

The impact of dung beetles on the free-living stages of ruminant parasites in faeces and their role as biological control agents in grazing livestock

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Highlights

- Dung beetle activity can impact parasitic nematode epidemiology.
- Beetles burying dung ≥ 15 cm can reduce pasture larval populations.
- Shallowly buried and fragmented dung affect larval survival inconsistently.
- Little evidence that beetles affect coccidial, cestode or trematode epidemiology.

Abstract

Dung beetles provide a variety of ecosystem services in both natural and farmed landscapes. Amongst these services, reductions in the abundance of the free-living stages of pests and parasites that develop in faeces is considered to be of great importance. There is evidence from Australia that enhanced dung beetle populations can reduce populations of pest fly species, particularly the bush fly, however, there is little empirical evidence for reductions in the incidence and impact of nematode parasitism in grazing ruminants. There are two main pathways whereby beetles can disrupt worm life-cycles: predaceous species that feed on eggs or larvae can directly reduce populations in dung whereas coprophagous species can affect parasite development, survival and translocation by altering the location, microclimate and infrastructure of dung deposits. In addition, predaceous mites that are phoretic on dung beetles, can also prey on larval stages in the faeces. To date, reductions in both larval survival and the acquisition of gastrointestinal nematode burdens in ruminants on pasture has been reported only in association with the activity of large tunnelers that bury dung 15 cm or more below ground. The activity of dwellers, rollers and shallow tunnelers can either limit or enhance larval development and translocation, depending on the influence of other factors, notably rainfall. Currently, the scientific evidence for dung beetles playing a major role in the control of gastrointestinal nematodes in domestic ruminants is very limited and may have been overestimated in assessments of their ecosystem services.

Keywords: Dung beetles; Nematodes; Larvae; Species interactions; Control

1. Introduction

The ecosystem services provided by dung beetles are diverse and, in addition to their role in the decomposer community, they have potential value as biological control agents of both insect pests and gastrointestinal nematodes (GIN) on livestock farms (Bornemissza, 1976, deCastro-Arrazola et al., 2023, Doube, 2018, Nichols et al., 2008). Considerable financial value has been placed on biological control of parasitism by dung beetles (Losey and Vaughan, 2006); in a UK study over 50 % of the estimated financial benefit of dung beetles on cattle

farms was attributed to their control of parasitic gastroenteritis (PGE), outweighing the combined value of controlling pest flies, reduced pasture fouling and increased nutrient cycling (Beynon et al., 2015).

In this overview the evidence for the disruption of parasite life-cycles by the dung fauna and its consequences for the epidemiology and control of parasitism in domestic ruminants in pastoral regions of the world is examined. The focus is on the impact of coprophagous dung beetles on GIN of cattle, but sheep and their parasites are also included, as are some other, relevant interactions amongst the dung fauna of domestic ruminants. Dung beetle interactions with parasites take place within dung deposits and their surroundings, both above and below ground. In order to place these relationships within context, ruminant dung, its characteristics and the biology and ecology of its fauna need to be understood and these are briefly summarised below.

2. Dung and the dung fauna

Freshly excreted herbivore dung comprises an aqueous matrix of undigested plant material, minerals, microorganisms, cellular debris, mucus and metabolites; in addition, it can contain oocysts, eggs, gravid proglottids and larvae from internal parasite infections. Ruminants deposit dung as pats (cattle and adult sheep grazing lush herbage) or pellets (lambs and ewes grazing dry vegetation). The quantity and composition of dung produced by herbivores can vary widely through differences in factors such as feed intake, diet, liveweight (LW), physiological status, parasitism and disease. The typical daily output of fresh faeces from healthy cattle approximates to ~5 % of LW, per day and the average number of defecations per day for adult cows is 11–12, so each deposition is around 2.5 kg fresh weight for a 600 kg animal (Marsh and Campling, 1970). Bovine dung pats have an initial moisture content of $\pm 85\%$ (Barth et al., 1995), though in the dry season in the sub-tropics, this can fall to $\pm 70\%$ (Rougon et al., 1990).

In ecological terms, natural deposits of dung are described as patchy and ephemeral and each can be considered as a distinct ecological unit (Hanski, 1991a, Mohr, 1943). The physicochemical and biological properties of faeces begin to change almost immediately after deposition, influenced in the first place by the weather and subsequently by the activities of myriad invertebrates, fungi and bacteria and subject to mechanical damage through trampling by livestock and foraging behaviour of insectivorous birds and mammals (Putman, 1983). The dung invertebrate fauna comprises free-living nematodes, earthworms and arthropods, including beetles, flies, springtails and mites, (Skidmore, 1991), as well as termites in subtropical regions (Ferrar and Watson, 1970, Freymann et al., 2008). This community includes not only obligatory and facultative coprophages, but also saprophages, fungivores, predators and parasitoids; such functional diversity contributes to complex food-webs within and beyond the pat (Skidmore, 1991). The relative occurrence and abundance of individual species within dung depends on several factors including geographical location, the age of the pat, its size and site of deposition, the season of the year and the prevailing weather (Wassmer, 2014, Wassmer, 2020). Examples of some abiotic and biotic factors that can influence dung fauna (Edwards, 1991, Seeman and Walter, 2023, Sulgostowska et al., 2015, Wratten and Forbes, 1996, Young, 2015), are shown in Table 1.

Table 1. Factors that can affect breeding and feeding biology of dung insects.

Abiotic	Biotic
Temperature, Rainfall, Season Weather-induced or mechanical disturbance and disruption of pat integrity Moisture content of faeces at deposition and subsequently pH and nutrient composition of faeces Site of deposition and soil characteristics Presence of insecticidal residues in dung	Bacterial content (feed source for larvae) Interspecific and Intraspecific competition Parasitism Phoresy Predation by invertebrates and vertebrates Disturbance and disruption of pat integrity by foraging birds and mammals

Typically, there is a succession of the various members of the dung fauna, fungi and bacteria over time as the pat ages and changes in its form and composition (Gittings and Giller, 1998, Sladeczek et al., 2017, Sladeczek et al., 2021a). At one extreme, horn flies (*Haematobia irritans irritans*) have been observed laying their eggs in cow dung as it is falling to the ground and where peak oviposition occurs within two minutes of deposition (Sanders and Dobson, 1969), whereas detritivores such as earthworms, termites and ants generally do not utilise faeces until they are fragmented and desiccated several weeks after deposition (Freymann et al., 2008, Knight et al., 1992). Given that dung is a discrete and finite resource, it is inevitable that there are interactions amongst the colonising species, many of which are competitive in nature (Finn and Gittings, 2003, Ridsdill-Smith et al., 1986), though some may be facultative (Sladeczek et al., 2021b, Sullivan et al., 2017).

3. Dung beetles

Coprophilous (‘dung-loving’) beetles that are commonly associated with herbivore dung can be broadly classified into a number of groups that comprise coprophagous (‘dung-eating’), predaceous or mixed-diet species (Table 2), in some of which the adults and larvae have different feeding preferences and behaviours (Hanski, 1991a). Coprophagous species can also be classified by various traits, such as their size, feeding and nesting behaviour into at least 7 functional groups (deCastro-Arrazola et al., 2023, Doube, 1990), but three broad categories suffice to understand beetle/parasite interactions:

- Tunnelers (Paracoprids), which bury dung beneath the pat in tunnels of varying depths
- Rollers (Telecoprids), which roll dung balls away from pats and then bury them shallowly
- Dwellers (Endocoprids), which feed and lay their eggs within or immediately below the pat

Table 2. Feeding and Breeding Behaviour in Coprophilous Beetles.

Beetle Taxa	Adult	Larvae	Guild
Aphodians	Coprophagous ^a	Coprophagous ^b	Dwellers
Geotrupids	Coprophagous ^a	Coprophagous ^b	Tunnelers
Histerids	Predaceous	Predaceous	
Hydrophilids	Mixed diet	Predaceous	
Scarabs	Coprophagous ^a	Coprophagous ^b	Tunnelers & Rollers
Staphylinids	Predaceous	Predaceous	

^aAdult coprophagous beetles are filter-feeders whose diet comprises mainly the liquid component of dung.

^bLarval coprophagous beetles feed on whole dung including the fibrous, cellular, microbiological and liquid content.

The typical species composition differs quite markedly in various geographical zones, for example in northern temperate regions, dwellers predominate and rollers are rare or absent (Hanski, 1991b), whereas in southern Africa, tunneler species are most abundant, followed by rollers, while dwellers are less common (Doube, 1991).

The function of coprophilous beetles in the families Histeridae (Clown Beetles), Hydrophilidae (Water Scavenger Beetles) and Staphylinidae (Rove Beetles) is mainly predation, either as adults or larvae or both (Floate, 2023). Most Staphylinids are small to medium-sized (1–20 mm long) beetles in which both adults and larvae are predatory, occurring mostly in moist situations such as humus, herbivore dung and carrion, where they prey on mites, insect eggs and soft-bodied insects such as worms and maggots. Histerids are oval, shiny beetles that vary in length between about 1 mm and 20 mm. Most species are active predators and adults and larvae may be found together where potential prey occurs of which fly eggs and maggots and other soft-bodied invertebrates are important items. The coprophilic Hydrophilids are medium-sized, 4–7 mm long and the adults mainly colonise fresh dung that is quite liquid, through which they move in a swimming-like manner. Though adults may have a mixed diet (Holter, 2004), they are largely predaceous, as are their larvae, feeding mainly on dipteran larvae.

Predatory beetles can be very abundant in dung, for example a study in South Africa recorded 134 species of non-scarabaeid beetles in cattle dung exposed for 12 hours, including 100 species of Staphylinidae and 21 of Histeridae (Davis et al., 1988). Similarly in northern temperate dung beetle assemblages, predators are common and frequently outnumber coprophages (Barth et al., 1994, Koskela, 1972, Lee and Wall, 2006, Merritt and Anderson, 1977, Schmid et al., 2024). The presence of so many different beetle species in a single dung pat alongside other insects, such as flies, and invertebrates from different taxa, results in multiple interactions, which in turn are also influenced by the physical and chemical changes in the pat as it ages.

4. Dung flies

There are a number of flies that associate with dung for nutrition or breeding; most adult flies are active on the surface of faecal deposits where they feed, mate or predate other insects (Hammer, 1941), while most of their larvae inhabit the interior where they may be coprophagous or predaceous, with some species switching their diet according to their age and the availability of food (Laurence, 1954). Adult flies can be scavengers or predators and some are pest species of livestock and man, for example *Haematobia* and *Musca* species. Numerous factors can affect the hatching of fly eggs, their subsequent development through larval (maggot) stages, pupation and adult emergence (Table 1).

The interactions of most relevance to pest fly populations are those between fly eggs or larvae and predaceous and coprophagous beetle species. In both controlled experiments and field studies, there is typically an inverse relationship between the density of dung beetles in a pat and the survival of fly larvae (Bornemissza, 1970, Tyndale-Biscoe and Vogt, 1991) and these in turn can be influenced by season, the moisture content and nutritional quality of the dung (Ridsdill-Smith et al., 1986). These relationships can be seen when the beetle fauna comprise coprophages, predators or both (Fay and Doube, 1983, Wallace and Tyndale-Biscoe, 1983). The predaceous species directly reduce fly numbers by feeding on their eggs and larvae, while the coprophages affect fly biology by disrupting microhabitats within the dung, rendering the maggots liable to desiccation or predation. In addition, tunnelers and rollers can incorporate

eggs and larvae in their food/brood balls and remove them from development sites, such that they cannot continue their life-cycles (Doube, 1986, Edwards and Aschenborn, 1987).

Studies in Australia after the introduction of no-native, mainly African, dung beetle species recorded large decreases in bush fly numbers in dung pats colonised by beetles compared with those without (Hughes et al., 1978), however, the impact of coprophagous dung beetles on buffalo fly populations was less marked. A possible explanation can be found in South Africa, where populations of the congeneric African buffalo fly (*Haematobia thirouxi potans*) are kept in check through the activity not only of coprophagous beetles, but also a suite of predatory beetles and mites (Doube, 2018, Doube et al., 1988).

5. Dung beetle interactions with free-living stages of livestock helminth and protozoan parasites

Many species of gastrointestinal helminths and protozoa are transmitted via the faecal-oral route in which parasite oocysts, eggs, tapeworm segments or larvae, produced by adult parasites in the host, are excreted in the faeces onto the pasture, where development *in situ* takes place. With adequate oxygenation and appropriate temperatures, coccidial oocysts sporulate in the faeces from which they can only disperse passively and generally remain at the soil/herbage interface until ingested by a grazing animal. Nematode larvae either move actively a short distance from the faeces onto the surrounding herbage or are passively translocated further through the action of agents such as rainfall (Gronvold, 1987a), coprophilous fungi (Robinson, 1962), invertebrates (Durie, 1975, Grønvoid, 1979, Tod et al., 1971), wildlife (Gronvold, 1984) or livestock (Hertzberg et al., 1992).

Trematodes and cestodes have indirect life-cycles that require the intervention of intermediate hosts before reaching the infective stages that can be ingested by the final hosts, where the parasites can establish. For ruminant tapeworms belonging to the genus *Moniezia*, their eggs must be eaten by Oribatid mites, which are common in the soil and herbage of pastures (Forbes, 2021), so it seems unlikely that the activities of dung beetles would disrupt this process. The eggs of liver and rumen fluke embryonate in dung, but do not hatch and release miracidia unless they are free of faeces and in a liquid environment (Rowcliffe and Ollerenshaw, 1960), which could make them susceptible to the actions of dung beetles that bury or fragment faeces. Evidence for such effects is very limited, but there is a study which noted that the eggs of *Fasciola hepatica* survived for considerably shorter time when exposed to natural or simulated dung fauna, including insects and earthworms, compared with comparatively low mortality rates in faeces with no fauna (Over, 1982).

The potential of dung beetles as aids to the control of parasitic helminths and protozoa in livestock has been recognised for several decades (Szewc et al., 2021), with several examples of interactions between beetles and the gastrointestinal nematodes of cattle (Bryan, 1973, Fincher, 1973, Reinecke, 1960). The mechanisms through which beetles may inhibit development, increase mortality or reduce transmission of coprophilous parasite stages include:

- Directly damaging to eggs (or larvae) through
 - Predation by carnivorous beetles
 - Incidental ingestion by adult coprophagous beetles
- Disrupting the milieu of the dung deposit, which can lead to:
 - Unfavourable conditions for parasite development, such as rapid desiccation

- Interference with translocation of larvae away from the pat
 - Invasion by predatory insects and parasitoids
- Burying dung in the soil to depths from which larvae are unable to return to the soil surface and hence the vegetation
 - Acting as vectors for predatory mites that feed on nematodes and arthropods

5.1. Direct damage to eggs or larvae through ingestion

There seems to be no reason why adult and larval predatory beetles would not feed on parasite eggs or larvae in the dung, given their powerful mouth-parts, however there do not appear to be any published data on this aspect of feeding behaviour. It is well documented that arthropods prey on free-living nematodes in the soil (Walter and Ikonen, 1989), so it is not unreasonable to assume that predaceous beetles could reduce the abundance of parasite larvae in dung, but without further research, this cannot be quantified. The concentration of parasite eggs in the dung can range from essentially zero eggs per gram (EPG) through $10-10^2$ in trematodes, $10-10^3$ in nematodes and $10-10^{4/5}$ in coccidiosis and these concentrations will determine the frequency with which beetles may encounter eggs or subsequent developmental stages during feeding.

The larvae of coprophagous beetles could potentially damage parasite eggs in the dung while feeding, but, because insect larvae typically emerge after nematode eggs have hatched and larval development has been completed, they are considered to have few, if any, direct effects on parasite development and survival. Adult coprophagous dung beetles are filter-feeders and there is a limit on the particle size that they can readily ingest; this ranges from 5 to 150 μm , depending on their body size and functional group (Holter and Scholtz, 2007). The approximate size of helminth and coccidial eggs (Deplazes et al., 2016, Foreyt, 2001) relative to the ingestive capacity of coprophagous beetles is shown in Table 3, along with an assessment of the likelihood of being eaten:

Table 3. Comparison between size of parasites stages and dimensions of beetle mouthparts.

Parasite Stage	Dimensions (μm)	Beetle Mouthparts 5–150 μm Potential to ingest eggs or larvae
Strongyle eggs	95×50	Large species
Strongyle larvae	400–900	Highly unlikely
Nematodirus eggs	200×90	Highly unlikely
Nematodirus larvae	750–1100	Highly unlikely
Lungworm larvae	420–480	Highly unlikely
Fluke eggs	140×80	Large species
Tapeworm eggs	60×60	Medium to Large species
Coccidial oocysts	40×25	Medium to Large species

From these measurements, it can be deduced that it is mainly the larger species of dung beetle that may be capable of ingesting or damaging nematode or trematode eggs, whereas tapeworm eggs and coccidial oocysts could be vulnerable to medium-sized species as well. This interpretation may overestimate potential for damage, as the majority of dung beetles have a maximum ingestible particle diameter of around 20 μm (Holter and Scholtz, 2007). Although destruction of parasite eggs or oocysts by ingestion may seem unlikely, during feeding, adult dung beetles compress the faeces and squeeze and expel excess moisture (Scholtz et al., 2009), actions that could damage parasite eggs. It can be concluded from this analysis that direct

ingestion of free-living stages of helminth and protozoal parasites by larval or adult dung beetles is unlikely to have any major effects on helminth populations, (Nichols et al., 2008).

5.2. Disruption of the milieu of the dung deposit, which renders it unfavourable for parasite development and transmission

Each of the functional groups (guilds; rollers, tunnellers or dwellers) of dung beetles causes some level of disturbance to a dung deposit; either by burying, translocating, shredding and fragmenting it or creating cavities and tunnels that provide access to a range of invertebrate predators including mites, ants and various beetle groups such as hister beetles (Histeridae) and rove beetles (Staphylinidae).

Endocoprid dung beetles (dwellers), the functional group that predominates in northern temperate regions (Hanski, 1991b), feed and breed within faeces and are partly responsible for fragmenting the dung on the soil surface. The beetles play a role in the decomposition of dung on pasture during the grazing season (Spring/Summer/Autumn) alongside earthworms (Gittings et al., 1994, Holter, 1979), other invertebrates, fungi, bacteria (Putman, 1983) and abiotic factors, notably rainfall (Barth et al., 1995, Dickinson et al., 1981).

Though aeration of the dung pat by endocoprid beetles is postulated to facilitate the hatching of nematode eggs and the development of larvae, there is little evidence to support this. Although aeration of eggs stored in water facilitates embryonation under laboratory conditions (Silverman and Campbell, 1959), oxygenation does not seem to be a limiting factor for the free-living stages in natural pats in the field. The microclimate within dung initially is largely anaerobic or microaerophilic (Holter, 1991), but under optimum conditions of moisture and temperature, egg hatching and larval development take place readily within a few days of deposition in undisturbed pats, indicating that sufficient oxygen is present for embryonation and hatching (Rose, 1961, Rose, 1963a, Rose, 1963b).

On the other hand, moisture is very important in all egg and larval stages, so if fragmentation of the dung occurs within the first 1–2 weeks after deposition and this leads to desiccation, then hatching and development can be severely retarded and mortality increased. This has been demonstrated experimentally by placing dung in small amounts on plots and comparing larval emergence with that in the same weight of faeces in a single pat (Rose, 1962, Rose, 1963a, Rose, 1963b, Shorb, 1943); in all cases, considerably fewer larvae were recovered from the fragmented faeces. These outcomes can be modulated by weather conditions and the microclimate surrounding the dung, which, under field conditions is typically a function of the height, density and composition of the surrounding vegetation. Herbage provides shade, which lowers the temperature and limits moisture loss (Rose, 1964) and also diffuses ultra-violet light, which can adversely affect nematode larvae (van Dijk et al., 2009).

Given the variable and contrasting outcomes of endocoprid/parasite/pasture/weather interactions, it is not surprising that the net effects on parasite epidemiology are similarly unpredictable (deCastro-Arrazola et al., 2023) and this is reflected in studies that produced conflicting results, including both inhibited and enhanced development and survival of GIN larvae (Chirico et al., 2003, Sands et al., 2017). Coprophagous pest fly larvae can also affect the microclimate within dung, which in turn can affect the survival of infective nematode larvae (Devaney et al., 1990).

In summary, the potential impact of endocoprid beetle activity on the epidemiology of PGE, and possibly other helminth infections (Gormally, 1993), is highly context-driven. Beetle-driven dispersion of faeces containing parasites could increase their development and survival if conditions are moist/wet, whereas if the dung is not exposed to rain or dew, then desiccation is likely to reduce parasite numbers considerably in the immediate environs of co-colonised pats.

Additionally, alterations in the milieu of dung by endocoprids could affect free-living parasite stages through interactions with dung-associated bacteria and fungi, examples of which include:

- Faecal bacterial populations; bacteria are important in the diet of developing nematode larvae (Lee and Atkinson, 1976).
- Coprophilous fungi (Biggane and Gormally, 1994), some of which are important in the translocation of infective larvae away from the pat onto the surrounding herbage (Robinson, 1962).
- Nematophagous fungi, which feed on nematode larvae (Healey et al., 2018).

5.3. Burying dung in the soil to depths from which larvae or eggs are unable to return to the soil surface and hence the grazing horizon

Dung beetles that are classed as either tunnellers (paracoprids) or rollers (telecoprids) comprise an important component of the dung insect fauna, particularly in tropical and subtropical regions (Doube, 1990, Halffter and Edmonds, 1982); several species within these groups have been included in introduction programmes in Australasia and the Americas (Pokhrel et al., 2021). When present in sufficient numbers, dung beetles in these groups can fragment and disperse a dung pat within a few hours either by rolling and then burying dung balls some distance from the original deposition or by burying dung directly below the pat (Doube, 1990). Rollers and tunnellers frequently colonise dung simultaneously, so there is competition for a limited resource, but the net effect is that faeces can disappear rapidly from the soil surface (Hanski and Cambefort, 1991a).

In temperate and subtropical regions that experience two or more seasons a year, most dung beetles are active during the warm, wet seasons, while dry and/or cold conditions generally render them inactive (Davis, 1996b, Hanski, 1980). When they are active, paracoprids and telecoprids will rapidly fragment and bury fresh faeces before any nematode eggs present have had time to hatch, so their role in limiting further development rests on how much the dung is disturbed and how deep in the soil the dung is buried. These variables will determine whether larval development can take place amongst the fragments and whether infective larvae that are buried can find their way back to the soil surface, where they can translocate to herbage and become available to grazing animals. For parasites other than GIN, burying faeces in soil probably results in a dead-end because coccidial oocysts are non-motile and would therefore require some sort of passive movement to reach the soil surface, while fluke eggs only hatch in a liquid, faeces-free medium. Lungworm (*Dictyocaulus viviparus*) larvae are relatively sluggish and largely rely on passive transport by coprophilous fungi or rainfall to move from dung to herbage, so again, they are unlikely to translocate following deep burial in the soil, although they can survive there for several months and be transported by earthworms to the soil surface (Oakley, 1981).

An important criterion that determines the likelihood that nematode eggs will hatch, larvae develop and infective larvae reach the soil surface is the depth of burial of the food and brood balls in the soil. As a general rule, the greater the depth of dung burial, the fewer larvae emerge (Gronvold et al., 1992, Persson, 1974), though larval migration can also be influenced by soil type (Lucker, 1938). Nematode larvae can reach the soil surface from depths of 10–15 cm (Krecek and Murrell, 1988, Rose and Small, 1985) and sometimes more (Fincher and Stewart, 1979). There do not appear to be distinct thresholds for larval migration in soil, but beyond a depth of 15 cm or more, larval recoveries are low; this means that dung beetles that bury faeces deeply could play an important role in the epidemiology of PGE – these tend to be the larger species of paracoprids (Gregory et al., 2015, Nervo et al., 2014).

Generally, telecoprids do not bury dung deeply – a few centimetres below the soil surface (Halfpenny and Edmonds, 1982) - hence it is unlikely that their activity will reduce larval survival to any great extent (Gregory et al., 2015). Furthermore, shallow burial of faeces may facilitate larval development, survival and subsequent migration (Waghorn et al., 2002), however, incorporation of faeces in soil by earthworms at shallow depths can reduce parasite numbers (Gronvold, 1987b, Waghorn et al., 2011), possibly through ingestion of larvae (Curry and Schmidt, 2007). The upper layers of soil can act as important reservoirs for infective larvae and thus play an important role in the epidemiology of PGE (Al Saqur et al., 1982, Kauzal, 1941).

Examples of interactions between paracoprid dung beetles and GINs can be found in studies including species such as *Digitonthophagus gazella*, an Afro-Asian native that has been introduced into Australia and several countries in the Americas. This beetle is medium-sized (10–13 mm) and typically buries dung to a depth of 20–25 cm (Tyndale-Biscoe, 1990), so it might be predicted to reduce GIN larval populations and pasture contamination. Under controlled conditions, the presence of beetles reduced larval recoveries on herbage surrounding pats by between ~50–90 %, the lower values were associated with moisture resulting from natural rainfall or irrigation (Bryan, 1973, Bryan, 1976), which permitted more larvae to survive. Under both natural and controlled exposure to dung beetles, the deleterious effects on GIN nematodes were greater when large numbers of beetles were present and tunnelling activity was high (Bryan, 1973, Bryan, 1976, Bryan and Kerr, 1989). Similar responses were observed with *Geotrupes spiniger*, a large (16–26 mm), deep tunnelling, temperate paracoprid (Skidmore, 1991), which has been introduced into Australia and New Zealand. In a pilot study with three introduced species of deep tunnelers – *G. spiniger*, *Onthophagus binodis* and *D. gazella* in New Zealand, pasture larval counts in the vicinity of the faeces were reduced by ~70 % through beetle activity (Forgie et al., 2018).

Euoniticellus intermedius is a smaller paracoprid (7–9 mm) that buries dung up to 15 cm below the soil surface (Tyndale-Biscoe, 1990) and a study in Mexico showed that this species was capable of burying considerable numbers of nematode eggs, more so during the rainy season, when both beetle activity and GIN transmission coincide (Martinez et al., 2018), but no data were provided on subsequent larval development or emergence. *Diastellopalpus quinquegens* is a large (18 mm) African species (Davis et al., 2008) that buries dung up to 40 cm below the pat causing rapid disintegration of the pat; such activity not only reduced the number of GIN larvae in the remaining faeces on the soil surface, but also reduced the number of larvae that splashed out of the faeces on to the surrounding vegetation (Gronvold et al., 1992).

5.4. Acting as vectors for predatory mites that feed on nematodes and arthropods

Mesostigmatic mites are amongst the most numerous nematophagous arthropods in grassland soils where they predate soil nematodes and regulate their populations (Curry, 1994, Walter and Ikonen, 1989); whether they also feed on free-living stages of parasitic nematodes is not recorded, but it seems reasonable to assume that they would feed on them opportunistically. A family within the Mesostigmatic mites, the Macrochelidae, has become specialised in exploiting dung and have adopted a phoretic life-style, which depends on dung beetles as vectors (Krantz, 1998). These mites appear to be generalist predators that can feed on nematodes and arthropods in the soil or dung (Walter and Proctor, 2013), with the potential to limit populations of their prey. This has been exploited in attempts to control buffalo fly in Australia through the joint action of dung beetles and their phoretic mites introduced from Africa (Wallace and Holm, 1983). Macrochelid mites can be associated with the different groups of dung beetles, with some species associating specifically with rollers, thus potentially synergising in reducing GIN larval emergence from buried dung (Niogret et al., 2010). Recent *in vitro* studies have shown significant reductions in larval emergence of *Haemonchus contortus*, a common and pathogenic nematode parasite of sheep, when exposed to certain species of Macrochelid mites (Aguilar-Marcelino et al., 2014, Dos Anjos et al., 2024). As yet, there are no definitive data to verify any measurable effects of phoretic mites on PGE in ruminants, but there is a strong rationale for their potential as biological control agents.

6. Sheep

Typically, lambs and adult sheep pass dung as discrete pellets but ewes can produce large pats, particularly when grazing forage with a high moisture content. Faecal output for adult sheep is in the range of 1–1.5 kg daily in 6–8 deposits, each with an average mass of 100–200 g (Frame, 1992). Sheep pellets have a water content of $\pm 70\%$ (Lumaret et al., 1992) and dry out quickly, especially in hot dry weather, because of their small mass and relatively large surface area and sheep faeces do not form protective crusts overlying a moist interior (Hirschberger and Bauer, 1994a). Generally, it appears that sheep dung, particularly in pelleted form, is a less suitable habitat for dung-dwelling insects than cattle dung (Lumaret and Kirk, 1987, Sowig and Wassmer, 1994). However, when sheep faeces are bulked to pats of one litre and compared with 1–2 litre cattle dung, pats, they can yield equivalent or greater density and abundance of beetles (Finn and Giller, 2002, Rainio, 1966).

The beetle fauna found in sheep faeces are generally similar to those found in cattle dung in the same region, though abundance and species diversity can vary. The dung beetles associated with ruminants have been described as ‘choosy generalists’, insofar as they are opportunistic feeders that do not discriminate strongly between dung from different sources (Frank et al., 2018). In northern temperate and Mediterranean regions, *Aphodius* and *Onthophagus* species are common inhabitants of sheep dung, as are some typical predatory species (Adam, 1986, Breymeyer, 1974, Finn and Giller, 2002, Kessler et al., 1974, Lobo et al., 2006, Lumaret et al., 1992, Lumaret and Kirk, 1987, Rainio, 1966).

In the limited published information available on the dipteran fauna associated with sheep dung, a diverse fauna, including common species like the yellow dung fly, *Scathophaga stercoraria*, with considerable overlap with the bovine dung fauna, appears to be typical (Coffey, 1966, Papp, 1985, Skidmore, 1991, Wilson, 1932). In addition, some pest species such as the sheep blowfly, *Lucilia cuprina* and the bush fly, *Musca vetustissima* utilize sheep faeces for feeding and breeding, though protein concentrations may be suboptimal (Hughes et al.,

2007, Vogt et al., 1985). In general, adult flies are attracted only to very fresh dung with a high moisture content; because sheep pellets dry out quickly, they rapidly become unattractive to early colonising insects, typically within the first few days after deposition.

There are few references to interactions between the sheep dung-associated fauna and the free-living stages of parasitic helminths and protozoa. Observations on dispersal and disintegration of sheep dung by insect fauna generally indicate that insects play a minor role in faecal degradation in temperate regions, but assume greater importance in more arid regions where herbivore dung is commonly in pelleted form (Tshikae et al., 2013). In temperate regions during the months when beetles are active, up to 40 % of dung can be buried, but over a whole grazing season, dung removal by beetles is reported as being less than 20 % of the initial deposits, with earthworms playing a more important role in dung degradation and decomposition (Brey Meyer, 1974, Hirschberger and Bauer, 1994a, Hirschberger and Bauer, 1994b).

Given the limited effects of coprophagous beetles on the relocation and restructuring of sheep dung, the mechanism for indirect effects on sheep parasites appears to be correspondingly small. Although adult sheep can suffer from haemonchosis, clinical PGE is typically associated with lambs, which produce pelleted faeces, unless diarrhoeic. Ewes can be important epidemiologically, because they can contribute to pasture contamination, particularly around lambing (Forbes, 2021) and they produce a relatively high volume of faeces that is attractive to dung insects. Potential useful contributions of dung beetles to worm control in lambs therefore could take place in ewe dung pats in the peri-parturient period and subsequently in lamb pellets. Predaceous beetles might feed on nematode larvae in sheep faeces, though evidence for this is currently lacking and phoretic mites have potential as biocontrol agents in sheep (Dos Anjos et al., 2024).

7. Temporal and spatial coincidence of dung beetle activity with parasite transmission

It is axiomatic that for dung beetles to interfere with parasite development and transmission, they must be active when eggs or larvae are present in the faeces deposited on pasture. In tropical regions of the world, this may be the case all year round, but in subtropical and temperate regions, where most livestock farming takes place, dung beetles are seasonal, being active only, when climatic conditions are favourable (Davis et al., 1988, Hanski and Cambefort, 1991b, Wassmer, 2014). Fortunately, such periods may coincide with parasite reproduction and transmission as there is commonly an overlap in favourable conditions for these invertebrates, which typically thrive in warm, moist conditions. However, livestock can harbour parasites all year round, though their populations may fluctuate through epidemiological factors and host responses, so control measures must be considered all year round.

The seasonality of beetle/nematode interactions in the dung has been noted by several authors (Bryan and Kerr, 1989, Martinez et al., 2018, Reinecke, 1960) and in some regions, the period of coincidence was considered to be too short for dung beetles to exert any epidemiologically useful impact on parasite transmission (English, 1979). A broad generalisation is that beetles tend to be inactive during cold winters in northern temperate regions and dry (winter) seasons in the southern hemisphere; these are times also when parasite transmission is low and larval mortality can be high, particularly when faeces and vegetation become desiccated. On a shorter time-scale, there are successional changes in the composition of the dung fauna within a pat as

some species arrive and others disappear, consequently (Gittings and Giller, 1998), the interactions with any parasite stages present will also vary accordingly.

Colonisation of faeces by dung beetles is affected by myriad factors such as site of deposition (Errouissi et al., 2004b), soil type (Davis, 1996a), pat or pellet form (Tshikae et al., 2008), chemical composition (Frank et al., 2017), size (Errouissi et al., 2004a) and the release of volatile attractants (Frank et al., 2018). For example, as a general rule, the larger the deposit, the greater the number of colonising beetles (Finn and Giller, 2000), hence pats produced by adult animals are likely to harbour more beetle biomass and diversity than those of calves or lambs. Adult cattle and sheep can be important epidemiologically, particularly in infections by parasites like liver fluke (Durbin, 1952, Ross, 1968), lungworm (Eysker et al., 1994) and GINs (Crofton, 1954, Stromberg and Averbeck, 1999), less so for coccidia, but youngstock are highly significant contributors to pasture contamination with parasite eggs, particularly those of GINs and coccidia (Forbes, 2021). Thus, differential dung beetle behaviour with respect to differences in faecal mass and characteristics can affect their ability to interact with parasites and contribute to their control in vulnerable stock.

At a local scale, aggregation of beetles has also to be considered as this means that even where beetle populations are present, not all pats will be colonised equally (Hanski and Cambefort, 1991c, Wall and Lee, 2010), so interactions between insects and helminth eggs or larvae are correspondingly variable. As a consequence of aggregation, competition amongst beetles can be intense, both within species and between functional groups as they contest the limited resource of a dung pat (Davis, 1996b, Finn and Gittings, 2003, Hanski and Cambefort, 1991a). Inevitably this in turn affects other fauna and interactions with parasites. Depending on the location, beetles belonging to different guilds can be present simultaneously in the same pat, so the net outcome of their interactions and consequent effects on parasitic nematode populations will vary according to the dominant species and their composition.

8. Dung beetles and their impact on the epidemiology, transmission and impact of livestock parasites

All the studies in the preceding sections have examined the effects of dung beetle activity on the eggs or larvae of (mainly GIN) parasites, but none have followed these findings through to actual measured effects on parasitism in the final hosts – mainly cattle and sheep - however, such data are available in two trials conducted in the USA. Both natural and augmented beetle communities were used in which the commonest species was the paracoprid, *Phanaeus vindex*, the rainbow scarab; this is a large beetle (16–18 mm) that buries dung to depths of 30 cm or more (Blume and Aga, 1976, Wassmer and Armstrong, 2023). Pastures grazed by young cattle were manipulated to provide three contrasts: minimal colonisation by dung beetles; natural populations of endemic dung beetles and natural populations augmented by periodic additions of beetles caught in local pit-fall traps (Fincher, 1973, Fincher, 1975).

Compared with the control paddocks with minimal numbers of beetles, the presence of endemic populations of dung beetles reduced the recovery of *Ostertagia ostertagi* larvae on herbage by 3.7 times while the augmented beetle communities reduced the number of larvae 14.7 times (Fincher, 1973). Corresponding mean *O. ostertagi* counts from tracer calves grazed for three weeks on each paddock were 1782, 499 and 537 on the minimal, natural and augmented pastures respectively (Fig. 1). Worm populations acquired by tracer calves in the second study were similar, with mean *O. ostertagi* counts of 1356, 680 and 117 (Fincher, 1975). These results provide support for the assumptions that reduced larval contamination of pastures

through the activity of dung beetles can reduce parasite populations in the grazing animal, however, such worm burdens are well below those typically associated with clinical PGE or subclinical losses in cattle (Forbes, 2021), so more research needs to be conducted under conditions where the parasite challenge is higher and parasitism in grazing animals is measured over at least a year in order to fully understand and quantify the role of dung beetles in PGE control.

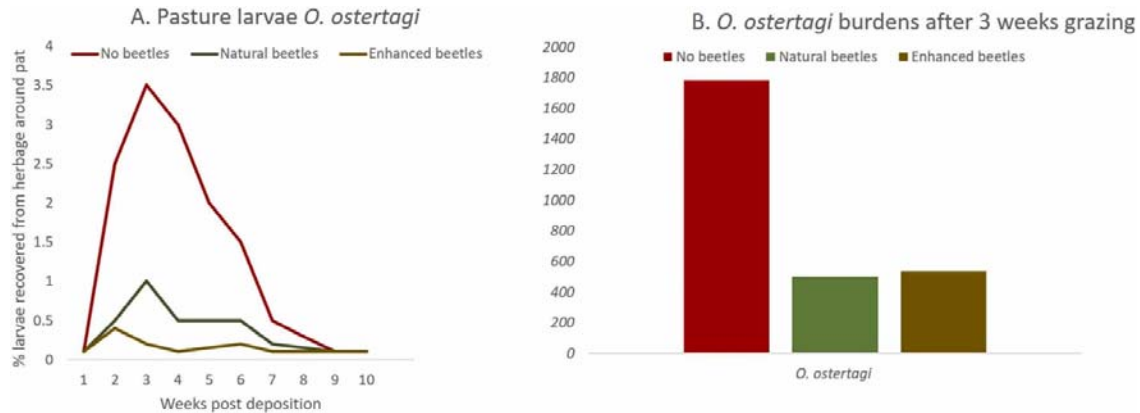


Fig. 1. A. Pasture larval populations on paddocks with minimal, natural and enhanced beetle numbers. B. *Ostertagia ostertagi* burdens in tracer calves grazed for three weeks on these paddocks. Redrawn from data in Fincher. Journal of Parasitology, 1973, 59:396–399.

9. Conclusions

At global, regional and local scales, parasitism is the most common infectious disease syndrome of livestock and its impact on animal health, welfare and productivity is substantial, resulting in enormous direct and indirect economic losses (Charlier et al., 2020, Perry and Randolph, 1999, Strydom et al., 2023). Control of parasitic disease in ruminants through the use of parasiticides is common, but not without some drawbacks, notably resistance in target parasites and potential negative effects on the functionality and populations of beneficial, non-target insect species, including dung beetles. Current trends are to control parasites through a multi-faceted, holistic approach, commonly referred to under the umbrella term Integrated Parasite Management (IPM). Biocontrol through agents such as the dung fauna has obvious appeal as a component of such approaches (Forbes et al., 2023, Szewc et al., 2021).

There is some evidence that the dung beetle fauna is richer and more abundant on organic farms compared with conventional farms (Geiger et al., 2010, Hutton and Giller, 2003), though this is not always the case (Piccini et al., 2019). However, healthy dung beetle populations alone do not seem to limit parasitic disease in livestock, as organic farms, with prescribed limits in parasiticide use, tend to have higher levels of parasitism, particularly in sheep, than other farming systems (Åkerfeldt et al., 2021). It is clear that there are multiple factors that can affect the outcome of beetle – livestock parasite interactions in dung, these include: biogeography, season, weather, beetle numbers, size, feeding and nesting behaviour, which in turn operate within a more general framework of parasite epidemiology, grazing management and farming practices.

There is very little evidence for any effects of dung beetles on the free-living stages of coccidia, tapeworms or fluke, though, from a knowledge of the biology of these stages, it might be surmised that dung beetles could reduce the transmission of coccidial oocysts and the survival

of rumen and liver fluke eggs, but have little impact on tapeworm eggs. Amongst the common nematode parasites, beetle activity can disrupt some elements of the lungworm life-cycle, including larval survival and translocation. Much of the research on GIN has been conducted under experimental/controlled conditions using larval emergence as the measure of effect, implicitly linked to potential transmission to the final hosts; only two short-term studies actually measured responses in grazing animals. Deep burial of faeces is the facet of dung beetle behaviour most likely to lead to a reduction in pasture larval populations. Shallow burial and fragmentation of dung can reduce larval populations, particularly when accompanied by desiccation, but when conditions are warm and moist, larval development and survival can be enhanced (Chirico et al., 2003, Sands et al., 2017).

Few would argue with the important role that dung beetles play in the dispersal and decomposition of livestock faeces and their value in agricultural settings (Stanbrook-Buyer et al., 2024), albeit constrained by factors such as the guild composition and seasonality. However, their ability to significantly contribute positively to the control of parasitic helminths on livestock farms appears to have a limited scientific evidence base and is to some degree equivocal. In turn, this suggests that some of the estimated economic benefits attributed to this element of ecosystem services have been overestimated (Beynon et al., 2015). This should not detract from the many and diverse benefits associated with dung beetles in agriculture and other, more natural, habitats (Davis et al., 2004, Scholtz et al., 2009).

CRedit authorship contribution statement

Andrew B Forbes: Writing – review & editing, Writing – original draft, Conceptualization.
Clarke H. Scholtz: Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare no competing interest.

References

- Adam, L., 1986. Beetles (Coleoptera) inhabiting sheep droppings in dry pastures of Hungary. *Folia Entomol. Hung.* 47, 5–12.
- Aguilar-Marcelino, L., Quintero-Martinez, M.T., Mendoza de Gives, P., Lopez-Arellano, M.E., Liebano-Hernandez, E., Torres-Hernandez, G., Gonzalez-Camacho, J. M., Cid del Prado, I., 2014. Evaluation of predation of the mite *Lasioseius penicilliger* (Aracnida: Mesostigmata) on *Haemonchus contortus* and bacteria-feeding nematodes. *J. Helminthol.* 88, 20–23.
- Åkerfeldt, M.P., Gunnarsson, S., Bernes, G., Blanco-Penedo, I., 2021. Health and welfare in organic livestock production systems—a systematic mapping of current knowledge. *Org. Agric.* 11, 105–132.
- Al Saqur, I., Bairden, K., Armour, J., Gettinby, G., 1982. Population study of bovine *Ostertagia* spp infective larvae on herbage and soil. *Res Vet. Sci.* 32, 332–337.
- Barth, D., Karrer, M., Heinze-Mutz, E.M., 1995. Significance of moisture content of dung pats for colonisation and degradation of cattle dung. *Appl. Parasitol.* 36, 11–21.

- Barth, D., Karrer, M., Heinze-Mutz, E.M., Elster, N., 1994. Colonization and degradation of cattle dung: aspects of sampling, fecal composition, and artificially formed pats. *Environ. Entomol.* 23, 571–578.
- Beynon, S.A., Wainwright, W.A., Christie, M., 2015. The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry. *Ecol. Entomol.* 40, 124–135.
- Biggane, R.P.J., 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.
- Blume, R.R., Aga, A., 1976. *Phanaeus difformis* LeConte (Coleoptera: Scarabaeidae): clarification of published descriptions, Notes on biology and distribution in Texas. *Coleopt. Bull.* 30, 199–205.
- Bornemissza, G.F., 1970. Insectary studies on the control of dung breeding flies by the activity of the dung beetle, *Onthophagus gazella* F. (Coleoptera: Scarabaeinae). *J. Aust. Entom Soc.* 9, 31–41.
- Bornemissza, G.F., 1976. The Australian Dung Beetle Project 1965-1975. *Aust. Meat Res. Comm. Rev.* 30, 1–30.
- Breymeyer, A., 1974. Analysis of a sheep pasture ecosystem in the Pieniny mountains (The Carpathians). XI. The role of coprophagous beetles (Coleoptera, Scarabaeidae) in the utilization of sheep dung. *Ekol. Pol.* 22, 617–634.
- Bryan, R.P., 1973. The effects of dung beetle activity on the numbers of parasitic gastrointestinal helminth larvae recovered from pasture samples. *Aus. J. Agric. Res* 24, 161–168.
- Bryan, R.P., 1976. The effect of the dung beetle, *Onthophagus gazella*, on the ecology of the infective larvae of gastrointestinal nematodes of cattle. *Aus. J. Agric. Res* 27, 567–574.
- Bryan, R.P., Kerr, J.D., 1989. Factors affecting the survival and migration of the free-living stages of gastrointestinal nematode parasites of cattle in central Queensland. *Vet. Parasitol.* 30, 315–326.
- Charlier, J., Rinaldi, L., Musella, V., Ploeger, H.W., Chartier, C., Vineer, H.R., Hinney, B., von Samson-Himmelstjerna, G., Băcescu, B., Mickiewicz, M., Mateus, T.L., Martinez-Valladares, M., Quealy, S., Azaizeh, H., Sekovska, B., Akkari, H., Petkevicius, S., Hektoen, L., Höglund, J., Morgan, E.R., Bartley, D.J., Claerebout, E., 2020. Initial assessment of the economic burden of major parasitic helminth infections to the ruminant livestock industry in Europe. *Prev. Vet. Med.* 182, 105103.
- Chirico, J., Wiktelius, S., Waller, P.J., 2003. Dung beetle activity and the development of trichostrongylid eggs into infective larvae in cattle faeces. *Vet. Parasitol.* 118, 157–163.
- Coffey, M.D., 1966. Studies on the association of flies (Diptera) with dung in Southeastern Washington. *Ann. Entom Soc. Am.* 59, 207–218.

Crofton, H.D., 1954. Nematode parasite populations in sheep on lowland farms. I. Worm egg counts in ewes. *Parasitology* 44, 465–477.

Curry, J.P., 1994. *Grassland Invertebrates*. Chapman & Hall, UK.

Curry, J.P., Schmidt, O., 2007. The feeding ecology of earthworms – A review. *Pedobiologia* 50, 463–477.

Davis, A.L.V., 1996a. Community organisation of dung beetles (Coleoptera: Scarabaeidae): differences in body size and functional group structure between habitats. *Afr. J. Ecol.* 34, 258–275.

Davis, A.L.V., 1996b. Diel and seasonal community dynamics in an assemblage of coprophagous, Afro-tropical, dung beetles (Coleoptera: Scarabaeifae s. str., Aphodiidae, and Staphylinidae: Oxytelinae). *J. Afr. Zool.* 110, 291–308.

Davis, A.L.V., Doube, B.M., McLennan, P.D., 1988. Habitat associations and seasonal abundance of coprophilous coleoptera (Staphylinidae, Hydrophilidae and Histeridae) in the Hluhluwe region of South Africa. *Bull. Entomol. Res* 78, 425–434.

Davis, A.L.V., Frolov, A.V., Scholtz, C.H., 2008. *The African Dung Beetle Genera*. Protea Book House, Pretoria, South Africa, p. 272.

Davis, A.L.V., Scholtz, C.H., Dooley, P.W., Bham, N., Kryger, U., 2004. Scarabaeine dung beetles as indicators of biodiversity, habit transformation and pest control chemicals in agroecosystems. *S. Afr. J. Sci.* 100, 415–424.

deCastro-Arrazola, I., Andrew, N.R., Berg, M.P., Curtsdotter, A., Lumaret, J.P., Menendez, R., Moretti, M., Nervo, B., Nichols, E.S., Sanchez-Pinero, F., Santos, A.M. C., Sheldon, K.S., Slade, E.M., Hortal, J., 2023. A trait-based framework for dung beetle functional ecology. *J. Anim. Ecol.* 92, 44–65.

Deplazes, P., Eckert, J., Mathis, A., Von Samson-Himmelstjerna, G., Zahner, H., 2016. *Parasitology in Veterinary Medicine*. Wageningen Academic Publishers, Netherlands, 653 p.

Devaney, J.A., Miller, D.K., Craig, T.M., 1990. Effects of horn fly and house fly (Diptera: Muscidae) larvae on the development of parasitic nematodes in bovine dung. *J. Econ. Entomol.* 83, 1446–1448.

Dickinson, C.H., Underhay, V.S.H., Ross, V., 1981. Effect of season, soil fauna and water content on the decomposition of cattle dung pats. *N. Phyto* 88, 129–141.

van Dijk, J., de Louw, M.D., Kalis, L.P., Morgan, E.R., 2009. Ultraviolet light increases mortality of nematode larvae and can explain patterns of larval availability at pasture. *Int J. Parasitol.* 39, 1151–1156.

Dos Anjos, K.A., Duarte, F.C., Katiki, L.M., Giglioti, R., Santos, B.G., Mendes, M.C., 2024. In vitro evaluation of the potential of mites of the family Macrochelidae (Acari: Mesostigmata) as macrobiological agents against the nematode *Haemonchus contortus* (Strongylida: Trichostrongylidae). *Vet. Parasitol.* 328, 110191.

- Doube, B.M. 1986. Biological Control of the Buffalo Fly in Australia: The Potential of the Southern Africa Dung Fauna. In *Biological Control of Muscoid Flies*, Patterson, R.S., Rutz, D.A., eds. (Gainesville, FL 32604, USA, Miscellaneous Publications of the Entomological Society of America), pp. 16-34.
- Doube, B.M., 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecol. Entomol.* 15, 371–383.
- Doube, B.M., 1991. Dung Beetles of Southern Africa, In: Hanski, I., Cambefort, Y. (Eds.) *Dung Beetle Ecology*. Princeton University Press, USA, pp. 133-155.
- Doube, B.M., 2018. Ecosystem services provided by dung beetles in Australia. *Basic Appl. Ecol.* 26, 35–49.
- Doube, B.M., Macqueen, A., Fay, H.A.C., 1988. Effects of dung fauna on survival and size of Buffalo Flies (*Haematobia* ssp.) breeding in the field in South Africa and Australia. *J. Appl. Ecol.* 25, 523–536.
- Durbin, C.G., 1952. Longevity of the Liver Fluke, *Fasciola* sp. *Sheep. Proc. Helminth Soc. Wash.* 19, 120.
- Durie, P., 1975. Some possible effects of dung beetle activity on the infestation of pastures by intestinal worm larvae of cattle. *J. Appl. Ecol.* 12, 827–831.
- Edwards, P.B., 1991. Seasonal variation in the dung of African grazing mammals and its consequences for coprophagous insects. *Funct. Ecol.* 5, 617–628.
- Edwards, P.B., Aschenborn, H.H., 1987. Patterns of nesting and dung burial in *Onitis* dung beetles: implications for pasture productivity and fly control. *J. Appl. Ecol.* 24, 837–851.
- English, A.W., 1979. The effects of dung beetles (Coleoptera-Scarabaeinae) on the free-living stages of strongylid nematodes of the horse. *Aust. Vet. J.* 55, 315–321.
- Errouissi, F., Haloti, S., Jay-robot, P., Janati-idrissi, A., Lumaret, J.-P., 2004a. Effects of the attractiveness for dung beetles of dung pat origin and size along a climatic gradient. *Environ. Entomol.* 33, 45–53.
- Errouissi, F., Jay-robot, P., Lumaret, J.-p, Piau, O., 2004b. Composition and structure of Dung Beetle (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) assemblages in mountain grasslands of the Southern Alps. *Ann. Entomol. Soc. Am.* 97, 701–709.
- Eysker, M., Claessens, E.W., Lam, T.J., Moons, M.J., Pijpers, A., 1994. The prevalence of patent lungworm infections in herds of dairy cows in the Netherlands. *Vet. Parasitol.* 53, 263–267.
- Fay, H.A.C., Doube, B.M., 1983. The effect of some coprophagous and predatory beetles on the survival of immature stages of the African buffalo fly, *Haematobia thirouxii potans* in bovine dung. *Z. F. üR. Angew. Entomol.* 95, 460–466.

- Ferrar, P., Watson, J., 1970. Termites (Isoptera) associated with dung in Australia. *Aust. J. Entomol.* 9, 100–102.
- Fincher, G.T., 1973. Dung beetles as biological control agents for gastrointestinal parasites of livestock. *J. Parasitol.* 59, 396–399.
- Fincher, G.T., 1975. Effects of dung beetle activity on the number of nematode parasites acquired by grazing cattle. *J. Parasitol.* 61, 759–762.
- Fincher, G.T., Stewart, T.B., 1979. Vertical migration by nematode larvae of cattle parasites through soil. *Proc. Helminth Soc. Wash.* 46, 43–46.
- Finn, J.A., Giller, P.S., 2000. Patch size and colonisation patterns: an experimental analysis using North Temperate coprophagous dung beetles. *Ecography* 23, 315–327.
- Finn, J.A., Giller, P.S., 2002. Experimental investigations of colonisation by north temperate dung beetles of different types of domestic herbivore dung. *Appl. Soil Ecol.* 20, 1–13.
- Finn, J.A., Gittings, T., 2003. A review of competition in north temperate dung beetle communities. *Ecol. Entomol.* 28, 1–13.
- Floate, K., 2023. *Cow Patty Critters: An introduction to the ecology, biology and identification of insects in cattle dung on Canadian pastures.* Agriculture and Agri-Food Canada, Lethbridge, Alberta, Canada.
- Forbes, A.B., 2021. *Parasites of cattle and sheep.* CABI, Wallingford, UK, p. 379.
- Forbes, A., Ellis, B., K.A., 2023. Parasite control in regenerative livestock farming. *Livestock* 28, 112–120.
- Foreyt, W.J., 2001. *Veterinary parasitology reference manual, 5th Edition.* Iowa State University Press, USA.
- Forgie, S.A., Paynter, Q., Zhao, Z., Flowers, C., Fowler, S.V., 2018. Newly released non-native dung beetle species provide enhanced ecosystem services in New Zealand pastures. *Ecol. Entomol.* 10, 12513.
- Frank, K., Brückner, A., Bluthgen, N., Schmitt, T., 2018. In search of cues: dung beetle attraction and the significance of volatile composition of dung. *Chemoecology* 28, 145–152.
- Frank, K., Brückner, A., Hilpert, A., Heethoff, M., Blüthgen, N., 2017. Nutrient quality of vertebrate dung as a diet for dung beetles. *Sci. Rep.* 7, 12141.
- Freyman, P.B., Buitenwerf, R., Desouza, O., Olf, H., 2008. The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review. *Eur. J. Entomol.* 105, 165–173.
- Geiger, F., van der Lubbe, S.C.T.M., Brunsting, A.M.H., de Snoo, G.R., 2010. Insect abundance in cow dung pats of different farming systems. *Entomol. Ber.* 70, 106–110.

- Gittings, T., Giller, P.S., Stakelum, G., 1994. Dung decomposition in contrasting temperate pastures in relation to dung beetle and earthworm activity. *Pedobiologia* 38, 455–474.
- Gittings, T., Giller, P.S., 1998. Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography* 21, 581–592.
- Gormally, M.J., 1993. Laboratory investigations of *Aphodius* s beetles (Scarabaeidae) as biological control agents of the cattle lungworm, *Dictyocaulus viviparus* (Nematoda: Dictyocaulidae). *Biocontrol Sci. Tech.* 3, 499–502.
- Gregory, N., Gomez, A., Oliveira, T.M., Nichols, E., 2015. Big dung beetles dig deeper: trait-based consequences for faecal parasite transmission. *Int J. Parasitol.* 45, 101–105.
- Gronvold, J., 1984. On the possible role of birds as transport hosts of 3rd-stage trichostrongyle larvae. Preliminary results. *Acta Vet. Scan* 25, 143–144.
- Gronvold, J., 1987b. Field experiment on the ability of earthworms (Lumbricidae) to reduce the transmission of infective larvae of *Cooperia oncophora* (Trichostrongylidae) from cow pats to grass. *J. Parasitol.* 73, 1133–1137.
- Gronvold, J., 1987a. A field experiment on rain splash dispersal of infective larvae of *Ostertagia ostertagi* (Trichostrongylidae) from cow pats to surrounding grass. *Acta Vet. Scan* 28, 459–461.
- Gronvold, J., Sommer, C., Holter, P., Nansen, P., 1992. Reduced splash dispersal of bovine parasitic nematodes from cow pats by the dung beetle *Diastelopalpus quinque-dens*. *J. Parasitol.* 78, 845–848.
- Grøn-vold, J., 1979. On the possible role of Earthworms in the transmission of *Ostertagia ostertagi* third-stage larvae from feces to soil. *J. Parasitol.* 65, 831–832.
- Halffter, G., Edmonds, W.D., 1982. Patterns of nesting behavior in Scarabaeinae: An overview. In: *The Nesting Behavior of Dung Beetles (Scarabaeinae): An Ecological and Evolutionary Approach*. Instituto de Ecología, Mexico, pp. 31–50.
- Hammer, O., 1941. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Vidensk. Medd. fra Dan. Nat. Foren.* 105, 140–393.
- Hanski, I., 1980. Spatial variation in the timing of the seasonal occurrence in coprophagous beetles. *Oikos* 34, 311–321.
- Hanski, I., 1991b. North Temperate Dung Beetles. In: Hanski, I., Cambefort, Y. (Eds.), *Dung Beetle Ecology*. Princeton University Press, USA, pp. 75–96.
- Hanski, I., 1991a. The Dung Insect Community. In: Hanski, I., Cambefort, Y. (Eds.), *Dung Beetle Ecology*. Princeton University Press, USA, pp. 5–21.
- Hanski, I., Cambefort, Y., 1991a. Competition in dung beetles. In: Hanski, I., Cambefort, Y. (Eds.), *Dung Beetle Ecology*. Princeton University Press, USA, pp. 305–329.

- Hanski, I., Cambefort, Y., 1991c. Spatial Processes. In: Hanski, I., Cambefort, Y. (Eds.), *Dung Beetle Ecology*. Princeton University Press, USA, pp. 283–304.
- Hanski, I., Cambefort, Y. 1991b. *Dung Beetle Ecology (United States of America, Princeton University Press)*, p. 481.
- Healey, K., Lawlor, C., Knox, M.R., Chambers, M., Lamb, J., Groves, P., 2018. Field evaluation of *Duddingtonia flagrans* IAH 1297 for the reduction of worm burden in grazing animals: Pasture larval studies in horses, cattle and goats. *Vet. Parasitol.* 258, 124–132.
- Hertzberg, H., Schnieder, T., Lopmeier, F.J., Stoye, M., 1992. The influence of weather and egg contamination on the development of third-stage larvae of *Cooperia oncophora* on pasture. *Int J. Parasitol.* 22, 719–730.
- Hirschberger, P., Bauer, T., 1994a. The coprophagous insect fauna in sheep dung and its influence on dung disappearance. *Pedobiologia* 38, 375–384.
- Hirschberger, P., Bauer, T., 1994b. Influence of earthworms on the disappearance of sheep dung. *Pedobiologia* 38, 475–480.
- Holter, P., 1979. Effect of dung-beetles (*Aphodius* spp.) and earthworms on the disappearance of cattle dung. *Oikos* 32, 393–402.
- Holter, P., 1991. Concentration of oxygen, carbon dioxide and methane in the air within dung pats. *Pedobiologia* 35, 381–386.
- Holter, P., 2004. Dung feeding in hydrophilid, geotrupid and scarabaeid beetles: Examples of parallel evolution. *Eur. J. Entomol.* 101, 365–372.
- Holter, P., Scholtz, C.H., 2007. What do dung beetles eat? *Ecol. Entomol.* 32, 690–697.
- Hughes, R., Greenham, P., Tyndale-Biscoe, M., Walker, J., 2007. A synopsis of observations on the biology of the Australian Bushfly (*Musca vetustissima* Walker). *Aust. J. Entomol.* 11, 311–331.
- Hughes, R.D., Tyndale-Biscoe, M., Walker, J., 1978. Effects of introduced dung beetles (Coleoptera: Scarabaeidae) on the breeding and abundance of the Australian bushfly, *Musca vetustissima* Walker (Diptera: Muscidae). *Bull. Entomol. Res.* 68, 361–372.
- Hutton, S.A., Giller, P.S., 2003. The effects of the intensification of agriculture on northern temperate dung beetle communities. *J. Appl. Ecol.* 40, 994–1007.
- Kauzal, G.P., 1941. Examination of grass and soil to determine the population of infective larval nematodes on pastures. *Aust. Vet. J.* 17, 181–184.
- Kessler, H., Balsbaugh Jr., E.U., McDaniel, B., 1974. Faunistic comparison of adult Coleoptera recovered from cattle and sheep manure in east-central South Dakota. *Entomol. N.* 85, 67–71.
- Knight, D., Elliott, P.W., Anderson, J.M., Scholefield, D., 1992. The role of earthworms in managed, permanent pastures in Devon, England. *Soil Biol. Biochem.* 24, 1511–1517.

- Koskela, H., 1972. Habitat selection of dung-inhabiting Staphylinids (Coleoptera) in relation to age of the dung. *Ann. Zool. Fenn.* 9, 156–171.
- Krantz, G.W., 1998. Reflections on the biology, morphology and ecology of the Macrochelidae. *Exp. Appl. Acar* 22, 125–137.
- Krecek, R.C., Murrell, K.D., 1988. Observations on the ability of larval *Ostertagia ostertagi* to migrate through pasture soil. *Proc. Helminth Soc. Wash.* 55, 24–27.
- Laurence, B.R., 1954. The larval inhabitants of cow pats. *J. Anim. Ecol.* 23, 234–260.
- Lee, D.L., Atkinson, H.J., 1976. *Physiology of Nematodes*, Second Edition. The MacMillan Press Ltd, London, 215 p.
- Lee, C., Wall, R., 2006. Distribution and abundance of insects colonizing cattle dung in South West England. *J. Nat. Hist.* 40, 1167–1177.
- Lobo, J.M., Hortal, J., Cabrero-Sa~nudo, F.J., 2006. Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Divers Distrib.* 12, 111–123.
- Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *BioScience* 56, 311–323.
- Lucker, J.T., 1938. Vertical migration, distribution and survival of infective horse strongyle larvae developing in feces buried in different soils. *J. Ag. Res* 57, 335–348.
- Lumaret, J.P., Kadiri, N., Bertrand, M., 1992. Changes in resources: consequences for the dynamics of dung beetle communities. *J. Appl. Ecol.* 29, 349–356.
- Lumaret, J.P., Kirk, A., 1987. Ecology of dung beetles in the French Mediterranean region (Coleoptera:Scarabaeinae). *Acta Zool. Mex.* 24, 1–56.
- Marsh, R., Campling, R.C., 1970. Fouling of pastures by dung. *Herb. Abstr.* 40, 123–130.
- Martinez, I.M., Flota Ba~nuelos, C., Gonzalez-Tokman, D., Zayas, Md.R., 2018. Dung and gastrointestinal nematode eggs buried by *Euoniticellus intermedius* (Reiche) (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopt. Bull.* 72, 188–194.
- Merritt, R.W., Anderson, J.R., 1977. The effects of different pasture and rangeland ecosystems on the annual dynamics of insects in cattle droppings. *Hilgardia* 45, 31–71.
- Mohr, C.O., 1943. Cattle droppings as ecological units. *Ecol. Monogr.* 13, 275–298.
- Nervo, B., Tocco, C., Caprio, E., Palestini, C., Rolando, A., 2014. The effects of body mass on dung removal efficiency in Dung Beetles. *PloS One* 9, e107699.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv* 141, 1461–1474.

- Niogret, J., Lumaret, J.-P., Bertrand, M., 2010. Generalist and specialist strategies in macrochelid mites (Acari: Mesostigmata) phoretically associated with dung beetles (Coleoptera: Scarabaeidae). In: Trends in Acarology, Dordrecht, 2010//, pp. 343-347.
- Oakley, G.A., 1981. Survival of *Dictyocaulus viviparus* infection in earthworms. Res Vet. Sci. 30, 255–256.
- Over, H.J., 1982. Ecological basis of parasite control: trematodes with special reference to fascioliasis. Vet. Parasitol. 11, 85–97.
- Papp, L., 1985. Flies (Diptera) developing in sheep droppings in Hungary. Acta Zool. Hung. 31, 367–379.
- Perry, B.D., Randolph, T.F., 1999. Improving the assessment of the economic impact of parasitic diseases and of their control in production animals. Vet. Parasitol. 84, 145–168.
- Persson, L., 1974. Studies on the bionomics of eggs and infective larvae of *Ostertagia ostertagi* and *Cooperia oncophora* in soil. Zent. fur Vet. Reihe B. J. Vet. Med. Ser. B 21, 318–328.
- Piccini, I., Palestrini, C., Rolando, A., Roslin, T., 2019. Local management actions override farming systems in determining dung beetle species richness, abundance and biomass and associated ecosystem services. Basic Appl. Ecol. 41, 13–21.
- Pokhrel, M.R., Cairns, S.C., Hemmings, Z., Floate, K.D., Andrew, N.R., 2021. A review of dung beetle introductions in the antipodes and North America: status, opportunities, and challenges. Environ. Entomol. 50, 762–780.
- Putman, R.J., 1983. Carrion and Dung. The Decomposition of Animal Wastes. Edward Arnold, UK.
- Rainio, M., 1966. Abundance and phenology of some coprophagous beetles in different kinds of dung. Ann. Zool. Fenn. 3, 88–98.
- Reinecke, R.K., 1960. A field study of some of the nematode parasites of bovines in a semi-arid area, with special reference to their biology and possible methods of prophylaxis. Onderstepoort J. Vet. Res 28, 365–464.
- Ridsdill-Smith, T.J., Hayles, L., Palmer, M.J., 1986. Competition between the bush fly and a dung beetle in dung of differing characteristics. Entomol. Exp. Appl. 41, 83–90.
- Robinson, J., 1962. *Pilobolus* spp. and the translation of the infective larvae of *Dictyocaulus viviparus* from faeces to pastures. Nature 193, 353–354.
- Rose, J.H., 1961. Some observations on the free-living stages of *Ostertagia ostertagi*, a stomach worm of cattle. Parasitology 51, 295–307.
- Rose, J.H., 1962. Further observations on the free-living stages of *Ostertagia ostertagi* in cattle. J. Comp. Path 72, 11–18.

- Rose, J.H., 1963a. Ecological observations and laboratory experiments on the free-living stages of *Cooperia oncophora*. *J. Comp. Path* 73, 285–296.
- Rose, J.H., 1963b. Observations on the free-living stages of the stomach worm *Haemonchus contortus*. *Parasitology* 53, 469–481.
- Rose, J.H., 1964. Relationship between environment and the development and migration of the free-living stages of *Haemonchus contortus*. *J. Comp. Path* 74, 163–172.
- Rose, J.H., Small, A.J., 1985. The distribution of the infective larvae of sheep gastro-intestinal nematodes in soil and on herbage and the vertical migration of *Trichostrongylus vitrinus* larvae through the soil. *J. Helminthol.* 59, 127–135.
- Ross, J.G., 1968. The life span of *Fasciola hepatica* in cattle. *Vet. Rec.* 82, 587–589.
- Rougon, D., Rougon, C., Levieux, J., Trichet, J., 1990. Variations in the amino-acid content in Zebu dung in the Sahel during nesting by dung beetles (Coleoptera, Scarabaeidae). *Soil Biol. Biochem.* 22, 217–223.
- Rowcliffe, S.A., Ollerenshaw, C.B., 1960. Observations on the bionomics of the egg of *Fasciola hepatica*. *Ann. Trop. Med. Parasitol.* 54, 172–181.
- Sanders, D.P., Dobson, R.C., 1969. Contributions to the biology of the Horn Fly. *J. Econ. Entomol.* 62, 1362–1366.
- Sands, B., Wall, R., McCallum, H., 2017. Dung beetles reduce livestock gastrointestinal parasite availability on pasture. *J. Appl. Ecol.* 54, 1180–1189.
- Schmid, R.B., Welch, K.D., Lundgren, J.G., 2024. A survey of the dung-dwelling arthropod community in the pastures of the Northern Plains. *Insects* 15, 1–13.
- Scholtz, C.H., Davis, A.L.V., Kryger, U., 2009. *Evolutionary Biology and Conservation of Dung Beetles*. Pensoft, Bulgaria, 567 p.
- Seeman, O.D., Walter, D.E., 2023. Phoresy and mites: more than just a free ride. *Annu Rev. Entomol.* 68, 69–88.
- Shorb, D.A., 1943. Survival on grass plots of eggs and preinfective larvae of the common sheep stomach worm, *Haemonchus contortus*. *J. Parasitol.* 29, 284–289.
- Silverman, P.H., Campbell, J.A., 1959. Studies on parasitic worms of sheep in Scotland: I. Embryonic and larval development of *Haemonchus contortus* at constant conditions. *Parasitology* 49, 23–38.
- Skidmore, P., 1991. Insects of the British cow-dung community. *Field Stud. Counc.* 166.
- Sladeczek, F.X.J., Segar, S.T., Konvicka, M., 2021a. Early successional colonizers both facilitate and inhibit the late successional colonizers in communities of dung-inhabiting insects. *Eur. J. Entomol.* 118, 240–249.

- Sladeczek, F.X., Segar, S.T., Lee, C., Wall, R., Konvicka, M., 2017. Temporal segregation between dung-inhabiting beetle and fly species. *PloS One* 12 e0170426.
- Sladeczek, F.X.J., Zitek, T., Konvicka, M., Segar, S.T., 2021b. Evaluating the relative importance of habitat filtering and niche differentiation in shaping the food web of dung-inhabiting predators. *Acta Oecologica* 112, 103767.
- Sowig, P., Wassmer, T., 1994. Resource partitioning in coprophagous beetles from sheep dung: phenology and microhabitat preferences. *Zool. Jahr. Abt. fuer Syst. Oekologie und Geogr. der Tiere* 121, 171–192.
- Stanbrook-Buyer, R., Bhat, M., King, J.R., 2024. Economic value of dung removal by dung beetles in US sub-tropical pastures. *Basic and Applied Ecology*. In Press.
- Stromberg, B.E., Averbek, G.A., 1999. The role of parasite epidemiology in the management of grazing cattle. *Int J. Parasitol.* 29, 33–39.
- Strydom, T., Lavan, R.P., Torres, S., Heaney, K., 2023. The economic impact of parasitism from nematodes, trematodes and ticks on beef cattle production. *Anim.: Open Access J. MDPI* 13, 1599.
- Sulgostowska, T., Solarz, K., Madej, G., Klimaszewski, K., 2015. Mites and internal parasites associated with the common dung beetle *Geotrupes (Anoplotrupes) stercorosus* (Hartmann in Scriba, 1791) in Poland. *Acta Parasitol.* 60, 622–630.
- Sullivan, G.T., Ozman-Sullivan, S.K., Lumaret, J.P., Bourne, A., Zeybekoglu, U., Zalucki, M.P., Baxter, G., 2017. How guilds build success; aspects of temporal resource partitioning in a warm, temperate climate assemblage of Dung Beetles (Coleoptera: Scarabaeidae). *Environ. Entomol.* 46, 1060–1069.
- Szewc, M., De Waal, T., Zintl, A., 2021. Biological methods for the control of gastrointestinal nematodes. *Vet. J.* 268, 105602.
- Tod, M.E., Jacobs, D.E., Dunn, A.M., 1971. Mechanisms for the dispersal of parasitic nematode larvae. 1. Psychodid flies as transport hosts. *J. Helminthol.* 45, 133–137.
- Tshikae, B.P., Davis, A.L., Scholtz, C.H., 2008. Trophic associations of a dung beetle assemblage (Scarabaeidae: Scarabaeinae) in a woodland savanna of Botswana. *Environ. Entomol.* 37, 431–441.
- Tshikae, B.P., Davis, A.L.V., Scholtz, C.H., 2013. Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari? *Ecol. Entomol.* 38, 83–95.
- Tyndale-Biscoe, M., 1990. Common dung beetles in pastures of south-eastern Australia. CSIRO Australia, Australia, 71 p.
- Tyndale-Biscoe, M., Vogt, W.G., 1991. Effects of adding exotic dung beetles to native fauna on Bush Fly breeding in the field. *Entomophaga* 36, 395–401.

- Vogt, W.G., Woodburn, T.L., Ellem, B.A., van Gerwen, A.C.M., Browne, L.B., Wardhaugh, K.G., 1985. The relationship between fecundity and oocyte resorption in field populations of *Lucilia cuprina*. *Entomol. Exp. Appl.* 39, 91–99.
- Waghorn, T.S., Leathwick, D.M., Chen, L.Y., Gray, R.A., 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. *Vet. Parasitol.* 104, 119–129.
- Waghorn, T.S., Reynecke, D.P., Oliver, A.M., Miller, C.M., Vlassoff, A., Koolaard, J.P., Leathwick, D.M., 2011. Dynamics of the free-living stages of sheep intestinal parasites on pasture in the North Island of New Zealand. 1. Patterns of seasonal development. *N. Z. Vet. J.* 59, 279–286.
- Wall, R., Lee, C.M., 2010. Aggregation in insect communities colonizing cattle-dung. *Bull. Entomol. Res* 100, 481–487.
- Wallace, M.M.H., Holm, E., 1983. Establishment and dispersal of the introduced predatory mite, *Macrocheles peregrinus* Krantz, in Australia. *Aust. J. Entomol.* 22, 345–348.
- Wallace, M.M.H., Tyndale-Biscoe, M., 1983. Attempts to measure the influence of dung beetles (Coleoptera: Scarabaeidae) on the field mortality of the bush fly *Musca vetustissima* Walker (Diptera: Muscidae) in south-eastern Australia. *Bull. Entomol. Res* 73, 33–44.
- Walter, D.E., Ikonen, E.K., 1989. Species, guilds, and functional groups: taxonomy and behavior in nematophagous arthropods. *J. Nemat* 21, 315–327.
- Walter, D.E., Proctor, H.C., 2013. *Mites: Ecology, evolution & behaviour*, 2nd Edition. Springer, London, p. 494, 2nd Edition.
- Wassmer, T., 2014. Seasonal occurrence (Phenology) of coprophilous beetles (Coleoptera: Scarabaeidae and Hydrophilidae) from cattle and sheep farms in Southeastern Michigan, USA. *Coleopt. Bull.* 68, 603–618.
- Wassmer, T., 2020. Attractiveness of Cattle Dung to Coprophilous Beetles (Coleoptera: Scarabaeoidea and Sphaeridiinae) and their Segregation during the initial stages of the Heterotrophic Succession on a Pasture in Southeast Michigan. *J. Insect Sci.* 20.
- Wassmer, T., Armstrong, E., 2023. Population structure of *Phanaeus vindex* (Coleoptera: Scarabaeidae) in SE Michigan. *J. Insect Sci.* 23, 1–15.
- Wilson, J.W., 1932. Coleoptera and Diptera Collected from a New Jersey Sheep Pasture. *J. NY Entomol. Soc.* 40, 77–93.
- Wratten, S.D., Forbes, A.B., 1996. Environmental assessment of veterinary avermectins in temperate pastoral ecosystems. *Ann. Appl. Biol.* 128, 329–348.
- Young, O., 2015. Predation on Dung Beetles (Coleoptera: Scarabaeidae): a literature review. *Trans. Am. Entomol. Soc.* 141, 111–155.