Environmental Entomology, 50(4), 2021, 762–780
doi: 10.1093/ee/nvab025
Advance Access Publication Date: 16 April 2021
Review

Review

A Review of Dung Beetle Introductions in the Antipodes and North America: Status, Opportunities, and Challenges

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Subject Editor: Melody Keena

Received 11 June 2020; Editorial decision 2 March 2021

Abstract

Following the introduction of cattle, exotic dung beetles (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) were imported into the Antipodes (Australia and New Zealand) and North America (primarily the United States) to accelerate the degradation of cattle dung on pastures. The history of dung beetle introductions between the two regions is similar but has not previously been assessed: this is important as new introductions are continuing in the regions. Here, we review these introduction programs, report on their current status, and discuss methodological advances. In doing so, we examine the accidental introduction of exotic (i.e., adventive) species and the contribution of both deliberately introduced and adventive species to endemic dung beetle faunas. Further, we provide a list of pest and parasite species whose populations can be reduced by dung beetle activity. We also identify a combined total of 37 introduced and 47 adventive dung beetle species that have become established in the Antipodes and North America, with exotic species dominating dung beetle assemblages from pasture habitats. Climatic and edaphic matches, the size of founding populations, abiotic and biotic stressors, and the time of year when releases are made are all critical determinants that affect the success of dung beetle introduction programs. Finally, we discuss opportunities, plus the risks and challenges associated with dung beetle introductions. We hope that this review will aid in the success of future introduction programs, either to enhance ecosystem services in areas that they are needed, or potentially to reestablish native species in regions where they have been extirpated.

Key words: Scarabaeidae, adventive species, bioturbation, biological control, ecosystem service

Fresh dung of cattle (*Bos taurus indicus* Linnaeus, 1758), colloquially referred to as pads or pats, is about 80% water and rich in volatile organic compounds, nutrients, and microorganisms (Stavert et al. 2014, Frank et al. 2017). Accumulations of dung pollute water sources, foul pastures, provide breeding sites for pests and parasites of livestock, and represent a loss of soil nutrients from the pasture (Bornemissza 1960, 1976; Waterhouse 1974; Anduaga and Huerta 2007). However, fresh dung also attracts a diverse group of insects that function as coprophages, recyclers, decomposers, predators, and parasitoids (Hanski 1991, Floate 2011, Floate and Kadiri 2013). Through their activities, these insects scatter and bury dung, thus maintaining pasture quality and incorporating nutrients from the dung back into the soil. Dung beetles (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) are primary contributors to the rapid degradation of dung pads (Waterhouse 1974, Bornemissza 1976, Forgie et al. 2010).

As critical ecosystem function providers, dung beetles are recognized as ecosystem engineers (Nichols et al. 2008, Johnson et al. 2016). Adults arrive at fresh pads to lay eggs and feed on the pad's nutrient-rich fluids, whereas larvae develop on undigested plant fiber (Cambefort 1991, Errouissi et al. 2004). These feeding and nesting activities: 1) disrupt breeding habitat for pests and parasites affecting livestock (Hughes et al. 1978, Bornemissza 1979, Ridsdill-Smith and Kirk 1985, Nichols and Gomez 2014, Gregory et al.

2015); 2) reduce the spread of soil-borne human pathogens (Miller 1954, Jones et al. 2019); 3) accelerate the return of nutrients from the pad back into the soil (Owen et al. 2006, Yamada et al. 2007, Sitters et al. 2014); 4) improve soil aeration, water-holding capacity and soil fertility (Bang et al. 2005, Decaëns et al. 2006, Brown et al. 2010); 5) enhance plant growth (Macqueen and Beirne 1975b, Bang et al. 2005); 6) aid in seed dispersal (Nichols et al. 2008, Manns et al. 2020); and 7) also provide pollination services (Sakai and Inoue 1999). The potential benefits of these services, when converted to 2021 US dollars, have been estimated at $US 5.9 billion per annum in the United States (Fincher 1981, Losey and Vaughan 2006) and $US 425.9 million per annum in the United Kingdom (Beynon et al. 2015). The value of dung beetle service in Australia has not been estimated to date, but it is expected to be higher than that in the United Kingdom (Doube 2018a). The United Kingdom has a depauperate dung beetle fauna (Holter 1982, Gittings and Giller 1997), whereas the Australian native dung beetle fauna has been supplemented with more efficient dung-degrading and diverse exotic dung beetle species (Edwards 2007, Monteith 2015).

In terms of guilds, dung beetles are broadly classified as tunnelers, rollers, and dwellers, based on their adult reproductive behavior (Bornemissza 1976, Doube 1990, Tonelli 2021). Tunnellers relocate dung from the fresh pad into tunnels or galleries in the soil beneath or near the pad (Simmons and Ridsdill-Smith 2011). Females lay eggs beside the buried dung, which provides food for the larvae (Bornemissza 1976, Doube 1990). Rollers remove a portion of dung from the pad and form it into a ball, which they roll away for burial (Simmons and Ridsdill-Smith 2011). As with the tunnelers, female rollers lay eggs beside the buried dung. Dwellers include both non-nesters and endocoprids—those that feed and breed within the pad or in organic-rich soil immediately beneath the pad (Bornemissza 1976, Christensen and Dobson 1976, Tonelli 2021). Rollers are competitively superior to tunnellers, and tunnellers are competitively superior to dwellers (Hanski and Cambefort 1991a). However, tunnellers relocate dung deeper into the soil profile (Gittings and Giller 1997, Anduaga and Huerta 2007). In contrast, rollers and dwellers mostly scatter the pad or, for rollers, bury it in shallow tunnels (Doube and Marshall 2014).

Prior to European settlement, the dung faunas of North America were (and still are) dominated by species of dwellers (Aphodiidae: Aphodiinae) ill-suited to degrade the large pad-like deposits of dung left by cattle. In Australia, the native beetle species had evolved to feed on the drier, smaller, and more pellet-shaped dung of native marsupial species (Bornemissza 1970, 1976; Waterhouse 1974). With European settlement, cattle were introduced into these regions and became the dominant large grazing herbivore species. These introductions first occurred in what is now the continental United States in 1493 (Bowling 1942), in Canada in 1541 (MacLachlan 2006), Australia in 1788 (Redhead et al. 1991), and New Zealand in 1814 (Stringleman and Scrimgeour 2009). The Antipodes and North America (hereafter used in reference to Canada and the United States; i.e., north of Mexico) together comprise 19% of the global land area and now support 10% of the global herd of cattle (FAO 2017). The dung produced by these animals inevitably led to the aforementioned concerns of pasture quality, water pollution, and increased numbers of pests and parasites affecting livestock. To address concerns associated with accumulations of cattle dung, global searches were initiated to identify dung beetle species capable of quickly degrading dung pads for introduction into the Antipodes and the United States (Bornemissza 1970, 1976; Nakao and Funasaki 1979; Blank et al. 1983; Funasaki et al. 1988; Dymock 1993). Other species of dung beetles were accidentally introduced (i.e., adventive species) into the Antipodes and North America by human activity (Brown 1940, 1950; Emberson and Matthews 1973; Stebnicka 2009).

Within the context of almost half a millennium of European colonization and cattle production, we review the history and current status of dung beetles associated with cattle dung in the Antipodes and North America. More specifically, we examine: 1) the exotic species that have been deliberately introduced and methods/procedures used for their importation, 2) adventive species, 3) opportunities that potentially might be realized with additional introductions, and 4) risks associated with such introductions. We close with a series of recommendations for consideration in the development of potential further dung beetle introduction programs.

Deliberate Introductions

More than 100 species of dung beetles have been deliberately introduced into regions outside of their native range primarily to reduce populations of dung-breeding flies affecting cattle. At least 37 of these beetle species are now established in eight countries where they have been introduced (Table 1). Historical perspectives and the current status of dung beetle introduction programs, plus importation and quarantine procedures associated with these programs, are discussed below.

Historical Perspectives: Deliberate Introductions

Redistribution programs for dung beetles have been reported in the literature since the early 1900s. In 1909, dung beetles were introduced onto the Hawaiian islands to control horn fly, *Haematobia irritans irritans* Linnaeus, 1758 (Fullaway 1921, Markin and Yoshioka 1998). In 1929, *Copris incertus* Say, 1835 was imported into Fiji from Hawaii (Simmonds 1929). In 1956, New Zealand introduced *C. incertus* to control nuisance flies (Blank et al. 1983). The Australian organization CSIRO (Commonwealth Scientific and Industrial Research Organization) Entomology operated a dung beetle importation program from 1964 to 1986. Under that program, *Digitonthophagus gazella* (Fabricius, 1787) obtained from Hawaii were released in 1968 to reduce populations of bush fly (*Musca vetustissima* Walker, 1849) and buffalo fly (*H. irritans exigua* Linnaeus, 1758) (Bornemissza 1976, Roth et al. 1988, Edwards 2007). Ultimately, the program resulted in the establishment of 23 exotic dung beetle species throughout Australia (Edwards 2007). In 1978, releases of *D. gazella, Euoniticellus intermedius* (Reiche, 1849), and *Sisyphus spinipes* (Thunberg, 1818) were made on New Caledonia, and of *D. gazella*, *E. intermedius*, and *Liatongus militaris* (Castelnau, 1840) on Vanuatu, using beetles provided by CSIRO Australia (Gutierrez et al. 1988). In 1988, releases of *D. gazella* and *Onitis venderkelleni* Lansberge 1886 were made on Easter Island (Pacific Ocean) using beetles obtained from Australia (Ripa et al. 1995). In 1990, *D. gazella* obtained from the state of Texas in the United States were released into Brazil (Bianchin et al. 1992); it is the only dung beetle species to have been deliberately introduced in that country (Filho et al. 2018). The most comprehensive dung beetle introduction programs were those of Australia and the United States, which we assess further.

In the United States, releases on both the mainland and on the island state of Hawaii have resulted in the establishment of 23 exotic dung beetles species (Table 1). Indeed, Hawaii is a global pioneer of classical biological control efforts, having deliberately introduced at least 679 vertebrate and invertebrate species to control invasive exotic pests (Fullaway 1921, Funasaki et al. 1988). One such

Table 1. Deliberately introduced dung beetle species established in the countries around the world until 2021

Dung beetle species	Country of establishment								FG	Released in (year)	Origin of source material	References
	AU	NZ	US	BR	FJ	NC	VU	EI				
Aphodius fimetarius (Linnaeus, 1758)			+ + +						DW	HI (1909)	Europe	Markin and Yoshioka 1998
Ateuchus lecontei (Harold, 1868)			+ + +						TN	HI (1963)	US (Florida)	Davis and Krauss 1964
Bubas bison (Linnaeus, 1767)	+ + +								TN	AU (1983–1986)	Turkey	Tyndale-Biscoe 1996
Canthon humectus (Say, 1832)			+ + +						RL	HI (1923, 1952)	Mexico	Funasaki et al. 1988
Canthon indigaceus LeConte, 1866			+ + +						RL	HI (1954)	Mexico	Weber 1955
Canthon pilularius (Linnaeus, 1758)			+ + +						RL	HI (1963)	US (Florida)	Davis and Krauss 1964
Copris elphenor Klug, 1855	+ + +								TN	AU (1978–1983)	Southern Africa	Tyndale-Biscoe 1996
Copris hispanus Linnaeus, 1764	+ + +								TN	AU (1983)	France	Tyndale-Biscoe 1996
Copris incertus Say, 1835		+ + +	+ + +		+ + +				TN	HI (1922), NZ (1956), FJ (1929)	Mexico/Samoa	Simmonds 1929, Thomas 1960
Digitonthophagus gazella (Fabricius, 1787)	+ + +		+ + +	+ + +		+ + +	+ + +	+ + +	TN	AU (1968–1978), HI (1957) US (1972–1979), BR (1990), NC (1978), VU (1978), EI (1988)	South Africa, Zimbabwe	Fincher et al. 1983, Bianchin et al. 1992, Markin and Yoshioka 1998, Funasaki et al. 1988, Ripa et al. 1995
Euoniticellus fulvus (Goeze, 1777)	+ + +								TN	AU (1978–1982)	France	Tyndale-Biscoe 1996
Euoniticellus africanus (Harold, 1873)	+ + +		+ + +						TN	AU (1971–1977), US (1974)	South Africa	Nakao and Funasaki 1979, Tyndale-Biscoe 1996
Euoniticellus intermedius (Reiche, 1849)	+ + +		+ + +			+ + +	+ + +		TN	AU (1971), US (1979), NC (1978), VU (1978)	South Africa	Gutierrez et al. 1988, Nakao and Funasaki 1979
Euoniticellus pallipes (Fabricius, 1781)	+ + +								TN	AU (1977–1982)	Turkey, Iran	Tyndale-Biscoe 1996
Geotrupes spiniger Marsham, 1802	+ + +								TN	AU (1979–1980)	France	Tyndale-Biscoe 1996
Liatongus militaris (Castelnau, 1840)	+ + +						+ + +		TN	AU (1968–1979)	South Africa	Tyndale-Biscoe 1996
Oniticellus cinctus (Fabricius, 1775)			+ + +						DW	HI (1957)	Sri Lanka	Markin and Yoshioka 1998
Oniticellus militaris (Castelnau, 1840)			+ + +						DW	HI (1957)	Zimbabwe	Markin and Yoshioka 1998
Onitis alexis Klug, 1835	+ + +		+ + +						TN	AU (1972), US(1984)	South Africa	Nakao and Funasaki 1979
Onitis aygulus (Fabricius, 1781)	+ + +								TN	AU (1977–1982)	South Africa	Tyndale-Biscoe 1996
Onitis caffer Boheman, 1857	+ + +								TN	AU (1979–1984)	South Africa	Tyndale-Biscoe 1996

Table 1. Continued

Dung beetle species	Country of establishment								FG	Released in (year)	Origin of source material	References
	AU	NZ	US	BR	FJ	NC	VU	EI				
Onitis pecuarius Lansberge, 1875	+ + +								TN	AU (1976–1979)	South Africa	Tyndale-Biscoe 1996
Onitis vanderkelleni Lansberge, 1886	+ + +		+ + +					+ + +	TN	AU (1976), US (1976), EI (1988)	Kenya	Nakao and Funasaki 1979, Ripa et al. 1995
Onitis viridulus Boheman, 1857	+ + +								TN	AU (1976–1980)	South Africa	Tyndale-Biscoe 1996
Onthophagus binodis Thunberg, 1818	+ + +		+ + +						TN	AU (1971–1981), US (1973)	South Africa	Nakao and Funasaki 1979, Tyndale-Biscoe 1996
Onthophagus bonasus Fabricius, 1775			+ + +						TN	US (1980)	Pakistan	Fincher and Hunter 1989
Onthophagus catta (Fabricius, 1787)			+ + +						TN	HI (1957)	Kenya	Davis 1960
Onthophagus foliaceus Lansberge, 1886			+ + +						TN	HI (1975)	Angola	Nakao and Funasaki 1979
Onthophagus incensus Say, 1835			+ + +						TN	HI (1923)	US, Mexico	Markin and Yoshioka 1998
Onthophagus nigriventris d'Orbigny, 1902	+ + +		+ + +						TN	AU (1974–1982), US (1975)	Kenya	Edwards 2007, Nakao and Funasaki 1979
Onthophagus obliquus (Olivier, 1789)	+ + +								TN	AU (1976–1977)	Nigeria, Senegal, Zaire	Edwards 2007
Onthophagus oklahomensis Brown, 1927			+ + +						TN	HI (1963)	US (Florida)	Davis and Krauss 1964
Onthophagus sagittarius (Fabricius, 1781)	+ + +		+ + +						TN	HI (1985–1987), AU (1968–1977)	Sri Lanka	Markin and Yoshioka 1998, Tyndale-Biscoe 1996
Onthophagus taurus (Schreber, 1759)	+ + +		+ + +						TN	AU (1975), US (1984)	Greece	Hoebeke and Beucke 1997, Tyndale-Biscoe 1996
Onthophagus tuberculifrons Harold, 1871			+ + +						TN	HI (1963)	US (Florida)	Davis and Krauss 1964
Sisyphus rubrus Paschalidis, 1974	+ + +								RL	AU (1973–1980)	South Africa	Tyndale-Biscoe 1996
Sisyphus spinipes (Thunberg, 1818)	+ + +					+ + +			RL	AU (1972–1978), NC (1978)	South Africa	Gutierrez et al. 1988, Tyndale-Biscoe 1996
Total number of species	23	1	23	1	1	3	3	2				

The '+ + +' denote the countries where deliberately introduced dung beetle species have become established. The countries: AU-Australia, NZ-New Zealand, US-the United States of America, BR-Brazil, FJ-Fiji, NC-New Caledonia, VU-Vanuatu, EI-Ester Island, HI-the island state of Hawaii in the US. The functional group (FG): TN-tunneler, RL-roller, DW-dweller.

pest is the horn fly. Native to the Mediterranean region, horn fly was accidentally introduced onto Hawaii before 1897, became a significant threat to cattle production, and received considerable attention for almost a century from 1898 to 1982 (Funasaki et al. 1988). By the 1950s, Hawaii had introduced seven dung beetle species, along with 33 parasitoids and predators (including birds) for the biological control of horn fly (Markin and Yoshioka 1998). By the 1970s, the number of dung beetle species introduced into Hawaii reached 21 (Fincher 1981). In the continental United States, especially in the southeastern region where most of the high-density livestock grazing occurs, native dung beetles cannot effectively degrade the large amounts of cattle dung deposited on pastures (Fincher 1981). In the southeastern region, only ten of 40 native species are significant degraders of dung, and only three of these have a wide distribution (Fincher 1981). To augment the dung burial activities of native species and reduce horn fly populations, the United States Department of Agriculture's Agricultural Research Service (USDA/ARS) initiated a program in 1969 to introduce exotic species of dung beetles (Fincher and Hunter 1986). Several of the species subsequently released onto the mainland were obtained from Hawaii, with additional species obtained from Pakistan, Argentina, Egypt, and Mexico. Species of African and European origin were received from Australia via the CSIRO dung beetle project (Blume et al. 1973).

The CSIRO and the USDA/ARS projects coordinated their efforts for mutual benefit. CSIRO sent Dr. George Bornemissza to Hawaii to study local efforts to control horn fly for application to control bush fly and buffalo fly in Australia (Markin and Yoshioka 1998). In 1967 and 1968, Australia subsequently released nine dung beetle species of African and Asian origin, which were obtained from populations established in Hawaii (Markin and Yoshioka 1998). In return, Hawaii received nine dung beetle species that had successfully established following their release into Australia. These nine species were released onto Hawaii between 1973 and 1982, with eight species successfully becoming established (Funasaki et al. 1988, Markin and Yoshioka 1998). Largely because of these two projects, a total of 37 exotic species of dung beetles have been successfully established in the Antipodes (Australia – 23, New Zealand – 1) and 23 in the United States, including continental and the island state of Hawaii (Table 1).

One focus of the CSIRO project was to introduce into Australia, different climatic and genetic strains of a given dung beetle species; e.g., *D. gazella* (14 strains), *O. taurus* (Schreber, 1759) (7 strains), *E. fulvus* (Goeze, 1777) (5 strains), *E. pallipes* (Fabricius, 1781) (3 strains). This was done to increase the genetic diversity of introduced populations and enhance the likelihood of their establishment under different bioclimatic conditions (Bornemissza 1976, 1979; Edwards 2007). Thus, dung beetle surveys were conducted in six African, and 14 Asian and European countries, ranging from Morocco and Spain to Hong Kong, to identify suitable species and strains that are pre-adapted to bovine dung and to a wide range of climatic regions similar to those occurring in Australia (Bornemissza 1976, 1979; Edwards 2007). Particular care was taken to release beetles into regions with climates similar to the country of origin. For example, dung beetles released in southwestern Australia were introduced from countries with cold and moist winters, and warm and dry summers (Bornemissza 1979, Steinbauer and Wardhaugh 1992, Wright et al. 2015).

Current Status: Deliberate Introductions

Dung beetle introductions in the Antipodes continue intermittently (Steinbauer and Wardhaugh 1992, Mackereth et al. 2013, Forgie et al. 2014, Wright et al. 2015, Doube 2018a, Forgie et al. 2018). In Australia, two species of European origin have been continuously released since 2014 (Doube 2018b, DBEE 2021) with three additional species approved for introduction (CSIRO 2018, Doube 2018b, DBEE 2021). In New Zealand, 11 species were approved for introduction after years of intensive domestic field trials (Mackereth et al. 2013, Forgie et al. 2014, Forgie et al. 2018). Eight of these species have now been introduced, with seven of them being commercially available for release across New Zealand, at least up until 2021 (DBEE 2021).

In North America, there are no ongoing dung beetle introduction programs and little effort has been made to introduce or redistribute dung beetles since the 1990s (Table 1). There are three main reasons for this. Firstly, there are higher regulatory barriers for the importation of invertebrate biocontrol agents (IBCAs). There is now greater emphasis in classical biocontrol programs to assess the risk of exotic IBCAs introductions on native species (e.g., Sheppard et al. 2003, Hunt et al. 2008, Mason et al. 2017). Assessing this risk increases the cost and reduces the likelihood of biocontrol initiatives (Sheppard et al. 2003). Secondly, previous introduction programs were undertaken to control invasive species of dung-breeding pests, but there have been no recent such invasions to generate interest in new programs. Horn fly was first reported in North America on the east coast in 1887 and by 1897, it had spread across the continent and onto the Hawaiian Islands (Marlatt 1910). Its presence on the islands led to introductions of exotic dung beetle species from the early to mid-1900s (Table 1). Face fly (*Musca autumnalis* De Geer, 1776) was first reported in North America in the 1950s and, within 30 yr, it was present across southern Canada and in all but the most southern states of the United States (Krafsur and Moon 1997). Introductions of exotic dung beetles in the 1970s (Table 1) were undertaken to control this pest and also horn fly. This latter Introduction program coincided with CSIRO's dung beetle project (Bornemissza 1976), whose positive results undoubtedly facilitated research activity and producer support for efforts in North America. Thirdly, North America already has a diverse assemblage of tunneling and rolling dung beetles associated with cattle dung; i.e., eight species of Geotrupidae and 67 species of Scarabaeidae (Bezanson and Floate 2019). Thus, introductions of exotic species into North America are theoretically not needed to degrade cattle dung, but rather run the risk of supplanting the native species that already occupy this niche. The exception is the island state of Hawaii, which lacks a dung beetle assemblage that evolved jointly with large grassland herbivores.

The most recent redistribution efforts of dung beetles within North America occurred in 2008 when *D. gazella* and *O. taurus* were collected from the field in the United States and imported into Canada to establish research colonies. These colonies were used in laboratory and field cage studies to develop bioclimatic models to predict the eventual distributional limits of these species in North America (Floate et al. 2015, Floate et al. 2017). Despite the release of both species on pasture in southern Alberta, Canada (Floate et al. 2013), multiple years of dung-baited pitfall trapping have failed to provide evidence of their establishment (Floate and Kadiri 2013, Bezanson and Floate 2019). The import of these species into containment for scientific research and environmental release required applications and petitions to Canadian regulatory authorities concerning the potential impact of these IBCAs on the environment and native species (Hunt et al. 2008, Mason et al. 2017). The major points included in the petition were: 1) *D. gazella* is a Neotropical species not expected to overwinter in Canada, 2) *O. taurus* was present within 200 km of the Canadian border and possibly already established in parts of the country, and 3) dung beetle assemblages on pastures in Canada are overwhelmingly dominated by exotic species; e.g., *Onthophagus nuchicornis*.

Advances in Importation and Quarantine Procedures

Dung beetle introduction programs require a series of steps to reduce the risk of accidentally introducing pests or pathogens from the country of the beetle's origin. Because cattle dung may harbor such agents, beetles have been commonly shipped as surface-sterilized eggs. The sterilization process used in CSIRO's dung beetle project (1964–1986) was immersion in 3% formalin for 3 min (Bornemissza 1976). The surface-sterilized eggs were then packed in boxes with sterile peat and air-freighted to the recipient country into a specially designed and equipped sterilizing room. The eggs were subsequently placed into cavities within hand-formed balls of dung or in balls of dung obtained from cultures of donor beetles, and held until adult emergence (Bornemissza 1976, Fincher 1986). Rearing, breeding, mass production, and field release are the major steps to be carried out in the recipient country (Bornemissza 1976, Steinbauer and Wardhaugh 1992, Wright et al. 2015).

Initial introductions of dung beetles into Hawaii during the early 1900s used adult beetles imported without a sterilization process (Fullaway 1921). Most of the imported species failed to establish, perhaps due to an ecological mismatch (Fincher 1981). One species that did establish was *D. gazella*. CSIRO imported adult *D. gazella* from Hawaii in 1966 after first applying acaricide treatments to remove mites present on the beetles. However, upon receipt of the beetles at CSIRO's quarantine facility in the city of Canberra, live mites were still present and the beetles were destroyed without release (Bornemissza 1976). CSIRO subsequently obtained *D. gazella* from Hawaii as surface-sterilized eggs. These were reared to adults and released in the field on 30 January 1968 to become the first species of deliberately introduced dung beetle to successfully establish in Australia (Bornemissza 1976). Importation of surface-sterilized eggs became a standard practice for the CSIRO and the USDA/ARS dung beetle introduction programs (Waterhouse 1974, Fincher and Hunter 1986, Steinbauer and Wardhaugh 1992, Wright et al. 2015).

For the USDA/ARS program, the import permit process required the production and shipment of eggs from the country of origin under the supervision of a United States scientist (Fincher and Hunter 1986). The eggs were surface-sterilized, packed in boxes with moist peat moss from the United States and then shipped to an approved quarantine facility in the United States (Fincher and Hunter 1986). Eggs received for four species, two each from South Korea (in 1976) and Pakistan (in 1978), either failed to hatch or hatched during shipment with larvae dying en route (Fincher and Hunter 1986). These results stimulated research on alternative methods of egg-sterilization and shipment. In a comparison of ten methods, egg-to-adult survival of *D. gazella* was greatest when adults were allowed to make brood cells in autoclaved soil using rehydrated dung that had been freeze-dried (Fincher and Hunter 1986). In a comparison of different methods incorporating steps mandated by federal Animal and Plant Health Inspection Service guidelines, egg treatments inevitably reduced egg-to-adult survival (Fincher and Hunter 1987).

Further examination revealed additional consequences of importing beetles only as eggs, particularly for those species practicing brood care. For example, female *Onthophagus vacca* (Linnaeus, 1767) transfer their microbiome to the larvae by lining the egg chamber within the brood ball with regurgitated or fecal material (Doube 2018b). In *Copris hispanus* (Linnaeus, 1764), brood-care increases egg-to-pupal survival by 70–80%, and in *Kheper nigroaeneus* (Boheman, 1957), eggs cannot survive without maternal care (Edwards 1988, Halffter et al. 1996). The eggs of other dung beetle species are easily desiccated during shipment, which causes shrinkage, tearing or rupture of the egg membrane to kill the embryo (Bornemissza 1976). Furthermore, larvae that emerge from eggs during shipment perish in a few hours without food (Bornemissza 1976, Fincher and Hunter 1986). Therefore, alternatives to the importation of surface-sterilized eggs have been pursued.

Following the completion of the initial CSIRO dung beetle introduction project (1964–1986), subsequent projects in Australia have relied upon the importation of adults. Under a project conducted by CSIRO/WA Department of Agriculture (1990–1992), adult beetles were imported from Spain directly to quarantine facilities at the Australian Animal Health Laboratory (AAHL) in Geelong, Victoria (Steinbauer and Wardhaugh 1992). Projects operating from 2012 to 2014, and from 2017 to 2022 also imported beetles (Wright et al. 2015, DBEE 2021). For these latter projects, collected beetles were sieved, rinsed in water, transferred to buckets of moist vermiculite, and provided with fresh dung. Prior to shipment from the country of origin, five to ten females were dissected in saline to assess ovarian development and to ensure the absence of parasitic nematodes (Steinbauer and Wardhaugh 1992, Wright et al. 2015, DBEE 2021). If results of the assessment warranted, the remaining beetles were transferred to fresh or damp vermiculite in tightly sealed vials and held without food for 3–5 d to void their gut and reduce the chances of mite survival. The beetles, still in the vials, were then packed in large aluminum boxes with activated charcoal and air-freighted into Australia. The presence of activated charcoal reduced the likelihood of beetles being affected by the insecticidal sprays that are routinely sprayed in aircraft entering Australia to prevent the introduction of adventive species (Steinbauer and Wardhaugh 1992, Wright et al. 2015, DBEE 2021). Despite no food or water for a week, < 0.1% of the beetles shipped in this manner died in transit (Steinbauer and Wardhaugh 1992, Wright et al. 2015).

Species that have recently been imported into Australia (e.g., *Bubas bubalus* (Oliver, 1811) and *Onthophagus vacca*) were shipped as adults and held for rearing in AAHA ultra-high quarantine insectaries (Wright et al. 2015, Doube 2018b). After they laid eggs, the adults were destroyed to kill any mites or nematodes that they might have harbored. Adults developing from the eggs were held for one or more generations in quarantine to increase their numbers and then shipped as surface-sterilized eggs to distribution centers for additional rearing, multiplication and eventual field release (Steinbauer and Wardhaugh 1995, Doube 2018b). Surface-sterilization using formalin was replaced with use of Virkon, a new acid peroxygen system-based disinfectant. Established field populations of these species in Australia have provided source material for shipments of beetles into New Zealand, following layers of quarantine procedures and biosecurity guidelines (Pers. comm. Dr. Shaun Forgie, Dung Beetle Innovations).

Importing beetles as pupae, instead of as eggs or adults, may provide additional advantages. Pupae are less likely to carry contaminants (e.g., mites) and, because they are inactive, more easily handled during transport (Wright et al. 2015, Doube 2018b). Shipping the pupae of diapausing species also may reduce generation times and increase reproductive potential by accelerating the vernalization process as has been reported for *B. bubalus* (Wright et al. 2015, Doube 2018b).

In addition to how the beetles are shipped (egg, pupa or adult), other steps are taken to further mitigate the risk of accidentally introducing pests and diseases with shipments. The CSIRO and USDA/

ARS projects only collected beetles from regions within countries for which an occurrence of foot-and-mouth disease had not been reported for the previous 5 yr (Bornemissza 1976,1979; Fincher 1986, Wright et al. 2015). Prior to leaving quarantine, all packaging materials, residual dung, soil and dead beetles are autoclaved (Doube 1986, Fincher 1986, Fincher and Hunter 1986, Steinbauer and Wardhaugh 1992, Wright et al. 2015). Rearing and quarantine operations are undertaken in accordance with conditions stipulated as part of the import process approved by federal authorities (Bornemissza 1979, Fincher 1981).

Advances in Mass Rearing and Release Procedures

Methods used over the years in Australia have been modified to enhance the rearing and field establishment of imported dung beetles. Bornemissza (1976) describes the rearing methods used for the first CSIRO dung beetle project (1964–1986). Surface-sterilized eggs received at quarantine facilities were implanted in hand-formed or foster-parent brood balls. These brood balls were held for adult emergence in environmental growth chambers to simulate diapause and seasonal conditions specific to the given species. The new adults were then reared in insectaries or in breeding pens with subsoil heating to ensure continuous and rapid breeding. Using this method, 43 of the 53 species imported were successfully reared in quarantine (Edwards 2007). The failure of the remaining ten species was mainly due to low reproductive rates and a developmental diapause (Edwards 2007). Adults of the successfully reared species were then shipped for field release in damp peat moss in ventilated plastic containers in cardboard boxes.

For the first and second (1992–1994) CSIRO dung beetle projects, beetles were released into the paddocks on pasture by tipping them out onto fresh cattle dung pads (Bornemissza 1976, Steinbauer and Wardhaugh 1992). This method established field populations for 23 of the 43 species released during the first project, but failed to establish field populations for any of the species released during the second project. Failure to establish has been attributed by Edwards (2007) to: 1) the small number of beetles released, 2) unsuitable release sites in terms of soil type, habitat, and climate, 3) the weather conditions at the time of release and in the subsequent year, and 4) the use of pesticides and anthelmintics on cattle resulting in residues in dung detrimental to dung beetles (e.g., see Floate et al. 2005). The release of insufficient beetles is likely the main reason; i.e., 20 of the 21 species released in greatest numbers successfully established (Edwards 2007).

The field release method was altered for the third (2012–2014) and the current (2017–2022) dung beetle introduction projects as described by DBEE 2021), Doube (2018b), and Wright et al. (2015). Adults are released into field cages provisioned with fresh cattle dung each week and left to breed. The cages are screened to prevent dung beetles from leaving. Many cages at one site can be used as outdoor field nurseries to produce thousands of beetles over the course of several months. Field releases also can be made by placing brood balls in a special trench (20–40 cm deep) with drainage to prevent flooding and covered with a heavy wire mesh to exclude vertebrate predators. For introductions in New Zealand, the farmers rear and breed a starter colony (250 to 500 beetles) for almost 10 wk to produce thousands of new beetles. The sexually mature beetles are then released onto selected (sunny, sheltered, and centrally located) paddocks during appropriate times of the season when there is plenty of fresh dung from cattle that have not been recently treated with anthelmintics (DBEE 2021).

Accidental Introduction and Dispersal of Dung Beetle Species

In addition to those species deliberately introduced, a further 47 species have been accidentally introduced into the Antipodes and North America (Table 2). Many of these adventive species were likely introduced during European settlement when vessels from Europe discarded livestock bedding and soil ballast near ports of entry (Horn 1887, Emberson and Matthews 1973). This hypothesis explains the high number of adventive species of European origin in North America that were first reported along the eastern seaboard (Brown 1940, 1950). It also explains why most of these adventive species (38 of 47) are dwellers. Whereas rollers and tunnellers require fresh dung and undisturbed soils, dwellers tend to be generalists that do not need soil or fresh dung and can survive under a broad range of temperatures (Stebnicka 2001, 2009; Hemmings 2018).

Of the 39 adventive species that are dwellers, 12 are exclusively distributed throughout Australia, 1 throughout New Zealand, and 10 only in the United States—none exclusively occur in Canada (Table 2). *Aphodius fimetarius* (Linnaeus, 1758) and *Calamosternus granarius* (Linnaeus, 1767) are common throughout the Antipodes and North America (Table 2). *Labarrus lividus* (Olivier, 1789) is widespread in the tropical region of Australia, New Zealand, and in the United States, but has not been found in Canada (Table 2). *Australaphodius frenchi* (Blackburn, 1892) and *Parataenius simulator* (Harold, 1868) are common in Australia and New Zealand. *Otophorus haemorrhoidalis* (Linnaeus, 1758), *Teuchestes fossor* (Linnaeus, 1758), *Melinopterus prodromus* (Brahm, 1790) and *Acrossus rufipes* (Linnaeus, 1758) are common in both Canada and the United States.

Of the eight adventive species that are tunnellers, only *Onthophagus depressus* Harold, 1871, a species native to South Africa, is present in both the Antipodes (in Australia) and North America (in the southeastern United States) (Waterhouse 1974, Hoebeke and Beucke 1997, Bezanson and Floate 2019). Two native Australian species (*Onthophagus granulatus* Boheman 1858, *O. posticus* Erichson, 1842) are now common in New Zealand grasslands (Emberson and Matthews 1973). The South African species *Epirinus aeneus* (Wiedemann 1823) is widespread near Christchurch, New Zealand (Dymock 1993). *Onthophagus nuchicornis* (Linneaus, 1758), a Eurasian species, is common across southern Canada and adjacent states in the United States (Floate et al. 2017). *Onthophagus taurus* was first reported in the southeastern United States in the state of Florida (Fincher and Woodruff 1975). It has now spread across much of the eastern United States north to Canada and, because of redistribution programs, is established along the west coast in the state of California (Floate et al. 2017).

Dung Beetle Species Richness and Their Distribution

There is a global total of about 6,000 species of rollers and tunnellers (= true dung beetles) (Coleoptera: Geotrupidae, Scarabaeidae) (Davis and Scholtz 2001) and at least 2,000 species of dwellers (Aphodiidae: Aphodiinae) (Cabrero-Sañudo and Lobo 2009). Among the biogeographical regions, the Afrotropical region has the highest number of true dung beetle species (around 44% of the total), followed by the Neotropical region (24%), the Oriental region (14%), Australia (9%), the Palearctic region (7%) and the Nearctic region (2%) (Cambefort 1991) (Fig. 1). These same patterns are reflected in the species diversity of dung beetles at the scale of the individual dung pad. One pad in South Africa attracted 64 true dung beetle species

Table 2. Dung beetle species accidentally introduced into the Antipodes and North America known until 2021

Dung beetle species	Country of establishment				Taxa	FG	Native to	References
	AU	NZ	CA	US				
Acrossidius tasmaniae Hope, 1847		+ + +			AP	DW	Australia	Stebnicka 2001
Acrossus rufipes (Linnaeus, 1758)			+ + +	+ + +	AP	DW	Europe	Floate 2011, Horn 1887
Aganocrossus meticulosus Paulian, 1942	+ + +				AP	DW	South Africa	Stebnicka 2009
Airapus burrundieae Stebnicka & Howden, 1996	+ + +				AP	DW	PN Guinea	Stebnicka 2009
Aphodius fimetarius (Linnaeus, 1758)	+ + +	+ + +	+ + +	+ + +	AP	DW	Europe	Bezanson and Floate 2019; Stebnicka 2001, 2009; Tiberg and Floate 2011
Aphodius inquinatus Reeve, 1847				+ + +	AP	DW	Europe	Horn 1887
Aphodius pedellus (De Geer, 1774)			+ + +	+ + +	AP	DW	Europe	Bezanson and Floate 2019, Miraldo et al. 2014
Aphodius scrofa (Fabricius, 1787)				+ + +	AP	DW	Europe	Gordon 1983
Ataenius brouni (Sharp, 1876)		+ + +			AP	DW	Australia	Stebnicka 2001
Ataenius liogaster Bates, 1887	+ + +				AP	DW	Americas	Stebnicka 2009
Ataenius peregrinator Harold, 1877	+ + +				AP	DW	North America	Stebnicka 2009
Ataenius picinus Harold, 1867	+ + +	+ + +			AP	DW	Americas	Stebnicka 2001, 2009
*Australaphodius frenchi (*Blackburn, 1892)	+ + +	+ + +			AP	DW	South Africa	Stebnicka 2001, 2009
Calamosternus granarius (Linnaeus, 1767)	+ + +	+ + +	+ + +	+ + +	AP	DW	Europe	Horn 1887; Kadiri et al. 2013; Stebnicka 2001, 2009
Chilothorax distinctus (Muller, 1776)			+ + +	+ + +	AP	DW	Europe	Christensen and Dobson 1976, Tiberg and Floate 2011
Colobopterus erraticus (Linnaeus, 1758)			+ + +	+ + +	AP	TN	Europe	Floate and Kadiri 2013, Horn 1887, Rojewski 1983
Epirinus aeneus (Wiedemann, 1823)		+ + +			SC	TN	South Africa	Dymock 1993
Euoniticellus cubiensis (Laporte, 1840)				+ + +	SC	TN	Cuba	Almquist 2001
Eupleurus subterraneus (Linnaeus, 1758)				+ + +	AP	DW	Europe	Gordon 1983
Harmogaster geminatai Schmidt, 1911	+ + +				AP	DW	South Africa	Stebnicka 2009
Labarrus lividus (Olivier, 1789)	+ + +	+ + +		+ + +	AP	DW	Africa	Bezanson and Floate 2019; Horn 1887; Stebnicka 2001, 2009
Lorditomaeus bifidus Schmidt, 1980	+ + +				AP	DW	South Africa	Stebnicka 2009
Melinopterus prodromus (Brahm, 1790)			+ + +	+ + +	AP	DW	Europe	Horn 1887, Tiberg and Floate 2011
Nilaaphodius nigrita (Fabricius, 1801)				+ + +	AP	DW	Europe	Lobo 1996
Onthophagus depressus (Harold, 1871)	+ + +			+ + +	SC	TN	South Africa	Hoebeke and Beucke 1997, Waterhouse 1974
Onthophagus granulatus Boheman, 1858		+ + +			SC	TN	Australia	Emberson and Matthews 1973
Onthophagus nuchicornis (Linnaeus, 1758)			+ + +	+ + +	SC	TN	Eurasia	Hoebeke and Beucke 1997, Melsheimer 1844
Onthophagus posticus Erichson, 1842		+ + +			SC	TN	Australia	Emberson and Matthews 1973
Onthophagus taurus (Schreber, 1759)				+ + +	SC	TN	Spain	Fincher and Woodruff 1975, Fincher et al. 1983
Otophorus haemorrhoidalis (Linnaeus, 1758)			+ + +	+ + +	AP	DW	Europe	Tiberg and Floate 2011
Oxyomus porcatus (Fabricius, 1775)				+ + +	AP	DW	Europe	Horn 1887
Parataenius simulator (Harold, 1868)	+ + +	+ + +			AP	DW	South America	Stebnicka 2001, 2009
Phycochus graniceps Broun, 1886	+ + +				AP	DW	New Zealand	Stebnicka 2009
Planolinum tenellus Fabricius, 1775				+ + +	AP	DW	Europe	Gordon and Skelley 2007
Platytomus tibialis (Fabricius, 1798)	+ + +				AP	DW	Holomediterranean	Stebnicka 2009
Pleuraphodius lewisi (Waterhouse, 1875)	+ + +				AP	DW	Asia	Stebnicka 2009
Pleurophorus caesus (Panzer, 1796)				+ + +	AP	DW	Europe	Horn 1887
Proctophanes minor (Blackburn, 1897)		+ + +			AP	DW	Australia	Stebnicka 2001
Proctophanes sculptus (Hope, 1847)		+ + +			AP	DW	Australia	Stebnicka 2001
Psammodius nanus DeGeer, 1867				+ + +	AP	DW	South America	Horn 1887
Rhyparus helephoroides Fairmaire, 1893	+ + +				AP	DW	Asia	Stebnicka 2009
Rhyssemus inscitus (Walker, 1858)	+ + +				AP	DW	Afro Asia	Stebnicka 2009
Saprosites mendax (Blackburn, 1892)		+ + +			AP	DW	Australia	Stebnicka 2001

Table 2. Continued

Dung beetle species	Country of establishment				Taxa	FG	Native to	References
	AU	NZ	CA	US				
Tesarius sulcipennis (Lea, 1981)		+ + +			AP	DW	Australia	Stebnicka 2001
Teuchestes fossor (Linnaeus, 1758)			+ + +	+ + +	AP	DW	Europe	Horn 1887
Trichaphodius paradivisus Balthasar, 1960	+ + +				AP	DW	South Africa	Stebnicka 2009
Trichaphodius reichei Harold, 1859	+ + +				AP	DW	Asia	Stebnicka 2009
Total number of species	20	15	11	22				

The '+ + +' denote the countries where accidentally introduced dung beetle species are established. Countries: AU-Australia, NZ-New Zealand, CA-Canada, US-the United States of America, PN Guinea-Papua New Guinea. Functional group (FG): TN-tunneler, RL-roller, DW-dweller, AP-Aphodiinae, SC-Scarabaeinae.

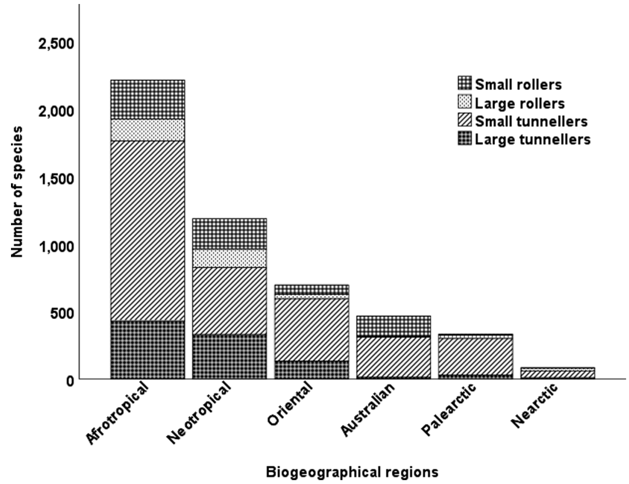

Fig. 1. Total number of true dung beetle (Scarabaeidae: Scarabaeinae) species represented in global biogeographical regions. Dung beetles with body size < 13mm are small and >13 mm are large. The information for the diagram is derived from Cambefort (1991).

and four dweller species (Hanski and Camberfort 1991b), versus 16 true and three dweller dung beetle species in Australia (Doube et al. 1991), versus four true and 18 dweller dung beetle species in temperate North America (Hanski and Camberfort 1991b). For fast and sustainable dung disposal and to fill ecological niches, a diverse, stable, and efficient dung beetle community is necessary (Yoshihara and Sato 2015, Soliveres et al. 2016).

Origin of Native Species in the Antipodes and North America

The native dung beetle species of the Antipodes evolved in the absence of large, pad-like deposits of herbivore dung. The landmasses that were to become Australia and New Zealand (the Antipodes) were separated from Gondwana, 99 and 80 million years before present (MYBP), respectively. Ancestors of current-day reptiles and mammals were the dominant terrestrial vertebrates in Australia during Mesozoic era (252 to 66 MYBP). Terrestrial marsupials and placental mammals coexisted in Australia in the Eocene (56 to 33.9 MYBP), but only the marsupials survived from that period to the present (Godthelp et al. 1992). Since 25 MYBP, marsupials with about fifty extant species have been the dominant herbivores and dung producers (Godthelp et al. 1992). Dung beetles have an evolutionary association with dung resources available (Gunter et al. 2016), such that the majority of Australian native dung beetle species co-evolved with marsupial dung (Waterhouse 1974, Doube and Marshall 2014). Unlike Australia, New Zealand did not have terrestrial mammals with the exception of a few small species of bats (Stringleman and Scrimgeour 2009). Therefore, New Zealand dung beetles co-evolved to use droppings from native species of bats, birds, reptiles and giant snails (Watt 1984).

Unlike in the Antipodes, a diverse and abundant assemblage of dung beetles associated with the pad-like dung of large grassland herbivores was present in North America at the time of European settlement and the introduction of cattle. The origins of this assemblage are summarized by Davis et al. (2002) and reflect the occurrence of two separate events. The first event, described in detail by Webb (1977; 1978), was the transition from forests to grasslands across large regions of North America (Nearctic) and South America (Neotropic) during the Cenozoic (66–0 MYBP) at a time when the two continents were physically separated.

This change led to the evolutionary diversification of large grazing ungulate species and their associated dung beetle faunas. The subsequent formation of an isthmus about 3 MYBP connected the two continents, which allowed for the interchange of species and the establishment of Nearctic and Neotropical elements in the dung beetle fauna in southern regions of North America. The second event was associated with the Bering Land Bridge, which existed up until about 11,000 yr ago between what is now present-day Siberia and Alaska (Elias et al. 1996). This land bridge allowed for the movement of Palearctic species into the Nearctic, including ancestors of the American bison, *Bison bison* (Linnaeus, 1758) (Artiodactyla: Bovidae) and their associated dung beetle faunas. Historically, bison roamed east of the Rocky Mountains from northern Canada south into Mexico and numbered an estimated 40 to 60 million animals (Hornaday 1889, Soper 1941). When cattle were introduced into North America prior to the 1640s (Bowling 1942), the coprophagous insects associated with bison were readily able to breed in cattle dung (Tiberg and Floate 2011).

Composition of Dung Beetles and Introduction Programs in Australia

There are 679 species of native and exotic dung beetles in Australia (Table 4). This includes 474 native true dung beetles (Scarabaeidae: Scarabaeinae), of which only 346 species have been described, in three tribes and 20 genera (Matthews 1972, 1974, 1976; Monteith 2015). They mainly inhabit forests and woodland habitats and feed on small, hard, and dry, pellet-like dung produced by marsupial and other small mammalian species (Waterhouse 1974, Doube and Marshall 2014). Many native dung beetles are generalist detritivores and feed on a range of food such as rotten fruits, mushrooms, carrion, and decayed forest litter (Matthews 1972, Doube et al. 1991, Monteith 2015, Ebert et al. 2019). There are limited studies on ecology and behavior, but many of these native beetles are captured in cattle dung baits (Edwards 2003). The 162 species of native dwellers (Aphodiidae: Aphodiinae) comprise eight tribes and 30 genera (Stebnicka 2009). The exotic species comprised 23 species that were deliberately introduced plus 20 adventive species (Table 1, 2, and 4).

The introduction of cattle into Australia created a need for dung beetle species capable of degrading large and wet cattle dung pads on open grasslands (Waterhouse 1974). To address this need, CSIRO Entomology imported into quarantine >114,000 eggs of 53 potentially suitable species (Bornemissza 1979). Of these, 43 species (1.73 million adult dung beetles) were released between 1964 and 1986 into mainland Australia (Bornemissza 1976, 1979; Edwards 2007). Only 23 species of the released species became established (Table 1), with 14 now at the limits of their expected distribution (Edwards 2007, Doube 2018a). The remaining nine species occupy only a fraction of their expected distributions (Tyndale-Biscoe 1990, Edwards 2007, Johnston et al. 2008, Doube 2018a).

Dung beetle introduction programs continue in Australia. Field releases of the early spring-active species *B. bubalus* and *O. vacca* were made in 2014 (Edwards et al. 2015, Doube 2018a). The Dung Beetle Ecosystem Engineers (DBEE) project, the successor to the original CSIRO Entomology project, began in 2017. The major aims of DBEE are: 1) to quantify the economic benefits of introduced dung beetles to the Australian livestock industry, 2) to identify spatial and temporal gaps in dung beetle activity and, 3) to import, rear, and release a Moroccan strain of *O. vacca* and three other dung beetle species (DBEE 2021). Currently, three new dung beetle species—*Euonthophagus crocatus* (Mulsant and Godart 1870), *Onthophagus andalusicus* (Waltl, 1835), and *Gymnopleurus sturmi* (MacLeay, 1821)—have been approved for importation and release to enrich the late winter through to spring gaps in dung beetle activity (CSIRO 2018).

Composition of Dung Beetles and Introduction Programs in New Zealand

New Zealand has a total of 41 dung beetle species; i.e., 25 native, 15 adventive, and one deliberately introduced (Table 1, 2, and 4). The native fauna include 16 species of rollers in the genera *Saphobius*, *Saphobiamorpha,* and *Boreobius* (Watt 1984, Stavert et al. 2014, DBEE 2021). There are also nine native species of dwellers in the genera *Phycocus, Saprosites, Tesarius,* and *Ataenius* (Stebnicka 2001). In 1956, the Mexican species *C. incertus* was deliberately introduced via Samoa to control cattle dung and dung-breeding flies (Thomas 1960, Emberson and Matthews 1973). Two species native to Australia (*O. granulatus* and *O. posticus*) were accidentally introduced with livestock bedding over 150 yr ago (Emberson and Matthews 1973). The South African species *Epirinus aeneus* (Wiedemann, 1823) is also adventive (Dymock 1993). The origins of the 12 adventive dweller species include six from Australia, two from North America, two from Europe, and two from Africa (Table 2).

New Zealand's Environmental Protection Authority has approved the importation and release of 11 dung beetle species (ERMA 2011). Initially, farmers, environmentalists, academics and the general public raised concerns about potential risks to human health and the environment that might arise from these releases. Therefore, exhaustive laboratory and field trials were carried out to address these concerns (e.g., Mackereth et al. 2013, Forgie et al. 2014, Forgie et al. 2018). The approved species are: *D. gazella, Onthophagus binodis* (Thunberg, 1818), *O. vacca*, *O. taurus, Euoniticellus fulvus*, *Onitis alexis* Klug, 1835, *Bubas bison* (Linnaeus, 1767), *B. bubalus, Copris hispanus, C. lunaris* (Linnaeus, 1758) and *Geotrupes spiniger* (Marsham, 1802). With the exception of *C. lunaris*, all of these species were previously introduced to Australia (Edwards 2007, ERMA 2011). Seven of the 11 species (except *C. lunaris, E. fulvus, O. vacca* and *B. bubalus*) are commercially available (https://dungbeetles.co.nz/orders) for release and four species (*O. binodis*, *O. taurus, Geotrupes spiniger,* and *Onitis alexis*) have been already released (DBEE 2021).

Composition of Dung Beetles and Introduction Programs in Canada

A total of 44 dung beetle species associated with cattle dung have been reported from Canada, comprising 34 native and 10 adventive species of European origin (Tables 2 and 4). The adventive species are abundant across southern Canada and extend further south into the United States (Hoebeke and Beucke 1997, Floate and Gill 1998). *Onthophagus nuchicornis* was present in the United States prior to 1844 (Melsheimer 1844) and is now the most common adventive tunneling species in Canada. It provides significant dung burial services on native grasslands, but is not effective in controlling horn flies—possibly because the adult beetles are not active throughout the summer (Macqueen and Beirne 1975a). *Onthophagus taurus* is an efficient tunneler species that is established in the northeastern United States at sites close to the Canadian border and potentially already may be present in southern regions of the provinces of Ontario, Quebec (Rounds and Floate 2012, Floate et al. 2017). The adventive *Colobopterus erraticus* (Linnaeus, 1758) is a rarity among aphodiine species. Whereas other members of this group are dwellers, *C. erraticus* is a tunneler (Rojewski 1983) and has been expanding its distribution across western Canada in recent years (Floate and Kadiri 2013). Where comparisons have been done, the number of individuals representing adventive species in cattle dung greatly exceeds that of native species (e.g., Floate and Gill 1998, Floate 2011, Floate and Kadiri 2013).

Native dung beetle species in Canada (and in the United States) that bred in the pad-like dung of American bison, *Bison bison* were pre-adapted to breed to the similar dung of cattle, when the latter were introduced to North America during European settlement (Tiberg and Floate 2011). This includes, for example, the roller species *Canthon pilularius* (Linnaeus, 1758) and *C. praticola* LeConte, 1859, the tunneler species *Onthophagus hecate* (Panzer, 1794) and *O. pennsylvanicus* Harold, 1871, and several species of dwellers (Howden and Cartwright 1963, Floate 2011). It has been hypothesized that the near extirpation of bison in North America during European settlement may have caused the extinction of some native species, but this has been refuted by Tiberg and Floate (2011). Rather, European settlement and the attendant introduction of adventive species has enhanced the overall diversity of dung beetle species in North America (Bousquet et al. 2013, Bezanson and Floate 2019).

There has been no formal program to deliberately introduce exotic species of dung beetles into Canada. However, *O. taurus* and *D. gazella* were imported as part of a laboratory and field cage study to predict their eventual distributions in North America (Floate et al. 2015, Floate et al. 2017). At the completion of the study, releases of both species were made on native grassland in southern Alberta (Floate et al. 2013). There was a slight possibility of establishment by the more cold-tolerant *O. taurus*, but no expectation of establishment by the semi-tropical *D. gazella*. Sequential years of pitfall trapping at the site have failed to recover either species (Floate and Kadiri 2013, Bezanson et al. 2020).

Composition of Dung Beetles and Introduction Programs in the United States

Species of dung beetles in the United States are particularly diverse, reflecting a country that includes regions that are subarctic (Alaska), tropical (Hawaii), and almost a full spectrum of intervening climates (the lower 48 contiguous states). The Nearctic region (encompasses the United States, Canada, Greenland, and parts of Mexico) supports 8 tribes, 10 genera, and 86 species of true dung beetles (Scarabaeidae: Scarabaeinae) (Cambefort 1991, Davis and Scholtz 2001). These comprise four genera and 24 species of rollers and six genera and 64 species of tunnellers (Cambefort 1991). Furthermore, the dweller dung beetles (Aphodiidae: Aphodiinae) comprise nine genera, including 118 native, three deliberately introduced, and 16 accidentally introduced species (Tables 1, 2, and 4). The 37 species of *Onthophagus* originally reported in the United States and Canada (Howden and Cartwright 1963) have been reduced to 29 species following taxonomic revisions (Bezanson and Floate 2019). A total of 158 dung beetle species have been updated in Scarabaeinae across America north of Mexico (Bezanson and Floate 2019).

There have been no dung beetle introduction programs in the United States since the 1990s (Table 1). Twenty-three species introduced prior to this time have become established (Table 1). Releases made to control horn fly included 29 species of which 14 species became established in Hawaii (Table 1). These include eight of nine species imported from Australia between 1973 and 1982; i.e., *D. gazella, Euoniticellus africanus* (Harold, 1873)*, E. intermedius, Onitis alexis, Onitis vandekelleni* Lansberge, 1886, *Onthophagus binodis, O. foliaceus* Lansberge, 1886, and *O. nigriventris* d'Orbigny, 1905) (Table 1). Fincher (1981) summarizes the history of deliberate releases of exotic species onto the mainland. These include *D. gazella*, *E. intermedius,* and *O. alexis*. All three species have established, but remain restricted to the southern United States (Bezanson and Floate 2019).

A reported 22 adventive species occur in the United States and generally are common and widespread (Horn 1887, Brown 1940, Bertone et al. 2005) (Tables 2 and 4). Among the more prominent of these is the tunneler *O. taurus*. First reported in Florida in 1971 (Fincher and Woodruff 1975), it is now common on pastures from North Carolina (Bertone et al. 2005) and north to the Canadian border (Rounds and Floate 2012). Common adventive dweller species include *A. fimetarius, C. distinctus* (Muller, 1776), *C. granarius, O. haemorrhoidalis, M. prodromus, and L. lividus* (Gordon 1983, Floate and Gill 1998, Fiene et al. 2011).

Opportunities Through Dung Beetle Introduction Programs

Dung beetle introduction programs enhance the ecosystem services provided by dung beetles and build knowledge networks to foster technology transfer. We examine these aspects in more detail in the following paragraphs.

Controlling Pests, Parasites, and Diseases

By scattering, shredding, and burying dung, dung beetles reduce the suitability of cattle pads as breeding sites for pests and parasites that affect livestock and humans (Horgan 2001, Forgie et al. 2010, Ryan et al. 2011). Some of these pests attack animals directly to feed on their blood, whereas others are vectors of parasites, bacteria, and viruses that are pathogenic in humans and livestock (Table 3). Evidence of these benefits is provided by numerous studies conducted indoors or under semi-natural field conditions (Blume et al. 1973, Fincher 1975, Doube and Moola 1988, Roth et al. 1988, Tyndale-Biscoe and Vogt 1991, Bishop et al. 2005, Gregory et al. 2015, Forgie et al. 2018). However, documenting these benefits in the field—where conditions are more difficult to control—is more challenging.

Dung Burial, Nutrient Recycling, and Carbon Sequestration

Regardless of their effects in reducing populations of pest species, dung beetles remove dung pads from the pasture surface—increasingly so when present in high numbers (Macqueen and Beirne 1975b, Tyndale-Biscoe 1994). By burying the dung, the beetles return labile nutrients, including nitrogen, phosphorus, and potassium to plants, and improve nutrient levels in the soil, soil aeration and water percolation, and reduce run-off into surface waters (Bornemissza 1960, Fincher 1981, Nichols et al. 2008). The provision of these services by introduced dung beetles is especially valuable when seasonal, local, or geographic niches are not fully occupied by native species. (Fincher 1981, Forgie et al. 2010, Ridsdill-Smith and Edwards 2011). Dung beetles sequester carbon, reduce carbon content and methane emissions in fresh dung pads (Iwasa et al. 2015).

Scientific Understanding, Expertise, and Collaboration

Introduction programs have increased opportunities for dung beetle research and scientific understanding. Before the initiation

Table 3. Examples of economically important flies and parasites that dung beetles are reported to reduce their populations until 2021

Common, scientific name	Taxa (Class: Order: Family)	Problem as	Native/ endemic to	Problematic to	References	Experimental evidences	Remarks
Horn fly, *Haematobia irritans irritans* (Linnaeus, 1758)	Insecta: Diptera: Muscidae	Blood-feeder	Europe	North America	Macqueen and Beirne 1975a, Markin and Yoshioka 1998	Greenhouse	Hawaii paid long attention from 1898 to 1982 to its biological control. Widespread at 0–2000 mASL and causes $1Bn per annum losses in the United States. Horn flies lay eggs in fresh dung and dung burial destroys their breeding ground.
Asian buffalo fly, *Haematobia irritans exigua* de Meijere, 1903	Insecta: Diptera: Muscidae	Blood-feeder	Asia, Indonesia (Timor)	Australia	Doube 1986, Roth et al. 1988, Wharton and Norris 1980	Laboratory	Accidentally introduced into northern Australia. Females lay eggs on fresh cattle dung on which the larvae feed. This is an obligate blood sucking fly: Both the male and female flies suck blood of cattle.
Bush fly, *Musca vetustissima* Walker, 1849	Insecta: Diptera: Muscidae	Nuisance pest	Australia	Australia	Blume et al. 1973, Bornemissza 1970, Hughes et al. 1978	Insectary	Female lays eggs on dung and larvae feed exclusively on dung, passive vector of trachoma and enteric diseases. Dung burial by beetles reduces survival of eggs and fly emergence.
African buffalo fly, *Haematobia thirouxi potans* (Bezzi, 1907)	Insecta: Diptera: Muscidae	Blood-feeder	southern Africa	southern Africa	Doube and Moola 1988, Doube et al. 1982	Laboratory	Female lays eggs exclusively on fresh dung; eggs hatch within 24 h and the larvae feed on dung Is a parasite of cattle and buffalo.
Face fly, *Musca autumnalis* De Geer, 1776	Insecta: Diptera: Muscidae	Pest	Europe/ Western Asia	North America	Fincher 1986, Krafsur and Moon 1997	Laboratory	Eggs and larvae occur exclusively in the fresh dung pads of cattle and bison in North America. Transfers causative agent of eyeworms and pinkeye in cattle.
Oriental face fly, *Musca hervei* Villeneuve, 1922	Insecta: Diptera: Muscidae	Nuisance and vector	Asia	Japan	Yamashita 2000	Field cages	The larvae develop in fresh cattle dung and the adults annoy livestock and are intermediate host of eyeworms.
Blue bottle fly, *Calliphora vomitora* Linnaeus, 1758	Insecta: Diptera: Calliphoridae	Vector	Cosmopolitan	United States	Jones et al. 2019	Laboratory	A fly species common on the farms, colonizes a variety of vertebrate dung and transmits enteric pathogens. Dung beetles supress these co-occurring flies in dung pads.
Stripped dung fly, *Oxysarcodexia varia* (Walker, 1836)	Insecta: Diptera: Sarcophagidae	Nuisance and vector	South America	New Zealand. Australia	Meiklejohn et al. 2012	Laboratory	Female prefers cattle and sheep dung to lay eggs, larvae feed on dung, vector of tapeworms, virus and zoonotic diseases. Also has forensic importance.
Blood sucking midge, *Culicoides brevitarsis* Kieffer, 1917	Insecta: Diptera: Ceratopogonidae	Parasite and vector	Asia	Australia	Bishop et al. 2005, Carpenter et al. 2013	Lab and field	This midge prefers moisture-rich dung pads for egg, larvae and pupae development, and causes blue tongue disease in ruminants. Increase of dung beetles and dung burial decreased their populations.
Medium gut worm, *Ostertagia ostertagi* (Stiles, 1892)	Chromadorea: Rhabditida: Trichostrongylidae	Gut parasite in cattle	Cosmopolitan	Australia, United States	Fincher 1975	Open pasture	Infects cattle and other ruminants, causes a fatal disease called ostertagiosis to calves. Dung beetles bury the eggs- contaminated dung and reduce the number of the infective stages.
Cattle nematode, *Cooperia oncophora* (Railliet, 1898)	Chromadorea: Rhabditida: Cooperiidae	Gut parasite	Europe, Americas	Australia, New Zealand, United States	Dorny et al. 1997, Fincher 1975, Forgie et al. 2018	Field cages	Eggs hatch in dung and the infective third-stage emerge from the dung, and disperse onto pasture foliage, and infect livestock. Dung beetles bury the eggs-contaminated dung and reduce the number of infective stages.
Bovine lungworm, *Dictyocaulus viviparus* (Bloch, 1782)	Chromadorea: Rhabditida: Dictyocaulidae	Cattle lung parasite	Europe	United States	Gormally 1993	Laboratory	Infected animals pass the eggs in feces, the first and second stage larvae develop in the dung and infective third-stage migrate onto grass. Dung beetles reduce larvae numbers in dung pads.

Table 3. Continued

Common, scientific name	Taxa (Class: Order: Family)	Problem as	Native/ endemic to	Problematic to	References	Experi-mental evidences	Remarks
New World hookworm, *Necator americanus* (Stiles, 1902)	Rhabditia: Strongylida: Ancylostomatidae	Human enteric parasite	North America	United States	Miller 1954	Field and lab	Dung burial and ingestion of feces by dung beetles reduce chances of exposure of the obligatory small intestine parasite that causes necatoriasis.
Enteric parasite, *Cryptosporidium parvum* Tyzzer, 1912	Conoidasida: Eucoccidiorida: Cryptosporidiidae	Enteric disease agent	Cosmopolitan	Europe, North America	Ryan et al. 2011	Laboratory	A dung pad may load thousands of oocytes, infection is through fecal-oral route and is one of the major cause of water contamination in Europe and North America, dung burial reduce their spread.
Pathogenic *E. coli*, *Escherichia coli* (Migula, 1895)	Gammaproteobacteria: Enterobacterales: Enterobacteriace	Enteric disease agent	Cosmopolitan	North America	Jones et al. 2019	Laboratory	Dung beetles supress pathogenic *E. coli* in the soil and co-occurring flies in vertebrate feces.

of dung beetle introduction projects (e.g., from the 1940s to 1970s), dung beetles were not well studied and were the subject of only a few publications per year (Hemmings 2018). The number of scientific publications per year increased to 10+ by the mid-1980s and rose dramatically after the mid-1990s (Hemmings 2018). One likely explanation for this increase are the introduction programs launched in the late 1960s and early 1970s in Australia and in the United States, subsequently followed by increased concerns of parasiticide residues in dung, which necessarily led to dedicated international studies on dung beetle ecology, biology, and taxonomy (Hemmings 2018). As an outcome of the first Australian project, over 600 species (50,000+ specimens) were classified and are now stored in the Dung Beetle Research Unit, Pretoria, South Africa (Bornemissza 1979). These programs also strengthened the expertise and capacity of government and private institutions (Edwards 2007, DBEE 2021). For example, Dung Beetle Solutions International (https://www.dungbeetlesolutions.com.au), SoilCam (https://dungbeetleexpert.com.au) and Dung Beetle Innovations (https://dungbeetles.co.nz) are private firms that conduct dung beetle research, sales, and training activities (DBEE 2021). The collaboration among government agencies, universities, schools, citizen scientists, councils, land care groups and committees, and private agencies in dung beetle research and introduction program (Edwards 2003, 2007; DBEE 2021) definitely indicates increased public interest, demand, scope and importance of dung beetles. Further evidence of this interest is the large and expanding number of studies examining the potential adverse effects on dung beetles, of parasiticide residues in dung of treated livestock (Floate et al. 2005, Lumaret et al. 2012, Junco et al. 2021). Concerns of these potential non-target effects are such that they have to be considered in the registration of new veterinary products (VICH 2004).

Challenges in Dung Beetle Introduction Programs

The dung beetles that have been introduced in the Antipodes and into North America facilitate dung burial, pest control and provide critical ecosystem services. However, the introductions of the past have had to surmount technical and regulatory challenges that will continue, and possibly increase, as barriers that will have to be addressed in future introduction programs. These are discussed below.

The Spread of Pests, Diseases, and Weeds

Dung beetles are unlikely to become pests, but their introduction into new regions may potentially result in the spread of mites, invasive weeds, and pathogens affecting livestock and humans (Bornemissza 1979, Janzen 1984, Funasaki et al. 1988, Niogret et al. 2006, Niogret et al. 2009, Mackereth et al. 2013). Because of these biosecurity concerns, introduction programs have heightened regulatory, research, and rearing requirements that increase program costs (Bornemissza 1979, Fincher and Hunter 1986, Hunt et al. 2008). To import beetles across international or interstate borders, there is typically a requirement for an import permit issued by the appropriate authorities. These permits specify conditions that must be met by the importer to avoid potential legal action (e.g., for Canada, see Mason et al. 2017). Previous programs in Australia and the United States mandated quarantine operations under the strict supervision of scientists and authorities in the country of origin, which increased costs associated with travel and logistics (Bornemissza 1976, Fincher

Table 4. Reported number of native and introduced dung beetle species in the Antipodes and North America[a]

<table>
<tr><th rowspan="2">Countries</th><th colspan="3">Native</th><th colspan="3">Deliberately introduced</th><th colspan="3">Adventive</th></tr>
<tr><th>Tunnellers</th><th>Rollers</th><th>Dwellers</th><th>Tunnellers</th><th>Rollers</th><th>Dwellers</th><th>Tunnellers</th><th>Rollers</th><th>Dwellers</th></tr>
<tr><td>Australia</td><td colspan="2">474</td><td>162</td><td>21</td><td>2</td><td>0</td><td>1</td><td>0</td><td>19</td></tr>
<tr><td>New Zealand</td><td>0</td><td>16</td><td>9</td><td>1</td><td>0</td><td>0</td><td>3</td><td>0</td><td>12</td></tr>
<tr><td>Canada</td><td rowspan="2">62</td><td rowspan="2">24</td><td rowspan="2">118</td><td>0</td><td>0</td><td>0</td><td>4</td><td>0</td><td>6</td></tr>
<tr><td>United States</td><td>17</td><td>3</td><td>3</td><td>6</td><td>0</td><td>16</td></tr>
</table>

[a]Source: Bezanson and Floate 2019; Cambefort 1991; Edwards 2007; Emberson and Matthews 1973; Floate 2011; Gordon 1983; Gordon and Skelley 2007; Horn 1887; Howden and Cartwright 1963; Matthews 1972, 1974, 1976; Monteith 2015; Stebnicka 2001, 2009.

and Hunter 1987). If a suitable quarantine facility does not exist, there are added (perhaps insurmountable) costs incurred in building such a facility and developing the necessary quarantine procedures (Wright et al. 2015, Doube 2018b).

Spread to Unintended Areas and Native Species Displacement

If releases are successful, the introduced species will spread and become abundant, but in doing so they may outcompete native species (Kohlmann 1994, de Oca and Halffter 1998, Vidaurre et al. 2008, Medina 2016, Genier and Davis 2017, Filho et al. 2018, Pokhrel et al. 2020). Within a few years after its introduction into southwestern Western Australia, the exotic species *O. binodis* displaced the native species *O. ferox* Harold, 1867 (Ridsdill-Smith and Edwards 2011) and, in turn, was displaced within 6 yr by the exotic species *O. taurus* (Ridsdill-Smith and Edwards 2011). Sampling conducted across Queensland, Australia recognizes *D. gazella* and *E. intermedius* as predominant species. These species were sampled from almost all of the sites and at several sites a single trap captured thousands of these beetles (Edwards 2003). In Brazil, introductions of the exotic species *D. gazella* have been reported to cause local extinctions of six native dung beetle species (Filho et al. 2018). Pokhrel et al. (2020) have examined the competitive success of the exotic species *D. gazella*, *O. taurus*, and *E. intermedius* in regions of introduction. They note that deliberate introductions allow beetles to establish in regions that might otherwise inaccessible due to climatic and geographic barriers. Also, they may adjust their life-history traits to adapt to novel environments, as has reportedly occurred for *O. taurus* within 100 generations of release (Macagno et al. 2016). Although one or more exotic species may provide the desired level of ecosystem services (Manning and Cutler 2018), this benefit may be offset by declines in assemblages of native dung beetle species (Aizen et al. 2018, Filho et al. 2018, Pokhrel et al. 2020).

Failure in Quarantine Rearing and Multiplication

Many dung beetle species have complex reproductive behaviors, biparental care, an obligate diapause and special breeding requirements, and others that are poorly understood (Bornemissza 1976, Davis 1996, Hunt and Simmons 2002, Daniel et al. 2014). Knowledge of these requirements is needed to facilitate egg-to-adult production of each species being reared in quarantine; either in the source or recipient country (Bornemissza 1976, Wright et al. 2015). For example, rearing large numbers of a large-bodied brood caring species such as *Copris hispanus* is difficult because 6 mo is required by the female to care for each brood (Bornemissza 1976, Kirk and Feehan 1984). *Onthophagus nuchicornis* appears to have an obligate diapause, restricting its production to one generation per year (Floate et al. 2015). Simply because of their biologies, some species may be immediately excluded from consideration in an introduction program as being too difficult to mass-rear. Mass-reproduction of other species in quarantine may be hindered by high mortality rates of different life stages (Bornemissza 1976, Chown et al. 1995, Edwards 2007, Wright et al. 2015) as occurred for 10 species considered for introduction in Australia (Edwards 2007).

Failure to Establish in the Field

Because dung beetle species have specific climatic and edaphic needs (Barkhouse and Ridsdill-Smith 1986, Brown et al. 2010, Braga et al. 2013, Hemmings 2018, Holley and Andrew 2019), they may fail to establish if released at sites with inappropriate climatic and soil conditions (Floate et al. 2015, Floate et al. 2017, Doube 2018a). For this reason, thorough consideration of both climatic (temperature, precipitation) and non-climatic (e.g., dispersal barriers, food resources, natural enemies) factors is essential (Edwards 2007; Duncan 2009, 2016; Yelenik and Levine 2010). For example, models relying solely on climatic factors performed poorly to predict regions of potential establishment for three of five species released in Australia (Duncan et al. 2009). In the earlier Australian dung beetle projects, a total of 20 species released in the field failed to establish (Edwards 2007). Examination of these failures suggested that this outcome could have been avoided by matching the physiology of the beetles to the season of release, by increasing the number of beetles released at a given site, and by increasing the number of release sites (Edwards 2007, Wright et al. 2015). In some cases, conclusions of failure may be premature; e.g., *B. bubalus* was only recovered 9 yr after the original release (Edwards 2007). Other factors preventing establishment or causing local extirpation can include drought, fire, predators, and parasitoids (Noriega 2010, Smith et al. 2019). Lastly, the widespread usage of chemical insecticides, herbicides, fungicides, and anthelmintics can impact survival and establishment of dung beetle species (Floate et al. 2005, Lumaret et al. 2012, Gonzalez-Tokman et al. 2017, Junco et al. 2021).

Recommendations

We recommend a number of points to consider in relation to the development of a dung beetle introduction program.

First, clearly identify the goals of the introduction program based on unoccupied ecological niches as characterized by seasonality, geography, and habitat. Then identify dung beetle species capable of achieving these goals by reviewing the literature (e.g., reports, theses, archives, scientific papers) and/or by conducting preliminary trials (Bornemissza 1970; Edwards 2003, 2007).

Secondly, develop species distribution models that incorporate both climatic (temperature and precipitation) and non-climatic (environmental, biotic, and dispersal) factors to predict precisely the native and introduced ranges. New technologies such as NicheMapR

(Kearney and Porter 2017) can be used to identify suitable species or group of species as it can more correctly predict species distribution ranges.

Thirdly, it is essential to undertake research to answer fundamental questions regarding reproductive biology, thermal physiology, and population genetics of candidate species (Edwards 2007, Hemmings 2018). A thorough understanding in terms of reproductive biology, thermal behavior, and genetics of the species can help to select climatic and genetic strains of a species to enhance its establishment in regions of introduction.

Fourthly, the importation and rearing of beetles in quarantine are the most challenging steps in introductions because of biosecurity issues (Steinbauer and Wardhaugh 1992, Wright et al. 2015). Precise protocols are needed to rear and mass-produce, under quarantine conditions, sufficient numbers of individuals for release. An inability to achieve this goal in the laboratory may exclude consideration of some species for release; e.g., *Copris hispanus* (Kirk and Feehan 1984). However, greater success may be possible by rearing beetles using semi-controlled field conditions (Doube 2018b, DBEE 2021).

Fifthly, the overall success of introduction programs depends on the success of the species release and establishment. The appropriate timing and season of release (Bornemissza 1979, Edwards 2007), adequately-sized founding populations and an adequate number of release sites (Edwards 2007, Duncan 2016), and restriction in the use of parasiticides, insecticides, herbicides, and fertilizers that can harm dung beetles at these sites (Floate et al. 2005, Lumaret et al. 2012, Gonzalez-Tokman et al. 2017, Righi et al. 2018) should be considered during species release.

Sixthly, the redistribution programs should identify promising native and already established exotic species that are efficient dung degraders but limited in their distribution because they are slow breeding and slow spreading. This minimizes project cost and the risks associated with the spread of pests and diseases, and native species displacement (Edwards 2007, Medina 2016, Pokhrel et al. 2020).

Finally, it may take years for dung beetle populations to become locally abundant after their release. Therefore, long-term monitoring of release sites is essential to evaluate post-release success. Factors such as efficacy of dung burial, pest and parasite control, and native-introduced dung beetle assemblages are to be considered in post-release monitoring (Edwards 2007, Medina 2016, Doube 2018b).

Conclusion

Exotic species of dung beetles that have either been deliberately introduced or are adventive are widespread in grassland habitats in the Antipodes and North America. They often dominate local assemblages of dung beetles in cattle dung to support the conclusion that they fill niches unoccupied by native species and enhance dung degradation. Dung beetle introduction programs have adopted a standard set of procedures to optimize the selection of potentially suitable species, their mass rearing, field release, and eventual establishment. But there is equally a need for post-release monitoring to assess the effect of these introductions on native species, the speed of dung degradation, and its concomitant benefits; e.g., pasture productivity, suppression of dung-breeding pests, and parasite affecting livestock. By reviewing the history of dung beetle introduction programs in the Antipodes and North America, including both failed and successful efforts, we hope to inform the decision-making process to aid the development of future such programs.

Acknowledgments

The Australian Government's Endeavour Leadership Program provided scholarship to the lead author, MRP for his Ph.D. Program. Agriculture and Forestry University, Nepal granted him study leave during the program period. We appreciate and acknowledge the scholarship and study leave providers. We thank Eric Sinclair for his comments and English edits on the initial draft and three anonymous reviewers for their constructive criticisms on previous version of this manuscript. This publication is a part of the lead author's Ph.D. project. Holsworth Wildlife Research Endowment and University of New England Higher Degree Research provided grants to conduct research on native and introduced dung beetles. The research brought MRP the insights to conceptualize this review. All of these funders are highly acknowledged.

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