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Variation in Dung Removal Rates by Dung Beetles (Coleoptera: Scarabaeoidea) in a Temperate, Dry Steppe Ecosystem

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Abstract: During their feeding process, dung beetles perform a series of ecosystem functions that provide valuable ecosystem services, such as soil fertilization, improvement of soil properties, plant growth enhancement, and biological pest control. However, in the grasslands of the Central Asian dry steppe, the effects of dung beetles on dung removal remain almost unstudied. Here, we examined dung removal by different dung beetle species (*Colobterus erraticus* (Linnaeus, 1758), *Onthophagus bivertex* Heyden, 1887, *Onthophagus gibbulus* (Pallas, 1781), *Gymnopleurus mopsus* (Pallas, 1781), *Cheironitis eumenes* Motschulsky, 1859, and *Geotrupes koltzei* Reitter, 1892), and compared the impacts with control treatments (without beetles) under natural pasture conditions and in the laboratory. We examined the influence of different variables on dung removal rates, such as dung type and dung beetle traits (nesting strategies, abundance, body size, and biomass). We found higher dung removal rates during the initial 48 h in field and laboratory conditions. Among nesting strategies, tunnellers demonstrated significantly higher dung removal rates than dweller and roller species. The highest amount of dung removal was estimated for *C. eumenes* (6.5 g/day by seven individuals). We found no significant relationship between dung removal rates and dung beetle body size or biomass, but we observed a strong negative correlation between dung beetle abundance and dung removal rates. Our findings highlight the importance of dung type and age, nesting strategies and abundances of dung beetles, and experimental conditions, which are the main factors driving the process of dung removal.

Keywords: dung decomposition; functional groups; body size; biomass; abundance; dung types; experimental condition

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1. Introduction

Dung beetles (Coleoptera: Scarabaeoidea) play an important role in dung decomposition, especially in herbivore manure [1–3]. Most dung beetles highly affect dung removal through their nesting and feeding activities [4–6], serving as ecosystem engineers that increase soil nutrients and properties and, therefore, enhance plant growth [6–8], these beetles play a crucial role in the biological control of dung breeding pest flies [9–13].

In previous studies, dung removal rates by dung beetles were examined with respect to several biological variables in natural and artificial pastures. These studies found that dung removal rates are closely associated with functional groups, body size, biomass of dung beetles [2,14–19], and dung type [18,20,21]. There are both diurnal and nocturnal dung beetles, and because dung is often removed within hours or a few days of deposition, diffuse competition between nocturnal and diurnal guilds is likely to be of great importance [22,23]. Alvarado et al. [5] suggested that dung beetle activity represents an important aspect of the dung decomposition process in which body size and abundance of beetle species are important. Functional groups of dung beetles have different dung removal rates depending on feeding, nesting, and breeding patterns [9,24]. Overall, tunnellers have higher dung decomposition rates compared to the other functional groups [3,19,25].

Moreover, dung beetles have different choices of dung types associated with dung decomposition. For instance, Holter and Scholtz [26], Bogoni and Hernández [27] found that dung beetle species differed in their preferences depending on the nutritional and moisture content of dung. According to Holter [28], some dung beetles prefer dung with higher moisture content and smaller fiber particles, because such dung is protein-rich and contains more microbial biomass. Dung types and moisture content depend greatly on the geographical region, varying with pasture quality and climatic conditions [29,30].

Some studies examined the effects of dung beetle abundance on dung removal within different beetle communities [22,31,32]. Researchers found that competition between functional groups of dung beetles and breeding succession depend on habitat type, dung age, and body size of beetles [33–36]. However, few studies have examined the effects of dung beetle abundance or density on dung decomposition [16]. The colonization of dung by a high-density of dung beetles belonging to different species has been reported from tropical and sub-tropical regions [37,38], where trapping can yield several hundred to thousands of individuals per trap [24,39]. Alternatively, the dry steppes of the temperate region support a low density of dung beetles [40], with an average number of individuals varying between 14 and 64, depending on dung types [41]. Little is known about dung removal rates by different dung beetles, and about intraspecific competition among dung beetles in this region.

According to Yamada et al. [31], a high abundance of beetles leads to rapid removal of dung, with differences of dung removal rates among the functional groups of dung beetles. Biological aspects, such as functional groups, body size, biomass and abundance are not only an important factor in dung removal, but also closely associated with environmental conditions, such as temperature, humidity, wind, and more [42]. Climatic conditions are an essential aspect of dung degradation by dung beetles. According to Buse and Enthling [25], dung removal by dung beetles was strongly affected by habitat types as well as geographical localities [2,43], and anthropogenic perturbation level [32].

Currently, there are 129 known species of scarabaeoid beetles belonging to 42 genera and 11 families in Mongolia, of which 80 species from 15 genera and four families belong to the coprophagous dung beetle clade, while others to the phytophagous scarab beetle clade [44]. Fifteen species of dung beetles from three families composed by dwellers and tunnellers were found in Khar Yamaat Nature Reserve [41], where we conducted the field experiments of the present study. However, completely lacking is the data on the contribution of dung beetles to livestock dung decomposition in Mongolia, although the country has extensive traditional nomadic animal husbandry.

We investigated the effects of different dung beetle species on dung decomposition in a dry steppe ecosystem of Mongolia. We examined the influence of biological traits of beetles and environmental types on dung removal rates, specifically the nesting strategy, abundance, body size, and weight of the dung beetles involved, dung types, experimental conditions (field vs. laboratory), and age of dung. We addressed the following hypotheses: (1) Both the age and type of dung have an important effect on the dung removal activities by dung beetles; (2) The dung removal rate by dung beetles is higher in the natural environment than in laboratory conditions; (3) Tunneller and roller species remove more dung than dwellers; (4) The body size and biomass of dung beetles have clear relationships with dung decomposition rate; (5) The abundance of beetles has a positive effect on the decomposition of livestock dung.

2. Materials and Methods

2.1. Study Area

The field study was performed in Khar Yamaat Nature Reserve (N47°38′, E112°05′, 1350–1380 m a.s.l.), eastern Mongolia, which has year-round grazing. This nature reserve is located at the junction between Central-Khalkh dry steppe, Mongol-Dahurian forest-steppe, and Eastern-Mongolian tall-grass steppe [45]. The climate is arid and continental, characterized by relatively hot summers (mean summer temperature in July: 19.5 °C), cold winters (mean winter temperature in January: −22.5 °C), dry and windy springs, and cool autumns with low humidity. Precipitation is low and seasonal (mean annual precipitation

= 250−280 mm), with most precipitation falling in the summer as rain [46,47]. Soils are characterized by three main types: chestnut brown, kastanozem, and dark gray [45]. The region is a high upland (altitude 800–1380 m a.s.l.) with steppe vegetation dominated by *Stipa grandis* (Smirnov, 1929) and *Polygonum divaricatum* (Linnaeus, 1753) [48]. Livestock have grazed the nature reserve for more than 2000 years, with additional grazing by wild herbivores, including roe deer (*Capreolus pygargus* (Pallas, 1771)), Mongolian gazelle (*Procapra gutturosa* (Pallas, 1777)), and red deer (*Cervus elaphus* Linnaeus, 1758). Study areas such as the Khar Yamaat Nature Reserve, where significant numbers of both wild and domestic herbivores remain extant, can be an ideal subject for studying the ecology of dung beetle communities.

During the field experiments, there were no rainy days. Additionally, we performed laboratory experiments using dung beetles collected from the field.

2.2. Dung Beetles

We conducted field experiments in natural pasturelands in August 2019. We collected dung beetles of six species for our field and laboratory experiments from two different eco-regions. We captured two species of dung beetles (*Gymnopleurus mopsus* (Pallas, 1781) and *Cheironitis eumenes* (Motschulsky, 1859)) from desert steppes and four species (*Colopterus erraticus* (Linnaeus, 1758), *Onthophagus bivertex* Heyden, 1887, *Onthophagus gibbulus* (Pallas, 1781), and *Geotrupes koltzei* Reitter, 1892) from mountain steppes. These species were the most common and abundant in the study area, that is why we selected them for our experiments. Selected species represent different functional traits (nesting strategies) of dung beetles including dwellers (endocoprids), tunnellers (paracoprids), and rollers (telecoprids). We tried to include all nesting strategies of dung beetles, in our experiments, but their representation was not equal in the study area. We collected live beetles by hand from fresh dung of cattle and horses in the pastures.

We measured body size (average body length and width) of dung beetles using a caliper to the nearest 0.01 mm, randomly selecting 45–54 individuals from each species. We expressed biomass of each species as dry body weight, which we oven-dried at 60 °C for 48 h (Table 1). We weighed the body mass of beetle individuals using an analytic digital scale to 0.0001 g. These measurements were made to clarify whether there is a relationship between the body size, biomass of dung beetles, and the dung decomposition rate.

Table 1. Nesting strategies, body size, and biomass of dung beetle species used in the field and laboratory experiments.

Species	Nesting Strategies	Body Length (mm)	Body Width (mm)	Dry Weight (mg)
Colobterus erraticus	Dweller (D)	7.7 (±0.43)	3.9 (±0.25)	11 (±0.00)
Onthophagus bivertex	Tunneller (T_1)	7.4 (±0.40)	4.2 (±0.23)	17 (±0.00)
Onthophagus gibbulus	Tunneller (T_2)	10.5 (±1.04)	6.0 (±0.65)	53 (±0.06)
Gymnopleurus mopsus	Roller (R)	14.1 (±1.27)	9.2 (±1.05)	120 (±0.04)
Cheironitis eumenes	Tunneller (T_3)	15.0 (±0.87)	8.1 (±0.45)	78 (±0.03)
Geotrupes koltzei	Tunneller (T_4)	20.2 (±1.52)	11.5 (±0.86)	260 (±0.06)

2.3. Dung and Soil Sampling

During field experiments we collected fresh dung from horses and cattle (newly dropped on the ground, i.e., before they were colonized by invertebrates) from grazing areas in the mountain steppes and examined the dung to remove and exclude other invertebrates using tweezers if one occurred there (not disturbing dung structure). For the laboratory experiments, we brought fresh dung from the field and preserved it in a freezer. Before the experiments, we examined the moisture content of the dung. We calculated water content of dung as the difference between fresh and dry weight. We determined the dry weight of dung after oven-drying it for 48 h at 60 °C. In both field and laboratory experiments, we used the same chestnut brown soil, which we collected from the upper soil layer in the steppe (up to 10 cm).

2.4. Experimental Design

Part of this research was conducted in the field and others in the laboratory (see below). We planned to conduct all the experiments in both the field and laboratory, but due to the drastic changes in the climatic conditions of the study area, some experiments were carried out only in the laboratory. We used a plastic bucket (25 cm diameter, 18 cm deep) filled with approximately 1–1.5 kg of dry and sieved natural brown soil. Each experimental unit consisted of 5 buckets placed two meters apart with 5 replicates, i.e., a total of 25 buckets. We placed a plastic mesh with 10 mm holes on the soil surface of the bucket to make it easier to separate the residual dung from the soil, and then we put in 100 g of fresh dung. This mesh has large holes and fine fibers, it does not interfere with the dung removal capacity.

We then released a variable number of dung beetles into the buckets. Finally, we covered the buckets with a 1 mm fiber mesh to prevent the entry of other dung feeders. To measure the dung removal rate, we introduced 1, 3, 7, 14, and 28 individual dung beetles (depending on body size) to the buckets in each of 5 replicates (buckets). After taking body measurements of each species, we determined the above numbers based on how many times a species was larger in body size than the other species. We tested all species in horse and cattle dung and compared those buckets with controls (buckets without beetles). At the start of both the field and laboratory experiments, we fasted dung beetles for 8–10 h in a plastic box with soil and air.

During the experiments, we measured the dung removal rate for 96 h (at time intervals of 24, 48, 72, and 96 h), because after 4 days the dung became completely dry in both field and laboratory conditions. We used seven dung beetle individuals of each species in the laboratory experiments except for the study of the relationships between dung beetle numbers and dung decomposition (see below).

We considered dung removal rate to be the sum of both buried (dung mass carried into the soil) and consumed dung by beetles. We calculated the removal of dung by beetles using two different methods: (a) dung removal (DR) was the weight difference between the initial and residual dung on the soil surface, and (b) net removal (NR) was calculated by comparing the residual dung of experiments and control dung (evaporation weight). We calculated the mean weight of the removed dung (g) per individual by dividing the weight by the number of individuals in each bucket averaged over the five replicates.

2.5. Data Analysis

As all data were normally distributed, we used unpaired *t*-tests for independent variables and determined the variation in dung removal rates with different dung types (horse and cattle dung), and different experimental conditions (field and laboratory). We used paired *t*-tests to investigate differences in dung removal per hour. We examined the variation between functional traits through one-way ANOVA. For laboratory experiments, we tested the relationship among the dung removal, the body size, and dry biomass of beetles using generalized linear models (GLM) with the Gaussian error distribution. We examined relationships between the number of dung beetles and dung removal rates of different beetle species using Pearson's correlation. We set the significance level at $p \leq 0.05$. All data presented as means ± 1 standard error (SE). We conducted all statistical analyses using the *R* statistic package version 3.4.4 [49].

3. Results

3.1. Dung Age

Dung removal (DR) was higher in the first 48 h than in the subsequent 48 h ($t = 5.69$; $df = 11$; $p < 0.0001$), and then slowed down markedly for all investigated species except for *G. mopsus* and controls. The mean amount of dung removed by six species after 24 h and 48 h were an average of 4.68 ± 1.40 g and 3.52 ± 1.42 g, respectively, with weight loss of the control dung being much less (an average 1.37 ± 0.26 g and 0.96 ± 0.51 g, respectively). After 48 h, the mean dung removal rate by dung beetles decreased greatly. Over the next two days (72 h and 96 h), dung beetles removed an average of 1.84 ± 0.59 g and 1.13 ± 0.54 g of dung, respectively. Over the same time intervals, the weight loss of control dung was an average of 1.13 ± 0.63 g for 72 h, and 0.97 ± 0.08 g for 96 h (Figure 1). In the first 48 h, net removal (NR) was the highest at 96.5%, and in the next 48 h was removed from 0.6 to 1.4% of dung, depending on dung beetle species (Table 2).

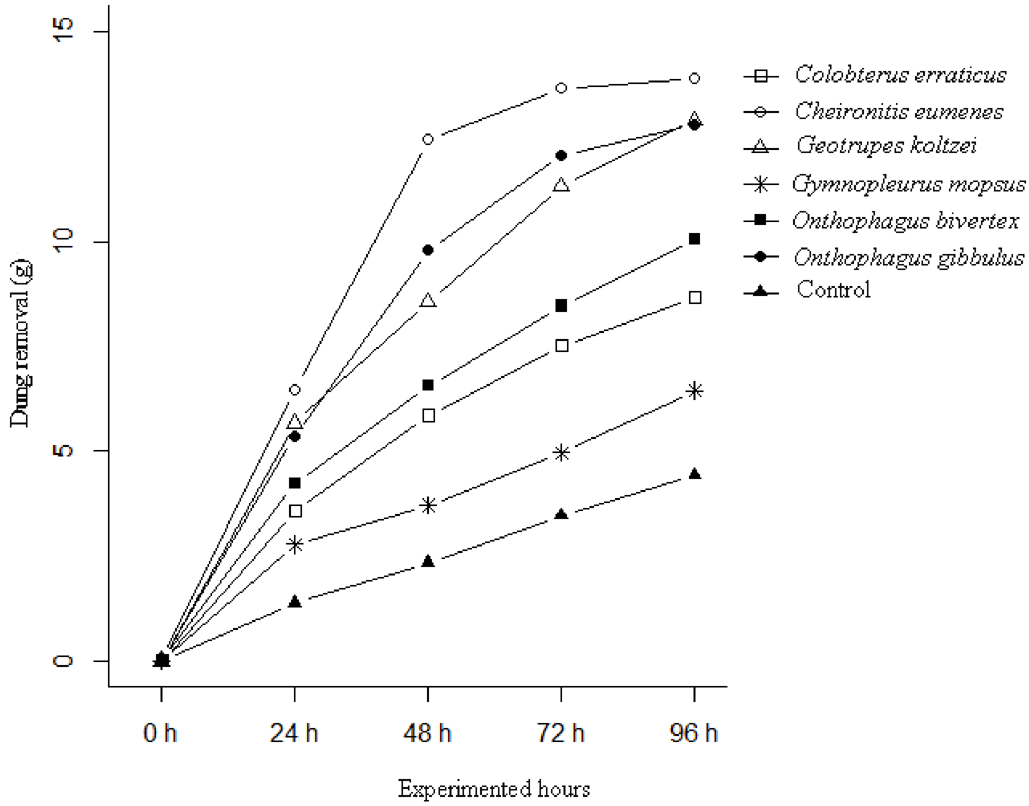

Figure 1. Dung removal (DR) by six dung beetle species and weight loss of control dung in the laboratory over four days (experimented with cattle dung).

Table 2. Net removal (NR) by different dung beetle species over four days (experimented with cattle dung in the laboratory).

Species	24 h	48 h	%	72 h	96 h	%
	Net Weight (g)			Net Weight (g)		
Colobterus erraticus	2.19	1.33	96.5	0.52	0.19	0.7
Onthophagus bivertex	2.86	1.37	95.8	0.76	0.61	1.4
Onthophagus gibbulus	3.99	3.46	92.6	1.15	0.00	1.2
Gymnopleurus mopsus	1.40	2.26	96.3	0.13	0.51	0.6
Cheironitis eumenes	5.10	4.98	89.9	0.10	0.00	0.1
Geotrupes koltzei	4.30	1.93	93.8	1.62	0.60	2.2

3.2. Nesting Strategies

Nesting strategies of dung beetles differed significantly ($F_{6,28} = 93.89$, $p < 0.0001$) in dung decomposition rates. All tunnellers removed significantly higher amounts of dung than dweller and roller species (Figure 2). The amount of removed dung was the highest for *C. eumenes* (T_3) compared to the other three tunneller species; this species reduced the total mass of dung by 12.4 ± 1.1 g after two days.

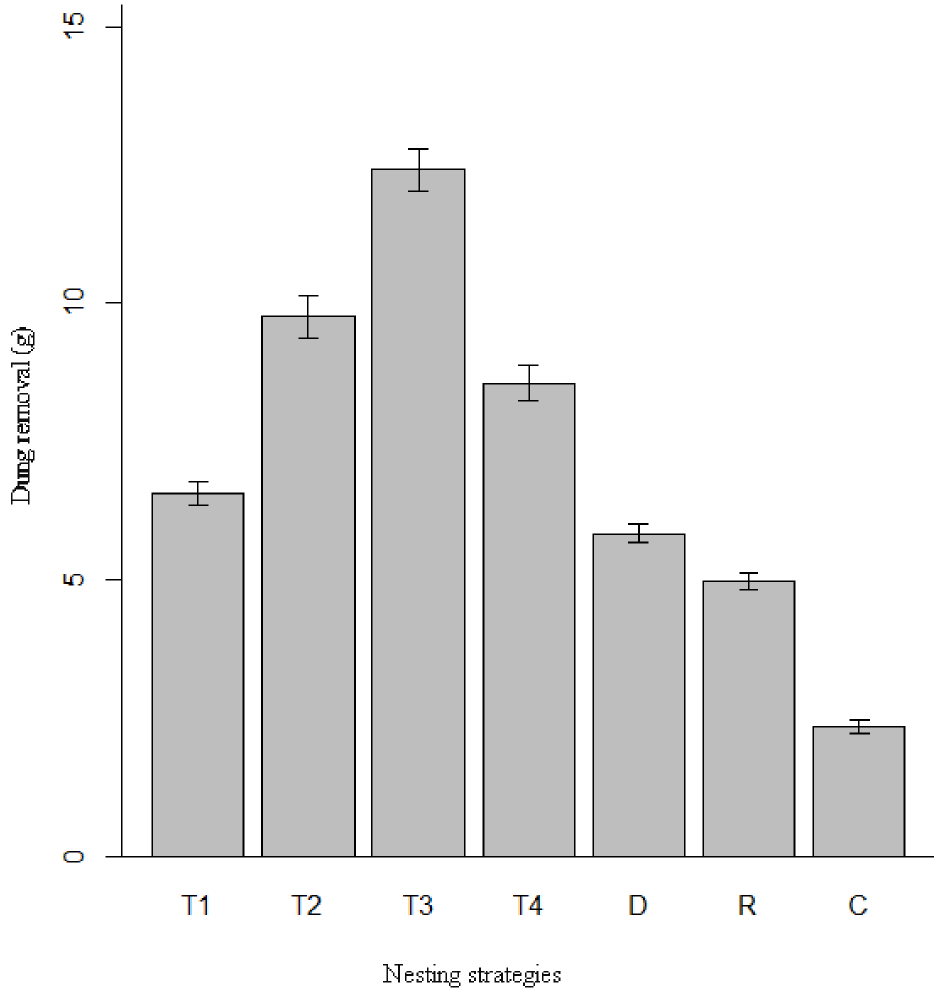

Figure 2. Differences in dung removal by dung beetles of different nesting strategies after 48 h in the laboratory (experimented with cattle dung). See Table 1 for nesting strategy abbreviations.

Dung decomposition by both dweller (t = 33.37; df = 4; $p < 0.0001$) and roller species (t = 38.92; df = 4; $p < 0.0001$) was higher than the weight loss of control dung, and these beetles removed an average of 5.9 ± 0.5 g and 5.0 ± 0.4 g, respectively. In comparison, dung in the control buckets lost a mean of 2.3 ± 0.3 g after 48 h under laboratory conditions.

3.3. Body Size and Biomass

We found no significant relationship between the mean body size of beetles and dung removal rate (Figure 3). Indeed, we found no significant relationships between the removed dung and beetle biomass (R^2 = 0.0008; $F_{1,4}$ = 0.003, p = 0.95), body length (R^2 = 0.13; $F_{1,4}$ = 0.60, p = 0.48), and body size (R^2 = 0.05; $F_{1,4}$ = 7.85, p = 0.66).

3.4. Dung Types

The water content in dung differed significantly depending on dung type (t = 9.82; df = 21; $p < 0.001$). Horse and cattle dung contained 79% and 84% water content, respectively, and each species of dung beetle displayed different decomposition effects. Dung removal rates of the horse and cattle dung by most beetle species differed significantly over 24 h and 48 h (Table 3). Dung removal rates for two dung beetle species (*O. bivertex* and *C. eumenes*) differed significantly over 24 h and 48 h (Table 3). Two other species, *O. gibbulus* and *G. mopsus* had significantly different dung decomposition rates only after 48 h (Table 3).

Weight loss of dung in the control buckets also differed significantly by dung type (Table 3). One of the species used in the experiment, *C. erraticus*, was excluded due to its excessive mortality during this experiment.

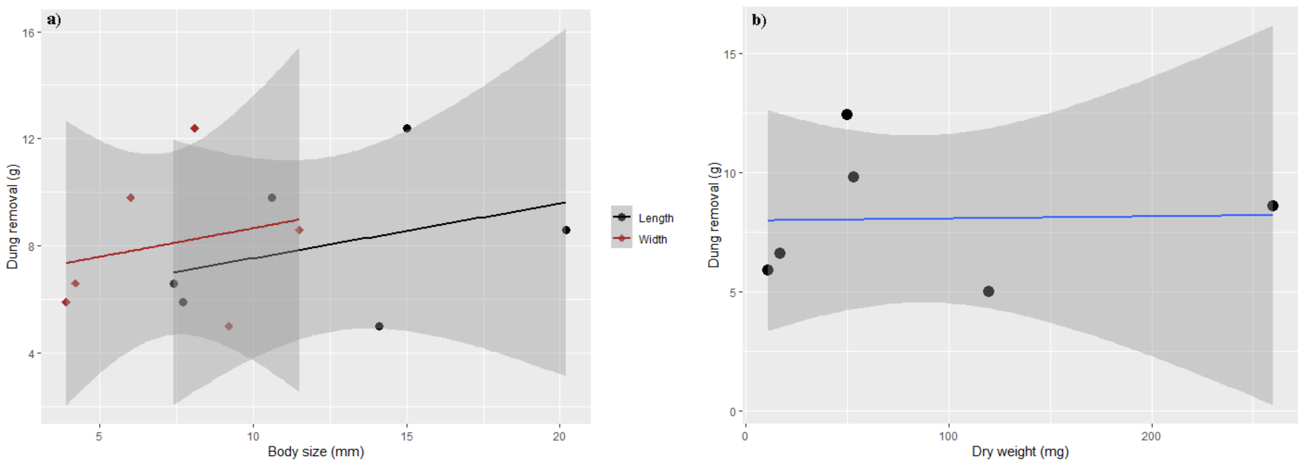

Figure 3. Relationships between the mean amount of removed dung and (**a**) body size (**b**) beetle biomass, after 48 h (experimented in the laboratory with cattle dung). Color lines represent insignificant linear regressions between the removed dung and beetle body size and biomass (t = 2.34; df = 6; $p > 0.05$).

Table 3. Mean (±SE) dung removal (g) by different dung beetle species after 24 h and 48 h in the laboratory.

Species	**24 h**		*t*	**df**	*p*	**48 h**		*t*	**df**	*p*
	Horse Dung	**Cattle Dung**				**Horse Dung**	**Cattle Dung**			
Onthophagus bivertex	3.59 ± 0.54	4.23 ± 0.30	2.34	6	0.05	3.01 ± 0.25	2.33 ± 0.37	−3.42	7	0.01
Onthophagus gibbulus	6.27 ± 1.17	5.36 ± 0.27	−1.68	4	0.16	3.34 ± 0.48	4.42 ± 0.89	2.34	6	0.05
Gymnopleurus mopsus	3.38 ± 0.41	3.71 ± 0.40	1.28	8	0.23	2.67 ± 0.31	1.26 ±0.19	−8.61	7	0.0005
Chironistis eumenes	10.05 ± 1.01	6.47 ±1.82	−3.84	6	0.007	0.66 ± 0.41	5.94 ± 1.10	10.08	5	0.0001
Geotrupes koltzei	5.22 ± 1.35	5.67 ± 0.47	0.70	5	0.51	3.34 ± 0.37	2.73 ± 1.09	−0.86	5	0.42
Control	1.96 ± 0.12	1.37 ± 0.26	−4.59	6	0.004	1.81 ± 0.35	0.96 ± 0.51	−3.04	7	0.01

3.5. Beetle Abundance

For all species, the amount of dung removed correlated strongly and negatively with the number of dung beetles in each bucket (Figure 4; Table 4). In other words, dung removal rates decreased with an increased number of dung beetle individuals. We observed that over two days (24 and 48 h intervals), dung decomposition rates (g/d/# beetles) dropped by about $\frac{1}{2}$ for every doubling of beetle numbers (Table 4).

3.6. Experimental Conditions

We compared the variation in dung removal rates for the three tunnellers, which were the species that removed the most dung, in laboratory and field conditions. *Cheironitis eumenes* showed a significant difference (t = −5.61; df = 4; $p < 0.01$) in dung removal between the two experimental conditions (11.81 ± 0.44 g in the field, 7.75 ± 1.43 g in the laboratory). We found no significant differences in dung removal for the two other species, *G. koltzei* (t = −1.27; df = 5; p = 0.25) and *O. gibbulus* (t = −0.80; df = 6; p = 0.45). As for the control, the dung weight loss was significantly different (t = 2.86; df = 8; p = 0.02) between the laboratory (3.76 ± 0.26 g) and field (3.34 ± 0.26 g) (Figure 5).

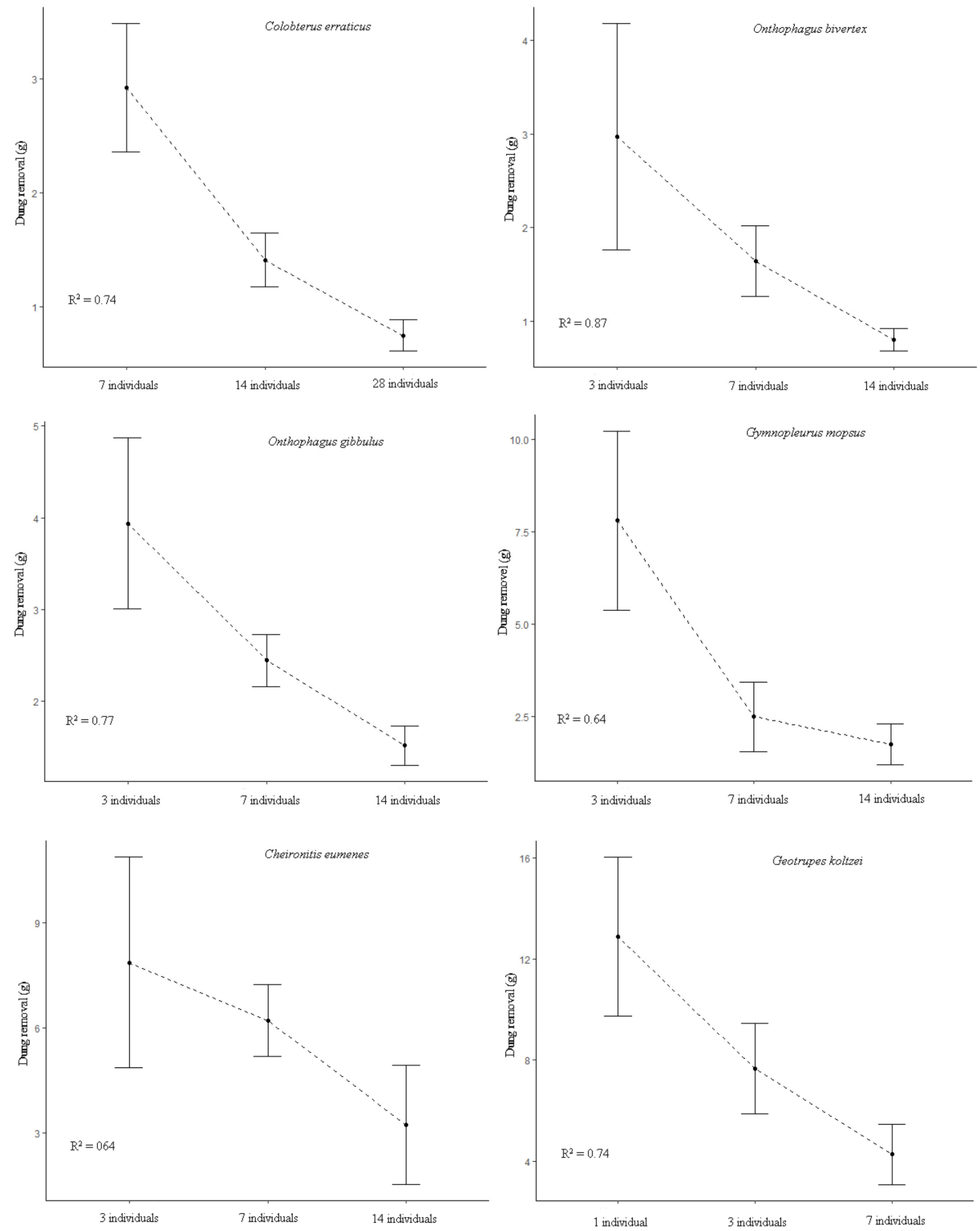

Figure 4. Relationships between the abundance of various beetle species and dung removal rates after 48 h in the laboratory (experimented with cattle dung).

Table 4. Relationships between beetle abundances and dung decomposition rates (g/d) (experimented with cattle dung during 24 and 48 h in the laboratory).

Species	**Number of Individuals**	**Dung Removal (g)**									
		24 h	R^2	F	df	p	**48 h**	R^2	F	df	p
Colobterus erraticus	7	3.56 ± 0.30	0.78	47.53	13	<0.0001	2.29 ± 0.54	0.74	37.74	13	<0.0001
	14	1.64 ± 0.34					1.18 ± 0.03				
	28	0.89 ± 0.15					0.61 ± 0.10				
Onthophagus bivertex	3	4.32 ± 0.12	0.87	67.51	10	<0.00001	1.62 ± 0.06	0.87	71.95	10	<0.00001
	7	2.11 ± 0.15					1.16 ± 0.18				
	14	0.90 ± 0.06					0.70 ± 0.04				

Table 4. *Cont.*

Species	Number of Individuals	Dung Removal (g)									
		24 h	R^2	*F*	*df*	*p*	**48 h**	R^2	*F*	*df*	*p*
Onthophagus gibbulus	3	5.03 ± 0.79	0.77	44.36	13	<0.0001	2.84 ± 0.45	0.77	43.59	13	<0.0001
	7	2.68 ± 0.13					2.21 ± 0.45				
	14	1.69 ± 0.35					1.35 ± 0.06				
Gymnopleurus mopsus	3	10.89 ± 1.25	0.71	32.37	13	<0.0001	4.71 ± 0.58	0.61	20.88	13	<0.001
	7	3.71 ± 0.40					1.26 ± 0.19				
	14	2.40 ± 0.36					1.08 ± 0.36				
Cheironitis eumenes	3	9.98 ± 2.34	0.55	11.08	9	<0.01	5.73 ± 1.24	0.64	16.68	9	<0.01
	7	6.47 ± 1.82					5.94 ± 1.10				
	14	4.65 ± 0.30					1.81 ± 0.56				
Geotrupes koltzei	1	16.39 ± 2.89	0.79	47.03	12	<0.0001	9.40 ± 2.12	0.75	37.34	12	<0.0001
	3	9.46 ± 0.74					5.88 ± 1.24				
	7	5.67 ± 0.47					2.89 ± 1.09				

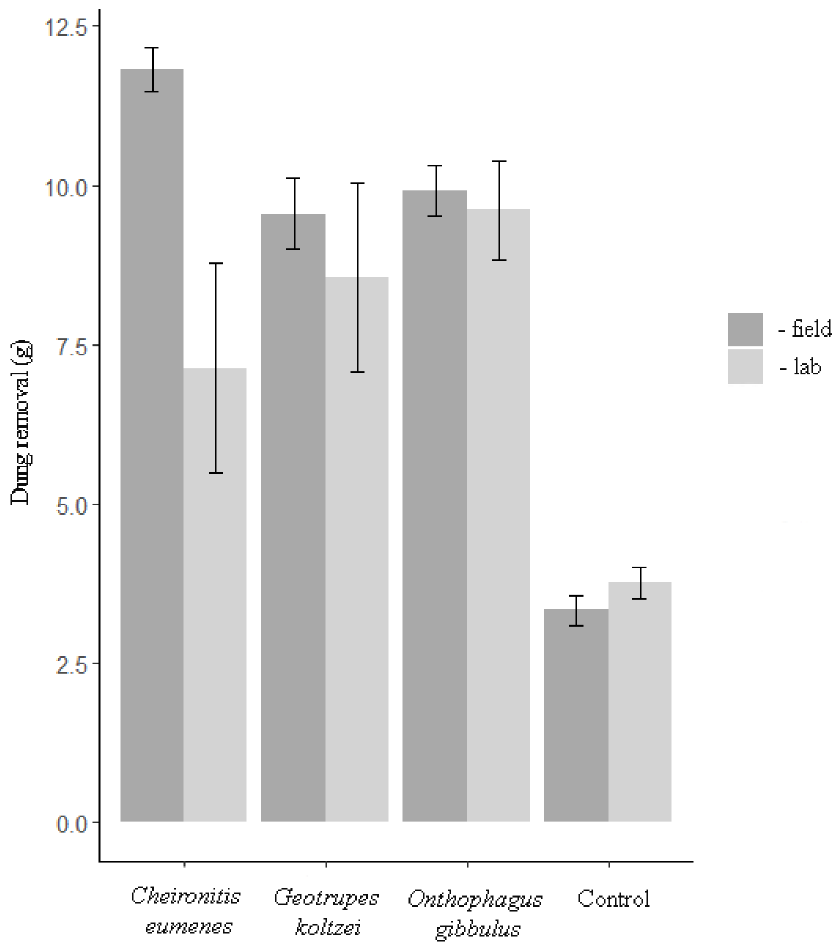

Figure 5. Comparison of dung removal rates by tunneller species in laboratory and field conditions after 48 h (experimented with horse dung).

4. Discussion

Our study represents one of the first efforts to systematically understand the effects of dung beetles on dung decomposition in the steppes of Mongolia, including the effects of functional groups, body size, biomass, and number of individuals, and time (dung age) on dung removal rates. We observed a significantly larger amount of dung removal by most dung beetle species during the first 48 h than in the next 48 h of the experiment, which we explain as follows. Higher moisture content in the first phase of the experiments probably led to the higher rates of dung removal we observed in the initial 48 h of our experiments, followed by dramatically decreasing rates. Dung of domestic herbivores contains between 70–89% water by weight [26,28], and it is well documented that most dung beetles prefer newly dropped fresh dung as they feed on its microorganism-rich liquid component [28,42]. Our results are in some agreement with other studies in which dung beetles are able to transfer all deposited herbivore dung into the soil within hours after deposition [42,50], but we believe that this is related to the biological characteristics of the beetle species and, in addition, dung removal rates appear to differ by ecological region. *Cheironitis eumenes* and *Onthophagus gibbulus* could be the most important species for dung removal in the dry steppe of Mongolia. Thus, our hypothesis, suggesting an importance of dung age, could be partly verified. We showed that dung beetle species affected dung removal differently. A previous study reported that over 70% of dung mass was lost during three days in the dry and wet prairie habitats of the USA [51], far less than the 90–97% dung mass loss we observed in just two days in the dry steppe habitat of Mongolia.

Differences in dung removal rates among nesting strategies of dung beetles is also important. The paracoprids (tunnellers) were the dominant functional trait in the study area and were responsible for a significantly greater proportion of dung removal than roller and dweller species. This is probably explained by their greater activities in dung recycling, favoring the productivity of pastures in temperate grasslands. Many previous studies in other regions of the world found the same results [19,25,50,52]. Other researchers found that tunnellers collected and buried a greater amount of dung during a shorter time than did rollers [53]. The relatively low dung decomposition rate by dweller and roller species in our experiments can be explained as follows. The endocoprids (dwellers) feed directly on the dung, but they do not relocate the food, and so are less important in the dung removal process, in terms of the amount of dung removed (see [17]). The telocoprids (rollers) require special conditions, such as a wide space for the rolling, carrying, and burying of dung balls [54,55]. It is evident that in our experimental condition, the rollers were not provided with sufficient spaces to roll and relocate their food ball. Thus, our hypothesis is partially confirmed that the dung beetle nesting strategy is crucial to the dung decomposition. Future research should examine how various biological attributes of dung beetle species, such as differences in feeding phases, breeding periods, etc., influence dung removal [9].

Some recent research showed that dung decomposition by dung beetles positively correlated to the beetle body size [14] and biomass [15,18]. However, we found no significant relationship between these variables (i.e., among and within functional traits), suggesting that beetle nesting strategy is more important than body size and biomass. For example, we found that smaller tunneller species had higher dung removal rates than larger species from other functional groups. Other researchers highlighted the importance of body size within each functional trait to differences in dung removal rates [56]. The biomass and body size of dung beetles are ecologically relevant characteristics, because large-sized species with high biomass remove and bury large amounts of dung faster than smaller species do [52]. Our results suggest, however, that in the dry grassland of Mongolia, a few, abundant, middle-sized species are responsible of the incorporation of dung into the soil (see also [3]). Thus, our hypothesis that beetle body size and biomass are important for dung removal could not be supported by this study.

Differences in removal rates among various dung types based on beetle species' feeding choices are well documented [27,57,58] and reflect dung quality and moisture content [26]. We observed that the dung removal by two dung beetle species differs significantly between dung types (cattle and horse dung) in the initial 48 h of experiments, but in the subsequent 48 h, dung removal by most beetle species (except only *G. koltzei*) differed depending on dung type, possibly because of different moisture content in the horse and cattle dung. There are at least two possible explanations for differences in dung removal rates between various beetle species. First, dung beetles restrict their ingested food to very small particles, while large particles in the fresh dung are rejected by the mouthparts [26]. Horse dung is much coarser than cattle dung, but has a lower water content, and most of this coarse material is likely to consist of lignocellulosic plant fibers. These biopolymers are too hard to digest for small to medium sized dung beetles, but large bodied dung beetles such as *G. koltzei* may easily digest both horse and cattle dung, and that is why there was no difference for this species. Second, besides water contents and particle structure, horse and cattle dung are different in microbial biomass, which is the main food of dung beetles. With the ageing of dung, its moisture content decreases, and the content of organic and inorganic matters also changes [28]. It is possible that the nitrogen and other nutrient contents in the cow and horse dung, mainly associated with dead and alive microbial biomass from the herbivore's gut, are different, as one of these herbivores is ruminant. Therefore, we believe that there is a difference in the dung removal rates of beetles feeding on ageing dung of horses and cattle. Our hypothesis on the importance of dung type could be thus supported by this study.

Several researchers have discussed the influence of inter- and intra-specific competition among dung beetles for food, and found higher complexity within intraspecific competition than with interspecific competition in natural pastures [23,36]. These studies showed that beetle competition was closely related to dung size. Other researchers reported positive relationships between beetle abundance and total dung removal in the field [22,32]. Similarly, our results showed a positive relationship between total dung removal and beetle abundance. However, the amount of removed dung per individual decreased as the number of beetles increased. These findings support the hypothesis that intraspecific competition influences the amount of dung removed per individual. As in our study, Giller and Doube [23] found decreasing dung removal rates per individual with increased beetle numbers for three tunneller species. It is evident that under experimental conditions, as the number of beetles feeding on the same droppings increases, the competition between the individuals undoubtedly increases, thus reducing the rates of dung decomposition by an individual beetle.

We hypothesized that dung beetles would remove a significantly higher amount of dung in the field than in the laboratory, where fresh dung dried more rapidly. Amore et al. [42] showed that higher air temperatures reduced dung removal rates. In our study, only *C. eumenes* demonstrated significant higher dung removal rates in the field compared to the laboratory. We found no significant differences in dung removal rates for two other tunneller species. It is not easy to interpret why there is such a difference between tunneller species, but we suggest the following. As mentioned above, *C. eumenes* inhabit the lowland desert steppe, while two other species, *G. koltzei* and *O. gibbulus* occur in mountain steppes. The desert steppe habitat has a warmer, drier condition than the mountain steppe. Therefore, it is likely that individuals of *C. eumenes* were more stressed under laboratory conditions, which may have affected their performance in dung removal.

Overall, our results demonstrated the importance of functional group, dung type, beetle abundance, and environmental conditions associated with the drying of dung pads on dung removal rates by dung beetle species in the dry steppes of Central Asia. Future research should examine changes in the dung removal rates by different beetle species within and among seasons.

It should be noted that there are some limitations of this study, e.g., we could not conduct all the experiments under both field and laboratory conditions, the functional traits of the beetles used in the experiment were not equally representative, and environmental factors such as temperature, precipitation, and season were not considered. Therefore, our future research will be focused on taking into account various environmental factors and including equal representation of functional traits of dung beetles in both natural and laboratory conditions. This could shed some light on the effect of the ecological function of this important insect group in the sustainability of livestock production systems in Mongolia.

5. Conclusions

The results of our experiments demonstrate that there is a relationship between a set of traits (e.g., dung age, dung type, nesting strategies and abundance of dung beetles, experimental conditions), and dung removal functions provided by dung beetles. In the dry steppe of Mongolia, by preferring newly dropped fresh dung, these beetles are able to transfer herbivore dung into the soil within hours or few days after deposition, which is related to the biological characteristics of the beetle species; such species as *Cheironitis eumenes* and *Onthophagus gibbulus* are considered the most important species for dung removal. The tunnellers were responsible for a significantly greater proportion of dung removal than other traits, which is explained by their greater activities in dung recycling in temperate grassland. This study revealed the different decomposition rates by various beetles depending on the dung type, which appears to be related to the moisture and microbial contents as well as organic and inorganic nutrients in horse and cattle dung. Dung removal rates of different dung beetles varied between field and laboratory conditions, and this was considered to be related to the habitats of the beetle species.

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