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Pasture diet of cattle contributes to the reproductive success of dung beetles

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Abstract

1. Cattle diet plays a crucial role in the quality of dung and the consequent reproductive capacity of dung beetles. We investigated how three pasture types (improved native, forage oat and inter-sown rye/clover) influence the dung quality, the number of broods and reproductive output measured as brood size (dry weight and ellipsoid volume), development time and F_1 progeny size (beetle length and pronotum width) of *Onthophagus binodis*, *Euoniticellus africanus* and *Euoniticellus intermedius*.
2. Nitrogen content was highest in rye/clover-derived dung compared with improved native and forage oat. Improved native-derived dung had the highest carbon, energy, organic matter, pH and insoluble non-starch polysaccharide content, whereas forage oat had the lowest contents. Forage oat had the highest moisture content, ash and soluble non-starch polysaccharide content compared with the other pastures.
3. Progeny length was influenced by pasture type, with female *E. intermedius*, and males and females of *O. binodis* being 11.4%, 11.2% and 7.3% longer, respectively, in rye/clover-derived dung than forage oat dung. The pronotum width of *O. binodis* F_1 progeny was 9.8% wider when produced from rye/clover dung than forage oat.
4. Rye/clover- and improved native-derived dung provided the best resource for dung beetle reproduction compared with forage oat dung. Based on this study, cattle diet is important for consideration when evaluating reproductive ability and progeny measurements. Cattle diet should be further investigated as only three pasture types were investigated out of a numerous number of species and combinations.

KEYWORDS
Coleoptera, dung beetles, forage oat, improved native, pasture type, reproduction, rye/clover, Scarabaeidae

INTRODUCTION

Dung beetles (Coleoptera: Scarabaeidae) are important ecosystem engineers, which rely upon an ephemeral resource (deCastro-Arrazola et al., 2023; Hanski & Cambefort, 2014; Nichols et al., 2008). Dung beetles feed upon the small particles within dung, which are primarily microbial biomass and small particles of organic matter (Holter, 2016).

Dung beetle larvae feed unselectively on the dung provided by adult dung beetles in brood balls (Holter, 2016). Herbivore dung varies physically and chemically depending on herbivore species, herbivore diet and seasonal conditions (Edwards, 1991; Gittings & Giller, 1998; Greenham, 1972; Hughes & Walker, 1970; Kaur et al., 2021; Kunz, 1980; Macqueen et al., 1986; Matthiessen & Hayles, 1983). Dung varies in its physical and chemical composition, including moisture content, C:N ratio, pH and organic matter content (Gittings & Giller, 1998). Specifically, in agricultural systems, cattle dung is a mixture of undigested plant material, intestinal secretions and microbes, such as bacteria and fungi (Holter & Scholtz, 2007), and the composition of cattle dung is influenced by the nature of the consumed material (Treece, 1966).

Abiotic factors influence the quality of fodder upon which domesticated herbivorous species rely (Edwards, 1991), with temperature and rainfall being key regulators of the moisture and chemical parameters within dung (Edwards, 1991; Kaur et al., 2021). Rainfall influences the moisture content of the dung of many species of herbivores with 5%–10% increase in dung moisture observed 2 weeks post rainfall (Edwards, 1991). Many dung studies have either focused on single parameters such as moisture content (Edwards, 1991), mineral content (Kaur et al., 2021) or pH (Dadour & Cook, 1996), with a few studies assessing multiple variables of dung quality among herbivores, carnivores and omnivores (Barth et al., 1994; Frank et al., 2017; Gittings & Giller, 1998; Kerley et al., 2018) with no definitive answer as to what constitutes a good quality dung resource for coprophagous insects.

The nutritional content of dung and how it influences coprophagous insect reproduction are poorly understood. However, the nitrogen content of dung is strongly influenced by the nitrogen content of the original feed (Dijkstra et al., 2013). Grain-fed, rather than pasture-grazed, animals produce dung with higher nitrogen, phosphorus and water-soluble NH_4^+ in proportion to the ratio of supplementary material within diet (Hao et al., 2009). The provision of grain to livestock can further influence the chemical properties of dung, including the pH and moisture content (Dadour & Cook, 1996; Hao et al., 2009; Meyer et al., 1978).

To enhance the grazing capacity of Australian landscapes, there have been multiple grass, legume and brassica species introduced as forage crops for livestock (Johnston et al., 1999; Lodge, 1996; Lodge et al., 2003; Mitchell et al., 2015; Whalley, 1970; Whalley et al., 2005). The pasture species and the associated land management influence the quality of livestock dung (Schick et al., 2019). In a comparison of brome grass inter-sown with legumes and brome grass with N-fertiliser and non-fertilised treatments, the inter-sown treatments resulted in less dietary fibre concentrations and higher nitrogen concentrations in livestock dung (Schick et al., 2019). In feedlots, diets with 40% and 60% dried distillers' grains achieved higher nitrogen, phosphorus and ammonium content than the control dung, in which all grain was steam-rolled barley (Hao et al., 2009). The pH of cattle dung also decreased with increasing proportions of dried distillers' grains (Hao et al., 2009). How dung chemically and physically varies from dung produced from different pasture species is poorly understood, with limited knowledge on the response from coprophagous insects.

The Australian native dung beetle fauna do not efficiently break down domesticated cattle dung (Bornemissza, 1976; Hughes, 1975; Tyndale-Biscoe, 1994); as a result, 43 species of dung beetle were released into Australia, between 1964 and 1986 (Edwards, 2007; Pokhrel et al., 2021; Tyndale-Biscoe, 1990, 1996). Dung beetles reproduce by laying an egg, which develops as a larva feeding upon the resources provisioned to it in a brood ball before pupating into an adult beetle (Bornemissza, 1969; Doube, 1990; Lumaret et al., 1992). How different species of dung beetle handle the egg and brood ball determines classification into a functional guild (Bornemissza, 1969; Doube, 1990; Heddle et al., 2021; Lumaret et al., 1992). The four guilds are the rollers (telecoprids), the tunnellers (paracoprids), the dwellers (endocoprids) and the stealers (kleptocoprids) (Bornemissza, 1969; Doube, 1990; Heddle et al., 2021; Lumaret et al., 1992). Australia's key agricultural dung beetle fauna include the paracoprid genera *Onthophagus*, *Euoniticellus* and *Onitis*, the telecoprid genera *Sisyphus* and the endocoprid genera *Aphodius* and *Labarrus* (Edwards, 2007; Tyndale-Biscoe, 1990, 1996).

Seasonal fluctuations in the nutrient quality and moisture content of dung influence dung beetle reproduction (Kaur, 2019; Kaur et al., 2021; Ridsdill-Smith et al., 1986), and dung pad moisture strongly impacts the reproduction of the dung beetle *Euoniticellus intermedius* (Reiche, 1849) (Edwards, 1991). Cattle diet changes the pH and nutrient availability within dung produced, which can lead to *Onthophagus binodis* Thunberg, 1818 females requiring additional nitrogen for egg maturation (Cambefort, 1984, 1991; Dadour & Cook, 1996; Madzivhe et al., 2021). The nutritional content and physical parameters of dung—that is, moisture content, pH, mineral content, energy content, and C:N ratio—affect the size of dung beetles, which, in turn, influences their capacity to compete within and between the species for resources (Dadour & Cook, 1996; Macqueen et al., 1986; Shymanovich et al., 2020). Seasonality of pastures and subsequent dung composition affect dung beetle reproduction (Edwards, 1991; Greenham, 1972; Hughes & Walker, 1970; Kaur et al., 2021; Kunz, 1980; Macqueen et al., 1986; Matthiessen & Hayles, 1983), and there is currently only a single study into the influence of pasture species on the dung quality and the subsequent influence on dung beetle reproduction (Ridsdill-Smith, 1986). Ridsdill-Smith (1986) found that the reproductive output of *Onitis alexis* (Klug, 1835) ehxhibited relatively little seasonal variation between the annual and perennial pastures compared to *O. binodis*, which had higher reproduction on green annual and irrigated perennial pastures in spring than dead annual pasture (Ridsdill-Smith, 1986). In these studies, the annual and perennial pasture species composition was not documented, limiting extrapolation of managing pastures on the overall dung beetle communities.

Little is known about the influence of cattle dung derived from common pasture types, such as forage oat, mixed rye/clover pastures and improved native pastures, on the fecundity and reproduction of temperate-introduced dung beetles. In this study, we assess the influence of pasture type on dung quality—moisture content, pH, energy content, insoluble and soluble non-starch polysaccharides, starch, organic matter, carbon, nitrogen and C/N ratio—to provide a resource for optimal dung beetle reproduction. Specifically, we investigated how the different pasture types influence the dung quality, number of broods and reproductive output measured as brood size, development time and progeny size. We hypothesise that a diverse pasture (improved native) will foster greater fecundity for all dung beetle species than mono- (forage oat) or bi-culture (ryegrass/clover) pasture due to the high number of pasture species providing a range of nutrients, moisture content and pH in the subsequent dung.

METHODS

Dung collection

Fresh cattle dung (<12 h old) derived from three pasture types—improved native pasture (IMP), forage oat (Oat) and ryegrass/clover pasture (RC)—was collected directly from the paddock from three cattle farms on the New England Tablelands, NSW, Australia (Table 1, Appendix Table 1). These pastures are commonly used for improving growth rates of cattle across southern Australia. The improved native pasture was improved through the intersowing of many pasture species into a native pasture base. These inter-sown species include phalaris, cocksfoot, kikuya, Italian ryegrass, clover and medics, whereas no fertiliser was applied. Cattle were actively grazing within paddocks of a selected pasture type and were not provided with additional feed types such as hay or grain. Dung from each pasture type was collected from large paddocks, which varied for soil type, moisture content and landscape topography, with collection focusing on overnight cattle camps where dung pads were at the highest density. Dung pads with signs of current dung beetle activity were excluded to prevent contamination from dung beetles. If cattle parasiticide treatments occurred on site, dung was not collected for at least 2 months post-drenching (Kryger et al., 2006; Martínez et al., 2018; Sands et al., 2018; Vale et al., 2015; Wardhaugh, 2005). The timing of dung collection was scheduled to coincide with mid-stem elongation and booting of grass species (Z31-49) (Table 1) (Zadoks et al., 1974), which is when the plants have a balance between nutritient content and that of digestibility (Albon & Langvatn, 1992; Demment & van Soest, 1985; Fryxell, 1991; Hansen et al., 2009; Mårell et al., 2006). A total of 150 kg of each dung-derived pasture type was collected, homogenised using a motorised paint stirrer and stored at −10°C in 3 kg bags. When required, bags were defrosted 24 h prior to use and homogenised.

Dung nutritional content

For each dung type, five individual fresh dung pads were collected and returned to the laboratory for quality analysis. pH was measured directly using a pH electrode (HANNA, pHep4: HI98127), and the mass of wet dung was recorded. Samples were oven-dried for 7 days at 60°C and then weighed for dry mass. Dried samples were ground (0.5 mm) for further analysis using a food processor.

To determine the organic matter content of dung, four replicates of each dung-derived pasture type were analysed for loss on ignition. Samples of ground dung were weighed to approximately 10.0 g, the weight recorded and placed into a ceramic crucible with a ceramic lid. After drying samples at 105°C overnight, the samples were placed into a furnace at 500°C for 8 h. Ash weight provided the loss on ignition, leaving minerals behind and providing the organic content of samples (Davies, 1974).

To determine the energy content of dung samples, 1 g of ground sample was pressed into a pellet, which was subsequently weighed to 1 mg. The pellet was placed into a bomb calorimeter (Parr 6400 Bomb Calorimeter) and ignited. Energy released (MJ/kg) was recorded twice for the five-dung pad replicates for each dung-derived pasture type.

The ground dung was additionally analysed for carbon and nitrogen content with an LECO carbon analyser, which was coupled to an infrared CO_2 detector for nitrogen. A TruSpec Series Carbon and Nitrogen Analyser (LECO Corporation, United States) was used for the analysis, using standard procedures (Sample Preparation for the LECO TruMac, UNE). Dried manure samples of 0.5 mm-diameter-sized fractions were weighed to 0.10–0.11 g into individual porcelain boats for analysis. The amount of carbon (%) was divided by the nitrogen (%) content to provide C:N ratio. Soluble and insoluble non-starch polysaccharides of the ground samples were measured as described by Englyst and Hudson (1993) and Theander and Westerlund (1993).

Dung beetle cultures

Euoniticellus africanus (Harold, 1873), *E. intermedius* and *O. binodis* were collected from Premer and Armidale, NSW, where these species are commonly found in cattle dung (Heddle et al., 2023). In the laboratory, beetles were sorted, counted and stored by species and sex in separate shallow culture boxes (5L, 31L × 22W × 18H cm). This was to stop the reproduction of field-captured beetles before use in the experiment. Cultures were maintained in a glass house at 25 ± 2°C (day) and 20 ± 2°C (night) (16L:8D) for at least a week prior to the experiments (Iwasa et al., 2008; Schwab et al., 2016) and were fed dung derived from a control plantain pasture. Beetles were utilised from the field as previous work has indicated age did not influence the reproductive output of *O. binodis* (Ridsdill-Smith et al., 1982).

Experimental design

Experiments were set up in 3L plastic cylindrical containers three quarters filled with a 50:50 sand/vermiculite mixture, which was moistened to 10% (±2%) (ICT International Moisture probe MPM-160-B). Experiments were run for 3 weeks in a temperature-controlled glasshouse (day 25 ± 2°C, night 20 ± 2°C, 16L:8D). The experiment

TABLE 1 Site information for dung collection.

Town	Pasture type	Collection date	Last drench date	Latitude	Longitude
Armidale	Oat	2/11/2020	Feb-2020	−30.44	151.53
Armidale	Rye/clover	27/10/2020	Feb-2020	−30.46	151.56
Ebor	Improved	18/1/2021	Nov-2020	−30.32	152.39

was set up as a randomised complete block design using Agricolae (de Mendiburu & de Mendiburu, 2019), with two treatments, beetle species (three levels) and dung type (three levels), with a total of 10 replicates for each combination. One pair (one male and one female) of beetles were added to each replicate and left for 7 days to maximise the number of broods produced per female (Ridsdill-Smith et al., 1982). Beetles were not standardised for size, but rather randomly allocated to each treatment, and size was distributed across treatments (Appendix Table 2). Based on preliminary experiments, *E. intermedius* was fed 150 g of dung twice a week (300 g/week), whereas *E. africanus* and *O. binodis* were fed 200 g twice weekly as these species showed the capability to bury the entire 150 g dung pad in 4 days. Old dung was removed, checked for live beetles and replaced with the same dung type. This was done to ensure that brood production was not limited by the availability of fresh dung. At the end of each 7-day period, each container was emptied and sifted to remove beetles and whole broods. Incomplete broods were excluded from brood calculations. Live beetles were placed into fresh containers of the same treatment as they had previously occupied. In the event that males died, the death was noted, and a new male was added to the replicate and the replicate continued. When a female beetle died, this replicate was reset to week zero and run for a further 3 weeks.

To determine if the pasture types had an influence on reproduction and progeny size, broods from the same container were split into two groups. The first group was used for destructive measurements, whereas the second was used for progeny development. The first group was cleaned of sand and vermiculite; the fresh weight of broods was taken using a 120 g scale. Using callipers (precise to 0.01 mm), two equatorial and one polar diameters were recorded and then halved to get the radius. Then, using the equation 4/3.π.a.b.c (a = first equatorial radius; b = second polar radius; c = first polar radius), we determined the ellipsoid volume of the brood (Kishi, 2014).

The second group was used for progeny development by placing the broods into individual containers filled with moistened vermiculite. Containers were placed in a thermocline at 23°C (TRH-300-SD), and water was applied as required to maintain moisture contents. After 30 days, containers were checked on a daily basis for emerging beetles. The date of emergence for individual beetles was recorded, and the average start date was determined by taking the initial start date and the changeover (7 days) date to provide the 'average' start date. The number of days between the emergence date and the average start date was used as the average days to emerge. Finally, progeny was measured for pronotum width and pronotum and elytra length to determine the influence of pasture types on the progeny beetle size.

Statistical analysis

All statistical analyses were implemented in R studio 3.4.3 (R Core Team, 2022). For dung quality parameters, analysis of variance (St & Wold, 1989) was conducted to examine differences across dung types for soluble non-starch polysaccharide (SNSP), organic matter (OM), energy, moisture content and pH. Post hoc Tukey tests of multiple comparisons were carried out (Abdi & Williams, 2010). Due to non-normality, Kruskal–Wallis tests (Kruskal & Wallis, 1952) were conducted to examine differences in insoluble non-starch polysaccharides (INSP), starch and C/N ratio. Post hoc Dunn tests (Dunn, 1964) of multiple comparisons were carried out with p-values adjusted by the Holm method (Aickin & Gensler, 1996).

Generalized linear mixed-effect models were fitted with a Gaussian family and were fitted with the functions 'glmmTMB' from the package glmmTMB (Magnusson et al., 2017). For generalized linear mixed models, we checked for under- and overdispersions with the functions 'simulateResiduals' and 'testResiduals' from the DHARMa package (Hartig & Hartig, 2017). An analysis of deviance table was run using a type 3 chi-square test. Models were adjusted using Bonferroni in the function 'emmeans' from the package emmeans (Lenth et al., 2019). Model predicted values were determined using 'emmeans,' with final values showing 95% confidence intervals and letters used to notify where significant differences were observed. All models used the Gaussian family, with brood production not requiring a log link. Dry weight, ellipsoid volume and pronotum width used a log-link and F1 progeny development and length used an identity link.

To determine the influence of dung quality parameters on beetle progeny, we used correlation and direction to determine the strength of correlation. As F1 progeny length and pronotum width were strongly correlated ($r^2 = 0.736$), we used progeny length as the main measurement for dung quality parameter analysis. We analysed correlation between beetle length and individual dung parameters by measuring Spearman's rho (Puth et al., 2015). Results are written in the language of evidence (Muff et al., 2022).

RESULTS

Dung quality

Very strong evidence was found for differences among the dung sources for organic matter content ($F_{2,9} = 89.5$, $p < 0.0001$), energy content ($F_{2,26} = 99.9$, $p < 0.0001$), pH ($F_{2,12} = 55.8$, $p < 0.0001$), nitrogen content ($F_{2,12} = 14.6$, $p = 0.0006$) and carbon content ($F_{2,12} = 59.7$, $p < 0.0001$, Table 2, Appendix Figure 1). Strong evidence was found for an effect of dung source on the C:N ratio ($\chi^2(2) = 10.8$, $p = 0.0045$). Moderate evidence was found for differences between the dung sources for soluble non-starch polysaccharide ($F_{2,6} = 6.1$, $p = 0.036$) and insoluble non-starch polysaccharides ($\chi^2(2) = 6.5$, $p = 0.039$). Weak evidence was found for differences between the dung sources for starch content ($\chi^2(2) = 5.4$, $p = 0.066$). No evidence was found for differences between the dung sources for dung moisture content ($F_{2,18} = 1.4$, $p = 0.26$).

Brood production

In total, 2242 broods were produced across all dung beetle species and pasture types (Table 3). Brood production of *O. binodis* was

TABLE 2 Nutritional content of the three pasture types used in the experiments.

	Improved	Forage oat	Rye/clover	*p*-value
SNSP (g/kg)	5.71 ± 0.64[a]	8.48 ± 0.44[b]	6.98 ± 0.58[ab]	**0.036**
INSP (g/kg)	103.33 ± 0.39[a]	101.37 ± 0.75[ab]	77.27 ± 0.85[b]	**0.039**
Starch (%)	0.38 ± 0.007[a]	0.38 ± 0.013[a]	1.01 ± 0.03[a]	0.066
Organic matter (proportion)	0.71 ± 0.0061[a]	0.63 ± 0.0015[b]	0.66 ± 0.0041[c]	**<0.0001**
Energy (MJ/kg)	18.36 ± 0.13[a]	15.36 ± 0.22[c]	16.9 ± 0.054[b]	**<0.0001**
Moisture (%)	85.97 ± 0.53	88.03 ± 0.86	87.18 ± 1.10	0.26
pH	7.36 ± 0.06[a]	6.66 ± 0.04[c]	6.98 ± 0.037[b]	**<0.0001**
C/N ratio	16.14 ± 0.33[a]	13.93 ± 0.12[ab]	13.46 ± 0.21[b]	**0.0045**
Carbon (%)	43.2 ± 0.21[a]	36.18 ± 0.71[c]	40.22 ± 0.28[b]	**<0.0001**
Nitrogen (%)	2.68 ± 0.058[b]	2.6 ± 0.058[b]	2.99 ± 0.049[a]	**0.00061**

Note: Mean and standard error are provided for all variables. SNSP—Soluble non-starch polysaccharide, INSP—Insoluble non-starch polysaccharide. Units where 'g/kg' is given refer to grams of variable per kg of dried sample, similarly with MH/kg. Superscript letters indicate significant differences.

TABLE 3 Broods produced and broods used for destructive sampling to take measurements of brood ball dry weight and ellipsoid volume, and for progeny measurements by the dung beetle species on each pasture type.

		Euoniticellus africanus	*Euoniticellus intermedius*	*Onthophagus binodis*
Total production	Improved native	228	270	336
	Rye/clover	138	283	298
	Forage oat	173	282	234
	Total	**539**	**835**	**868**
Brood ball measurements	Improved native	97	115	152
	Rye/clover	55	116	111
	Forage oat	69	120	88
	Total	**221**	**351**	**351**
Progeny development and measurements	Improved native	95	151	148
	Rye/clover	52	122	137
	Forage oat	68	114	96
	Total	**215**	**381**	**381**

Note: Total broods used is provided in bold.

highest in improved native-derived dung but lowest in forage oat-derived dung. Highest brood production for *E. africanus* was found in improved native dung, whereas the lowest brood production was from rye/clover-derived dung. Highest brood production for *E. intermedius* was found in rye/clover- and forage oat-derived dung compared with improved native-derived dung.

We found very strong evidence indicating reduced dung beetle reproduction over time (weeks) ($\chi^2_1 = 22.8, p < 0.0001$). More broods were produced in week 1 than week 2 ($p = 0.003$), and very strong evidence for more broods is produced in week 1 than week 3 ($p = 0.0002$). There was moderate evidence for differences in broods produced between the dung beetle species ($\chi^2_1 = 6.1, p = 0.048$) (Figure 1). There was no evidence for differences between the pasture types for brood production ($\chi^2_1 = 3.8, p = 0.15$), and no evidence was found to indicate interactions between any parameters. Weak evidence was found to indicate that fewer broods overall were produced by *E. africanus* compared with *E. intermedius* ($p = 0.098$) and *O. binodis* ($p = 0.05$). No evidence was found to indicate differences between *E. intermedius* and *O. binodis* ($p = 0.97$).

Dry weight of broods

In total, 923 broods were measured from all dung beetle species and pasture types (Table 3). Mean brood dry weight varied between species with *E. africanus* ranging from 1.4 to 1.6 g, *E. intermedius* ranging from 0.7 to 0.9 g and *O. binodis* ranging from 2.5 to 2.9 g. Very strong evidence was found for differences between dung beetle species for the dry weight of broods ($\chi^2_1 = 403.3, p < 0.0001$) (Figure 2a). Weak evidence was found for differences in dry weight between the pasture types ($\chi^2_1 = 4.9, p = 0.086$). There was no evidence for any interaction between dung beetle species and pasture type ($\chi^4_1 = 2.01, p = 0.73$). No evidence was found to indicate differences within *E. africanus* between native- and oat-derived dung ($p = 0.98$), native- and

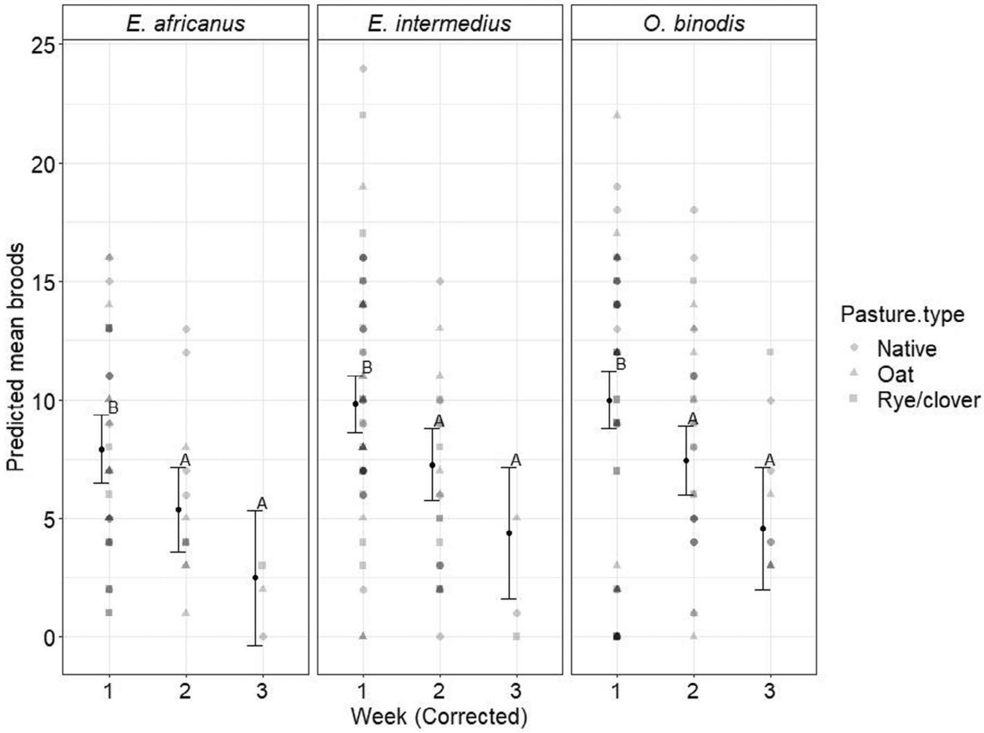

FIGURE 1 Brood production by *Euoniticellus africanus*, *Euoniticellus intermedius* and *Onthophagus binodis* across 3 weeks and three different pasture types. Dots represent raw data with 95% confidence intervals with circles being native improved dung, triangles being forage oat dung and squares being rye/clover dung. Dots represent raw data with predicted mean and 95% confidence intervals to the left of raw data. Significant differences were indicated by different letters, where the same letters indicate similarities.

rye/clover-derived dung ($p = 0.4$) or between oat and rye/clover ($p = 0.99$). No evidence was found for differences within *E. intermedius* between native- and rye/clover-derived dung ($p = 0.99$), native and forage oat ($p = 1$) or between oat and rye/clover ($p = 1.0$). For *O. binodis*, there was no evidence for differences between dung-derived pastures of native and oat ($p = 1.0$), native and rye/clover-derived dung ($p = 0.67$) or between oat and rye/clover ($p = 0.74$).

Ellipsoid volume of broods

Very strong evidence was found for differences between dung beetle species ($\chi^2_1 = 1102.2, p < 0.0001$) and pasture type ($\chi^2_1 = 11.3, p = 0.004$) (Figure 2b). There was moderate evidence within *E. africanus* for larger broods being produced in native dung compared with forage oat ($p = 0.02$), whereas no evidence was found for differences between native- and rye/clover-derived dung ($p = 0.13$). For *E. africanus*, there was no evidence found to indicate the differences between forage oat and rye clover dung ($p = 0.97$). There was moderate evidence for *E. intermedius* that larger broods were produced in native dung than forage oat ($p = 0.02$), whereas no evidence was observed between native- and rye/clover-derived dung ($p = 0.13$). No evidence was found between oat and rye clover dung ($p = 0.9686$). There was moderate evidence found for *O. binodis* producing larger broods in native dung compared with forage oat ($p = 0.02$), whereas no evidence was found for differences between native dung and rye/clover dung ($p = 0.13$). Furthermore, no evidence was found between oat and rye clover dung ($p = 0.97$).

F_1 progeny development (days)

In total, 983 beetles of all species emerged from 1319 brood balls from all species and pasture types (Table 3). Mean development days ranged from 42 days under forage oat dung in *E. intermedius* to 49 days in *O. binodis* from forage oat. There was no evidence for differences between dung beetle species for development days ($\chi^2_1 = 1.5, p = 0.48$) nor was there evidence for differences between pasture types ($\chi^2_1 = 4.1, p = 0.13$) or the interaction between the two ($\chi^4_1 = 6.2, p = 0.19$).

Beetle length

For F_1 progeny beetle length, there was very strong evidence for differences among beetle species ($\chi^2_1 = 121.7, p < 0.0001$), pasture type ($\chi^2_1 = 13.4, p = 0.001$), sex ($\chi^1_1 = 151.2, p < 0.0001$) and moderate evidence for a three-way interaction among dung beetle species, pasture type and sex ($\chi^4_1 = 44.6, p = 0.02$) (Figure 3). Post hoc testing of *E. africanus* females revealed no evidence for differences in length

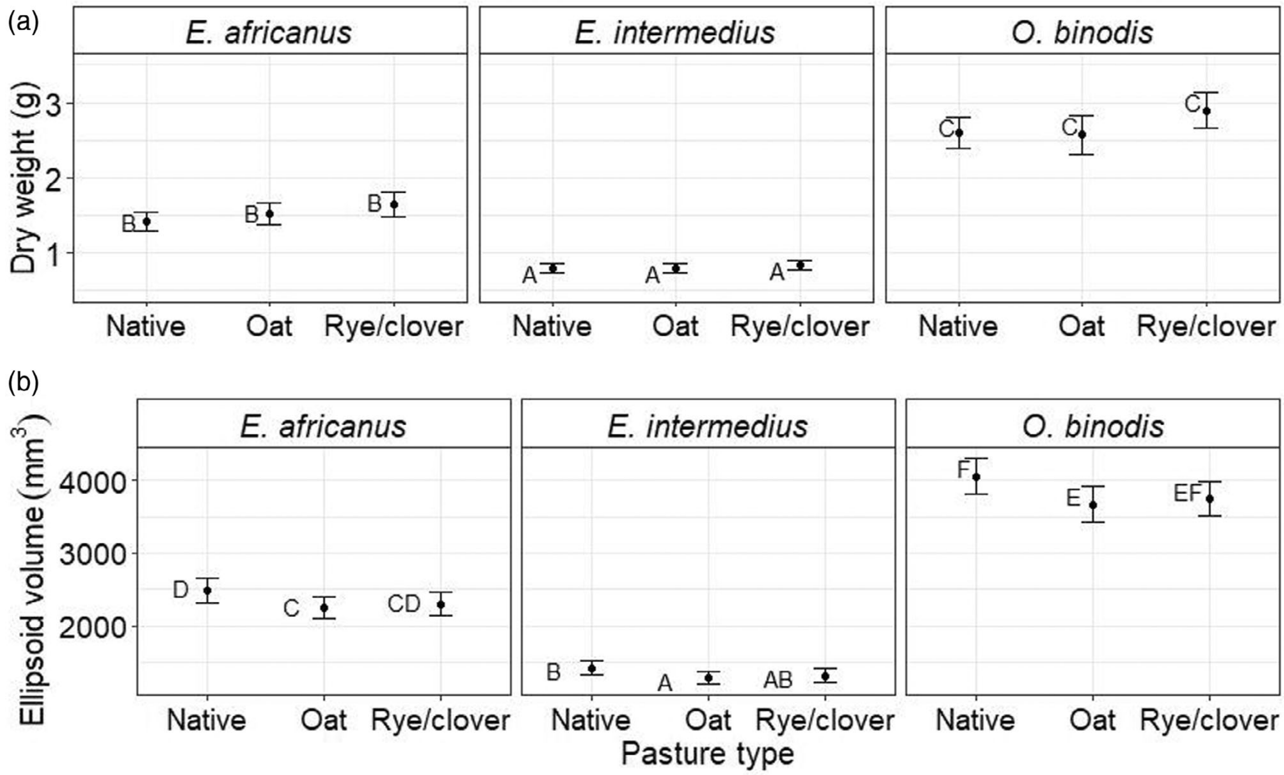

FIGURE 2 Influence of pasture-derived dung on (a) dry weight and (b) ellipsoid volume of broods for *Euoniticellus africanus*, *Euoniticellus intermedius* and *Onthophagus binodis*, male and females. Predicted mean and 95% confidence intervals with significant differences were indicated by different letters, where the same letters indicate similarities.

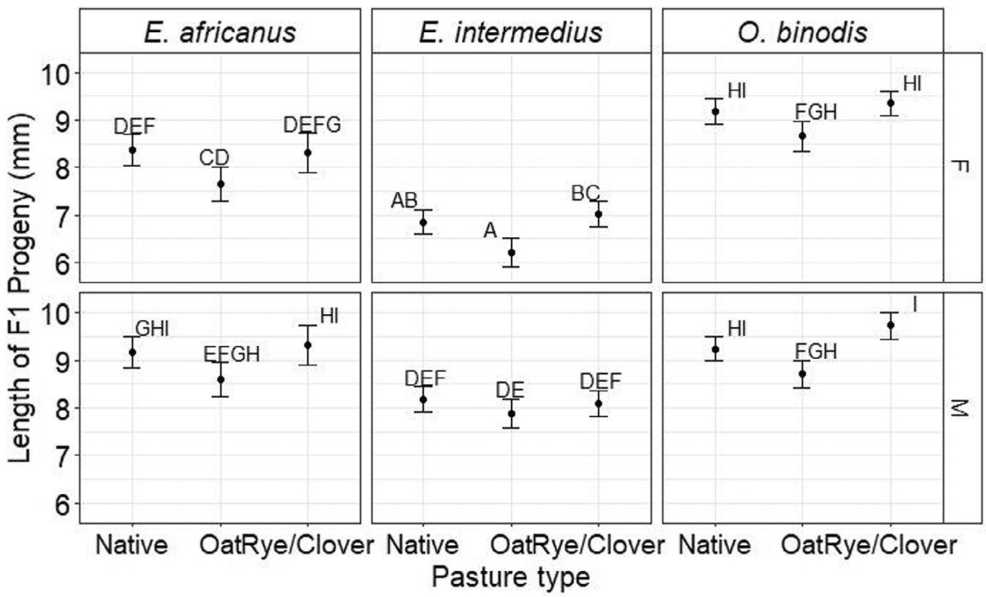

FIGURE 3 Influence of pasture-derived dung on the length of the F_1 progeny (mm) for *Euoniticellus africanus*, *Euoniticellus intermedius* and *Onthophagus binodis*, male and females. Predicted mean and 95% confidence intervals with significant differences were indicated by different letters, where the same letters indicate similarities.

between improved native and forage oat ($p = 0.26$), improved native- and rye/clover-derived dung ($p = 1.0$) or between forage oat- and rye/clover-derived dung ($p = 0.6$). For males of *E. africanus*, there was no evidence for differences in length between improved native and forage oat ($p = 0.67$), improved native- and rye/clover-derived dung ($p = 1.0$) or between forage oat- and rye/clover-derived dung ($p = 0.47$).

For *E. intermedius* females, post hoc testing revealed weak evidence for differences between improved native- and forage oat-derived dung ($p = 0.06$), no evidence between improved native- and rye/clover-derived dung ($p = 1.0$) and strong evidence for differences between forage oat- and rye/clover-derived dung ($p = 0.002$). Female *E. intermedius* reared from rye/clover dung were 11.7% longer than those reared from forage oat dung. The females reared from improved native dung were 6.0% longer than those reared from forage oat. For the males of *E. intermedius*, no evidence for differences was found between improved native- and forage oat- ($p = 0.99$), improved native- and rye/clover- ($p = 1.0$) and between forage oat- and rye/clover-derived dung ($p = 1.0$).

For *O. binodis* females, post hoc testing revealed no evidence for differences between improved native- and forage oat-derived dung ($p = 0.55$), improved native- and rye/clover-derived dung ($p = 1.0$) but weak evidence for differences between forage oat- and rye/clover-derived dung ($p = 0.07$). Female *O. binodis* reared from rye/clover dung were 7.4% longer than those reared from forage oat dung. For the males of *O. binodis*, no evidence for differences was found between improved native and forage oat ($p = 0.7$), and improved native and rye/clover ($p = 0.49$). Very strong evidence was found for differences between forage oat- and rye/clover-derived dung ($p = 0.0001$). Male *O. binodis* reared from rye/clover dung were 10.5% longer than those reared from forage oat dung.

Beetle width

For pronotum width, moderate evidence was found for a three-way interaction between dung beetle species, pasture type and sex ($\chi^4_1 = 11.4, p = 0.02$) (Figure 4). Post hoc testing of *E. africanus* females revealed no evidence for differences in length between improved native- and forage oat-derived dung ($p = 0.21$), improved native- and rye/clover-derived dung ($p = 1.0$) or between forage oat- and rye/clover-derived dung ($p = 0.67$). For males of *E. africanus*, there was no evidence for differences in width between improved native- and forage oat-derived ($p = 0.57$), improved native- and rye/clover-derived ($p = 1.0$) or between forage oat- and rye/clover-derived dung ($p = 0.67$).

For *E. intermedius* females, post hoc testing revealed weak evidence for differences between improved native- and forage oat-derived dung ($p = 1.0$), and no evidence between improved native- and rye/clover-derived dung ($p = 0.95$) and between forage oat- and rye/clover-derived dung ($p = 0.99$). For the males of *E. intermedius*, no evidence for differences was found between improved native- and forage oat- ($p = 1.0$), improved native- and rye/clover- ($p = 0.81$) and between forage oat- and rye/clover-derived dung ($p = 0.5$).

For *O. binodis* females, post hoc testing revealed no evidence for differences between improved native- and forage oat-derived dung ($p = 0.77$) and between improved native- and rye/clover-derived dung ($p = 0.94$). There was moderate evidence for differences between forage oat- and rye/clover-derived dung ($p = 0.02$). Female *O. binodis* reared from rye/clover dung were 8.0% wider than those reared from forage oat dung. For the males of *O. binodis*, no evidence for differences was found between improved native and forage oat ($p = 0.22$), and improved native and rye/clover ($p = 0.32$). Very strong evidence was found for differences between forage oat- and rye/clover-derived dung ($p < 0.0001$). Male *O. binodis* reared from rye/clover dung were 11.1% wider than those reared from forage oat dung.

Dung quality interaction with F_1 progeny

All species F_1 progeny length had a negative correlation with SNSP and moisture content, whereas positive correlations were identified

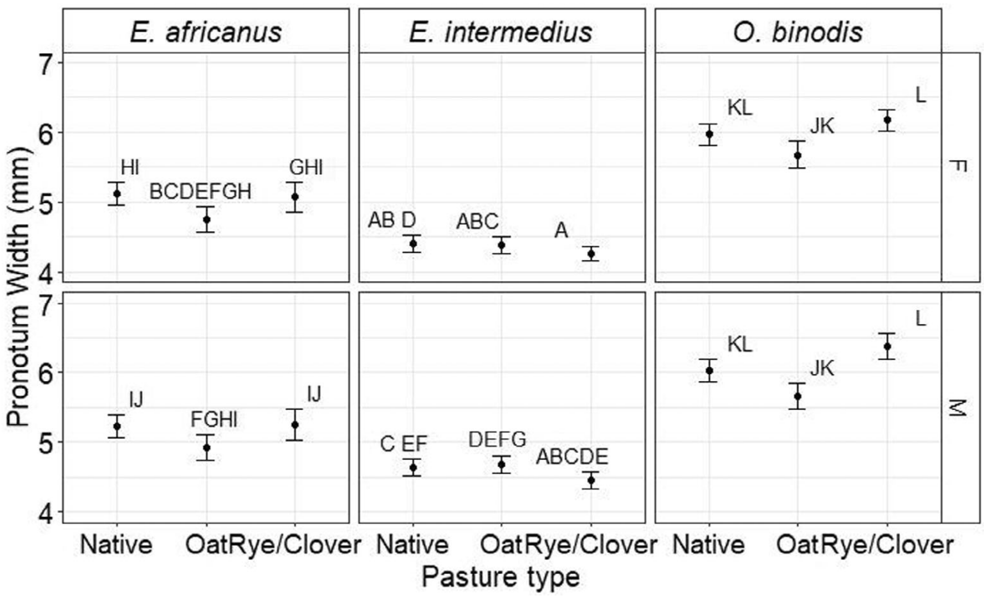

FIGURE 4 Influence of pasture-derived dung on the pronotum width of the F_1 progeny (mm) for *Euoniticellus africanus*, *Euoniticellus intermedius* and *Onthophagus binodis*, male and females. Predicted mean and 95% confidence intervals with significant differences were indicated by different letters, where the same letters indicate similarities.

TABLE 4 Spearman's rho values for the correlation between dung parameters and F_1 progeny beetle length.

Dung quality parameters	Overall	*E. africanus*	*E. intermedius*	*O. binodis*
SNSP	**−0.16**	**−0.22**	**−0.18**	**−0.18**
INSP	−0.02	−0.052	0.015	**−0.12**
Starch	**0.13**	0.11	**0.1**	**0.26**
Organic matter	**0.16**	**0.22**	**0.18**	**0.18**
Moisture content (%)	**−0.16**	**−0.22**	**−0.18**	**−0.18**
Energy content	**0.16**	**0.22**	**0.18**	**0.18**
pH	**0.16**	**0.22**	**0.18**	**0.18**
Carbon content	**0.16**	**0.22**	**0.18**	**0.18**
Nitrogen content	**0.21**	**0.23**	**0.19**	**0.34**
C:N ratio	−0.02	0.052	0.015	**−0.12**

Note: Positive values indicate a positive correlation, whereas negative values indicate a negative correlation. Bold values indicate significant correlations based on p-values provided by Spearman's correlation test. SNSP—Soluble non-starch polysaccharide, INSP—Insoluble non-starch polysaccharide.

with organic matter, energy content, dung pH, carbon content and nitrogen content (Table 4, Appendix Figure 1). In *O. binodis* only, there was a negative correlation between beetle length and INSP and the C:N ratio. Starch content had positive correlations with F_1 progeny in *E. intermedius* and *O. binodis* but not *E. africanus*. All correlations were weak due to variation in beetle length.

DISCUSSION

We investigated how different pasture types influence the dung quality (moisture content, pH, energy content, insoluble and soluble non-starch polysaccharides, starch, organic matter, carbon, nitrogen and C/N ratio) to provide a resource for optimal dung beetle reproduction. Specifically, we experimentally assessed how the different pasture types influence the dung quality, number of broods and reproductive output measured as brood size, development time and progeny size. From this study, evidence partially supported our original hypothesis that a diverse pasture (improved native) will foster greater fecundity for all dung beetle species than mono- (forage oat) or bi-culture (ryegrass/clover) pasture. This study has shown that three common pasture diets influenced cattle dung composition. The breeding success of dung beetles saw similar patterns with longer and wider F_1 progeny from native improved derived dung pastures compared to forage oat dung. This indicates that the diet of cattle, typically pasture, is important for the reproduction and development of phenotypic traits of certain dung beetle species but not others.

Dung quality

Many dung quality parameters, including pH and moisture, have been indicated as important factors for dung beetle reproduction (Dadour & Cook, 1996; Edwards, 1991), yet limited work has been conducted to determine the impact these factors have on dung beetle reproduction. Moisture content of dung can vary across seasons and years (Edwards, 1991; Kaur et al., 2021); however, moisture content in our study of dung was not influenced by pasture type sampled at one growth stage. Dung moisture influenced the reproductive response of *E. intermedius* in wildebeest dung (Edwards, 1991) with a strong correlation between increasing moisture content and increasing brood production; however, moisture content was not found to be strongly correlated with beetle length in this study.

The rye/clover pasture used in the present study was inter-sown, and dung from this pasture source had a higher nitrogen content than the improved native- and forage oat-derived dung (Table 2), as expected from previous legume-based dung studies (e.g., Schick et al., 2019). Increasing grain concentration within feedlot diets increases nitrogen, phosphorus and water-soluble ammonium (Hao et al., 2009); it can also affect pH and moisture content, which are limiting variables for brood production by dung beetles (Dadour & Cook, 1996). Nitrogen content in dung is important for the development of progeny, with higher nitrogen concentrations resulting in large beetles (Cambefort, 1984, 1991). This higher nitrogen content may have produced longer and wider offspring in *E. intermedius* and *O. binodis*.

Reproduction

Brood size is influenced by a range of factors including mammalian dung source, dung beetle species, pasture management and seasonal variation (Kaur et al., 2021; Moczek, 1998; Ridsdill-Smith et al., 1982). *O. binodis* typically produces a brood between 5 and 6 g fresh weight (Kaur et al., 2021; Ridsdill-Smith et al., 1982). Our study showed that brood balls were larger in native improved and rye/clover-derived dung, indicating that parents were provisioning broods with more dung (Emlen, 1994; Hunt & Simmons, 1997; Hunt & Simmons, 2000; Lee & Peng, 1981). Despite the larger broods in all three species of dung beetle, only *E. intermedius* and *O. binodis* recorded longer and wider progeny. The response from *E. africanus* showed weak evidence of different responses to pasture types, suggesting that further investigation is required.

The brood provisioning of all dung beetle species indicates that potential differences and limitations exist for different species with the potential for seasonal variation and quality of dung influencing beetle size (Kaur, 2019; Kaur et al., 2021). While seasonal variation in dung influenced the brood size of *O. binodis*, there was no further analysis to determine whether there was an influence on the progeny resulting from these broods (Kaur et al., 2021). Further issues arise in that there was no mention of variation in pasture species (Kaur et al., 2021) nor age of the pasture species sampled, which could alter the nutritional content. Life stage-identification techniques of agricultural grass crops should be used in future dung research to determine differences in grass pasture age (Zadoks et al., 1974). This information on pasture species and subsequent dung quality is important as our study adds to current knowledge (Treece, 1966; Walsh & Birrell, 1987) in that different pasture types do influence not only the dung but also the response by dung beetles, and warrants further investigation.

Previous research has shown that bigger dung beetles (body mass) across species bury more dung (Gregory et al., 2015), with greater burial of dung resulting in improved ecosystem services provided by dung beetles (Doube, 2018; Nichols et al., 2008). Our study has shown that improved native-derived dung (improved through sowing more pasture species) is important for producing longer beetles with wider pronotums, though how the pastures have been improved and the diversity of pasture species influences the size of emerging beetles are yet to be investigated. Two studies in Australia have investigated diet, with seasonal pasture variations (Ridsdill-Smith, 1986) and between pasture and feedlot diets (Dadour & Cook, 1996). If pasture type influences the dung quality and the subsequent reproductive capacity of dung beetles, it is likely that this will result in a change in the ecosystem service efficiency provided by dung beetles. If cattle dung from a given pasture type results in larger dung beetles, this would result in increased tunnel size for burial, with more dung likely to be buried (Gregory et al., 2015), which, in turn, will increase the ecosystem services (i.e., soil aeration, water infiltration, and pest control) provided by dung beetles.

Based on this investigation, *O. binodis* has a reproductive advantage on the locally common native improved and rye/clover pastures compared with forage oat. The populations of *E. africanus* and *E. intermedius* were collected from areas with different native pastures and are more likely to interact with forage oat or ryegrass/clover mixes. Dung beetle F_1 progeny size is influenced by the provisioning of brood balls by the adults (Hunt & Simmons, 2004), with the first to third instar larvae feeding on the inner brood surface, which has a higher C:N ratio than the original dung deposit (Holter & Scholtz, 2007). The internal surface of the brood is covered with important microbes, which allow for the digestion of cellulose and increased nitrogen fixation (Shukla et al., 2016). The microbiome community of dung beetle guts is influenced by the cellulose concentration of the diet (Shukla et al., 2016), indicating that, in this study, *O. binodis* may be deficient critical microbes for the digestion of the cellulose concentration in forage oat dung. Both *Euoniticellus* species did not display the differences in brood production as observed in *O. binodis*, indicating there is the potential for these species to utilise more variable resources and still produce large healthy progeny. This may be due to the ability of *Euoniticellus* species utilising a large diversity of dung types and qualities, as previously found in the African savanna (Edwards, 1991; Sands et al., 2022).

Volatile organic compounds (VOCs) are released by dung beetles and are used by them to choose a suitable resource for feeding and reproduction (Dormont et al., 2004, 2007; Dormont et al., 2010). The key volatile used by dung beetles is a shikimic product, *p*-cresol (Dormont et al., 2010), though there are a wide array of VOCs with combinations, which are as attractive as fresh dung (Frank et al., 2017). Volatiles released by dung vary by animal species (Dormont et al., 2004, 2010; Perera et al., 2022) and the presence of other insects in the dung (Dormont et al., 2010), but only a single study demonstrates that diet of animals influences the volatile composition released (Perera et al., 2022). Specifically, the dung beetle *Bubas bison* (L., 1767) preferred dung from horses fed pasture compared with lucerne hay-fed animals (Perera et al., 2022). How pasture diets influence the volatiles released by cattle dung and the colonisation of cattle dung-by-dung beetles in the field is unknown and warrants further investigation.

CONCLUSION

Dung beetles are important ecosystem service providers in agricultural systems; however, the ability for species to do so requires strong viable offspring. From our study, we conclude that dung beetle species are influenced by the different dung resources, which either increases or decreases the size (length and width) of progeny. The response of dung beetle species to different resources is influenced by both spatial variation across local populations and landscape response of populations. The diet of cattle plays a key role in the quality of dung and the consequent reproductive capacity of dung beetles, with larger beetles produced on dung with higher organic matter, energy and nitrogen content. In this study, rye/clover- and improved native-derived dung provided the best resource for dung beetle reproduction compared with forage oat dung. Therefore, pasture management of livestock production will influence the overall ecosystem service provided by dung beetle communities.

AUTHOR CONTRIBUTIONS

Thomas Heddle: Conceptualization; data curation; formal analysis; investigation; methodology; writing – original draft. **Zac Hemmings:** Conceptualization; project administration; supervision; validation; writing – review and editing. **Adrienne Burns:** Formal analysis; supervision; writing – original draft; writing – review and editing. **N. R. Andrew:** Funding acquisition; project administration; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

Data used in the paper are currently archived in the online database, Figshare (https://doi.org/10.6084/m9.figshare.22705351).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix Table 1. Information regarding the biomass and moisture content of pasture when dung was collected.

Appendix Table 2. Mean fresh weight (mg ± standard deviation) of parental dung beetles across the different pasture types.

Appendix Figure 1. Dung quality parameters across pasture types. Moisture content, ash, organic matter content, carbon and nitrogen content are a percentage (%). Insoluble non-starch polysaccharides (INSP), Soluble non-starch polysaccharide (SNSP) and starch are presented as grams per kg dry matter (g/kg) and energy content is presented as megajoules per kilogram dry matter (MJ/kg). C:N ratio and pH are presented as themselves with no units.

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