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

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

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

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

8

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

11

12 **Abstract**

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

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

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

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

37 **Introduction**

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

45 Tunnelling and dung burial by paracoprid beetles have a vital role in semiarid ecosystems. Their
46 ecosystem services include removing dung from the soil surface (Holter, 1979; Carvalho et al., 2018),
47 bioturbation (Mittal, 1993) and nutrient cycling (Bang et al., 2005). For example, the presence of the
48 paracoprid beetles *Copris ochus* and *Copris tripartitus* increased the total crude protein in forage
49 growth by 33%, and total digestible nutrient in grass shoots by 1.3% compared to beetle-free
50 controls (Bang et al., 2005). Furthermore, activity of *Digitonthophagus gazella* and *Onthophagus*
51 *taurus* improved the physiochemical characteristics of soil, significantly increasing pH and soil
52 nutrients (P, Ca and Zn) compared to beetle-free controls (Bertone et al., 2006). Improvements in
53 soil health are likely to result in increased yield, for example plots of coastal bermudagrass with
54 dung beetle activity had significantly higher yield over the season than those without (Fincher,
55 1981).

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

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

70 Formulations of the pyrethroids deltamethrin and cypermethrin are widely used for biting-fly and
71 tick control (Lovemore, 1992; Spickett & Fivaz, 1992; Alexander & Wardhaugh, 2001). Following
72 treatment, the main route of pyrethroid excretion in cattle is faecal (Floate et al., 2005) and residues
73 are excreted into the dung of cattle at concentrations of about 0.01-0.4 ppm for up to two weeks
74 after treatment (Wardhaugh, Longstaff & Lacey, 1998; Vale et al., 2004). In faeces, excreted
75 unmetabolized drug or metabolites (Venant et al., 1990), may retain insecticidal properties (Floate
76 et al., 2005; Wardhaugh, 2005). Dung spiked with 10 ppm deltamethrin or alphacypermethrin and
77 analysed for residues showed that there was no change in concentration over two months following
78 field exposure (Vale et al., 2004). Dung contaminated with deltamethrin, cypermethrin, cyalothrin,
79 flumethrin and alphamethrin, has been shown to adversely affect several dung beetle species
80 leading to mortality and disruption of reproduction (Bianchin et al., 1992; Bianchin, Alves & Koller,
81 1997; 1998; Wardhaugh, Longstaff & Lacey, 1998; Vale et al., 2004; Bang et al., 2007).

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

91

92 **Methods**

93 **Study area**

94 The study was conducted at Khumaga Village in north-eastern Botswana (S20° 28.165', E24° 30.875')
95 and in the Makgadikgadi Pans National Park (MPNP) (S20°26.947', E24°36.988'). A permit to conduct
96 the research was granted from the Ministry of Environment, Wildlife and Tourism Botswana
97 [number EWT 8/36/4 XXXIII (9)]. The region is characterized by a summer rainfall season between
98 November – March with annual rainfall between 450 – 500 mm, although periodic drought occurs,
99 which is an intrinsic characteristic of a southern African system (Krüger & Scholtz, 1998). Sampling
100 was undertaken between December 2015 – February 2016, during which time southern Africa
101 experienced a severe drought with Botswana receiving <65% of the average annual rainfall (FEWS,
102 2016). The results of this study are therefore in the context of low rainfall and the dung beetle
103 assemblages reported here may not be representative of high rainfall years.

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

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

116

117 **Pitfall trap bait**

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

133

134 **Trapping**

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

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

143 three 560 mL plastic cups, each half-filled with water containing 0.5mL detergent and buried
144 alongside each other to form a triangle level with the soil surface. Above the cups, 150 g of dung
145 wrapped in muslin was suspended at a height of 150 mm, and to prevent flooding, a plastic rain
146 guard was placed 50 mm above the dung. Each 24 h trapping session was set up at 07:00 h and
147 emptied at 18:30 h for collection of diurnal species, then immediately re-baited with fresh dung and
148 emptied at 07:00 h the following morning for collection of nocturnal and crepuscular species.
149 Trapping was repeated on three separate occasions for both surveys, two weeks apart to allow
150 movement of individuals in the area without bait interference (da Silva & Hernández, 2015), with
151 locations surveyed simultaneously to control for climatic variation. This gave a total of nine trapping
152 sessions for the cattle dung survey and six for the trophic association survey. This survey was
153 conducted over a period of 12-weeks between December 2015 and February 2016. Beetles were
154 stored in absolute ethanol prior to counting and identification.

155 Scarabaeinae dung beetles were identified to species level where possible using morphological and
156 ecological characteristics (Davis et al., 2008) and compared to reference collections at the National
157 History Museum (London, UK) and the University of Pretoria (South Africa).

158

159 **Data analysis**

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

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

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

193 2008). Permutation tests ($n = 999$) were then performed, and species with high (≥ 0.75) and
194 significant IndVals were considered specialists for that group.

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

203

204 **Results**

205 **Cattle dung survey**

206 *Dung beetle assemblage structure*

207 There were 12,013 dung beetles collected from the cow-dung baited pitfall traps between December
208 2015 – February 2016, belonging to 40 species and representing all of the 9 dung beetle tribes found
209 in Africa (Dichotomiini, Coprini, Canthonini, Gymnopleurini, Scarabaeini, Sisyphini, Onitini,
210 Onthophagini, Oniticellini). Paracoprid beetles were the most dominant functional group comprising
211 58% of individuals and 52.5% of species. There were six (15%) putative kleptocoprids (species in the
212 genera *Caccobius* and *Cleptocaccobius*, and *Onthophagus pullus*) which comprised 19% of
213 individuals. For two abundant species (*Onthophagus vincus* and *Onthophagus nr. sugillatus*) which
214 comprised 10% of individuals trapped, dung-use behaviour is not clear and may be a combination of
215 paracoprid and kleptocoprid types (Davis, 1996). There were 11 species of telocoprid (27.5%) which
216 comprised 12.5% of total individuals.

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

225 Of the 40 species collected, 24 (60%) were nocturnal or crepuscular, 13 (32.5%) were diurnal and 3
226 (7.5%) were collected in both diurnal and nocturnal traps. There were 27 species (67.5%) found in all
227 three locations (national park, riverside and village) and 2 (5%), 5 (12.5%) and 1 (2.5%) species
228 collected from the national park, riverside or village only. Most individuals were collected in the
229 national park (5554; 46.2%), with 2673 (22.3%) collected at the riverside and 3792 (31.6%) in the
230 village (Table 1).

231

232 *Diel activity and habitat*

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

240

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.

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

272 Of the 48 species collected, 34 (70.8%) were nocturnal or crepuscular, 13 (27.1%) were diurnal and 1
 273 (2.1%) was collected in both diurnal and nocturnal traps. Fourteen species (29.2%) were collected
 274 from all four dung types and 4 (8.3%), 3 (6.3%) and 7 (14.6%) were found exclusively in traps baited
 275 with elephant, zebra and cattle dung respectively. Non-ruminant dung attracted the most
 276 individuals, with 5347 (41.0%) collected from elephant and 5126 (39.3%) from zebra dung traps.
 277 Ruminant dung attracted 2380 (18.2%) and 196 (1.5%) individuals from cattle and giraffe dung traps
 278 respectively.

279

280 *Diel activity and habitat*

281 There was significantly higher abundance ($X^2_1=48.1$, $P<0.001$), species richness ($X^2_1=37.79$, $P<0.001$),
 282 dominance concentration ($t_{40}=3.75$, $P<0.001$) and diversity ($t_{47}=4.45$, $P<0.001$) of dung beetle
 283 communities attracted to nocturnal and crepuscular compared to diurnal pitfall traps. Six dung
 284 beetle species were associated with the national park habitat: *Metacatharsius opacus* (IndVal =
 285 0.69), *Caccobius cavatus* (IndVal = 0.67), *Caccobius nigrifulus* (IndVal = 0.64), *Pedaria sp. (Kalahari)*
 286 (IndVal = 0.59), *Catharsius calaharicus* (IndVal = 0.59) and *S. goryi* (IndVal = 0.56). Sixteen species
 287 were nocturnal/crepuscular specialists ($P<0.05$, IndVal ≥ 0.75) (Supplementary Table S2). Of these, *M.*
 288 *troglydites*, *D. gazella*, *Onthophagus fimetarius*, *O. stellio* and *C. ferrugineus* were equally good
 289 indicator species for nocturnal/crepuscular dung beetle communities (IndVal = 1). Four species

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

292

293 *Trophic associations*

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

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

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

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

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

323 There were no species that specialized on one particular dung type. Three species showed an
324 association with cattle dung: *G. ignitus* (IndVal 0.61), *Euoniticellus intermedius* (IndVal = 0.61) and
325 *Neosisyphus calcaratus* (IndVal = 0.7). Eight species showed an association with nonruminant (zebra
326 and elephant) dung: *Onthophagiini sp. 2* (IndVal = 0.71), *O. vinctus* (IndVal = 0.70), *C. cavatus* (IndVal
327 = 0.67), *Onitis sp. 1* (IndVal = 0.61), *Onthophagus sp. 13* (IndVal = 0.61), *C. calaharicus* (IndVal =
328 0.59), *Pedaria sp. (Kalahari)* (IndVal = 0.52) and *Afrostrandius plebejus* (IndVal = 0.51). There were 15
329 species associated with all dung types except giraffe (IndVal = 0.58 – 0.92) (Supplementary Table S2),
330 and six species were identified as generalists, being found in all four dung types with no particular
331 association: *S. zambeziensis*, *S. goryi*, *M. troglodytes*, *D. gazella*, *O. fimetarius* and *K. quadriceps*.

332

333 *Ordination*

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

337 Permutation tests indicated that dung beetle community composition varied significantly in relation
338 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).

339

340 Discussion

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

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

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

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

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

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

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

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

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

439 evident that although true specialisation is rare in dung breeding beetles, except on non-dung food
440 resources such as carrion or fungus (Larsen et al., 2006; Tshikae et al., 2008), many species show
441 some level of association with a particular dung type (Martin-Piera & Lobo 1996; Larsen et al., 2006;
442 Frank et al., 2017; Wurmitzer et al., 2017; Tocco et al., 2018). Studies along the aridity gradient of
443 the Botswana Kalahari (mesic northeast – arid southwest) have also shown separation between
444 ruminant (cattle, sheep) and nonruminant (elephant) dung beetle communities (Tshikae et al.,
445 2013a), and the species found in the present study most closely reflect those of the mesic northeast.
446 However, Tshikae et al. (2013a) show that towards the arid southeast of Botswana, where there is
447 an absence of native large mammal (elephant) dung, there is more species generalisation, lower
448 separation in communities between ruminant and nonruminant dung, and reduced species richness.
449 Decline in indigenous mammal densities due to expansion of the livestock sector, veterinary fences
450 and ranching areas which interrupt routes of migration, and drought (Moleele & Mainah 2003;
451 Tshikae et al., 2013b), may therefore result in shifts in dung beetle species communities. Nocturnal
452 or crepuscular species which are associated with native nonruminant herbivore dung, as well as
453 those species associated with protected areas such as the National Park, may be replaced in favour
454 of diurnal species associated with domestic ruminant (cattle) dung.

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

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

472

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481

482 **Conflicts of interest**

483 The authors declare no competing interests.

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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. ($P < 0.05$, $\text{glm.nb}(\text{link}=\log)$).

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 $\text{glm.nb}(\text{link}=\log)$), Dw and diversity ($P < 0.05$, $\text{glm}(\text{quasipoisson}(\text{link}=\log))$).

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. ($P < 0.05$, $\text{glm.nb}(\text{link}=\log)$).

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. zambezius*.

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