Sands, B. O., Mgidiswa, N., Curson, S., Nyamukondiwa, C., & Wall, R. (2021). Dung beetle community assemblages in a southern African landscape: niche overlap between domestic and wild herbivore dung. *Bulletin of Entomological Research*.
<https://doi.org/10.1017/S0007485321000742>

Peer reviewed version

License (if available):
CC BY-NC-ND

Link to published version (if available):
[10.1017/S0007485321000742](https://doi.org/10.1017/S0007485321000742)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Cambridge University Press at <https://doi.org/10.1017/S0007485321000742> . Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

Dung beetle community assemblages in a southern African landscape: niche overlap between domestic and wild herbivore dung

SANDS, B.¹, MGIDISWA, N.², CURSON, S¹., NYAMUKONDIWA, C². & WALL, R.¹

¹School of Biological Sciences, University of Bristol, UK.

²Department of Biological Sciences and Biotechnology, Botswana International University of Science and Technology, Botswana.

Corresponding author: Bryony Sands, Bristol Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TH, UK. bryony.sands@bristol.ac.uk. Tel: 01173941385

Abstract

Dung beetles provide important ecosystem functions in semiarid environments, improving the physiochemical characteristics of the soil through tunnelling and burying nutrient-rich dung. In sub-Saharan Africa, diverse indigenous mammal communities support highly abundant dung beetle populations in savannah ecosystems. However, the conversion of landscapes to livestock agriculture may result in changes in the abundance and diversity of wild mammal species. This is likely to have significant impacts on dung beetle communities, particularly because domestic livestock dung may be contaminated with toxic residues of veterinary parasiticides. The environmental impact is likely to be affected by the degree of niche overlap between the beetle communities that colonize cattle dung and those that colonize the dung of wild mammals. We compared dung beetle communities

between a pristine national park habitat dominated by large wild herbivores, and a pastoral farming community dominated by domestic livestock. Diurnal dung beetles were attracted to cattle dung in greater abundance and diversity than to elephant, zebra or giraffe dung. Nocturnal/crepuscular dung beetles were attracted to non-ruminant dung (elephant and zebra) in higher abundance than ruminant dung (cattle and giraffe). While there were no clear trophic specializations, three diurnal species showed an association with cattle dung, whereas eight nocturnal/crepuscular species showed an association with nonruminant (elephant and zebra) dung. Diurnal species may be at greater risk from the toxic effects of residues of veterinary parasiticides in domestic livestock dung. Although many species showed trophic associations with wild herbivore dung, these beetles can utilize a wide range of dung and will readily colonize cattle dung in the absence of other options. As more land is converted to livestock agriculture, the contamination of dung with toxic residues from veterinary parasiticides could therefore negatively impact the majority of dung beetle species.

Running head Dung beetle niche overlap between cattle and wild animal dung

Keywords Scarabaeinae, livestock, agriculture, veterinary parasiticides, native herbivore, sub-Saharan Africa

Introduction

Dung beetles in the subfamily Scarabaeinae are a diverse and abundant component of the savannah ecosystem in sub-Saharan Africa, which supports some of the richest and most diverse mammalian communities in the world (Nieto et al., 2005; Tshikae et al., 2008). The majority of African Scarabaeinae are tunnelling (paracoprid) beetles, which comprise approximately 70% of species found (Davis et al., 2008, Stanbrook et al., 2021). However, ball-rolling species (telocoprid) and species which colonize and breed in the dung balls of other beetle species (kleptocoprid) may also be abundant (Davis et al., 2008).

Tunnelling and dung burial by paracoprid beetles have a vital role in semiarid ecosystems. Their ecosystem services include removing dung from the soil surface (Holter, 1979; Carvalho et al., 2018), bioturbation (Mittal, 1993) and nutrient cycling (Bang et al., 2005). For example, the presence of the paracoprid beetles *Copris ochus* and *Copris tripartitus* increased the total crude protein in forage growth by 33%, and total digestible nutrient in grass shoots by 1.3% compared to beetle-free controls (Bang et al., 2005). Furthermore, activity of *Digitonthophagus gazella* and *Onthophagus taurus* improved the physiochemical characteristics of soil, significantly increasing pH and soil nutrients (P, Ca and Zn) compared to beetle-free controls (Bertone et al., 2006). Improvements in soil health are likely to result in increased yield, for example plots of coastal bermudagrass with dung beetle activity had significantly higher yield over the season than those without (Fincher, 1981).

Advances in our understanding of dung beetle functional contributions to ecosystems have not been matched by an understanding of the consequences of anthropogenic activities such as the conversion of landscapes to livestock agriculture (Raine & Slade, 2019). In these landscapes, there has been a decrease in wild indigenous mammal density and an increase in the abundance of domesticated livestock (largely cattle and goats). A 38 % reduction in the species richness of indigenous mammals was shown to alter patterns of dung association, and reduce dung beetle species richness by 43 % across the Botswana Kalahari aridity gradient (Tshiake et al., 2013). Raine & Slade (2019) report consistent trends towards co-declines of dung beetles and mammals, and changes in the abundance and diversity of indigenous mammal species as a result of habitat disturbance are likely to have significant impacts on dung beetle communities. Coupled with anthropogenic related climate change, this represents a substantial threat to coprophagous beetle species (Pamesan & Yohe, 2003; Thomas et al., 2004).

The impacts of agricultural intensification are likely to be particularly concerning in the context of the treatment of livestock with veterinary parasiticides (Verdú et al., 2015; Sands et al., 2018).

Formulations of the pyrethroids deltamethrin and cypermethrin are widely used for biting-fly and tick control (Lovemore, 1992; Spickett & Fivaz, 1992; Alexander & Wardhaugh, 2001). Following treatment, the main route of pyrethroid excretion in cattle is faecal (Floate et al., 2005) and residues are excreted into the dung of cattle at concentrations of about 0.01-0.4 ppm for up to two weeks after treatment (Wardhaugh, Longstaff & Lacey, 1998; Vale et al., 2004). In faeces, excreted unmetabolized drug or metabolites (Venant et al., 1990), may retain insecticidal properties (Floate et al., 2005; Wardhaugh, 2005). Dung spiked with 10 ppm deltamethrin or alphacypermethrin and analysed for residues showed that there was no change in concentration over two months following field exposure (Vale et al., 2004). Dung contaminated with deltamethrin, cypermethrin, cyalothrin, flumethrin and alphasmethrin, has been shown to adversely affect several dung beetle species leading to mortality and disruption of reproduction (Bianchin et al., 1992; Bianchin, Alves & Koller, 1997; 1998; Wardhaugh, Longstaff & Lacey, 1998; Vale et al., 2004; Bang et al., 2007).

The environmental impact of widespread treatment of cattle with parasiticides is likely to be affected by the degree of niche overlap between the beetle communities that colonize cattle dung and those that colonize the dung of indigenous mammals. Beetles colonising wild herbivore dung are not likely to encounter toxic faecal residues from veterinary parasiticides, whereas the greater the degree of niche overlap the greater the potential negative consequences. The aims of this study were therefore to assess dung beetle diversity and community structure across habitats and dung types in a grassland savannah region of the Makgadikgadi, Botswana, in an area which facilitated comparison between a pristine national park habitat dominated by large indigenous mammals, and a pastoral farming community dominated by domestic livestock.

Methods

Study area

The study was conducted at Khumaga Village in north-eastern Botswana (S20° 28.165', E24° 30.875') and in the Makgadikgadi Pans National Park (MPNP) (S20°26.947', E24°36.988'). A permit to conduct the research was granted from the Ministry of Environment, Wildlife and Tourism Botswana [number EWT 8/36/4 XXXIII (9)]. The region is characterized by a summer rainfall season between November – March with annual rainfall between 450 – 500 mm, although periodic drought occurs, which is an intrinsic characteristic of a southern African system (Krüger & Scholtz, 1998). Sampling was undertaken between December 2015 – February 2016, during which time southern Africa experienced a severe drought with Botswana receiving <65% of the average annual rainfall (FEWS, 2016). The results of this study are therefore in the context of low rainfall and the dung beetle assemblages reported here may not be representative of high rainfall years.

The study site is situated at a transition between two ecoregions (Olson et al., 2001) bordered by the Boteti River. On the east of the river is Khumaga Village, characterized by Kalahari Acacia-Baikiaea Woodland (AT0709), and on the western side is the Makgadikgadi Pans National Park, a Zambezian Halophytic (AT0908) ecoregion (Fig. 1). The landform is lacustrine plain with fossil river courses and recent fluvial deposits from the present channel of the Boteti (Venema & Kgaswanyane, 1996), with Kalahari sand soils consisting of haplic arenosols in Khumaga Village and calcaric arenosols in the Makgadikgadi Pans (De Wit & Nachtergaele, 1990).

Khumaga Village is a rural area characterized by small scale cattle and goat pastoralists, whereas the Makgadikgadi Pans National Park represents a protected area with populations of large indigenous mammals including nonruminant (elephant, zebra) and ruminant (blue wildebeest, giraffe, gemsbok, springbok and impala) herbivores, carnivores (lion, leopard) and omnivores (vervet monkey, baboon, warthog) (DWNP, 2012).

Pitfall trap bait

Four different types of dung were used to bait pitfall traps, representing the most common large mammals in the area. Wild animal dung was obtained from elephant (*Loxodonta africana* (Blumenbach)), zebra (*Equus quagga burchellii* (Gray)), and giraffe (*Giraffa camelopardalis giraffa* (von Schreber)) which roamed freely in the national park. Dung was also collected from Tswana/Sanga-type cattle (*Bos taurus africanus* Linnaeus) that foraged freely in the village during the day, were corralled overnight and had never been treated with parasiticides. These bait types represent both ruminant (cattle and giraffe) and non-ruminant (elephant and zebra) herbivores, and include small dry pellets (giraffe), large moderately dry coarse-fibred boluses (elephant, zebra) and large moist fine-fibred pats (cattle) (Davis & Scholtz, 2001). Freshly voided cattle dung was collected from the village at 06:30 h on the day of use. Elephant, giraffe and zebra dung were collected from the national park between 16:00h and 18:00h on the evening prior to trapping, by observing animals with binoculars and collecting any freshly voided dung, which was stored overnight in sealed buckets for use the following morning. Dung was collected from wild animals at this time for logistical reasons, due to it being the latest period of daylight activity before the trapping commenced the following day.

Trapping

Two separate trapping surveys were performed. The first used pitfall traps baited with cattle dung at three different sites: in the village, on the western bank of the Boteti which was the border of the national park, and 5 km inside the national park. The second survey, designed to identify trophic associations, used cattle, giraffe, elephant and zebra dung to bait pitfall traps at two different sites: within the village and 5 km inside the national park.

Eight pitfall traps were set up at 10 m intervals along a transect at each of the locations. For the second survey, two traps were randomly allocated to each of the four dung types and were pooled for analysis giving an adequate sample for analysis based on preliminary data. Traps consisted of

three 560 mL plastic cups, each half-filled with water containing 0.5mL detergent and buried alongside each other to form a triangle level with the soil surface. Above the cups, 150 g of dung wrapped in muslin was suspended at a height of 150 mm, and to prevent flooding, a plastic rain guard was placed 50 mm above the dung. Each 24 h trapping session was set up at 07:00 h and emptied at 18:30 h for collection of diurnal species, then immediately re-baited with fresh dung and emptied at 07:00 h the following morning for collection of nocturnal and crepuscular species. Trapping was repeated on three separate occasions for both surveys, two weeks apart to allow movement of individuals in the area without bait interference (da Silva & Hernández, 2015), with locations surveyed simultaneously to control for climatic variation. This gave a total of nine trapping sessions for the cattle dung survey and six for the trophic association survey. This survey was conducted over a period of 12-weeks between December 2015 and February 2016. Beetles were stored in absolute ethanol prior to counting and identification. Scarabaeinae dung beetles were identified to species level where possible using morphological and ecological characteristics (Davis et al., 2008) and compared to reference collections at the National History Museum (London, UK) and the University of Pretoria (South Africa).

Data analysis

All statistical analyses were performed using RStudio (Version 1.2.1578, RStudio Team, 2019). The cattle dung survey and the trophic association survey were analysed separately. Dung beetle communities were described by total abundance, species richness, dominance concentration (D_w) (Strong, 2002) and asymptotic Shannon diversity (Hill number order $q = 1$). Furthermore, to overcome the ‘sampling problem’ in which species richness is highly sensitive to sample size and completeness and underestimates true species richness (Chao et al., 2014), interpolation and extrapolation procedures were used to facilitate comparison of dung beetle assemblages using the R package ‘iNEXT’ (Chao et al., 2014; Hsieh et al., 2020).

A generalized linear model with a negative binomial error distribution was used to analyse count data of species abundance, including diel period, location and dung type (for the trophic association survey only) and their interactions as explanatory variables. The same model was used with species richness as the response variable for the trophic association survey, whereas a generalized linear model with a Poisson error distribution was a better fitting model for species richness in the cattle dung survey. Model assumptions were checked by the distribution of residuals (normality), residual deviance $< 2 \times$ residual degrees of freedom (dispersion) and plotting the residuals against the dependent variable (homoscedasticity). For the dominance (D_w) and diversity (Shannon) indices, a generalized linear model with a quasipoisson error distribution was performed with the above explanatory variables. If diel period was a significant factor, data from diurnal and nocturnal traps were analysed separately. Models were simplified by stepwise removal of non-significant factors and the resulting minimal model contrasted with Akaike's Information Criterion (AIC) to the global model, until the best fitting model was found (Bozdogan, 1987). Post-hoc analysis for generalized linear models was performed using the R package 'multcomp' (Hothorn et al., 2008) with Tukey multiple comparisons of means. Separate analysis was carried out as described above for the explanatory variable herbivore type (ruminant or nonruminant) due to non-independence of this variable from dung type.

The IndVal method (Dufrêne & Legendre, 1997) is a technique used to find indicator species and species assemblages characterising groups of sites, and was used to identify species that were associated with particular pitfall trap 'groups' such as diel period, location and dung type. The R package 'indicspecies' (De Cáceres & Legendre, 2009) was used to calculate the IndVal index between dung beetle species and pitfall trap groups, and to identify groups with the highest species association values. The IndVal index is a value between 0 – 1, and species with a value of ≥ 0.75 were considered indicators for a group, 0.5 – 0.75 of showing a degree of association, and ≤ 0.5 indicating no association or generalist behaviour (subjective benchmark; Stanbrook et al 2021; Tshikae et al

2008). Permutation tests ($n = 999$) were then performed, and species with high (≥ 0.75) and significant IndVals were considered specialists for that group.

Canonical Correspondence Analysis (CCA) was used to analyse dung beetle community composition between pitfall trap groups. The R package *vegan* (Oksanen et al., 2019) was used initially to confirm that the data were suitable for unimodal ordination, by running a Detrended Correspondence Analysis in which the first DCA axis was > 3 standard deviations (Lepš & Šmilauer, 2003), and subsequently to perform the CCA. Finally, ANOVA-like permutation tests were used to assess the significance ($P < 0.05$) of environmental variables (habitat and dung type). Diurnal traps did not collect adequate species samples for reliable ordination, so analysis focused on nocturnal and crepuscular traps.

Results

Cattle dung survey

Dung beetle assemblage structure

There were 12,013 dung beetles collected from the cow-dung baited pitfall traps between December 2015 – February 2016, belonging to 40 species and representing all of the 9 dung beetle tribes found in Africa (Dichotomiini, Coprini, Canthonini, Gymnopleurini, Scarabaeini, Sisyphini, Onitini, Onthophagini, Oniticellini). Paracoprid beetles were the most dominant functional group comprising 58% of individuals and 52.5% of species. There were six (15%) putative kleptocoprids (species in the genera *Caccobius* and *Cleptocaccobius*, and *Onthophagus pullus*) which comprised 19% of individuals. For two abundant species (*Onthophagus vincus* and *Onthophagus nr. sugillatus*) which comprised 10% of individuals trapped, dung-use behaviour is not clear and may be a combination of paracoprid and kleptocoprid types (Davis, 1996). There were 11 species of telocoprid (27.5%) which comprised 12.5% of total individuals.

Dung beetles in the tribe Onthophagini were the most abundant, comprising 79.3% of all individuals trapped. Canthonini, Dichotomini and Onitini were the most poorly represented tribes, with just 3, 7 and 1 individual(s) respectively. *Kurtops signatus* (tribe Onthophagini) was the most abundant species and accounted for 25.4% of all individuals. There were four highly abundant species, *Scarabeus zambezianus* (tribe Scarabaeini), and *K. signatus*, *Onthophagus stellio* and *Caccobius ferrugineus* (all tribe Onthophagini) which together comprised 65.8% of all dung beetles trapped. There were 11 rare species (<5 individuals trapped) (Table 1) which together comprised just 0.17% of the total beetles trapped.

Of the 40 species collected, 24 (60%) were nocturnal or crepuscular, 13 (32.5%) were diurnal and 3 (7.5%) were collected in both diurnal and nocturnal traps. There were 27 species (67.5%) found in all three locations (national park, riverside and village) and 2 (5%), 5 (12.5%) and 1 (2.5%) species collected from the national park, riverside or village only. Most individuals were collected in the national park (5554; 46.2%), with 2673 (22.3%) collected at the riverside and 3792 (31.6%) in the village (Table 1).

Diel activity and habitat

There was significantly higher abundance ($\chi^2_1=64.6$, $P<0.001$), species richness ($\chi^2_1=39.1$, $P<0.001$), dominance concentration ($t_{17}=2.67$, $P<0.05$) and Shannon diversity ($t_{17}=2.16$, $P<0.05$) in dung beetle communities attracted to nocturnal and crepuscular pitfall traps compared to diurnal traps. In the nocturnal and crepuscular traps, a greater abundance of dung beetles were trapped in the national park (Fig. 2), but this relationship was only significant between the national park and the riverside ($Z_8=2.27$, $P<0.05$). There were no statistically significant differences in the abundance of beetles trapped in diurnal traps between the three habitats.

241 *Indicator species*

242 Three species showed an association with the national park: *Pedaria* sp. (Kalahari) (IndVal = 0.66),
 243 *Onthophagus aeruginosus* (IndVal = 0.65) and *Chalconotus convexus* (IndVal 0.58), and one species
 244 showed an association with the riverside, *Onthophagus fallax* (IndVal = 0.68). *Escarabeaus remii* was
 245 associated with all habitats except the national park (IndVal= 0.68), whereas *Copris cornifrons* was
 246 associated with all habitats except the village (IndVal = 0.63). Eighteen species were
 247 nocturnal/crepuscular specialists ($P < 0.05$, IndVal ≥ 0.75) (Supplementary Table S1). Five of these had
 248 Indval = 1 and were equally good indicator species for nocturnal/crepuscular dung beetle
 249 communities (*S. zambeziensis*, *Scarabeaus goryi*, *Metacatharsius troglodytes*, *Digitonthophagus*
 250 *gazella* and *O. vinctus*). Four species were diurnal specialists ($P < 0.05$, IndVal ≥ 0.75) (Supplementary
 251 Table S1) and *Gymnopleurus ignitus* was the best indicator species for diurnal communities (IndVal =
 252 1).

253

254 **Trophic association survey**

255 *Dung beetle assemblage structure*

256 There were 13,032 dung beetles collected from the pitfall traps baited with cattle, elephant, zebra
 257 and giraffe dung between December 2015 – February 2016, belonging to 48 species representing all
 258 9 tribes of dung beetle found in Africa. Paracoprid beetles were the most dominant functional group
 259 comprising 49% of individuals and 60% of species. There were seven (15%) putative kleptocoprids
 260 (species in the genera *Caccobius* and *Cleptocaccobius*, and *O. pullus*) which comprised 19% of the
 261 individuals. For two abundant species, *O. vincus* and *O. nr. Sugillatus*, which comprised 29% of
 262 individuals trapped, dung-use behaviour is not clear and may be a combination of paracoprid and
 263 kleptocoprid types (Davis, 1996). There were 10 species of telocoprid (21%) which comprised just 2%
 264 of the total number of individuals.

Dung beetles in the tribe Onthophagini were the most abundant, comprising 90.4% of all the individuals trapped. Canthonini, Onitini and Oniticellini were the most poorly represented tribes, with just 1, 9 and 8 individual(s) respectively. *O. stellio* (tribe Onthophagini) was the most abundant species and accounted for 31.1% of all individuals. There were three highly abundant species, *O. stellio*, *O. vinctus* and *C. ferrugineus*, which together accounted for 70.4% of all the dung beetles trapped. There were 20 rare species (<5 individuals) (Table 1) which together comprised just 0.28% of the total beetles trapped.

Of the 48 species collected, 34 (70.8%) were nocturnal or crepuscular, 13 (27.1%) were diurnal and 1 (2.1%) was collected in both diurnal and nocturnal traps. Fourteen species (29.2%) were collected from all four dung types and 4 (8.3%), 3 (6.3%) and 7 (14.6%) were found exclusively in traps baited with elephant, zebra and cattle dung respectively. Non-ruminant dung attracted the most individuals, with 5347 (41.0%) collected from elephant and 5126 (39.3%) from zebra dung traps. Ruminant dung attracted 2380 (18.2%) and 196 (1.5%) individuals from cattle and giraffe dung traps respectively.

Diel activity and habitat

There was significantly higher abundance ($X^2_1=48.1$, $P<0.001$), species richness ($X^2_1=37.79$, $P<0.001$), dominance concentration ($t_{40}=3.75$, $P<0.001$) and diversity ($t_{47}=4.45$, $P<0.001$) of dung beetle communities attracted to nocturnal and crepuscular compared to diurnal pitfall traps. Six dung beetle species were associated with the national park habitat: *Metacatharsius opacus* (IndVal = 0.69), *Caccobius cavatus* (IndVal = 0.67), *Caccobius nigrifolius* (IndVal = 0.64), *Pedaria sp. (Kalahari)* (IndVal = 0.59), *Catharsius calaharicus* (IndVal = 0.59) and *S. goryi* (IndVal = 0.56). Sixteen species were nocturnal/crepuscular specialists ($P<0.05$, IndVal ≥ 0.75) (Supplementary Table S2). Of these, *M. troglodytes*, *D. gazella*, *Onthophagus fimetarius*, *O. stellio* and *C. ferrugineus* were equally good indicator species for nocturnal/crepuscular dung beetle communities (IndVal = 1). Four species

showed an association with diurnal traps (Supplementary Table S2), and *Kurtops quadriceps* was a diurnal specialist ($P < 0.05$, IndVal = 0.85).

Trophic associations

For diurnal traps, there was a significant association between dung type and dung beetle abundance ($\chi^2_3 = 26.27$, $P < 0.001$). Significantly more dung beetles were attracted to cattle than to elephant ($P < 0.05$) or giraffe ($P < 0.001$) dung, and to zebra than giraffe dung ($P < 0.05$; Fig. 3). For nocturnal and crepuscular traps, there was also a significant association between dung type and dung beetle abundance ($\chi^2_3 = 14.07$, $P < 0.05$). Significantly fewer dung beetles were attracted to giraffe dung than to cattle ($P < 0.05$), elephant ($P < 0.001$) or zebra ($P < 0.001$) dung (Fig. 3).

There was a significant association between dung type and species richness for diurnal traps ($\chi^2_3 = 24.15$, $P < 0.001$). Dung beetle communities attracted to cattle dung had significantly higher species richness than those attracted to giraffe ($P < 0.05$) or elephant ($P < 0.05$) dung, but not zebra (Fig. 3). For nocturnal and crepuscular traps, there was also a significant association between dung type and species richness ($\chi^2_3 = 13.58$, $P < 0.05$). Dung beetle communities attracted to giraffe dung had significantly lower species richness than those attracted to cattle ($P < 0.05$) or elephant ($P < 0.05$) dung (Fig. 3).

There were significant differences in dominance between dung beetle communities attracted to the different dung types for diurnal traps ($F_3 = 6.51$, $P < 0.05$). There was significantly higher dominance in dung beetle communities attracted to cattle dung than to giraffe ($P < 0.001$) or elephant ($P < 0.05$) dung, and to zebra than giraffe dung ($P < 0.05$; Fig. 3). For nocturnal and crepuscular traps, there was a significant association between dung type and dominance ($\chi^2_3 = 7.63$, $P < 0.05$). Dung beetle communities attracted to cattle dung had significantly higher dominance than those attracted to giraffe dung ($P < 0.05$).

There were significant differences in diversity between dung beetle communities attracted to the different dung types for diurnal traps, ($F_3=7.68$, $P<0.05$). Dung beetle communities attracted to cattle dung had significantly higher diversity than those attracted to giraffe ($P<0.001$) or elephant ($P<0.05$; Fig. 3). There were no significant differences in diversity for nocturnal or crepuscular traps.

There was no significant association between herbivore dung type and beetle abundance for diurnal traps. For nocturnal and crepuscular traps, there was a significant association between dung type and dung beetle abundance ($\chi^2_1=5.09$, $P<0.05$). Non-ruminant dung attracted significantly more beetles than ruminant dung ($P<0.05$; Fig. 4). There were no significant differences in species richness, dominance concentration or diversity between ruminant and non-ruminant dung.

There were no species that specialized on one particular dung type. Three species showed an association with cattle dung: *G. ignitus* (IndVal 0.61), *Euoniticellus intermedius* (IndVal = 0.61) and *Neosisyphus calcaratus* (IndVal = 0.7). Eight species showed an association with nonruminant (zebra and elephant) dung: *Onthophagiini sp. 2* (IndVal = 0.71), *O. vinctus* (IndVal = 0.70), *C. cavatus* (IndVal = 0.67), *Onitis sp. 1* (IndVal = 0.61), *Onthophagus sp. 13* (IndVal = 0.61), *C. calaharicus* (IndVal = 0.59), *Pedaria sp. (Kalahari)* (IndVal = 0.52) and *Afrostrandius plebejus* (IndVal = 0.51). There were 15 species associated with all dung types except giraffe (IndVal = 0.58 – 0.92) (Supplementary Table S2), and six species were identified as generalists, being found in all four dung types with no particular association: *S. zambezianus*, *S. goryi*, *M. troglodytes*, *D. gazella*, *O. fimetarius* and *K. quadriceps*.

Ordination

The proportion of the total variability captured by the CCA was 30%. The first canonical axis corresponded to dung type and accounted for approximately 56% of the constrained variability, and the second axis corresponded to habitat type and accounted for 28% of the constrained variability.

Permutation tests indicated that dung beetle community composition varied significantly in relation to both dung type ($\chi^2_3=0.23$. $P<0.05$) and habitat type ($\chi^2_1=0.092$. $P<0.05$) (Fig. 5).

Discussion

Dung beetle nesting behaviour is broadly classified into four functional groups: the telecoprids (ball rollers), paracoprids (tunnellers), endocoprids (dung dwellers) and kleptocoprids (brood parasites) (Simmons & Ridsill-Smith, 2011). Paracoprids dig tunnels in the soil beneath the dung pat and pack dung into brood masses at the end of these tunnels, laying a single egg in each mass. Telecoprid males form balls of dung which they roll away and bury below ground, where the female creates a brood ball. Endocoprids create broods within the dung pat itself and kleptocoprid females deposit their eggs into the brood masses already provisioned by telecoprids or paracoprids. Paracoprid Scarabaeinae are commonly the most abundant functional beetle group in African savannah landscapes (Davis et al., 2008). Of the Scarabaeine dung beetles collected in the present study, 60% were paracoprids while 15% were putative kleptocoprid species consisting of small bodied Onthophagini or Dichotomiini, which colonize and breed in the dung balls of large telocoprid (ball-rolling) Scarabaeini (Davis et al., 2008). The kleptocoprid genus *Pedaria* observed in this study has previously been recorded in the brood balls of the large paracoprid *Heliocopris* (Davis 1996a). Two species were collected, *O. sp. nr sugillatus* and the highly abundant *O. vinctus*, which have been recorded colonising the dung balls of larger species, but it is not clear whether they breed in these dung balls, therefore they have been grouped as an intermediate between paracoprid and kleptocoprid (Davis, 1996a). Of the seven most highly abundant species collected, 40% were putative kleptocoprids indicating that using the dung already claimed by larger beetles is a highly competitive strategy.

For both the cattle dung and the trophic association survey, there was significantly higher abundance, species richness, dominance and diversity in dung beetles collected from nocturnal and

crepuscular rather than diurnal traps. This contrasts with previous data from the Ivory Coast which shows a diurnal peak in abundance (Krell-Westerwalbesloh et al., 2004), and from South Africa which found the species richness of diurnal Scarabaeidae to be greater than that of dusk fliers (Davis, 1996b). Data from Neotropical regions also suggest that diurnal species are at least twice as abundant as nocturnal or crepuscular species (Davis, 1999; Feer & Pincebourde, 2005). These studies used buffalo, cattle (ruminant herbivore) or human/howler monkey (omnivore) dung as bait. It has been suggested that dung beetle flight periods may be correlated with the defecation patterns of mammals (Simmons & Ridsill-Smith, 2011) and in the present study all three dung beetle species that showed an association with cattle (ruminant herbivore) dung were diurnal: *G. ignitus*, *E. intermedius* and *N. calcaratus*. Conversely, all eight dung beetle species that were associated with nonruminant herbivore (elephant and zebra) dung were associated with nocturnal and crepuscular activity. Cattle produce dung mostly during the day with peaks in early morning and mid-afternoon (Simmonds & Ridsill-Smith, 2011), whereas elephants are also active during the night, particularly in areas of human disturbance such as close to settlements (Gaynor et al., 2018). Therefore, it may be that night-flying dung beetle species are prevalent in the present study area due to the abundance of dung from large monogastric wild animals which may also be active at these times. Studies have also shown that organisms may shift their foraging patterns in response to changing environments (Hamer et al., 2009), and behavioural shifts in activity and foraging timing may be one of the compensatory mechanisms used by dung beetles in avoiding diurnal high temperature stress (Gotcha et al., 2020). The drought conditions experienced during the present study could have contributed to the low diurnal activity, and future trends under scenarios of climate change may include shifts in diel activity as diurnal organisms move towards crepuscular or nocturnal foraging behaviour.

Differences in diel flight activity between dung beetle species is a mechanism for temporal resource partitioning that is thought to reduce competition (Hanski & Cambefort, 1991). These activity periods may be based on body size, for example large dung beetles can regulate their body

temperatures to allow them to fly in cooler periods, whereas for smaller species low temperatures may constrain their ability to fly at night (Philips, 2011). In the present study, several species of large bodied Coprini and Scarabaeini were associated with nocturnal and crepuscular traps. However, some small bodied species of Onthophagini were also found. These included the kleptocoprids *C. cavatus*, *C. ferrugineus* and *C. nigrutilus*, which must synchronise their activity with the large beetles whose dung balls they utilise, as well as several species of paracoprid *Onthophagus*. Krell-Westerwalbesloh et al. (2004) found the peak activity time of paracoprid dung beetles in the Ivory Coast to be between 18:00 – 22:00 hrs. In South Africa, dusk activity by small-bodied paracoprid and kleptocoprid *Onthopagus spp.* has been shown to be concentrated between 18:30 – 18:50 h, while large-bodied paracoprids including *Copris*, *Catharsius*, *Heliocopris* and the kleptocoprid *Pediaria* all flew later between 18:50 – 19:50 h (Davis 1996b). In the current work, the nocturnal trapping period began at 18:30 h and therefore may have included crepuscular species, so it is likely that the smaller bodied paracoprids active in this period were flying at dusk rather than during the night when temperatures were cooler. Although significantly associated with nocturnal and crepuscular traps in both surveys of the current study, *C. nigrutilus* and *O. sp. nr. sugillatus* have been reported elsewhere to be diurnal species (Davis 1996b; Davis et al. 2008). Further research is needed to determine peak activity times of these species, which may be affected by climate change.

Telecoprid dung beetle activity has been shown to peak during the hottest part of the day (Krell-Westerwalbesloh et al., 2004), which may facilitate the energetically costly rolling behaviour at the highest possible speed. Two diurnal species in the present study were indeed small bodied telecoprids (*G. ignitus* and *N. calcaratus*), however the large-bodied telecoprids *S. zambeziensis* and *S. goryi* were strongly associated with nocturnal or crepuscular activity. Large beetle species take longer to dissipate heat due to higher thermal inertia than small species (Gotcha et al., 2020), so are at greater risk of overheating and may therefore avoid diurnal activity. As well as maintaining an elevated body temperature, the large size of these telecoprid beetles may have enabled them to be active in low light levels by the evolution of more sensitive eyes, since the superposition aperture

and rhabdoms can be larger (Byrne & Dacke, 2011). The rhabdoms of *S. zambezianus* have been found to contain microvilli at two orthogonal orientations indicating adaptation for polarisation sensitivity (Dacke et al., 2003). Indeed, *Scarabeaus satyrus* has been shown to use celestial cues, including the polarised skylight pattern at twilight, as well as the stars, to navigate straight line paths when rolling brood balls away from dung pats (Dacke et al., 2003; 2013).

There were no dung beetle species particularly associated with the Khumaga Village habitat, whereas three and six species were associated with the MPNP habitat in the cattle dung and trophic association surveys, respectively. Almost 40% of the species associated with the national park habitat were also associated with non-ruminant herbivore (elephant and zebra) dung and were mainly nocturnal or crepuscular. The remainder showed no particular dung type association or were generalists. In the trophic association survey, diurnal dung beetle species were collected with higher abundance, species richness, diversity and dominance from cattle dung baits compared to all other dung types. Diurnal dung beetles may therefore be at greater risk from the toxic effects of residues of veterinary insecticides in cattle dung, which have been shown to reduce the survival and development of larval Scarabaeinae in Botswana (Sands et al., 2018). For nocturnal species, lowest abundance and species richness were found in giraffe dung baited traps, and highest abundance in nonruminant (elephant and zebra) traps. Sitters et al., (2013) also found that significantly more dung beetles were attracted to nonruminant (elephant and zebra) dung than ruminant (giraffe, wildebeest and buffalo) dung in a Tanzanian wildlife reserve. Dung of low moisture content is thought to be unsuitable for dung beetles (Edwards, 1991) since the adult beetles feed on the liquid portion which contains very small, nutritious particles as opposed to the larger indigestible plant remains (Holter et al., 2002). It is therefore unsurprising that the small dry pellets of giraffe dung attracted fewer dung beetles.

Community ordination revealed significantly distinct species assemblages between dung types, particularly between nonruminant (elephant and zebra) and ruminant (cattle and giraffe) dung. It is

evident that although true specialisation is rare in dung breeding beetles, except on non-dung food resources such as carrion or fungus (Larsen et al., 2006; Tshikae et al., 2008), many species show some level of association with a particular dung type (Martin-Piera & Lobo 1996; Larsen et al., 2006; Frank et al., 2017; Wurmitzer et al., 2017; Tocco et al., 2018). Studies along the aridity gradient of the Botswana Kalahari (mesic northeast – arid southwest) have also shown separation between ruminant (cattle, sheep) and nonruminant (elephant) dung beetle communities (Tshikae et al., 2013a), and the species found in the present study most closely reflect those of the mesic northeast. However, Tshikae et al. (2013a) show that towards the arid southeast of Botswana, where there is an absence of native large mammal (elephant) dung, there is more species generalisation, lower separation in communities between ruminant and nonruminant dung, and reduced species richness. Decline in indigenous mammal densities due to expansion of the livestock sector, veterinary fences and ranching areas which interrupt routes of migration, and drought (Moleele & Mainah 2003; Tshikae et al., 2013b), may therefore result in shifts in dung beetle species communities. Nocturnal or crepuscular species which are associated with native nonruminant herbivore dung, as well as those species associated with protected areas such as the National Park, may be replaced in favour of diurnal species associated with domestic ruminant (cattle) dung.

This study focused on the dung of large herbivores that were abundant in the area, including ruminant (cattle, giraffe) and non-ruminant (zebra, elephant) dung, and did not include carnivore, omnivore or carrion baits. It is therefore unlikely to represent the full dung beetle species complement. In addition, the drought that occurred during the study period may have negatively impacted dung beetle species richness and abundance, which have been shown to increase after substantial rainfall (Davis, 2002). Furthermore, care must be taken when interpreting results from baited pitfall traps, which reflect attraction to the bait and may not be a true representation of population abundance or structure. Nevertheless, the data highlight the potential impacts of livestock husbandry and the consequences that dung contaminated with pesticides or parasiticides may have on beetle diversity. This emphasises the importance of conserving areas which maintain

indigenous large mammal diversity and are protected from livestock incursions. Many dung beetle species show trophic associations with native nonruminant herbivore dung such as zebra and elephant, however, these beetles can utilise a wide range of dung and will readily colonize cattle dung in the absence of other options. As more land is converted to livestock agriculture, the treatment of cattle with veterinary insecticides and associated contamination of dung with toxic residues (Sands et al., 2018) could therefore negatively impact the majority of dung beetle species, especially in the absence of native nonruminant dung types due to the loss of protected areas.

Acknowledgements

The authors would like to thank Clarke Scholtz, Adrian Davies and Christian Deschodt (Scarab Research Group, University of Pretoria), and Max Barclay and Hitoshi Takano (NHM London) for taxonomic training and assistance. We thank Tiaan Theron and Heike Temme for providing the field site, Robert Bofedile for access to cattle for dung collection, and Jess Isden and Kate Evans of Elephants for Africa for practical support. Wayne L Strong provided statistical advice. BS was supported by a NERC GW4+ studentship for which Dr Sarah Beynon acted as a CASE partner. CN was supported through a BIUST grant number BIUST/ds/R&I/17/2016.

Conflicts of interest

The authors declare no competing interests.

488 **References**

- 489 **Alexander, M., & Wardhaugh, K.** (2001) Workshop on the effects of parasitocides on dung beetles
 490 report of proceedings. Technical Report No. 89. The Bardon Centre, Brisbane, Queensland, Australia.
- 491 **Bang, H. S., Lee, J-H., Kwon, O. A., Na, Y-E., Jang, Y. S. & Kim, W. H.** (2005) Effects of paracoprid
 492 dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying
 493 soil. *Applied Soil Ecology* DOI: 10.1016/j.apsoil.2004.11.001
- 494 **Bang, H. S., Lee, J.-H., Na, Y. E., & Wall, R.** (2007) Reproduction of the dung beetles (*Copris*
 495 *tripartitus*) in the dung of cattle treated with cis-cypermethrin and chlorpyrifos. *Applied Soil Ecology*
 496 **35**, 546–552.
- 497 **Bertone, M. A., Green, J. T., Washburn, S. P., Poore, M. H., & Watson, D. W.** (2006) The
 498 contribution of tunnelling dung beetles to pasture soil nutrition. *Forage and Grazinglands* **4**, 1-12.
- 499 **Bianchin, I., Alves, R. G. O., & Koller, W. W. (1997)** Efeito de alguns carrapaticides/insecticidas de
 500 aspersão sobre os adultos de *Onthophagus gazella* (F.). *Ecosistema* **22**, 116–119.
- 501 **Bianchin, I., Alves, R. G. O., & Koller, W. W. (1998)** Efeito de carrapaticides/insecticidas “pour-on”
 502 sobre adultos do besouro coprofago Africano *Onthophagus gazella* Fabr. (Coleoptera: Scarabaeidae).
 503 *Anais da Sociedade Entomologica do Brazil* **27**, 275–279.
- 504 **Bianchin, I., Honer, M. R., Gomes, A., & Koller, W. W. (1992)** Efeito de alguns
 505 carrapaticides/insecticidas sobre *Onthophagus gazella*. *EMBRAPA Comunicado Tecnico* **45**, 1–7.
- 506 **Bozdogan, H.** (1987) Model selection and Akaike’s information criterion (AIC): the general theory
 507 and its analytical extensions. *Psychometrika* **52**, 345-370.
- 508 **Byrne, M. & Dacke, M.** (2011) The visual ecology of dung beetles. In *Ecology and Evolution of Dung*
 509 *Beetles*, (ed. Simmons, L.W. and Ridsill-Smith, T. J.), pp 177-199. Sussex, UK: Wiley-Blackwell

- 510 **Carvalho, R., Frazao, F., Ferreira-Châline, R. S & França, F. M.** (2018) Dung burial by roller dung
 511 beetles (Coleoptera: Scarabaeinae): An individual and specific-level study. International Journal of
 512 Tropical Insect Science. DOI: 10.1017/S1742758418000206
- 513 **Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K. & Ellison, A. M.** (2014)
 514 Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species
 515 diversity studies. Ecological Monographs **84**, 45-76.
- 516 **da Silva, P. G. & Hernández, M. I. M.** (2015) Spatial patterns of movement of dung beetle species in
 517 a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. PloS ONE 10(5):
 518 e0126112. doi:10.1371/journal.pone.0126112
- 519 **Dacke, M., Nordström, P. & Scholtz, C. H.** (2003) Twilight orientation to polarised light in the
 520 crepuscular dung beetle *Scarabeaus zambezianus*. The Journal of Experimental Biology **206**, 1535-
 521 1543.
- 522 **Dacke, M., Baird, E., Byrne, M., Scholtz, C. & Warrant, E. J.** (2013) Dung beetles use the milky way
 523 for orientation. Current Biology **23**. 298-300.
- 524 **Davis, A. L. V.** (1996a) Community organization of dung beetles (Coleoptera: Scarabaeidae):
 525 differences in body size and functional group structure between habitats. African Journal of Ecology
 526 **34**, 258-275.
- 527 **Davis, A. L. V.** (1996b) Diel and seasonal community dynamics in an assemblage of coprophagous,
 528 Afrotropical, dung beetles (Coleoptera: Scarabaeidae s. str., Aphodiidae, and Staphylinidae:
 529 Oxytelinae). Journal of African Zoology **110**, 291-308.
- 530 **Davis, A. J.** (1999) Species packing in tropical forests: diel flight activity of rainforest dung-feeding
 531 beetles (Coleoptera: Aphodiidae, Scarabeisae, Hybosoridae) in Borneo. The Raffles Bulletin of
 532 Zoology **47**, 473-486.

- 533 **Davis, A.** (2002) Dung beetle diversity in South Africa: Influential factors, conservation status, data
534 inadequacies and survey design. *African Entomology* **10**, 53-65.
- 535 **Davis, A., Frolov, V., & Scholtz, C.** (2008) *The African Dung Beetle Genera*. Protea Book House. South
536 Africa.
- 537 **Davis, A. L. V. & Scholtz, C. H.** (2001) Historical vs. ecological factors influencing global patterns of
538 scarabaeine dung beetle diversity. *Diversity and Distributions* **7**, 161-174.
- 539 **D. E. A.** (2016) National Biodiversity Strategy and Action Plan. Department of Environmental Affairs,
540 Gaborone, Botswana.
- 541 **De Caceres, M., & Legendre, P.** (2009). Associations between species and groups of sites: indices an
542 d statistical inference. *Ecology* DOI: 10.1890/08-1823.1
- 543 **De Wit, P., & Nachtergaele, F.** (1990) Soil Map of the Republic of Botswana. Soil Mapping and
544 Advisory Services Project FAO/BOT/85/011. Map 1 of 2. FAO.
- 545 **Dufrêne, M. & Legendre, P.** (1997) Species assemblages and indicator species: the need for a flexible
546 asymmetrical approach. *Ecological Monographs*, **67**: 345-366
- 547 **DWNP** (2012) Aerial census of animals in Botswana 2012 dry season. Department of Wildlife and
548 National Parks. Gaborone, Republic of Botswana.
- 549 **Edwards, P. B.** (1991) Seasonal variation in the dung of African grazing mammals, and its consequen
550 ces for coprophagous insects. *Functional Ecology* **5**, 617 – 628.
- 551 **Feer, F.& Pincebourde** (2005) Diel flight activity and ecological segregation within an assemblage of t
552 ropical forest dung and carrion beetles. *Journal of Tropical Ecology* **21**, 21-30.
- 553 **FEWS** (2016) Illustrating he extent and severity of the 2015-16 drought. Southern Africa Special Repo
554 rt. Famine Early Warning Network, USAID.
- 555 **Fincher, G.** (1981) The potential value of dung beetles in pasture ecosystems [Texas]. *The Journal of*
556 *the Georgia Entomological Society*. **16**, 316-333.

- 557 **Floate, K. D., Wardhaugh, K. G., Boxall, A. B. A., & Sherratt, T. N.** (2005). Faecal residues of veterina
558 ry parasiticides: Nontarget effects in the pasture environment. *Annual Review of Entomology* **50**, 15
559 3–179.
- 560 **Frank, K., Brückner, A., Hilpert, A., Heethoff, M. & Blüthgen, N.** (2017) Nutrient quality of vertebrat
561 e dung as a diet for dung beetles. *Scientific reports* **7**, 12141.
- 562 **Gaynor, K. M., Branco, P. S., Long, R. A., Gonçalves, D. D., Granli, P. K. & Poole, J. H.** (2018) Effects
563 of human settlement and roads on diel activity patterns of elephants (*Loxodonta Africana*). *African J*
564 *ournal of Ecology* **56**, 872-881.
- 565 **Gotcha, N., Machekano, H., Cuthbert, R. N. & Nyamukondiwa, C.** (2020) Heat tolerance may deter
566 mine activity time in coprophagic beetle species (Coleoptera: Scarabaeidae). *Insect Science* DOI: 10.1
567 111/1744-7917.12844
- 568 **Hamer, K.C., Humphreys, E.M., Magalhaes, M.C., Garthe, S., Hennicke, J., Peters, G., Grémillet, D.,**
569 **Skov, H. & Wanless, S.** (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *J*
570 *ournal of Animal Ecology* **78**, 880-889
- 571 **Hanski, I. & Cambefort, Y.** (1991) *Dung Beetle Ecology*. Princeton, NJ: Princeton University Press.
- 572 **Holter, P.** (1979) Effect of dung-beetles (*Aphodius* spp.) and earthworms on the disappearance of cat
573 tle dung. *OIKOS* **32**, 393-402
- 574 **Holter, P., Scholtz, C. H., & Wardhaugh, K. G.** (2002) Dung feeding in adult scarabaeines (tunnellers
575 and endocoprids): even large dung beetles eat small particles. *Ecological Entomology* **27**, 169-176.
- 576 **Hothorn, T., Bretz, F. & Westfall, P.** (2008) Simultaneous inference in general parametric models. *Bi*
577 *ometric Journal* **50**, 346-363.
- 578 **Hsieh, T. C., Ma, K. H. & Chao, A.** (2020) iNEXT: iNterpolation and EXTrapolation for species diversity
579 . R package version 2.0.20 URL: <http://chao.stat.nthu.edu.tw/wordpress/software-download/>.
- 580 **Krell-Westerwalbesloh, S., Krell, F.T. & Linsenmair, K. E.** (2004) Diel separation of Afrotropical dung
581 beetle guilds – avoiding competition and neglecting resources (Coleoptera: Scarabaeoidea). *Journal*
582 *of Natural History* **38**, 2225-2249.

- 583 **Krüger, K. & Scholtz, C. H.** (1998) Changes in the structure of dung insect communities after ivermec
 584 tin usage in a grassland ecosystem. I. Impact of ivermectin under drought conditions. *Acta Oecologic*
 585 *a* **19**, 425-438.
- 586 **Larsen, T. H., Lopera, A. & Forsyth, A.** (2006) Extreme trophic and habitat specialisation by Peruvian
 587 dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin* **60**, 315-324.
- 588 **Lepš, J. & Šmilauer, P.** (2003) *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge
 589 Press. Supplementary materials
- 590 **Lovemore, D. F.** (1992). A regional approach to trypanosomiasis control: Activities and progress of
 591 the RTTCP (Regional Tsetse Trypanosomiasis Control Programme). Regional Tsetse and
 592 Trypanosomiasis Control Programme, Harare, Zimbabwe.
 593 <http://www.fao.org/docrep/004/T0599E/T0599E12.htm>
- 594 **Martin-Piera, F. & Lobo, J. M.** (1996) A comparative discussion of trophic preferences in dung beetle
 595 communities. *Miscellanea Zoologica* **19**, 13-31.
- 596 **Mittal, I.** (1993) Natural manuring and soil conditioning by dung beetles. *Tropical Ecology* **34**, 150-
 597 159.
- 598 **Moleele, N. M. & Mainah, J.** (2003) Resource use conflicts: the future of the Kalahari ecosystem.
 599 *Journal of Arid Environments* **54**, 405-423.
- 600 **Nieto, M., Hortal, J., Martínez-Maza, C., Morales, J., Ortiz-Jaureguizar, E., Pelaex-Campomanes, P.,**
 601 **Pickford, M., Prado, J. L., Rodríguez, J., Senut, B, Soria, D. & Varela, S.** (2005) *Historical*
 602 *Determinants of Mammal Diversity in Africa: Evolution of Mammalian Body Mass Distribution in*
 603 *Africa and South America During Neogene and Quarternary Times*. In: *African Biodiversity*. Springer,
 604 Boston, MA. DOI: 10.1007/0-387-24320-8_28
- 605 **Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R.,**
 606 **O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M., H., H., Szoecs, E. & Wagner, H.** (2019)

607 Vegan: Community Ecology Package. R package version 2.5-6. [[https://CRAN.R-](https://CRAN.R-project.org/package=vegan)
608 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan)]

609 **Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E.**
610 **C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H.,**
611 **Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. & Kassem, K. R.** (2001) Terrestrial ecoregions
612 of the world: a new map of life on earth: A new global map of terrestrial ecoregions provides an
613 innovative tool for conserving biodiversity. *BioScience* **51**, 933-938.

614 **Parmesan, C. & Yohe, G.** (2003) A globally coherent fingerprint of climate change impacts across
615 natural systems. *Nature*, **421**, 37-42.

616 **Philips, T. K.** (2011) The evolutionary history and diversification of dung beetles. In *Ecology and*
617 *Evolution of Dung Beetles*, (ed. Simmons, L.W. and Ridsill-Smith, T. J.), pp 21-46. Sussex, UK: Wiley-
618 Blackwell

619 **Raine, E. H. & Slade, E. M.** (2019) Dung beetle-mammal associations: methods, research trends and f
620 uture directions. *Proceedings of the Royal Society B* DOI: 10.1098/rspb.2018.2002

621 **RStudio Team** (2019). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL [http://](http://www.rstudio.com/)
622 www.rstudio.com/.

623 **Sands, B., Mgidiswa, N., Nyamukondiwa, C. & Wall, R.** (2018) Environmental consequences of
624 deltamethrin residues in cattle feces in an African agricultural landscape. *Ecology and Evolution*. **14**,
625 2938-2946.

626 **Simmons, L. W. & Ridsill-Smith, T. J** (2011) *Ecology and Evolution of Dung Beetles*. Sussex, UK:
627 Wiley-Blackwell

628 **Sitters, J., Maechler, M-J., Edwards, P. J., Suter, W. & Venterink, H. O.** (2013) Interactions between
629 C : N : P stoichiometry and soil macrofauna control dung decomposition of savanna herbivores.
630 *Functional Ecology* **28**, 776-786.

- 631 **Spickett, A. M., & Fivaz, B. H.** (1992). A survey of tick control practices in the Eastern Cape province
 632 of South Africa. *Onderstepoort Journal of Veterinary Research* **59**, 203–210.
- 633 **Stanbrook, R., Norrey, J., Kisingo, A.W. & Jones M.** (2021) Dung Beetle Diversity and Community
 634 Composition Along a Land Use Gradient in a Savannah Ecosystem of North Western
 635 Tanzania. *Tropical Conservation Science*. doi:[10.1177/19400829211008756](https://doi.org/10.1177/19400829211008756)
- 636 **Strong, W. L.** (2002) Assessing species abundance unevenness within and between plant
 637 communities. *Community Ecology* **3**, 237-246.
- 638 **Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus,**
 639 **B. F. N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.**
 640 **S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. & Williams, S. E.** (20
 641 04) Extinction risk from climate change. *Nature*, **427**, 145 – 148.
- 642 **Tshikae, B. P., Davis, A. L. V. & Scholtz, C. H.** (2008) Trophic associations of a dung beetle assemblag
 643 e (Scarabaeidae: Scarabaeinae) in a woodland savanna of Botswana. *Environmental Entomology* **37**,
 644 431-441.
- 645 **Tshikae, B. P., Davis, A. L. V. & Scholtz, C. H.** (2013a) Does an aridity and trophic resource gradient
 646 drive patterns of dung beetle food selection across the Botswana Kalahari? *Ecological Entomology*
 647 **38**, 83-95.
- 648 **Tshikae, B. P., Davis, A. L. V. & Scholtz, C. H.** (2013b) Dung beetle assemblage structure across the
 649 aridity and trophic resource gradient of the Botswana Kalahari: patterns and drivers at regional and
 650 local scales. *Journal of Insect Conservation* **17**, 623-636.
- 651 **Tocco, C., Balmer, J. P. & Villet, M. H.** (2018) Trophic preference of southern African dung beetles
 652 (Scarabaeoidea: Scarabaeinae and Aphodiinae) and its influence on bioindicator surveys. *African*
 653 *Journal of Ecology* **56**, 938-948.

- 654 **Vale, G. A., Grant, I. F., Dewhurst, C. F., & Aigreau, D.** (2004). Biological and chemical assays of
 655 pyrethroids in cattle dung. *Bulletin of Entomological Research* **94**, 273–282.
- 656 **Venema, J. H. & Kgaswanyane, M.** (1996) *Agricultural land use plan for Letlhakane agricultural*
 657 *district central region*. United Nations Development Programme. Food and Agriculture Organization
 658 of the United Nations.
- 659 **Venant, A., Belli, P., Borrel, S., & Mallet, J.** (1990). Excretion of deltamethrin in lactating dairy cows.
 660 *Food Additives and Contaminants* **7**, 535–543.
- 661 **Verdú, J. R., Cortez, V., Ortiz, A. J., González-Rodríguez, E., Martínez-Pinna, J., Lumaret, J-P., Lobo,**
 662 **J. M., Numa, C. & Sánchez-Piñero, F.** (2015) Low doses of ivermectin cause sensory and locomotor
 663 disorders in dung beetles. *Scientific Reports* **5**, 13912
- 664 **Wardhaugh, K. G.** (2005). Insecticidal activity of synthetic pyrethroids, organophosphates, insect
 665 growth regulators, and other livestock parasiticides: An Australian perspective. *Environmental*
 666 *Toxicology and Chemistry* **24**, 789–796.
- 667 **Wardhaugh, K. G., Longstaff, B. C., & Lacey, M. J.** (1998). Effects of residues of deltamethrin in cattle
 668 faeces on the development and survival of three species of dung-breeding insect. *Australian*
 669 *Veterinary Journal* **76**, 273–280.
- 670 **Wurmitzer, C., Blüthgen, N., Krell, F-T., Maldonado, B., Ocampo, F., Müller, J. & Schmitt, T.** (2017)
 671 Attraction of dung beetles to herbivore dung and synthetic compounds in a comparative field study.
 672 *Chemoecology* **27**, 75-84.

673

674

675

676 **Figure Legends**

677 Fig. 1 Map of Botswana indicating the study site at Khumaga Village and the Makgadikgadi Pans
678 National Park. The area shaded pink corresponds to Kalahari Acacia-Baikiaea Woodland (AT0709)
679 and white to Zambezian Halophytic (AT0908) ecoregions. Regions shaded grey indicate protected
680 areas. Adapted from D.E.A (2016).

681 Fig. 2 Abundance of dung beetles attracted to nocturnal and crepuscular (1830 – 0700 h) cattle dung
682 baited pitfall traps in the Makgadikgadi Pans National Park, the western bank of the Boteti river
683 which borders the park, and inside Khumaga Village. Boxes labelled with the same letters are not
684 statistically significant. ($P < 0.05$, glm.nb(link=log)).

685 Fig. 3 Abundance, species richness, dominance concentration (Dw) and diversity (asymptotic Hill
686 order $q = 1$) of dung beetle communities attracted to cattle, giraffe, elephant and zebra dung in
687 diurnal (0700 h – 1830 h) and nocturnal (1830 h – 0700 h) baited pitfall traps. Boxes labelled with
688 the same letters are not statistically significant. Abundance and species richness ($P < 0.05$,
689 glm.nb(link=log)), Dw and diversity ($P < 0.05$, glm(quasipoisson(link=log))).

690 Fig. 4 Abundance of dung beetles found in nocturnal or crepuscular (1830 – 0700 h) traps baited
691 with nonruminant (elephant and zebra) or ruminant (cattle and giraffe) herbivore dung. Boxes
692 labelled with the same letters are not statistically significant. ($P < 0.05$, glm.nb(link=log)).

693 Fig. 5 Canonical Correspondence analysis (CCA) ordination of dung beetle assemblages attracted to
694 nocturnal (1900 h – 0700 h) pitfall traps baited with cattle (o), giraffe (+), elephant (Δ) and zebra (x)
695 dung either inside Khumaga Village (grey points) or the Makgadikgadi Pans National Park (black
696 points). In the upper plot, traps with similar dung beetle communities are ordinated near to each
697 other, and corresponding environmental variables (dung type and habitat) are indicated by arrows.
698 The position of species on the lower plot correlate to their abundance in these traps. Key to species
699 codes: Afr.ple = *Afrostrandius plebejus*, All.tha = *Allogymnopleurus thalassinus*, Cac.cav = *Caccobius*

700 *cavatus*, Cac.fer = *C. ferrugineus*, Cac.nig = *C. nigrutilus*, Cac.6 = *Caccobius* sp. 6, Cat.cal = *Catharsius*
 701 *calaharicus*, Cha.con = *Chalconotus convexus*, Che.1 = *Cheironitis* sp. 1, Cle.vir = *Cleptocaccobius*
 702 *viridicollis*, Cop.cor = *Copris cornifrons*, Cop.ele = *C. elphenor*, Cop.3 = *C. sp. 3*, Dig.gaz =
 703 *Digitonthophagus gazella*, Esc.rem = *Escarabeaus remii*, Euo.int = *Euoniticellus intermedius*, Gym.aen
 704 = *Gymnopleurus aenescens*, Gym.ign = *G. ignitus*, Hel.1 = *Heliocopris* sp. 1, Het.1 = *Heteronitis* sp. 1,
 705 Kep.1 = *Kepher prodigiosus*, Kur.qua = *Kurtops quadriceps*, Kur.sig = *K. signatus*, Met.opa =
 706 *Metacatharsius opacus*, Met.tro = *M. troglodytes*, Neo.cal = *Neosisyphus calcaratus*, Oni.1 = *Onitis*
 707 sp. 1, Oni.2 = *O. sp. 2*, Oni.3 = *O. sp. 3*, Oni.4 = *O. sp. 4*, Ont.ste = *Onthophagus stellio*, Ont.aer = *O.*
 708 *aeruginosus*, Ont.fal = *O. fallax*, Ont.fim = *O. fimetarius*, Ont.gra = *O. granulatus*, Ont.pul = *O. pullus*,
 709 Ont.ras = *O. rasipennis*, Ont. 13 = *O. sp. 13*, Ont.14 = *O. sp. 14*, Ont.15 = *O. sp. 15*, Ont.16 = *O. sp. 16*,
 710 Ont.nr.pro = *O. sp. nr probus (granular)*, Ont.nr.sug = *O. sp. nr sugillatus*, Ont.vin = *O. vinctus*, Pac.1 =
 711 *Pachylomerus* sp. 1, Ped.kal = *Pedaria* sp. (Kalahari), Pha.bos = *Phalops boschas*, Pha.wit = *P. wittei*,
 712 Sca.gor = *Scarabeaus goryi*, Sca.zam = *S. zambeziensis*.

713