cycle) may play significant roles in regulating transmission success through predation on parasite eggs, cysts or larvae (Thieltges et al., 2008) or other types of mechanical interference (Johnson et al., 2010).

At least 19 families of helminths infecting terrestrial vertebrates have a faecal component to their life-cycle (Nichols and Gómez, 2014). For these parasites, transmission success is likely to be affected by interactions with coprophagous dung beetles. Globally, over 7000 species of the families Scarabaeidae, Aphodidae and Geotrupidae use vertebrate faeces as an adult and larval food resource.

The relocation of faeces by dung beetles during feeding and nesting activities may influence helminth survival and transmission through at least five underlying mechanisms (reviewed by Nichols and Gómez, 2014). Among these is indirect mechanical interference, wherein faeces that contain infective larval stages are buried beneath the soil surface. This mechanism is expected

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to buffer parasite transmission risk by reducing larval survival and emergence, subsequently lowering contact rates between larvae and definitive hosts. This reduction in parasite survival is contingent upon the burial of faeces at depths which exceed the maximum vertical migration distance (MVMD) of the larvae of a given parasite species, and is further dependent on local soil conditions (Lucker, 1938).

Efforts to understand the relevance of specific traits of both parasites and free-living species for transmission-relevant ecological interactions can improve our ability to understand and predict the ecological conditions that result in successful parasite transmission. As preliminary evidence suggests a positive relationship between the depth of faeces burial and beetle body mass (for review, see Nichols and Gómez, 2014), dung beetle body size may be a key species trait linking dung beetle community composition and helminth transmission outcomes. However, the relationship between beetle body size and burial depth has only been characterised for a limited number of species.

Here we report the results of a field-based mesocosm experiment that investigates the relationship between faeces burial depth and beetle body size. We additionally incorporate two relevant factors into our exploration of beetle trait-function relationships. First, does beetle infection status influence burial depth? Parasites commonly influence the behaviour of free-living species, including intermediate hosts (Holmes and Bethel, 1972), and recent evidence suggests that dung beetles infected with the swine nematode *Physocephalus sexalatus* dig shallower tunnels compared with uninfected individuals (Boze et al., 2012). Infection status may further interact with beetle sex to influence the role of species traits on faeces burial depth, given the oft-observed strong male bias in infection intensity across both vertebrate and invertebrate species (Córdoba-Aguilar and Munguía-Steyer, 2013). Second, although interactions between naturally co-existing species can strongly influence observed relationships between species, their traits, and their ecological function, the use of naturally assembled communities to explore these relationships remains relatively novel (Naem, 2008). We used a series of 25 naturally assembled Neotropical dung beetle communities to explore the relationships between beetle body mass, sex, infection intensity and nesting strategy with faeces burial depth. We discuss the implications of this relationship for the contribution of dung beetles to the reduction of parasitic helminth transmission.

Live dung beetles were collected using pitfall traps baited with human faeces – a broad spectrum attractant of Neotropical dung beetles (Nichols and Gardner, 2011). Each trap consisted of two halves of a 1.5 L plastic bottle fitted together, with the top inverted to create a funnel. Traps were buried in the ground, with the top rim flush with the soil surface, and were fitted with a plastic rain guard. Approximately 1 cm of soil was placed inside each trap to provide shelter for beetles following capture. Above each trap entrance, a single 25 g human dung bait was wrapped in mesh netting and hung from a bamboo skewer.

In an effort to maximise beetle taxonomic and functional diversity, dung beetles were sampled from two distinct biomes in the Cerrado (22°51'18"S, 46°19'4"W) and the Atlantic Forest biomes of São Paulo State (21°59'46"S, 47°25'33"W), Brazil. A total of 25 traps were set approximately 10 m apart, along transects into a total of three forest fragments in each biome. Traps were collected after 24 h and the beetle communities transported to the laboratory in 20 × 20 × 6 cm plastic containers, filled with approximately 2 cm of local soil.

A total of 25 experimental mesocosms were constructed using 34 × 40 × 70 cm plastic bins filled to within 3 cm of the surface with 70 L of hand-compressed, local latosol soil. To begin the experiments, 100 g of fresh, homogenised human faeces and a single dung beetle community were placed in each mesocosm at

the soil surface. The community composition of each naturally assembled beetle community differed, as each community represented the beetles attracted to and captured by a single pitfall trap, a direct and realistic representation of the ephemeral beetle communities that assemble on individual faecal deposits in nature. Each mesocosm was then covered with fine plastic netting to prevent beetle escape and a plastic lid was taped over each piece of mesh to protect mesocosms from rain. We added approximately 200 mL of water to the surface of each mesocosm twice during the trial period, to prevent desiccation of the top-most soil layer. Following a 1 week exposure period, mesocosms were opened and any remaining faecal masses were removed from the surface. Beetles and brood balls were excavated by hand, by scraping the soil surface away in 0.25 cm layers. The depth at which each beetle or brood ball was encountered was recorded. This approach does not distinguish between the type of tunnel created by beetles (e.g. for feeding, nesting or protection), but does realistically reflect beetles' per-capita burial capabilities. Individual beetles were preserved in alcohol-formalin-acetic acid solution (AFA), measured and then dissected to determine both sex and infection status, the latter through an examination of haemocoel contents under 40× magnification with a light microscope. Recovered brood balls were dried in a convection oven at 50 °C to constant weight. Dung beetles were identified to species by a Scarabaeinae taxonomist (Fernando A. B. Silva, Universidade Federal do Pará, Belém, Brazil). Experiments were conducted at the Multiuser Laboratory of Animal Health and Food Safety of the Faculty of Animal Science and Food Engineering at the University of São Paulo, Pirassununga, Brazil. All necessary permits were obtained for this work from the Brazilian Institute of Environmental and Renewable Natural Resources (IBAMA) under SISBIO permit 16620-1.

To preliminarily explore species-specific differences in burial depth and infection status, linear regression was performed using beetle species as the independent variable. We also contrasted mean tunnel depth, infection status and parasite prevalence between male and female dung beetles using Welch's *t*-tests. We modeled faeces burial depth as a function of beetle infection intensity, body mass and sex with generalised linear mixed models (Poisson errors), using mesocosm identity as the random effect. This analysis was restricted to species with a telocoprid or 'tunneling' nesting strategy, that excavate linear or branching tunnels directly below the faecal deposit (Halffter and Edmonds, 1982). Unlike 'dweller' species that nest within or immediately under the faecal deposit or 'roller' species that transport faecal matter some horizontal distance from the faecal deposit before excavating very shallow burial pits, tunneler species are likely to drive the majority of epidemiologically relevant faeces burial (Nichols and Gómez, 2014). The dredge function from the MuMIn package in R 2.15.2 was used to explore all additive combinations of these three variables on burial depth, and subsequent model selection was conducted with corrected Akaike Information Criterion (AICc). All analyses were conducted using the statistical package R 2.15.2 (Team 2005). *P*-values were considered significant below  $\alpha > 0.05$ .

A total of 124 beetles (60 females, 64 males), across 25 species in nine genera were (Table 1). Of these species, 13 used a tunneling nesting strategy, while nine were considered rollers and three were considered dwellers. Across all species, body mass ranged from 0.003 to 0.919 g (0.125 g ± 0.17, mean ± 1 S.D.), with the largest species belonging to tunneler species in the genus *Dichotomius* (0.283 g ± 0.21) and roller species in the genus *Deltochilum* (0.408 g ± 0.25). Across the 25 communities used in these trials, the average species richness ranged from 1 to 11 species (5 ± 3.38, mean ± 1 S.D.), while the average total abundance ranged from 1 to 27 species (9.2 ± 6.65, mean ± 1 S.D.).

The depth of faeces recovered from mesocosms ranged from 0 (at soil surface) – 54 cm (7.60 ± 0.84). While male beetles were

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