

# INDIGENOUS AND INTRODUCED DUNG BEETLES (COLEOPTERA: SCARABAEIDAE) OF TEMPERATE AUSTRALIA: A REVIEW OF BIOLOGY, IMPORTANCE AND EFFECT OF CLIMATE CHANGE ON POPULATION DISTRIBUTIONS.

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## Summary

Both indigenous and introduced Australian dung beetles (Coleoptera: Scarabaeoidea) play an important role in agricultural systems. Temperate grasslands in Australia are expected to have some of the greatest increases in temperature and reduction in precipitation due to climate change which may directly threaten dung beetles. Several biotic and abiotic factors affect the development of larvae and fitness of young dung beetles. To understand if dung beetles can continue to provide ecosystem services across temperate Australia under changing management and climate, we review what is known about their life history traits that will facilitate their adaptation.

We believe dung beetles will continue to provide valuable ecosystem services and have potential to aid in adapting and alleviating the impacts on crops and pastures from reduced and sporadic rainfall. However, the level of function, may be impeded due to climatic stress and a loss of diversity with thermal specialists and some indigenous species, expected to be displaced into narrower ranges. An increase in feeding competition from thermal generalists and introduced species will likely implement this movement. The evidence from naturalised introduced species indicate behavioural adaptations and/or phenotypic plasticity suggest some species will continue to provide services that improve pasture production despite changes to climate. Ongoing monitoring of phenological shifts will inform adaptive management of this vital group.

**Key Words:** dung beetles, Australia, climate change, Coleoptera, Scarabaeidae

## INTRODUCTION

Both indigenous and introduced Australian dung beetles (Coleoptera: Scarabaeoidea) play an important role in agricultural systems including nutrient cycling, soil aeration, seed burial, improved pasture production and pest suppression (Nichols *et al.* 2008, Simmons and Ridsdill-Smith 2011) by reducing the amount of time required for dung to break down. Dung beetle community composition depends upon the origin and intensity of their ecosystem, which has consequences for associated ecosystem functions (Fuzessy *et al.* 2021). Temperate grasslands in Australia are expected to have some of the greatest increases in temperature and reduction in precipitation due to climate change (Jakob and Walland 2016), which may directly threaten dung beetles by impacting on their development. Anthropogenic actions are likely to harm dung beetle communities throughout tropical forest ecosystems directly, by habitat loss, and indirectly through the depletion of large vertebrates (Fuzessy *et al.* 2021). Research is needed in temperate zones to investigate what might happen to these providers of ecosystem services.

Dung beetles already face indirect challenges in temperate grasslands due to changes in livestock management practices: including more intensive feeding regimes, and changes in patterns of endoparasitic chemicals administered to livestock, e.g., mectins are greatly more toxic than benzimidazole

to dung beetles. Ivermectin and abamectin cause a reduction in successful emergence and hatching of dung beetle larva (Ridsdill-Smith 1993c, Wardhaugh *et al.* 1993, Floate 1998, Dadour *et al.* 1999, Wardhaugh *et al.* 2001, Wardhaugh 2005, Beynon *et al.* 2012, Beynon 2012). To understand if dung beetles can continue to provide ecosystem services across temperate Australia under changing management and climate, we review what is known about their life history traits that will facilitate their adaptation.

## REPRODUCTION

### *Broods*

All dung beetles reproduce the same way with an egg laid inside a ball of dung. There are four different guilds; the rollers (telecoprids), the tunnellers (paracoprids), the dwellers (endocoprids) and the stealers (kleptocoprids) (Bornemissza 1969, Doube 1990, Lumaret *et al.* 1992). The first guild cut a ball out from the surface of the dung and attach it to the base of surrounding vegetation, above ground or buried away from the dung pad. The second guild tunnel beneath the dung pad to bury their brood balls, with some species laying individual eggs in broods (Tyndale-Biscoe 1990, Davis 1996a, Sowig 1996, Gregory *et al.* 2015). The tunnelling guild can be further divided into two sub-guilds with those that bury broods in brood masses, where broods are in close proximity to one another (Tyndale-Biscoe 1990, Davis 1996a, Sowig 1996, Gregory *et al.* 2015), and those

who bury individual broods in separate individual chambers. The third guild are dwellers or endocoprotophagus beetles that live and feed within the dung heap (Tyndale-Biscoe 1990, Lumaret *et al.* 1992). The fourth guild steals the brood ball of rollers in which to lay (parasitise) their own egg onto the stolen brood ball (Doube 1990).

Upon hatching, the larvae unselectively bulk feed on the organic matter in the brood, however feeding is restricted to the dung in the brood ball (Holter 2016). The larvae go through three instar phases. Upon ending the third instar the larvae cease feeding before changing into non-feeding pupae, later turning into adult beetles. At the third instar phase some species can cease development, which allows pupae to survive unfavourable conditions as they can remain inactive for many months (Tyndale-Biscoe 1990).

#### *Nulliparous*

Nulliparous beetles have three instars which are defined by Tyndale-Biscoe *et al.* (1981). The first instar (N1) is described as being newly emerged beetles that have a soft cuticle, no fat-body, an undeveloped reproductive system and unworn tibiae. The second instar (N2) changes to a hard cuticle, some body fat, an undeveloped or slightly developed reproductive system and a slightly worn tibiae. The third instar (N3) is defined as young beetles with a hard cuticle, have developed body fat, a developed reproductive system and slightly worn tibiae. The size of the adult dung beetle does not change after emerging from the nest (Tyndale-Biscoe 1990).

#### *Parous*

Older egg laying beetles, similar to nulliparous stage 3 (N3), with accumulations of yellow body fat at the base of the ovarioles along with an increasingly worn tibia are defined as parous (Tyndale-Biscoe *et al.* 1981).

#### *Resorbing*

Resorbing is a stage of beetle development where beetles of any age from N2 (Nulliparous 2) to the late parous stage (Parous 3) show visible signs of oocyte breakdown, or extrusion of oocyte sideways through the ovariole wall (Tyndale-Biscoe *et al.* 1981, Tyndale-Biscoe and Walker 1992). Visible signs of past resorption are yellow granules attached to the outside of the ovariole base. Beetles go through resorbing in response to stressful conditions unsuitable for breeding and when there is limited quality feed present.

#### *Reproduction conclusion*

The life cycle of dung beetles involves the placement of an egg inside a dung ball, the development of larvae

and the emergence of a young adult (nulliparous) before egg production (parous). If conditions for reproduction are not suitable, dung beetles will not develop eggs, or if eggs have developed, then eggs are resorbed (Tyndale-Biscoe and Watson 1977, Tyndale-Biscoe *et al.* 1981, Kirk 1983, Tyndale-Biscoe 1983, Tyndale-Biscoe and Walker 1992, Lopez-Guerrero 1996, Gonzalez-Vainer and Morelli 1999). Their reproduction cycle should be considered fragile, in that any disturbance to the egg or larvae may result in mortality of the larvae.

#### *Dung feeding*

There are several ways in which dung beetles remove dung. One is through burial for food storage and brood masses and chambers (egg development). Another is through rolling dung away and through shredding and feeding on dung (Tyndale-Biscoe 1990, Tyndale-Biscoe 1994).

Feeding is not based on the partly digested grass in the dung, but of the dead and alive biomass (Holter and Scholtz 2007, Holter 2016), that is between pieces of partly digested grass. The biomass provides essential nitrogen, steroids and amino acids for beetle reproduction. The dung beetles use specialised mouthparts to separate the biomass from the lignocellulose before ingestion (Holter 2016). Only a small proportion of fibre is ingested by dung beetles during feeding. The mandibular molars are used to reduce the moisture in fresh dung (70-90% water depending on the season (Holter 2016)) before concentrated material is swallowed (Holter 2000; Holter 2004).

### **ECOSYSTEM SERVICES PROVIDED BY DUNG BEETLES.**

Reproduction by both indigenous and introduced dung beetles provides a range of ecosystem services through the breakdown of dung pads. Dung beetles assist in nutrient cycling, improvement of soil structure and water infiltration (Bornemissza 1960), hence the regeneration of pastures (Bornemissza 1960, Davis 1996b, Miranda *et al.* 2000, Doube 2008, Pecenka and Lundgren 2018) and the reduction of pests (Wallace and Tyndale-Biscoe 1983, Ridsdill-Smith and Matthiessen 1988, Ridsdill-Smith and Hayles 1990). However, indigenous Australian dung beetles are not adapted to non-indigenous bovine dung (Waterhouse 1974, Tyndale-Biscoe 1994) and use a small amount, if any, of the large amounts of dung produced. Cattle can produce 30 kg of dung per animal a day under feedlot conditions (Dadour and Cook 1996). In the absence of introduced dung beetles adapted to utilise bovine dung pads, these often remain untouched,

smothering pasture, leading to reduced growth and providing a breeding resource for flies.

Dung beetles were introduced into Australia some 50 years ago, for example *Onthophagus taurus* (Schreber, 1759) and *O. binodis* Thunberg, 1818 were released on the Fleurieu peninsula of South Australia in the early 1970's. They have been active in the area for many years reducing dung and improving agricultural production. During the early 1990's beetles were harvested and released into other suitable regions of the state. Like many other introduced species across Australia, for these beetles to survive over many years they have probably adapted to the changing environment and agricultural practices. Historically these introductions are unique, and by studying responses gives insight into adaptive mechanisms which can be tested (e.g. Mamantov and Sheldon 2021).

Of the 43 species of dung beetle introduced into Australia by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) (Bornemissza 1960, Bornemissza 1976; Kabir *et al.* 1985, Wright *et al.* 2015, Doube 2016) to recycle bovine dung and aid in the management of the bush fly populations, 23 of these have become established (Bornemissza 1960, Bornemissza 1976, Kabir *et al.* 1985, Edwards 2007, Wright *et al.* 2015, Doube 2016). To protect indigenous dung beetles that specialize in marsupial dung (Bornemissza 1976), preference was given to releasing non-indigenous species that are primarily bovine dung feeders. Part of the problem of the lack of activity of indigenous beetles in non-indigenous dung may be a mismatch between beetle phenology and when large amounts of dung is present. Across south-eastern Australia, indigenous species are present during late spring and summer in low densities: for example, *O. australis* Guerin-Meneville 1838, *O. granulatus* Boheman 1858 and *O. pentacanthus* Harold 1867 (Tyndale-Biscoe *et al.* 1981, Tyndale-Biscoe and Walker 1992, Tyndale-Biscoe 1994). Hughes (1975) researched the burial of dung by indigenous species (predominantly *O. granulatus* and *O. australis*) in the Canberra region and found that in a 10-day period in spring and autumn, 60-93% of dung pads were buried but during the remainder of the season (summer and winter), pads were relatively untouched.

In comparison, non-indigenous species introduced into Australia were selected due to their ability to bury large amounts of dung across all seasons. Dung burial is largely related to the size of the beetle species (Davis 1996a). The *Onitis* genus represents a large family of dung beetles which are generally active between spring

and autumn (Weston 2020). *Onitis* are some of the largest species that have been successfully introduced to Australia (Weston 2020). Edwards and Aschenborn (1987) investigated the burial of several species of *Onitis* and found *On. caffer* Boheman 1857 (Autumn – spring active) and *On. aygulus* (Fabricius, 1781) commenced burial within 2-5 days of arriving at the dung pad burying between 57g and 92g per pair. *Onitis alexis* Klug 1835, *On. Pecurarius* Lansberge 1875 and *On. caffer* are such prolific buriers of cattle dung that no bush fly larvae survived dung burial in the presence of these species (Edwards and Aschenborn 1987). *Bubas bison* (L. 1767) is an autumn to early spring active dung beetle that has been estimated to bury 90% of cattle dung after 5 days (Ryan *et al.* 2011). In comparison, *O. gazella* (Fabricius, 1787), which is a spring-summer active beetle, was capable of breaking up entire dung pads within 30-40 hours of introduction, despite being a smaller beetle (Bornemissza 1970). Likewise, *O. taurus* dispersed more than 50% of dung within the first 24 hours (Dadour *et al.* 1999). Tyndale-Biscoe (1994) identified that in the field, dung burial was highly correlated with the biomass of dung beetles present. With the addition of more introduced species (in the case of Tyndale-Biscoe (1994), the arrival of *Euoniticellus fulvus* (Goeze, 1777)) increased the dung beetle biomass, thus increased the burial of dung. Introduced dung beetles have improved the burial of cattle dung by occupying underutilised niches (summer and winter dung pads) that the indigenous dung beetles did not (Hughes 1975; Tyndale-Biscoe 1994).

#### *Nutrient availability*

As the dung beetles in Australia bury large quantities of dung, not just for reproduction but also for food storage, not all of this is eaten and some of it is left behind in the soil. This provides nutrients for crops and has been shown to improve nutrient content of plants during drought conditions (Johnson *et al.* 2016). Johnson *et al.* (2016) found in the presence of *B. bison*, there was an increase in nutrient uptake which appeared to improve plant growth especially in the foliage. Doube and Marshall (2014) also found that, in low nutrient soils, the improvement of soil nutrient availability was due largely to the presence of dung beetles and remained so for up to a decade.

#### *Water penetration*

While dung beetles themselves are negatively associated with dry conditions, their activity can increase soil water by improving soil porosity. Brown *et al.* (2010) has shown that dung beetles improved water infiltration, soil porosity and reduced surface water run-off. Dung beetles aided pasture production

through improved water penetration, hence greater plant available water, with lasting effects of up to a decade (Doube 2008; Doube and Marshall 2014). Johnson *et al.* (2016) showed that dung beetle presence in the field during drought conditions improved plant health associated with increased soil water content. This has the potential to increase the ability of crops and pastures to withstand droughts, which are predicted to become more common (Johnson *et al.* 2016). Johnson *et al.* (2016) goes on to hypothesise that dung beetles could moderate the impacts of climate change by improving crop resilience to unpredictable rainfall events. More research is required to test this hypothesis.

#### *Pasture Improvement*

Intensive grazing practices utilising modern plant cultivars that increase production rely on the recycling of dung. Dung beetles aid in pasture improvement through cycling of nutrients by burying dung, aeration of the soil, improved water penetration and root penetration through digging tunnels for brood masses, individual broods and food balls (Edwards and Aschenborn 1987, Tyndale-Biscoe 1994, Hunt and Simmons 2004, Holter and Scholtz 2007, Doube 2008, Nichols *et al.* 2008, Gollan *et al.* 2013, Doube 2018). When dung beetles dig tunnels, soil casts are brought to the surface, which rotates and aerates the soil (Nichols *et al.* 2008; Simmons and Ridsdill-Smith 2011). With the presence of dung beetles, Doube (2008) found pasture production was improved by 30% which persisted for three years through many of the above mechanisms.

#### *Control of flies*

Dung beetles are used to aid in the management of the bush fly (Ridsdill-Smith and Matthiessen 1988; Ridsdill-Smith and Hayles 1990; Ridsdill-Smith 1993a) and the buffalo fly *Haematobia exigua* De Meijere 1903 (Bishop *et al.* 2005). Mortality of fly larvae can occur by shredding and disturbance of the dung pad, and through burial of dung.

Shredding by sexually mature and immature individuals during feeding (Tyndale-Biscoe 1994) controls flies as it reduces the dung pad moisture quickly. Shredding varies between seasons and sites and occurs when high populations interfere with each other's burial activities (Tyndale-Biscoe 1994). Tyndale-Biscoe (1994) found that mean seasonal quantity shredded never exceeded 12%. The level of shredding does fluctuate greatly (between 0 and 70%) throughout the season depending on the number of beetles in a dung pad (Tyndale-Biscoe 1994).

Ridsdill-Smith and Hayles (1990) studied the stages of bush fly killed by two species of dung beetle: *O. binodis* and *On. alexis*. There was a strong positive correlation between increased mortality of maggots and increasing dung beetle populations (Ridsdill-Smith and Hayles 1990). That trial was conducted using low quality dung, which is commonly seen during Mediterranean summers. Very low numbers of bush flies survived in both the laboratory and outside components of the experiment. The flies that did survive probably did so in small undisturbed pockets of dung. It has been found that fly mortality increases during summer as dung beetles become more abundant (Hughes *et al.* 1978, Ridsdill-Smith and Matthiessen 1988). There are other factors which effect mortality and success of the interactions between dung beetles and fly mortality; these include dung quality (Ridsdill-Smith 1986), moisture, concurrence of beetle entry, fly oviposition and the speed of burial (Bishop *et al.* 2005).

Some scenarios have appeared where the bush fly population does not change with the introduction of new dung beetle species (Wallace and Tyndale-Biscoe 1983). In south-western Australia, the indigenous dung beetle *O. ferox* Harold 1867 utilise kangaroo dung in undisturbed heath vegetation in spring (Ridsdill-Smith *et al.* 1983), yet is also found in cattle dung (Ridsdill-Smith 1993b). When *O. binodis* was introduced to south-western Australia, it was expected to reduce the bush fly population, however the fly population remained steady. Ridsdill-Smith (1993a) identified that *O. ferox* caused greater mortality to *bush fly* egg-puparia than *O. binodis*. It was also found that *O. binodis* egg production was substantially affected by the presence of *O. ferox*, though not vice versa due to the large size of *O. ferox* compared to *O. binodis*. Due to asymmetric competition at high densities between *O. ferox* and *O. binodis*, the introduction was not successful in terms of reducing the bush fly population.

### **INTERACTIONS BETWEEN DUNG BEETLES AND THEIR ENVIRONMENT**

#### *Factors that influence development*

Several biotic and abiotic factors affect the development of larvae and fitness of young dung beetles (Tyndale-Biscoe *et al.* 1981, Barkhouse and Ridsdill-Smith 1986, Sowig 1995, Dadour and Cook 1996, Menéndez *et al.* 2014, Holley and Andrew 2019a, Holley and Andrew 2019b). These include dung quality, such as moisture content (Edwards 1991) and pH, which is influenced by the diet of the livestock, such as grass diet verses grain (Dadour and Cook 1996), soil type (Sowig 1995), soil compaction (Dabrowski *et al.* 2019), fungal presence, soil

temperature and moisture (Tyndale-Biscoe *et al.* 1981, Barkhouse and Ridsdill-Smith 1986).

#### *Abiotic factors*

Atmospheric temperature plays a role in the survival and distribution of dung beetles (Gaston and Chown 1999, Nunes *et al.* 2016, Nunes *et al.* 2018, Holley and Andrew 2019a, Holley and Andrew 2019b, Holley and Andrew 2020). Tyndale-Biscoe and Walker (1992) found that optimum temperatures for *O. australis* brood production was between 20°C and 25°C compared to the optimum brood production temperature for *O. granulatus* was found to be 25°C and mortality rate increased when the temperature was above 30°C (Tyndale-Biscoe *et al.* 1981). There is an association between development rate and mortality as ambient temperature increases where *O. granulatus* developed more rapidly at higher temperatures but additionally died more rapidly (Tyndale-Biscoe *et al.* 1981).

Tyndale-Biscoe and Walker (1992) speculated that there was a reduction in survival of larvae during spring and summer due to very few rainfall events making the soil dry at their trial sites.

#### *Biotic factors*

Tyndale-Biscoe *et al.* (1981) identified that good quality dung increased brood production and decreased adult mortality. Good quality dung allows large quantities of body fat to be produced, which in turn allows beetles to survive harsher periods such as short-term droughts. Dung beetle reproduction is significantly influenced by dung pat moisture (Edwards 1991, Errouissi *et al.* 2004, Owen *et al.* 2006) as certain species can only develop in dung pads with a given moisture content, for example *E. intermedius* (Reiche, 1849) was unable to breed in wildebeest dung if the moisture content was less than 60% (Edwards 1991). Dadour and Cook (1996) concluded from their comparison of feedlot cattle dung compared to pasture dung that there was no significant difference in adult beetle mortality and no change in the emergence pattern of the F1 progeny. However, the number of brood masses was significantly increased on pasture fed cattle. They also found that dung from pasture fed cattle improved the survival rates of F1 progeny to adulthood. The progeny emerging from pasture fed cattle were much larger compared to progeny emerging from grain fed cattle dung (Dadour and Cook 1996). This was seen similarly by Lee and Peng (1981) who found that dung quality and nitrogen content had a significant effect on the progeny size while Ridsdill-Smith (1986) demonstrated that egg production of dung beetles was higher on green, annual

and/or irrigated pasture compared with dead annual pasture.

### RESPONSE TO CLIMATE CHANGE

Climate models project increases in temperature, more extreme rainfall and temperature patterns with shifts in seasonality, frequency and intensity (Garnaut 2011, Flato *et al.* 2013, Johnson *et al.* 2016). Walther *et al.* (2002) noted that the phenology, physiology and distribution of plants and animals will be affected by climate change. Evidence indicates plant production hence dung production, will also change (Wu *et al.* 2011, Fuzessy *et al.* 2021). How will dung beetles respond?

Dung beetles can adapt to changes by changing behaviour, distribution, both temporally and spatially, evolve or become extinct. Due to differences in phenotypic plasticity, indigenous species and introduced species may respond to climate change in different ways or to different degrees (Mamantov and Sheldon 2021). Given half the non-indigenous species introduced to Australia have adapted to novel ecosystems, as observed by successful establishment, due to their phenotypic plasticity we believe the provision of ecosystem services will continue. We examine the evidence from the literature to inform if dung beetles could persist despite rapidly changing climate across southern Australian landscapes, which they inhabit.

#### *Response to Temperature*

Direct physiological impacts of small increases in temperature on individual species has demonstrated quicker development, often associated with a fitness cost. Responses vary depending on the origin of species that may often provide a competitive advantage for those species with greater behavioural and phenotypic plasticity (Mamantov and Sheldon 2021).

Artificial warming by 2.3°C in Tibetan Alpine meadows advanced dung beetle egg laying and hatching by 4.1 and 7.2 days respectively (Wu and Sun 2012). In that study, Wu and Sun (2012) demonstrated the size of the larvae and eggs were reduced by 33.4% and 22.1% respectively. It should be noted that the species of dung beetle used for the trial was a cooler climatic dung beetle, *Aphodius erraticus* (L., 1758)), making it more prone to climatic change, concordant with Liu *et al.* (2011), and Bale *et al.* (2002). The advanced egg laying was attributed to cardiac stress caused by increasing temperature (Wu and Sun 2012). To reduce the stress of adult beetles and to maintain critical activities, females may have laid eggs to reduce allocation of energy for reproduction (Somero 2010).

Wu and Sun (2012) implied that early egg laying indicated a reduction in time for the acquirement of resources before reproduction, especially when compared to those in ambient chambers. As the eggs were laid at the interface between the soil and dung, it is possible that this left the eggs more prone to warming, advancing hatching, hence reducing the size of the larvae. Wu and Sun (2012) found that the smaller larvae may be directly linked to the smaller eggs in the warmed enclosures, as small eggs cannot deliver sufficient nutrients in early development stages of the larvae (Geister *et al.* 2009). It is also possible that the higher temperatures reduced the time for embryonic development, which can result in smaller larvae and egg size (Fox and Czesak 2000, Gillooly and Dodson 2000, Wu and Sun 2012). Steigenga and Fischer (2007) found that in butterflies the oocyte growth decreases with higher temperatures, while Fox and Czesak (2000) reported that with higher temperatures there may be an increased cost of somatic maintenance of adult arthropods. Our hypothesis is the reduced time to assimilate resources, due to advanced phenology and behavioural changes in response to warmer conditions led to a reduced egg size and production.

An American study compared response to temperature for two species, with the introduced *O. taurus* producing more brood balls and larger brood balls, buried brood balls deeper than the indigenous *O. hecate* (Panzer, 1794) in all treatments. The two species did not vary in the degree of behavioural plasticity in response to warming. However, different behavioural responses were observed: for example, *O. taurus* decreased brood ball production in response to warming, while *O. hecate* increased the number of brood balls in response to warming, but total numbers were still well below *O. taurus*. Both species survival was lower when brood balls were reared at 33°C. However, because *O. taurus* buried their brood balls deeper less offspring (23%) were exposed to 33°C during development. In contrast, a high proportion of *O. hecate* offspring (77%) were reared at 33°C as brood ball were buried close to the surface hence the lower survival rate for this species. Differences in reproductive behaviours did affect survival, suggesting those species with greater behavioural plasticity, i.e. invasive species, will displace less plastic, i.e. indigenous, species (Mamantov and Sheldon 2021).

In Australia, *E. fulvus* mortality increased, but not *Sisyphus rubrus* Paschalidis, 1974 when temperatures inside mesocosms were increased by 4°C from an average 24h baseline field temperature. An increase of 2°C did not increase mortality for either species, but increased the emigration out of the dung pat by *E.*

*fulvus*. No changes in the egg laying, brood size and number of broods of the two species were identified, which indicates that these species may be capable of surviving increased temperatures without biological trade-offs.

It is expected most introduced dung beetle species will respond positively to small increases in temperature projected for temperate Australia. What is less certain is how indigenous species will respond directly to changes in temperature, with the likelihood more will become extinct from bovine dung due to increased competition from introduced species.

#### *Temporal distribution – changes to phenology*

In response to warmer temperature, it is expected advances in reproductive phenology will occur (Walther *et al.* 2002; Wu and Sun 2012). However where behavioural and / or resource limitations exist these may stabilise selection for earlier breeders within a given population in response to warmer conditions. One hypothesis by Dortel *et al.* (2013) is early emergences in spring could allow the maintenance of local populations in southern France and reduce the decline in species richness. Currently Scarabaeidae are active from spring to summer throughout Europe.

An example of a plastic phenology, well suited to southern Australian environments, is the introduced species, *B. bison*. This species was introduced into Western Australia in 1983 from Europe, where it took about a decade to become widely distributed. This was partly due to natural spread and partly due to field-cropping and release in different locations. Since 1995, starter colonies have been released in all southern states. However, *B. bison* appears still to be absent from significant areas within its potential range.

In southern France, *B. bison* is active from September (March Australia) to the end of May (November Australia). Adult emergence lasted from September to January (March to July Australia); 8 % of the female population was parous and laying eggs in September, and 100% were parous from February to the end of June. Eggs laid in October, November, February and March hatched synchronously in May (November Australia). Adults resulting from eggs laid in March emerged in early September. Kirk (1983) concluded *B. bison* has the potential for recycling large amounts of dung in climatic areas of Australia equivalent to southern France.

Developmental thresholds of 7.2 °C are reported for the eggs of *B. bison*. Total degree days for egg development was 169, but hatching is linked to late

spring. Mortality of *B. bison* eggs was negligible up to 20°C, 50% at 25°C and 100% at 30°C (Kirk 1990).

In Australia this species can have a 1-, 2- or 3-year life cycle. The larvae remain underground through summer and in most regions emerge the following autumn. In colder regions, some larvae enter a form of arrested development (termed diapause) in which third instar larvae fail to transform into adult beetles in the first year but remain largely dormant for a period of time, emerging as adult beetles in the autumn one or two years later (Dung Beetle Ecosystem Engineers 2019).

Has *B. bison* phenology remained the same in their introduced, Australian, environment, or as temperatures have increased, are eggs hatching earlier or adult emergence later in Autumn to facilitated adaptation to changes in climate?

#### *Spatial Distribution*

Physiological requirements and thermal limits for insects, where body temperature is intrinsically linked to the thermal environment, determine the environments in which populations can persist, thus defining the potential geographic distributions of species (Hutchinson 1957, Addo-Bediako *et al.* 2000). Depending on a dung beetles' thermal tolerance, lower elevated species may be directly affected by climate change by reducing individual's survival rates, causing a shift in population range to higher elevations with suitable climates (Deutsch *et al.* 2008, Menéndez *et al.* 2014). If populations are unable to move, due to lack of suitable dung pads and / or competition, extinction of some thermal specialists will occur (Hughes 2000, McCarty 2001, Parmesan 2006). These shifts in range may change the services provided dung beetles (Huey and Tewksbury 2009). However, many insects have broad geographic distributions, raising the question of whether much of the variation among species from different environments reflects intraspecific variation rather than intrinsic differences among species (Hoffmann *et al.* 2013, Slatyer *et al.* 2016). Few tests of the relationship between inter- and intra-specific variation have so far been undertaken (Gaston and Chown 1999), with no research done on how ranges of the indigenous and exotic dung beetles will respond to climate change in Australia. It therefore remains unclear how often apparent species differences reflect plastic or locally adaptive variation among populations, rather than interspecific variation. Recent research on dung beetles' change in elevation and latitude is reviewed to provide insights into likely changes in Australian distributions.

In three research papers, similar results were found for historical data about temperature effects on dung beetle ranges (Dortel *et al.* 2013, Menéndez *et al.* 2014, Sheldon and Tewksbury 2014). To understand how temperature will affect the range of different dung beetles, one should note there are thermal specialists and thermal generalists (Sheldon and Tewksbury 2014). Thermal specialists are associated with narrow temperature variations (Janzen 1967) and are more likely to be displaced by increasing temperature as their fundamental niche becomes restricted. That is, they have a narrow temperature range and have a greater cost associated with dispersal up or down temperature gradients (e.g. elevation) seeking their thermal limits. Whereas thermal generalists are capable of living and reproducing at a greater temperature range.

Sheldon and Tewksbury (2014) found that tropical beetles had a lower tolerance to temperature change while temperate beetles have developed greater capacity for response due to temperature variations experienced while developing (Hoffmann *et al.* 2003). Sheldon and Tewksbury (2014) also suggest caution when predicting physiology using annual seasonality without considering that organisms filter the environment temperature they are exposed to (Kingsolver and Watt 1983) through behavioural means such as flying time, feeding and tunnelling. They conclude by saying that tropical thermal specialists are expected to demonstrate greater thermal sensitivity (Huey *et al.* 2009) and reduced fitness under climate change compared to temperate species (Sheldon and Tewksbury 2014).

Menéndez *et al.* (2014) highlights the point that the sensitivity of species to climate change in mountainous habitats will not only depend on the level of warming but also the geography of the mountain and characteristics of species present in terms of their thermal tolerance. They have shown that, in two mountain ranges in Europe, there has already been considerable movement of species, but not all species have moved up in elevation as there have been other biotic factors limiting species ranges. Nineteen out of the 30 species in the European alps and 17 out of 19 species in the Sierra Nevada had a mean shift upwards. This was consistent with the trend upwards for temperature and other shifts in elevation observed in other taxon (Chen *et al.* 2009, Forero-Medina *et al.* 2011, Feeley 2012). To move to higher elevations in response to increased temperature was species and region dependent. Only those of low- and mid-elevation shifted uphill in the European alps while high-elevation species remained unchanged. In the

In the Sierra Nevada, almost all species range shifted upwards. The regional differences may be explained by a number of factors including lack of significant warming at high elevations in the European alps (Menéndez et al. 2014). Menéndez et al. (2014) also reports that temperature affected the lower range of dung beetles in the Sierra Nevada. Temperature extremes may be more important in determining lower range limits due to the heat tolerance of given species (Menéndez et al. 2014). Despite the ability to change behaviourally, there is still the threat to fitness of beetles as it will reduce the time available for foraging and species niches will begin to overlap causing an increase in competition (Simmons and Ridsdill-Smith 2011, Menéndez et al. 2014).

A review by Dortel et al. (2013) reveals that the movement northwards of Mediterranean species will enrich the northern regions as climate change is likely to reduce the current distribution of many species. One species in particular, *On. belial* (Fabricius, 1978), which was restricted to the Mediterranean seashore in France, has been observed at an altitude of 900m in the Pyrenees, hence its range had moved up in elevation. Dortel et al. (2013) found that specialists had a poorer ability to cope with change compared to generalists, however migrations are severely limited by natural barriers such as largely un-grazed wooded habitats. This could exacerbate the effect of climate change as movement may become limited by such habitat. In southern France, Aphodiidae and Geotrupidae appear to be more sensitive to habitat heterogeneity than Scarabaeidae (Lobo et al. 1997, Lobo and Martín-Piera 1999), which will also see the diversity of niches diminish.

#### *Expected dung beetle community responses*

From the international evidence, it is expected in temperate Australia, changes in the current distributions of dung beetles will be observed. Species such as *O. nigriventris* D'Orbigny, 1902, *O. australis*, *O. chepara* Mathews, 1972 and *O. binodis* will be restricted as these species are found in cool, moist, temperate conditions (Tyndale-Biscoe 1990). These species may become isolated to pockets as they seek their preferred (niche) habitat. Species found in northern Australia such as *Liatongus militaris* (Castelnau, 1840), *On. alexis*, *On. caffer*, *On. pecuarius* Lansberge, 1875, *On. viridulus* Boheman 1857, *O. nigriventris*, *O. obliquus* (Olivier, 1789) and *O. Sagittarius* (Fabricius, 1781) may expand their ranges as tropical areas become wetter and shift further south as temperatures rise. Hence, there may additionally be an influx of species from tropical areas

into temperate areas where those species had previously been excluded due to unfavourable climate.

Some species such as *O. granulatus*, *E. intermedius* and *On. alexis* are likely to move into such niche habitats, restricting other species due to competition.

### CONCLUSION

Dung beetles maybe under threat from changes to climate and management, despite many species being introduced from sub-tropical regions, hence possess a level of tolerance to warmer conditions. We believe dung beetles will continue to provide valuable ecosystem services and have potential to aid in adapting and alleviating the impacts on crops and pastures from reduced and sporadic rainfall. However, the level of function, may be impeded by increased beetle mortality directly due to climatic stress and a loss of diversity. Thermal specialists and some indigenous species, are expected to be displaced into narrower ranges seeking available habitats due to increased feeding competition from thermal generalists and introduced species. The evidence from naturalised introduced species indicate behavioural adaptations and/or phenotypic plasticity suggest some species will continue to provide services that improve pasture production despite changes to climate. Research is needed on historical introductions, e.g. *O. taurus* and *B. bison*, to monitor shifts in species distribution and phenology in order to tease apart adaptive processes. Manipulative experiments to understand the interactions between genetics, environment and management are informative for sustainable land management. These types of experiments are needed to avoid disruptive practices; that is drenching or intensive feedlots when populations are actively breeding, and to ensure the continued benefits of dung beetles.

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