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A Comparison of Dung Beetle (Coleoptera: Scarabaeidae) Attraction to Native and Exotic Mammal Dung

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Abstract

Although the preference of dung beetles (Coleoptera: Scarabaeidae) for specific types and conditions of dung has been given substantial attention, little has been done to investigate the potential effects of exotic mammal introduction for game farms or rewilding projects. We used pitfall traps baited with various native and exotic herbivore, carnivore, and omnivore dung to evaluate dung beetle preference in the Great Plains of North America. Additionally, we analyzed the nutrient quality of each dung type. In total, 9,089 dung beetles from 15 species were captured in 2 yr of sampling. We found significant differences ($P < 0.05$) in mean dung beetle capture among omnivore, herbivore, and carnivore dung as well as differences in individual species preference for dung type. Omnivore dung was the most attractive with chimpanzee and human dung having the highest mean capture (291.1 ± 27.6 and 287.5 ± 28.5 respectively). Carrion also was highly attractive with a mean of 231.9 ± 20.6 beetles per trap ($N = 8$). Our results suggest definitive local preference of carrion in *Phanaeus vindex* Macleay and *Onthophagus hecate* (Panzer), while the congener, *O. pennsylvanicus* (Harold), was rarely captured in carrion and highly preferred omnivore dung. Preference for a specific bait type does not appear to be correlated with dung quality, mammalian diet, or origin of mammal. Results suggest niche segregation by dung type among dung beetle species.

Keywords: exotic species, feeding preference, niche partitioning, *Onthophagus*, *Phanaeus*

Although most dung beetles are generalist dung feeders, specialization can occur as a result of competition and scarcity of dung resources (Halffter and Matthews 1966, Howden and Young 1981, Young 1981, Hanski 1989, Davis and Sutton 1997). Previous research indicates that dung beetles differ in their preference for the type of dung (Estrada et al. 1993), the condition of dung (Doubé 1987, Yasuda 1987), and the odor (Dormont et al. 2004) of dung. However, most dung beetles have comparable ecological requirements, with the possibility for thousands of beetles from multiple species to arrive at a dung resource (Horgan 2005, Scholtz et al. 2009).

When native dung beetle faunas encounter dung from exotic animals, they may not use the new resource (Amézquita and Favila 2009). For example, European colonization of Australia in 1778 brought a variety of nonnative herbivores (Hanski and Cambefort 1991). Overgrazing, as well as an excess of flies, midges, and parasites resulted (Bornemissza 1970, Hanski and Cambefort 1991) because the native dung beetles, which had co-evolved with marsupials, did not adequately use bovine dung (Mathews 1972). In North America, the introduction of large domestic animals does not appear to have produced the same results as Australia, likely because the Great Plains had a diverse fauna of grazers and associated dung beetles.

However, it is possible that the introduction of exotic mammals has resulted in a shift in dung beetle species composition in the past 150 yr. Historically, the Great Plains were largely inhabited by nomadic people, following herds of bison (Van Every 1964). By the end of the 19th century, European settlers had colonized, bison were nearly exterminated, much of the grassland was fragmented by agriculture, and new livestock species had been introduced (Jones 1968). Compared with the dung generated by herds of bison that would normally congregate in an area and, after a limited stay, move on to new grounds (Benedict 1996, 2000, Scholtz et al. 2009), the dung resources generated by management practices for cattle and other domestic animals are more confined spatially and often with a single type of animal present. Previously, Barbero et al. (1999) found that land occupied by numerous species of livestock contained greater numbers and diversity of dung beetles compared with lands occupied by few species. Introduction of exotic mammals to North America as a result of exotic game farms or conservation programs (Rubenstein et al. 2006) may also affect dung beetle assemblages, although the response of dung beetles to novel resources has received little attention.

Game farms have introduced herbivores such as African antelope species and omnivores such as wild boars, *Sus scrofa* L., whereas zoological parks may include predatory species (Rubenstein et al. 2006). The dung characteristics and nutritional content of herbivores, carnivores, and omnivores differ and these factors may affect the attractiveness of dung to dung beetles (Scholtz et al. 2009). The dung of herbivores is mainly composed of cellulose, gut fragments, epithelium, and microbes (Hanski and Cambefort 1991, Scholtz et al. 2009), while the dung of carnivores is composed of undigested meat rather than cellulose. Omnivore dung will have a combination of the characteristics of herbivore and carnivore dung. In addition to using dung for feeding, many dung beetles can also obtain nutrients from carrion (Scholtz et al. 2009).

In this study, we used field sampling to determine the attractiveness of dung from native and exotic herbivores, carnivores, and omnivores, and provide nutritional analysis of

the tested dung types. We tested the null hypotheses that there would be no difference in attraction among dung types or nutrient content among different types of dung.

Materials and Methods

Field sampling took place from April through August of 2010 and 2011. The study site consisted of a large (> 4,000 ha) organic cattle ranch on the border of Banner, Morrill, and Cheyenne counties in western Nebraska (Latitude 41.469004°N, Longitude -103.340270°W). At the time of study, the ranch was stocked with $\approx$ 600 head of cattle, and a small number (< 20) of horses.

Pitfall traps (19-liter buckets) with soil in the bottom were baited using 113 g (0.25 lbs.) of mammal dung from various species of native and exotic herbivores, carnivores, and omnivores. Tested dung was from animals native to North America that included American bison (*Bison bison* L.), Shiras moose (*Alces alces* L.), and cougar (*Felis concolor* L.). Dung from animals that were originally introduced to North America but have become naturalized included donkey (*Equus asinus* L.), domestic pig (*Sus scrofa domestica* L.), and human (*Homo sapiens* L.). Dung from exotic animals included chimpanzee (*Pan troglodytes* Blumenbach), Bengal tiger (*Panthera tigris* L.), African lion (*Panthera leo* L.), zebra (*Equus burchellii* Gray), and waterbuck (*Kobus ellipsiprymnus* Ogilby). Carrion, which consisted of a whole rat (*Rattus norvegicus* L.), was prepared by rotting it in the sun for four days in a dark container. Rats were purchased from rodentpro.com, were previously frozen, and weighed between 175 and 250 g (0.3–0.5 lbs.).

Dung from animals was collected from Riverside Discovery Center in Scottsbluff, NE. Only fresh dung (defecation observed) was used, and dung from each type of mammal was mixed to ensure homogeneity, subdivided into 113 g (0.25 pound) bags, frozen, and then thawed before use. Four traps per dung type (48 total) were randomized and then baited for 24 h and checked for three consecutive days biweekly starting in late April and ending in early August. Traps were spaced a minimum of 100 m apart to ensure independence (Larsen and Forsyth 2005). All dung was replaced daily, and carrion was not replaced during the 3-d period of each trap session.

Beetles were counted and identified to species (Ratcliffe and Paulsen 2008), and then released at a location $\approx$ 1 km from the trap array. Members of the Aphodinae occasionally needed collection and storage to identify under magnification. Voucher specimens were placed in the collection of the Department of Biology at the University of Nebraska at Kearney. Total capture and numbers of each species were compared across years by bait type ($N = 8$) using Sigma-Plot 3.1 software (Jandel Scientific, Corte Madera, CA) with the Kruskal-Wallis one-way analysis of variance (ANOVA), which analyzes differences in median values. A Tukey test was used when differences were detected among treatments.

Nonmetric multidimensional scaling (NMDS) analysis was used to examine differences in dung beetle assemblages among dung types using Primer six software (Clarke and Gorley 2006). Total abundance data for each species of dung beetle captured were square-root transformed, and a Bray-Curtis index was used to measure similarities in attraction to omnivore, carnivore, and herbivore dung. Clusters created by the NMDS were measured using analysis of similarity with the same software (Clarke 1993).

Once dung was collected from each mammal species and mixed to ensure homogeneity, subsamples were analyzed by Ward Laboratories in Kearney, Nebraska, for pH, moisture, nitrogen, organic matter, ash content, sodium, zinc, iron, magnesium, manganese, copper, soluble salts, phosphorus, potassium, sulfur, calcium, and carbon-to-nitrogen ratio. Carrion was not included in the analysis because beetles could feed on different parts of the carcass and because the carbon-to-nitrogen ratio of the carcass is likely to change through time with microbial decomposition.

Results

Sampling in 2010 and 2011 yielded a total capture of 9,089 dung beetles from 15 species. There were significant differences (Kruskal-Wallis ANOVA, $P < 0.05$) in mean dung beetle capture within and among omnivores, herbivores, and carnivores (Table 1; Fig. 1). Omnivore dung was the most attractive with chimpanzee, human, and pig dung having higher mean capture per trap (291.1 ± 27.6 , 287.5 ± 28.5 , and 75.9 ± 9.6 , respectively) than all other bait types ($P < 0.05$) except tiger (42.0 ± 10.4), African lion (59.5 ± 3.9), zebra (44.9 ± 5.3), and carrion (231.9 ± 20.6) (Table 1). Carrion was more attractive than all types of herbivore dung except zebra ($P \pm 0.05$). Carnivore dung was more attractive than dung from most herbivore species (Table 1; Fig. 1), although mean beetle capture did not differ statistically between any of the three carnivore dung types and zebra dung. Bison dung was the least attractive; with only 38 beetles (mean 4.8 ± 0.9 per trap) captured from all samples (Table 1).

Figure 1. Mean capture ($\pm$ SE) of dung beetles during field sampling across all dates by dung type.

Table 1. Mean capture of each dung beetle species across all traps in 2010 and 2011 by bait type ($N = 8$)

	Chimpanzee	Human	Pig	Tiger	African lion	Cougar	Zebra	Waterbuck	Moose	Donkey	Bison	Carrión
<i>Aphodius coloradensis</i>	5.9 ± 1.1ab	8.1 ± 1.4a	3.3 ± 1abcd	0.9 ± 0.4bcd	2.8 ± 0.5abc	0.4 ± 0.2cd	1.0 ± 0.4bcd	1.4 ± 0.5abcd	0.3 ± 0.2cd	0.5 ± 0.2bcd	0.0 ± 0.0d	0.8 ± 0.3bcd
<i>Aphodius distinctus</i>	53.0 ± 2.6ab	34.3 ± 3.6a	11.4 ± 2.1abc	4.4 ± 1.3abcde	7.3 ± 1.2abcd	5.0 ± 1.3abcde	5.4 ± 0.8abcde	1.9 ± 0.5cde	2.1 ± 0.5cde	3.9 ± 0.8abcde	0.4 ± 0.2e	0.6 ± 0.3e
<i>Aphodius erraticus</i>	2.5 ± 0.6a	1.4 ± 0.5ab	0.4 ± 0.2ab	0.3 ± 0.2ab	0.5 ± 0.3ab	0.3 ± 0.2ab	0.1 ± 0.3b	0.4 ± 0.3ab	0.5 ± 0.2ab	0.5 ± 0.2ab	0.0 ± 0.0b	0.4 ± 0.2ab
<i>Aphodius fimetarius</i>	0.0 ± 0.0a	0.3 ± 0.2a	0.5 ± 0.3a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	1.5 ± 0.3a	0.1 ± 0.1a	0.1 ± 0.1a	1.9 ± 0.5a	0.3 ± 0.2a	0.0 ± 0.0a
<i>Aphodius grenarius</i>	1.0 ± 0.3a	0.9 ± 0.4a	0.4 ± 0.3a	0.5 ± 0.3a	0.1 ± 0.1a	0.5 ± 0.3a	0.0 ± 0.0a	0.4 ± 0.2a	0.0 ± 0.0a	0.4 ± 0.2a	0.0 ± 0.0a	1.0 ± 0.3a
<i>Aphodius prodromus</i>	0.8 ± 0.3a	1.1 ± 0.3a	0.0 ± 0.0a	0.3 ± 0.2a	0.3 ± 0.2a	0.0 ± 0.0a	0.6 ± 0.3a	0.0 ± 0.0a	0.4 ± 0.2a	0.1 ± 0.1a	0.0 ± 0.0a	0.5 ± 0.2a
<i>Aphodius testaceiventris</i>	0.5 ± 0.3a	0.8 ± 0.3a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a
<i>Aphodius walshii</i>	3.6 ± 0.9a	3.0 ± 0.7ab	0.8 ± 0.5abc	0.3 ± 0.2abc	1.1 ± 0.6abc	0.3 ± 0.2abc	0.3 ± 0.2abc	0.0 ± 0.0c	0.3 ± 0.2abc	0.4 ± 0.3abc	0.3 ± 0.2abc	0.5 ± 0.4abc
<i>Canthon pilularius</i>	7.4 ± 1.4abc	7.5 ± 1.4ab	1.9 ± 0.5abcd	1.6 ± 0.6bcd	2.4 ± 0.9abcd	1.3 ± 0.6bcd	1.0 ± 0.3bcd	0.1 ± 0.1d	0.4 ± 0.2d	0.5 ± 0.2d	0.1 ± 0.1d	20.3 ± 1.8a
<i>Copris fricator</i>	14.4 ± 2.6ab	13.0 ± 2.5abc	3.5 ± 0.7abcde	2.5 ± 0.8abcde	5.2 ± 1.0abcd	2.1 ± 1.0bcde	1.3 ± 0.6de	0.1 ± 0.1e	0.8 ± 0.2de	2.6 ± 0.8abcde	0.1 ± 0.1e	17.5 ± 3.1a
<i>Melanocanthon nigricornis</i>	6.9 ± 1.5ab	9.4 ± 2.6abc	2.1 ± 0.7abcde	1.8 ± 0.6abcde	2.9 ± 0.4abcd	1.9 ± 0.6abcde	1.3 ± 0.3bcde	0.8 ± 0.4de	0.6 ± 0.3de	1.1 ± 0.3bcde	0.0 ± 0.0e	15.0 ± 2.4a
<i>Onthophagus hecate</i>	61.0 ± 6.6abc	74.3 ± 7.1ab	21.4 ± 3.0abcde	16.5 ± 3.8bcde	21.5 ± 2.1abcd	13.6 ± 2.8bcde	12.9 ± 2.0bcde	8.9 ± 1.6de	4.4 ± 1.2de	7.1 ± 2.0de	2.9 ± 0.8e	128.3 ± 8.8a
<i>Onthophagus orpheus</i>	4.3 ± 1.2abc	4.6 ± 0.9ab	3.0 ± 0.8abcd	1.0 ± 0.5abcd	0.9 ± 0.4bcd	0.1 ± 0.1d	5.3 ± 0.6a	0.4 ± 0.2cd	0.9 ± 0.2abcd	2.3 ± 0.9abcd	0.2 ± 0.2d	0.2 ± 0.2d
<i>Onthophagus pennsylvanicus</i>	138.5 ± 15.5a	119.3 ± 17.2ab	25.1 ± 3.7abc	10.6 ± 3.1abcdef	11.9 ± 0.7abcd	7.6 ± 1.6cdef	13.9 ± 2.7abcde	6.5 ± 1.4cdef	4.1 ± 0.9def	6.8 ± 1.7cdef	0.5 ± 0.3f	2.6 ± 0.7def
<i>Phanaeus vindex</i>	11.5 ± 1.9ab	9.6 ± 1.7abc	2.3 ± 1.1abcd	1.5 ± 0.7bcd	2.9 ± 0.4abcd	1.9 ± 0.7abcd	0.5 ± 0.3d	0.1 ± 0.1d	0.0 ± 0.0d	0.1 ± 0.1d	0.0 ± 0.0d	44.3 ± 7.0a
Total	291.1 ± 27.6a	287.5 ± 28.5ab	75.9 ± 9.6abcd	42 ± 10.4abcdfg	59.5 ± 3.9abcdf	34.9 ± 5.6cdefg	44.9 ± 5.3abcdfg	21.0 ± 3.6efg	14.8 ± 1.9efg	28.1 ± 5.4efg	4.8 ± 0.9g	231.9 ± 20.6abc

Different letters indicate significance between dung types ($P < 0.05$, Kruskal-Wallis ANOVA, Tukey test post-hoc).

Table 2. Nutritional analysis of dung types used in field sampling

Dung type	Moisture (%)	Total N (%)	Organic N (%)	Organic C (%)	C:N ratio	Ash (%)	Phosphorus (%)	Potassium (%)	Calcium (%)	Magnesium (%)	Sodium (%)	Zinc (PPM)	Iron (PPM)	pH	Dry matter (%)
Human	75.71	5.74	5.54	51.96	9.1	10.69	3.28	1.33	2.31	0.73	0.14	796.9	391.1	5.8	24.29
Chimpanzee	79.29	3.33	3.25	43.71	13.1	17.88	4.78	2.77	2.88	0.48	0.03	366	487.1	6.2	20.71
Pig	62.23	2.00	1.96	33.49	16.7	38.65	3.19	0.75	2.86	0.54	0.20	442	2449.3	6.7	37.77
Bengal tiger	40.17	3.12	3.00	37.20	11.9	44.43	16.85	0.24	13.71	0.81	0.36	1240.2	2377.3	6.2	59.83
African lion	69.43	4.15	4.03	39.48	9.5	32.77	4.96	0.46	5.37	0.43	0.49	427	2616.2	6.2	30.57
Moose	70.37	2.28	2.21	45.75	20.1	13.81	2.76	0.26	2.68	0.92	0.06	424	1172.4	6.9	29.63
Bison	74.14	1.44	1.41	37.84	26.3	28.96	1.24	0.45	2.99	0.46	0.09	71.8	1694.3	8.1	25.86
Zebra	76.88	1.12	1.08	37.23	33.2	29.55	1.27	2.11	0.64	0.20	0.23	126.2	2198.2	7.1	23.12
Waterbuck	70.39	1.88	1.84	42.89	22.8	19.55	2.85	1.99	1.65	0.41	0.21	231.5	932.9	6.8	29.61

Although no differences were found when comparing overall mean capture within the native and exotic omnivore, carnivore, and herbivore groups, individual dung beetle species showed a high degree of variation in their attraction to dung types, as well as carrion (Table 1; Fig. 2). All *Aphodius* dung beetles were captured in the highest numbers in omnivore dung, with *A. coloradensis* Horn and *A. distinctus* (Müller) both being statistically greater with chimpanzee and human dung ($P < 0.05$) than moose, bison, and carrion bait types (Table 1). However, no differences in attraction were observed among dung types for *A. fimetarius* (L.), *A. granarius* (L.), *A. prodromus* (Brahm), or *A. testaceiventris* Fall.

Figure 2. Mean capture per trap of *O. hecate*, *O. orpheus*, and *O. pennsylvanicus* by bait type across traps in 2010 and 2011 ($N = 8$).

Canthon pilularius (L.), *Copris fricator* (F.), *Onthophagus hecate* (Panzer), *Melanocanthon nigricornis* (Say), and *Phanaeus vindex* MacLeay were all caught in the highest numbers with carrion, with chimpanzee or human dung being second most attractive (Table 1). In the case of *P. vindex*, carrion was more attractive than all herbivore dung types ($P < 0.05$); with 354 individuals captured with carrion while the next highest capture was chimpanzee dung accounting for only 92 total beetles. In contrast, *Onthophagus pennsylvanicus* Harold was more attracted to chimpanzee and human dung than carrion, as well as the dung of cougar, waterbuck, moose, donkey, and bison ($P < 0.05$). Only 21 *O. pennsylvanicus* were captured in carrion traps compared with 1,108 in chimpanzee dung and 954 in human dung (Table 1; Fig. 2). *Onthophagus orpheus pseudorpheus* (Howden and Cartwright) was also more attracted to human and chimpanzee dung than carrion ($P < 0.05$) (Table 1; Fig. 2).

Dung beetle community structure differed by dung type, with visible clustering among omnivore, carnivore, and herbivore feeding guilds on the NMDS plot (ANOSIM, $R = 0.48$, $P < 0.05$) and an overall stress level of 0.01 (Fig. 3). Carrion communities also differed

greatly from beetles attracted to all dung types ($P < 0.05$) (Fig. 3). Individuals from all species captured in this study were collected using human dung while only eight species were collected from traps baited with bison dung (Table 1; Fig. 3).

Figure 3. Two-dimensional nonmetric scaling ordination plot of communities of dung beetles, based on Bray-Curtis coefficient. Each point is a representation of composition of dung beetle species by bait type.

Dung composition differed among herbivores, carnivores, and omnivores as well as between exotic and native species. Nitrogen content (%) ranged from as low as 1.1 in zebra dung to 5.5 in human dung (Table 2). Organic carbon was also highest in human dung at 52.0%, while pig dung contained the lowest at 33.5% organic carbon. All omnivores and carnivores had lower C:N ratios than the herbivores tested. The ratio of carbon to nitrogen (C:N) varied from values of 9.1 in human dung to 33.1 in zebra. All measures of nutritional value and content of dung types are listed in Table 2.

Discussion

This study reveals variation in the attraction of dung beetles to native and exotic omnivore, herbivore, and carnivore dung. Our results support previous findings that omnivore dung is highly attractive when compared with that of herbivores and carnivores (Hanski and Cambefort 1991, Scholtz et al. 2009), although degree of attraction to a specific type of dung varied greatly among species (Table 1). This can largely be attributed to omnivore dung being more odiferous in comparison to that of a herbivore (Scholtz et al. 2009). Although differences in nutrient content are apparent among dung types (Table 2), no trends in capture appear to be correlated with nutritional value (Tables 1 and 2; Fig. 1).

Dung nutrient content differed greatly between mammals tested (Table 2). Nitrogen content is typically viewed as an estimation of dung quality in mammalian herbivores (Edwards 1991, Holter and Scholtz 2007). Human feces had the highest percent nitrogen (5.74%), which would be expected given the attractiveness (Table 2). However, zebra dung, which was more attractive than other herbivores, had the lowest nitrogen concentration at 1.18%. Because nitrogen is influenced by ash content, nutritional value may be better approximated by carbon-to-nitrogen ratio (Holter and Scholtz 2007, Scholtz et al. 2009). Holter and Scholtz (2007) showed that ratios should be between 10–20 to be most advantageous for dung beetles. The lowest C:N ratio was observed in human dung at 9.1. However, no correlation can be drawn between nutritional quality and attractiveness in this study, as the next lowest ratio was African lion dung at 9.5 (Table 2).

It is important to note that analysis of nutritional content may change over time because the concentration of microbes and fungi that inhabit all dung types will increase as decomposition takes place (Hanski and Cambefort 1991, Scholtz et al. 2009). To control for decomposition as much as possible, we replaced dung daily in the field so that no dung was > 24 h old. Further, because dung beetles are adapted to feed on liquid and small particles within the dung (Halffter and Matthews 1966, Halffter and Edmonds 1982, Holter 2000, Holter et al. 2002), during times of low dung availability, they will feed on other resources including rotting fruit and carrion (Hanski and Cambefort 1991, Scholtz et al. 2009). As a result of similar nitrogen content, resources such as carrion present an opportunity for generalist dung beetles to obtain nutrition, be it from the decaying carcass or the gut contents of the animal (Halffter and Matthews 1966, Scholtz et al. 2009). The dung beetles collected in the current study could have been attracted to a dung as a food source, rather than dung as a breeding resource and future studies should investigate the effects of exotic dung on breeding success.

Given the broad spatial and temporal distribution of a dung resource as well as intense competition for food and space (Anderson and Coe 1974, Cambefort 1982, Peck and Forsyth 1982, Hanski 1983, Janzen 1983, Doube 1987), utilization by dung beetles relies upon quickly locating a limited resource (Gillard 1967, Scholtz et al. 2009). Nonmetric multidimensional scaling analysis revealed that dung beetle community structure differed highly among mammalian feeding guilds and carrion, with omnivore, carnivore, and herbivore dung producing distinct groups on the nonmetric multidimensional scaling plot (Fig. 3). Nearly all species collected were caught in the highest numbers in chimpanzee and human dung, or carrion bait types (Table 1), which is likely a function of odor. Human feces is known to attract many species of dung beetle (Hanski 1983, Howden and Nealis 1975). However, this does not explain the observed differences in dung beetle attraction between omnivore dung and carrion, or among carnivores and herbivores with similar diets (Table 1; Figs. 1 and 2).

Halffter and Mathews (1966) noted that carnivore dung was much less sought after than the feces of herbivores and omnivores. In our study, omnivore dung was generally most attractive, but carnivore dung resulted in higher mean capture than nearly all herbivore dung types (Table 1; Fig. 1). In tropical forests, cattle dung represents an exotic resource that is competed for by a number of species belonging to different behavioral groups (Horgan 2005). The quantity of dung and spatial distribution of pats influences the number of

dung beetles and dung beetle species (Horgan 2005); however, the use of multiple dung types to determine total dung beetle community and the effects of proximity of different dung types has not been rigorously tested.

Our results support that most of the species captured are generalist feeders on all dung (Ratcliffe and Paulsen 2008). Although many of the dung beetle species collected are known to also be associated with carrion (Shea 2005, Price 2006, Ratcliffe and Paulsen 2008, Scholtz et al. 2009), our results suggest local preference of carrion in *Phanaeus vindex* and *Onthophagus hecate* (Table 1). For *O. hecate*, this is contrary to findings by Price (2006), who noted a significant preference for dung over carrion in New Jersey. While *O. hecate* and *O. orpheus* were readily captured in carrion (Table 1; Fig. 2), the congener, *O. pennsylvanicus*, was rarely captured in carrion (Table 1; Fig. 2). Our results suggest possible niche partitioning between *Onthophagus* species dung beetles; however, the results should be interpreted cautiously as they may be influenced by adult beetles seeking food resources rather than responding to a potential breeding resource. It should also be noted that dung beetles that use carrion for feeding will face greater competition from invertebrate necrophores, including maggots, carrion beetles, and ants and vertebrate scavengers, and thus carrion is likely to be a more ephemeral resource than dung (Horgan 2005). However, in an arid environment such as is found in western Nebraska, carrion may retain moisture longer than fresh dung and thus be attractive to dung beetles.

Attraction of dung beetles to dung from exotic and native species of the same feeding guild was similar. Exotic dung from zebra was generally more attractive than dung from other herbivores (Table 1) but was not statistically more attractive than donkey feces. Donkey and zebra are both members of the genus *Equus* and donkeys are a common livestock animal in the Great Plains. Additionally, bison dung, which would have been extremely common in the region < 150 yr ago, had the lowest capture of nearly all species collected (Table 1). It was surprising that native dung beetles, which coevolved with bison in this region (Van Every 1964, Jones 1968, Benedict 1996, 2000; Ratcliffe and Paulsen 2008), showed little attraction to this dung type (Table 1). Because the bison dung in our study was obtained from zoo animals, their diet was similar to the diet provided to the water-buck, zebra, donkey, and moose. Our results suggest dung beetle response to resource availability or preference for a novel food source. This information could hold further importance when considering that dung beetles can act as an indicator of change in an ecosystem (Davis et al. 2001).

It is also worth mentioning that because dung was collected from zoo animals, diet was nearly identical among herbivores and among carnivores from which dung was collected. This reinforces that overall dung quality and attractiveness are also a function of inherent physiology, digestion, and bacterial microflora present within the mammal (Scholtz et al. 2009), not a result of food type alone.

Our data indicate that dung beetle species in Nebraska differ in their attraction to mammalian dung and carrion, with many exhibiting strong preferences (Table 1; Fig. 2). With exotic game ranches increasing and further introduction of exotic megafauna being proposed to restore Pleistocene ecological potential (Rubenstein et al. 2006), dung beetle communities may be affected. More research is needed to identify specific preference for native

and exotic dung types, and future studies should be aimed at directly testing the effects of mammal diet, dung nutritional value, and the correlation with dung beetle attraction.

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